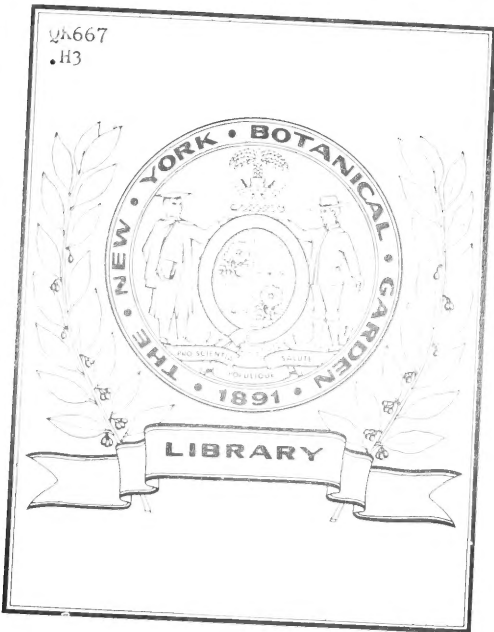
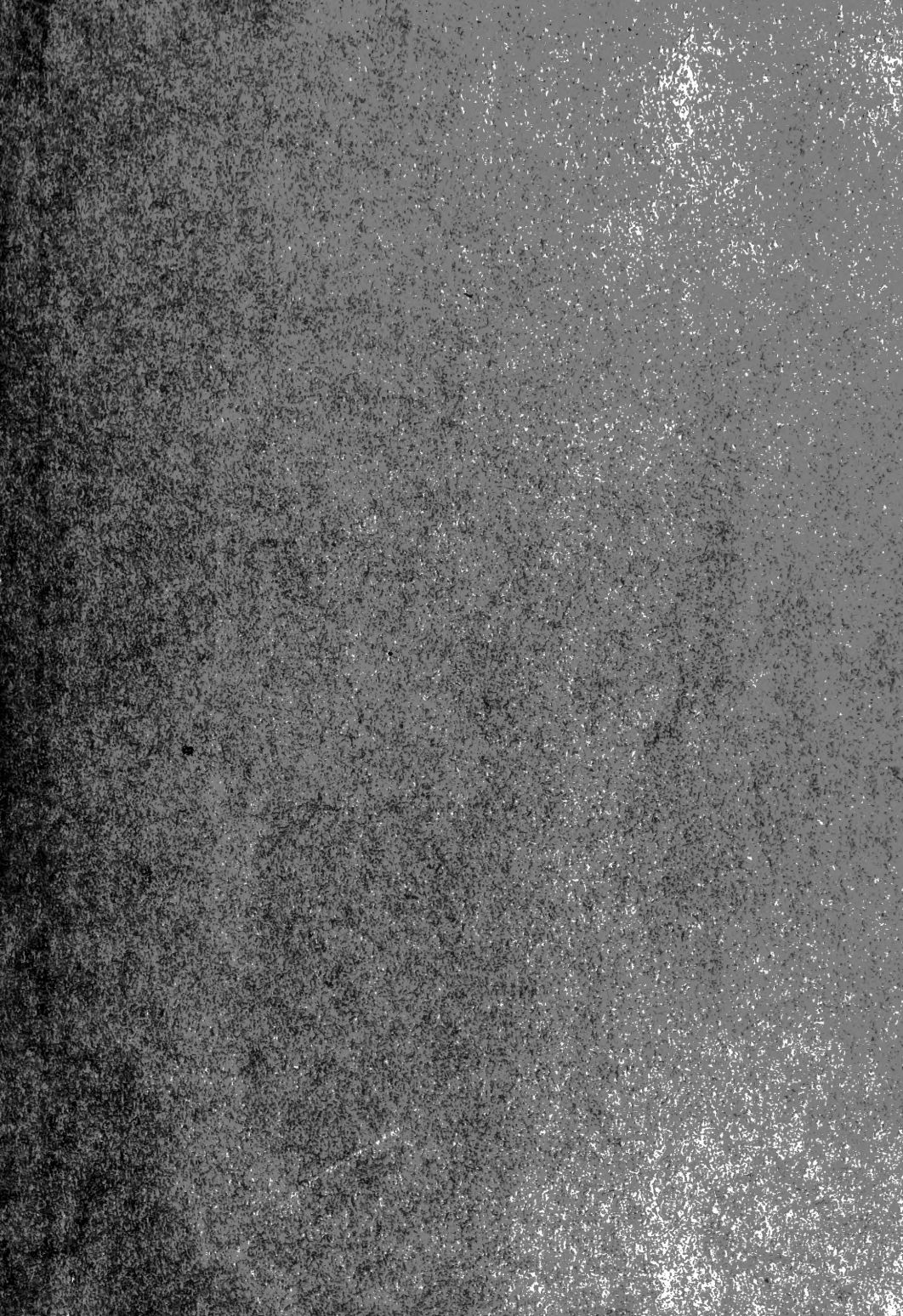


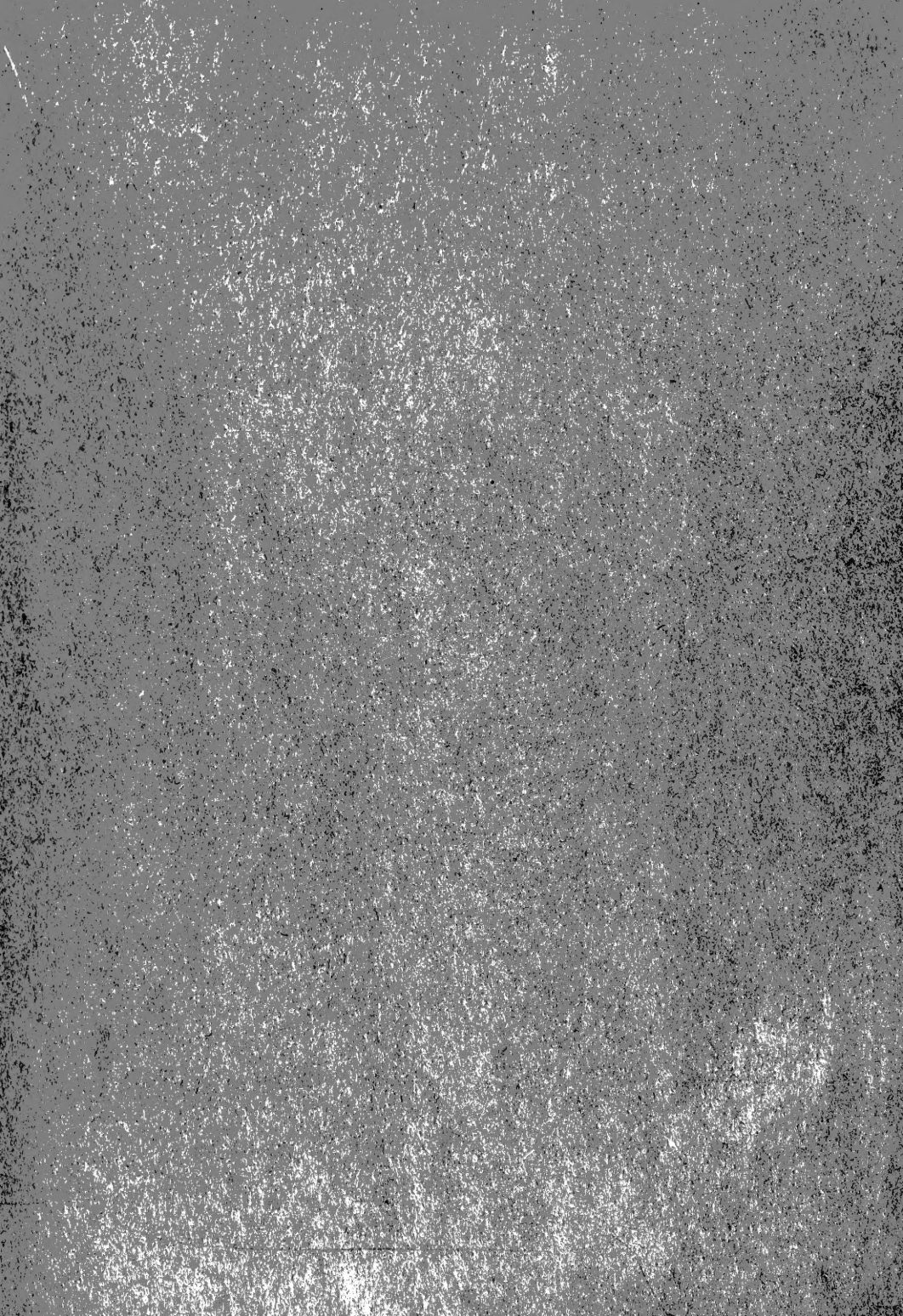


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THE PHYLOGENETIC METHOD IN TAXONOMY

THE NORTH AMERICAN SPECIES OF ARTEMISIA, CHRYSOTHAMNUS,
AND ATRIPLEX

BY

HARVEY M. HALL AND FREDERIC E. CLEMENTS



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INTRODUCTION.

SCOPE AND DUTY OF TAXONOMY.

Scope.—The essence of taxonomy is clearly indicated by the meaning of the word itself. It denotes the science of arrangement or system, and hence classification. While cataloguing is a part of it, it is a small part only. The naming of new forms is a necessary function of taxonomy, but it should always be incidental to giving them their proper meaning and relationship, and never an end in itself. In the case of plants, the mere recognition of supposed new species in the herbarium hardly merits the term descriptive botany, and it can in no wise be regarded as adequate taxonomic investigation. It has its value, and hence its excuse, in the biological exploration of new and distant countries, but, here as elsewhere, permanent taxonomic results must await the application of statistical and experimental methods in the field (Clements, 1905).

To be both comprehensive and thorough, taxonomy must draw its materials from all other fields, just as it must serve them in turn. While it leans most heavily upon morphology, it can not afford to neglect histology and physiology, and it must learn to go hand in hand with ecology and genetics in the future. Indeed, if it is to reflect evolution as accurately as it should, it must regard physiological adjustment as the basic process, and morphological and histological adaptations as the measurable results. This means that the taxonomist of the future will think in terms of evolutionary processes, and will learn to treat his morphological criteria as dynamic rather than static.

Relation to ecology and experimental evolution.—As a study of life in its environment, ecology deals with the motive force in evolution, and the experimental study of evolution is essentially ecological in nature. Quantitative ecology deals with the kind and amount of the stimulus initial to change, and likewise measures the corresponding response in terms of function and structure. It thus traces the evolution of new forms in minute detail, in so far as they arise through adaptation or variation, and consequently furnishes the only direct evidence of relationship by descent. It affords the sole method of testing the manifold assumptions of existing taxonomy, and provides the foundation upon which an objective and permanent taxonomy may be reared. If mutations prove to be but major variations in which the environic stimulus is hidden or indirect, it will become possible to study the origin of all new features or forms ecologically, since hybrids are to be regarded as new expressions of old forms. It appears probable that this method can be successfully applied to retracing the origin of existing species or stocks, and with increasing knowledge and skill in experimental manipulation, to repeating the change from a genus into a related one. Since tribes and families are but related phyla of genera, it seems not impossible to pass from one family to another experimentally, especially where the gap is slight, as between Ranunculaceae and Rosaceae, or Borraginaceae and Verbenaceae. In short, experimental and quantitative methods promise to turn taxonomy from a field overgrown with personal opinions to one in which scientific proof is supreme. Such a taxonomy is indispensable to the advance of ecology, and apparently can be attained only by adopting its methods.

The attitude of the ecologist has already been expressed by Clements (1905:12):

"Taxonomy is distinct from descriptive botany, which is merely a cataloguing of all known forms, with little regard to development and relationship. The consideration of the latter is peculiarly the problem of taxonomy, but the solution must be sought through experimental evolution. The first task of the latter is to determine the course of modification in related forms, and the relationships existing between them. With this information, taxonomy can group forms according to their rank, i.e., their descent. The same method is applicable to the species of a genus, and, in a less degree, perhaps, to the genera which constitute a family. The use to which it may be put in indicating family relationships will depend largely upon the gap existing

between the families concerned. While interpretation will always play a part in taxonomy, the general use of experiment will leave much less opportunity for the personal equation than is at present the case. Taxonomy, like descriptive botany, is based upon the species, but, while there may exist a passable kind of descriptive botany, there can be no real taxonomy as long as the sole criterion of a species is the difference which any observer thinks he sees between one plant and another. The so-called species of to-day range in value from mere variations to true species which are groups of great constancy and definiteness. The reasons for this are obvious when one recalls that 'species' are still the product of the herbarium, not of the field, and that the more intensive the study, the greater the output in 'species.' It would seem that careful field study of a form for several seasons would be the first requisite for the making of a species, but it is a precaution which is entirely ignored in the vast majority of cases. The thought of subjecting forms presumed to be species to conclusive test by experiment has apparently not even occurred to descriptive botanists as yet. Notwithstanding, there can be no serious doubt that the existing practice of re-splitting hairs must come to an end sooner or later. The remedy will come from without through the application of experimental methods in the hands of the ecologist,¹ and the cataloguing of slight and unrelated differences will yield to an ordered taxonomy."

Duty.—While the first duty of taxonomy is to furnish the best possible record of evolution and relationship, its next most important task is to be of the greatest usefulness. Fortunately, there is nothing antagonistic between these two needs, for the taxonomy that is based upon phylogeny is not only by far the most useful, but can also be made the most convenient and usable. For all who deal with plants, and even for the systematist outside his own groups, the most usable taxonomy is that in which relationship reaches its fullest expression, both in the forms recognized and the names applied. This leads to easier recognition of the plant and readier application of its name, a result to which even the specialist can not be indifferent, unless he be of the narrowest type. Even with our present unsatisfactory taxonomy, the number of people that make use of it has steadily increased, owing to the breaking down of the artificial barriers between the sciences and the rapid development of the practical fields of agriculture, grazing, and forestry. The time is past when even a morphologist or cytologist can afford to boast that he does not know a single plant by name, while for the geneticist and ecologist, species and variands² are the very essence of their work. The gradual disappearance of the unnatural boundary between botany and zoology makes it all the more necessary to have a kind of systematic botany that appeals to the zoologist, whose general use of the trinomial indicates a greater feeling for relationship. The use of genera and species by the agronomist, grazing expert, and forester is fundamental, and is limited only by the convenience and intelligence of the taxonomic treatment available. Even with those to whom plants are not the immediate object of attack, such as soil chemists and physicists, topographers, geologists, etc., much more attention would be given vegetation if manuals met their needs.

SCIENTIFIC BASIS OF TAXONOMY.

Classification and relationship.—The need of classifying plants has been felt since Aristotle (334 B. C.), and the history of classification is one of attempts to achieve a more natural system, except for the artificial system of Linnaeus (1737). The natural classification of flowering plants properly dates from Jussieu (1789), since which time progress has been chiefly crystallized in the systems proposed by DeCandolle (1813, 1819), Endlicher (1836), Lindley (1845), Bentham (1862), Eichler (1876), Luerssen (1882), Engler (1892), and Bessey (1896). In spite of its apparent simplicity and great popularity, the Linnaean system gradually yielded to the Candollean and Benthamian during the first half of the nineteenth century. The spirit of development that swept through botany with the rise of the cell-theory and the consequent impetus to physiology and morphology reacted favorably upon taxonomy. During the following half-century,

¹ By the term ecologist is understood anyone that employs quantitative and experimental methods in the study of plants or animals in the natural habitat.

² This term is employed for any form of the species, as discussed on p. 23.

the many relicts of artificial systems were eliminated by Luerssen, Engler, and Bessey, and it is perhaps not too much to say that the modified Besseyan system, which has drawn upon many others, is as natural as the present state of knowledge permits. Such systems have dealt chiefly with the relationships of orders and families, however, and are often very unsatisfactory in their treatment of genera and species.

Relationship is the very essence of classification. This axiom is universally accepted in theory, but too often ignored in practice, especially by the segregator. It is not sufficient that the relationship be felt, but it must also be shown. This can not be done by raising the sections of a genus to generic rank, or the variads of a species to specific rank, and this fact constitutes the most serious indictment against such practices. Moreover, while it is generally recognized that orders should be arranged and families grouped in such manner as to reveal their relationship, it is not usually realized that a similar relation should obtain between the genus and its sections, and between a species and its variads. This principle is later discussed in detail, and here it will suffice to point out its basic importance for a consistently natural system.

Evolution and phylogeny.—Evolution is the process and phylogeny the record of descent. Phylogeny is thus the measure of relationship, and is to be expressed in terms of community of ancestry; hence, if relationship is to express evolution adequately, it must take account of each change, from the branch to the variad. It must arrange these in their proper phylogenetic order, and denote them by such terms as will clearly indicate their fixed phylogenetic position. This has long been done for the most part, but the fact has too often been overlooked that the sequence of changes is fixed in practically all regions of intense evolution. The genus exhibits lines of evolution expressed in the sections, and the species shows more recent changes marked by variads. It serves no useful purpose, but merely obscures evolution and phylogeny to treat the sections of *Astragalus*, *Gentiana*, or *Pinus* as though they were genera, or the numerous variads of *Artemisia vulgaris* or *Chrysothamnus nauseosus* as species. A natural classification must maintain as well as reveal the different degrees of relationship as expressions of different stages of evolution, and it can do this most accurately with genera, sections, species, and variads, where the lines of evolution are still in a condition conducive to experimental study.

The evidences of evolution are the materials of phylogeny, and these have been almost exclusively morphological up to the present. Experimental studies, such as those of Bonnier (1895, 1920), Jordan (1873), and the geneticists, have been few, and for the most part without taxonomic objectives. Such work serves to prove that, while it is convenient to employ morphological observations, it is neither necessary nor desirable to do so without supplementing and checking them by means of statistical and experimental methods. Since the limits of orders and families are determined by genera, and the limits of genera by species, the whole problem resolves itself into a statistical and experimental study of species and their evolution. Pending the general adoption of such methods, morphology will continue to be employed, but it should be with due recognition of the fact that both criteria and results are tentative and must be confirmed by objective methods. While paleontology has often made brilliant use of morphology in connection with sequence in tracing the course of evolution, its criteria for genera and species have necessarily been drawn from existing units, and are similarly susceptible to refinement as a consequence of statistical and experimental studies.

Synthesis and analysis.—The prevailing practice in the segregation of genera and species is chiefly detached analysis, with little consideration of relationship and practically none of evolution. Superficially, this practice would seem to follow the course of evolution, since the latter is primarily a matter of differentiation. As a matter of fact this is usually expressed in a vast number of individuals scattered over a wide

territory and growing in a considerable range of differences within the habitat, or often in different habitats. An analysis based upon a few herbarium specimens or frequently indeed upon a single one can rarely be more than a personal opinion and usually affords but an erroneous or imperfect impression of the actual species. With reference to the evidence provided by Nature, then, the synthesis of data from various regions is imperative if a complete and exact picture of the species is to be obtained. The statistical method itself, while it is analytic in that it deals with individuals, is synthetic in as much as it relates the individuals studied to the mode for the locality as well as for the species. The experimental method appears to be intrinsically analytic, since it deals with the differentiation of the stock. However, its most successful use so far in the field has been to relate ecads to the parent stock and the so-called reciprocals to each other (Clements and Hall, 1922). Moreover, in working with the differentiation of a stock in various habitats, the synthetic factor is given full value at the outset, and the task is then merely one of analyzing the evolutionary possibilities of the species. Finally, the examination of any group of individuals produced experimentally involves the determination of the mode of the departure as well as the extremes. Thus, in building a natural system, synthesis and analysis must go hand in hand; it is the task of analysis to find new facts and of synthesis to give them their proper meaning.

THE GENUS CONCEPT.

Nature of the genus.—In the prevalent view the genus appears to be regarded merely as a concept, and it is often stated that it does not actually exist in nature. This is doubtless true for those who regard the genus merely as a pigeon-hole, chiefly convenient for the filing of new species. Such a view has its justification in the usual practice of making genera, and especially in the recent flood of generic segregation. It is not supported by the evidence drawn from the methods of evolution or the record of phylogeny. To the student of evolution, the genus represents a certain characteristic portion of the line or field of specialization, and its existence is as definite as that of the species which constitute it. It may be more difficult to recognize, but this is primarily the fault of outlook and method. In the absence of definite criteria, the chief difficulty centers about the rank and limits of genera. As a consequence of the unrestricted play of personal opinion, not infrequently aided by bias or carelessness, present-day taxonomy contains genera of every possible quality. Many of these disappear completely when the test of evolution is applied to them. Given the family, genus, and species as major units, these will regularly be differentiated into tribes, sections, and variads, respectively. This is a necessary corollary of the principle that the processes of evolution are constantly and universally at work. The basic laws of conservation of energy and material, division of labor, and increase of parental care lead inevitably to divergence, and hence to the splitting of the generic stock into sections, and of the specific stock into variads.

The question of generic limits is one of criteria. These have been of the most various kinds and quality, and have led to results of the most diverse value. It seems obvious that personal opinion is the poorest of bases for determining the relative merits of criteria, and that improvement in this respect can be effected only by means of experimental and statistical studies of the generic criteria in use. Until this is done, the segregation of well-established genera can have no standing in evolutionary taxonomy.

Genus and section.—The relation of the subgenus or section to the genus is a basic and natural one, arising out of evolution and serving as a record of it. It was inevitable that genera of wide extent in contact with many effective habitats, such as circumpolar ones, should show wide differentiation. The generic stock became split up into several or many lines of evolution, each with its secondary development. So funda-

mental and uniform was this process that its consequences are to be found in practically all genera that have attained considerable differentiation of species. It corresponds to the basic law of adaptation and specialization under the pressure of new conditions, and the maintenance of their evolutionary relationship is the chief task in the groups thus produced. The differentiation of the sections is subsequent and subordinate to that of the genus, and any treatment that ignores or obscures this fact is as undesirable as it is unnatural. To all who recognize that taxonomy should be the best possible interpretation of evolution, the confusion of genera and subgenera appears to negative all the principles upon which evolutionary taxonomy should rest.

Generic segregation.—The general tendency, during the last two decades in America at least, has been to segregate genera by raising their sections to generic rank. While the practice is not confined to this period, it is characteristic of it. Not all large genera have received this treatment as yet, but another decade or two will see this done, unless it is given a sharp check by the scientists who suffer from it. This tendency to assign generic rank to smaller and smaller divisions is the natural result of studies by specialists, who often focus their attention upon details to an extent that magnifies them out of all proportion to their value. Relationship and perspective are lost, and the results are both unnatural and unusable. It is necessarily in the largest and best-known genera that segregation has been rife, and it is these that offer the greatest opportunity for damage, both to phylogeny and to classification. In North America, *Astragalus* is unique in that it is now represented by 19 genera, so-called; *Aster* is segregated into 13, *Haplopappus* into 11, and *Gilia*, *Oenothera*, and *Saxifraga* are broken up into 10 or more each. *Habenaria* and *Polygonum* are each split into 6 parts, *Claytonia*, *Euphorbia*, *Lotus*, and *Ranunculus* into 5, and a large number of genera into 4 and 3.

While no complete presentation of the arguments for segregation seems to be available, the major reasons may be gained from various sources. It is contended that many genera, including those mentioned above, are unnatural groups of species of diverse habit and structure, and that they should be split into smaller and more natural ones. A second argument is that genera should be uniform, and that the criteria used in certain groups should be applied throughout. This is akin to the contention that many small genera are more convenient than a few large ones, and that a genus should be automatically split up when the species reach a certain number. Finally, it is sometimes maintained that justice to obscure workers demands that their genera should be adopted, since they are as good as many of those already in use.

Failures of segregation.—The most conspicuous failure of the method of generic segregation is in connection with phylogeny and classification. The 18 segregates of *Astragalus* are much more nearly related to each other than they are to *Robinia* or *Trifolium*, but there is no evidence of this fact in their treatment. The only possible phylogenetic and taxonomic treatment of these is to include them in *Astragalus* as sections, differentiated more or less recently from the same generic stock. This is likewise the answer to the contention that *Astragalus*, *Aster*, *Gilia*, *Gentiana*, *Oenothera*, etc., are unnatural groups, and that they are rendered more natural by raising their sections to generic rank. If further answer is sought, it may be obtained by trying to locate an *Astragalus* in the 18 segregates that represent its sections. The endeavor to give criteria the same value throughout and to make genera uniform fails because evolution is far from uniform, and its products share this quality. Moreover, it is significant that practically all such attempts confine themselves to reducing genera to the rank of the least valid, instead of combining the less natural genera to increase their validity in terms of evolution and relationship.

The assumption that many small genera are more convenient than fewer large ones shows a curious ignorance of the significance of system, and of the mechanism of memory.

It is the essence of a system to organize knowledge, and the conversion of generic sections into genera conceals their inherent relationship. The most striking feature of memory is its necessity for relating things to each other, and the multiplication of small genera without evident relationship to each other greatly increases the labor involved in remembering them, often to the degree that the worker can not or will not utilize them. The argument that generic segregates should be adopted in justice to the authors concerned, since they are quite as good as some accepted genera, is possible only because of the failure to realize that synthesis and not analysis is the corner-stone of classification. The question of justice is entirely subordinate to the demands of evolution and phylogeny, and it is certain that these can not be met by segregation of the usual sort.

It is clearly recognized that the making of new genera is purely a matter of personal judgment at the present time, and that this is profoundly affected by training and environment, and especially by prejudices in favor of uniformity, segregation, etc. There is no general agreement as to criteria, methods, or results, and the importance of evolution as the one safe guide is rarely if ever considered. A knowledge of the genus as a whole, especially when it includes exotic species, is too often lacking, and little or no thought is given to the phylogeny of the genus and its sections in relation to genera of the same evolutionary stock. More serious still is the all but inevitable magnifying of criteria in the detached herbarium study of a group or genus and the consequent lowering of the criteria for genera. The first cycle of this sort is nearing a close for lack of material for segregation, and it is confidently to be expected that the next generation will see a new lowering of criteria and a corresponding avalanche of segregates. This can be avoided only by a stern insistence on the part of conservative taxonomists, and of all non-taxonomists, that changes in generic concepts must be based upon evolution, and made only after the fullest statistical and experimental studies. An augury of the future of descriptive botany is furnished by the case of *Astragalus*, in which *Homalobus*, one of the 18 segregates, already has almost as many so-called species as the ecological treatment recognizes for the entire genus in North America.

With respect to usability, the segregation of genera is especially unfortunate. It is impossible for most botanists and practically all laymen to determine a large number of the generic segregates without recourse to the herbarium, and their recognition in the field is practically out of the question for all but the specialists in the group concerned. Ready recognition means carrying the distinctive criteria in mind, and only the specialist can hope to know the names of the segregates, to say nothing of their characters. Moreover, there is a definite limit to the number of names the taxonomist himself can readily command, and this limit is quickly reached with the great majority of those who use taxonomy merely as a tool. If the actual genera of the pea family are to be known and recognized on sight, it becomes a mental impossibility to deal with *Astragalus* when split into 19 parts. When the same process is carried into scores of genera, a working knowledge of flowering plants becomes impossible for anyone but the taxonomist, and it is possible for him only in the restricted groups with which he is working. As a consequence, taxonomy becomes an object of ridicule to those who would use it and can not, and this feeling is extended to the whole subject of botany by the layman, who properly looks upon the naming of plants as the first step in botanical knowledge.

Proper treatment of genera.—It has repeatedly been emphasized that the treatment of genera must be based upon evolution and phylogeny. This means the retention of the vast majority of genera as recognized by Linnaeus, Bentham, Gray, and others, together with the recognition of the subgenus or section as an essential unit for recording the course of evolution. From the evolutionary standpoint, this requires the replacing of generic segregates in their original genera, except in the rare cases where the genus

is plainly an artificial one. Since there is no intent to minimize analysis when it is in agreement with evolution, it would seem desirable to make rather more of sections as records of recent lines of specialization within the generic stock. This can readily be done by making them more prominent in the treatment of genera, and in special cases by the use of the sectional name or initial in a trinomial. With respect to practicality, the use of genus and section alone makes possible the correlations that are essential to a working knowledge of taxonomy. This likewise insures the smallest possible number of genera, which is also a cardinal point in usability. Moreover, this method permits the accumulation of a permanent body of knowledge, both for the subject and the individual, as the constitution of each genus is no longer subject to the personal judgment of every specialist. This is especially significant, in view of the fact that the raising of actual sections to genera does not represent new knowledge, but rather an ignoring of the essential facts of relationship. When the latter are given their full value, there will be no question as to the usability, convenience, and attractiveness of taxonomy for all those who wish to make use of it.

THE SPECIES CONCEPT.

Nature of the species.—As with the genus, there has been much divergence of views as to whether the species is merely a concept or an actual entity. Apparently, the general opinion is to the effect that the species is a concept, but this seems to deal with the term and its application rather than with the unit itself. Once granted that the term might have been applied to any other unit, or an altogether different term employed, it seems evident that the unit itself is as definite an entity as a plant community. In fact, with many dominants and subdominants, the species and the community are coextensive, and hence equally definite. Like the genus, the species represents a certain portion of the line of evolution, and it lacks definiteness only where evolution has progressed uniformly, without sharp divergences or breaks. Practically all species are still susceptible of modification, and many of them exhibit it most actively. If only the end results of this process are known, as in the case of herbarium studies, they appear to be distinct units, often with little or no evidence of their common origin. As a consequence, units of every possible degree of differentiation and value are masquerading as species in existing taxonomy. As long as species are made in the herbarium instead of the field, this condition must continue, at least in some degree, but it will disappear rapidly before statistical and experimental studies in the natural habitats. Such studies have already reached the point where it is possible to relate a number of recent segregates to their proper specific stock, and they indicate that this will be the regular outcome of such methods.

Definition of species.—Many attempts have been made to provide a working definition of the term species, but these have been successful only in leading to widely divergent usages. The old definition based upon sterility has long been discarded, but its place has been taken in some measure by the definition of the geneticists, which is based upon gametic purity. This basis has actually been proposed by Lotsy (1916), and it does have the advantage of being more objective than any other. It is a concept of use to geneticists alone, however, since gametic purity can only be determined by genetic analysis, and this is applicable so far to relatively few cases. Plants entirely identical in all external characters may exhibit a different gametic composition, as indicated by their behavior when hybridized, and would accordingly constitute different species. The classical example of this are the two strains of white sweet peas described by Bateson (1913), and a similar case is found in the 14 strains of corn, all with white aluerone (Babcock and Clausen, 1918). It is obvious that such a definition of the species is

wholly impracticable, and that genetic analysis can be of value taxonomically only in studying differentiation within the species itself.

Constancy.—A more generally accepted basis for the species is its constancy, or the ability to “breed true.” While it is doubtless true that practically all actual species do this, many of the segregates of to-day do not. More significant still is the fact that the adherents of this definition make no attempt to determine this point before describing a new species. Constancy is undoubtedly a factor to be regularly taken into account in the evolutionary study of species, but it is futile to attempt this without the aid of statistical and experimental methods. On the other hand, the test of constancy alone would require the acceptance of an absurd number of species. For example, Jordan (1873) recognized 200 species of *Draba verna*, the “Jordanons” of Lotsy (1916), and the United States Department of Agriculture recognizes 250 varieties of wheat, all of which breed true and would thus come to be species. But these are based upon characters that taxonomers regard as slight and non-specific. The case of *Draba verna* shows that this condition is not confined to cultivated plants, and this is borne out by studies of *Cerastium viscosum*, *Montia perfoliata*, and other species at the University of California.

Extensive field studies in connection with the present monograph have revealed innumerable examples of very similar forms that evidently breed true. The acceptance of this criterion would increase the number of species almost beyond belief, and it would throw taxonomy into inextricable confusion. The idea of constancy is helpful in distinguishing between fixed genetic units and ecads, and is one of the first points to be considered in the experimental analysis of a specific stock. It already appears probable, however, that the prevalent opinion that forms are constant or not constant will have to be modified, and that varying degrees of constancy must be recognized.

Distinctness.—Regardless of the fetish of constancy, the working definition of the average taxonomist is distinctness, by which he understands the ready recognition of a particular form. It may easily be shown that distinctness or recognizability in itself is no necessary test of a species. Nothing is more readily recognized than the albino mutants of blue and purple flowers, but even the most extreme segregator rarely proposes to call them species. Moreover, recognizability is too often a matter of the herbarium, and completely disappears in the field, or the limits of the unit fade away. It is peculiarly the faculty of the specialist, who sees the finest details in bold relief, and it frequently vanishes with adequate perspective. It ignores the various degrees of differentiation, and emphasizes apparent values at the expense of the real ones. Moreover, this working test is applied without any real attempt at consistency, since ecads are not regarded as species when their origin is known, but are called ecologic forms, in spite of the fact that a large number of the specific segregates of to-day are ecads, which are not generally recognized as such because they are known only in the herbarium.

The idea that recognizability was a test of the species was probably in the mind of Bateson, when he gave systematists the interesting advice to describe all the species that they could induce any reputable journal to print (1913²). This advice is so unsound as to bring its own condemnation, but it is useful in revealing the complete lack of understanding of the foundations of taxonomy. While it must be confessed that too much practice excuses the view that taxonomy is merely a matter of new species and many of them, no one who regards science as organized knowledge can fail to see that taxonomy has no real standing apart from evolution. To follow Bateson's advice would add enormously to the already immense accumulation of so-called species, the origin and relationship of which no one understands. What is now needed is not the further increase of such segregates, easy to discover and describe by the thousand, but the organization of this chaotic mass into natural groups. The method of the segregator is to take the scattered and broken twigs of the evolutionary tree and catalogue them

without concern as to their origin and relationship, while the true method of taxonomy is to deal with the tree as a whole, and to regard the units in it as so much correlated evidence of evolution.

The evolutionary definition.—To the student of evolution, all these proposed tests of species are gratuitous, arising from an incomplete view of the field and suffering from the bias of the specialist. While gametic purity, constancy, and recognizability all have their meaning, this is as yet too little understood to make them little more than interesting working hypotheses. There is no warrant in our present knowledge of the course of evolution for assuming that they have any more connection with the species than with the most recent ead or mutant. The evolutionary view of the species is that it is a definite phylogenetic stock, sprung from and related to similar stocks, and itself undergoing modification into a number of variads. As they have recently come from the same stock, these variads are more nearly related to each other than they are to those of any other species, and they represent a definite phylogenetic unit, the species, at the same time that they mark its further differentiation. The only definite measure of the progress of evolution is found in the degree of morphological difference, and species necessarily share this morphological basis with other units. To ask that all species show the same degree of morphological difference is to misunderstand the nature of evolution, but it is possible to demand that the great majority of them show a definite difference in the proper position in the sequence of units. In short, a species must not only show adequate morphological differentiation, but this must bear a definite relation to that of the genus on the one hand and of the variads on the other. It seems a truism to point out that in an evolutionary taxonomy each unit must be determined as much or more by its relation to the unit that precedes and the one that follows as by its purely structural characters.

The inadequacy of a strict morphological basis for species is due chiefly to the paramount rôle of divergence. If two species have been differentiated from an original stock by the impact of reciprocal factors, such as greater wetness on the one hand and dryness on the other, this very divergence will give opportunity for convergence when they invade reverse habitats. This convergence may sometimes become practical identity (Clements, 1904), but as a rule ancestral or related characters will furnish the clue to descent. Thus, while most species will show distinct gaps, it must be admitted that the gap may be quite or completely closed in some instances, in which evolutionary analysis is alone of avail. In this task ecology is often of great assistance in relating response to habitat and in connecting differentiating habitats with the habitat of the ancestral mass. Thus, while evolutionary taxonomy does not pretend to offer a definition of the species, it does provide the method by which species can be recognized and by which they can be related to each other as well as to the major and minor units. The consequences of various attitudes toward the species are discussed in the two following sections, and the details of the evolutionary method are dealt with in the last section, as well as under the later caption "Methods and results in evolutionary taxonomy."

The segregation of species.—The method of segregation that has characterized descriptive botany in America during the past quarter of a century is a necessary consequence of the idea that everything distinguishable is a species. Applied in the field, this definition would have worked little damage, as the abundance of material would quickly have set a limit to its operation. In the herbarium, however, the small number of individuals represented and the frequently incomplete nature of the specimens magnified small differences and gave the impression of gaps where none actually existed. In spite of the assumption of many descriptive botanists that much of their work is done in the field, this rarely amounts to little more than collecting a few individuals of the outstanding forms, and the describing is wholly a matter of the herbarium. Collecting for

a complete range of individual and specific variation, with thoroughgoing ecological analysis and statistical studies of the amount and direction of variation, is practically unknown. The usual practice has had its justification in the past, when actual species were still to be described, as shown by the results of Pursh, Nuttall, Torrey, Gray, and others, and these reasons still obtain in lands little known botanically, especially the tropics. For North America, however, the great majority of real species had been described by the close of Gray's work, and the vast increase of species since that time chiefly represents a change of personal views as to the criteria that mark this unit.

While there has been an unfortunate shifting of standards in descriptive botany generally, as shown by the almost universal raising of varieties to species (table 1), much of the existing confusion is due to the lack of sympathy and understanding shown by botanists toward the trinomial. It is probable that many segregators recognize that most of their new forms are not actual species at all, but the prevailing botanical attitude toward trinomials, and the failure of at least one code to give varietal names nomenclatorial standing, have discouraged thinking in relationships, since this demanded the use of the trinomial. The inconvenience of the latter is much more than offset by its value in relating forms to the specific stock, as is proven by the practice of mammalogists and ornithologists in particular. However, while it is quite possible that descriptive botanists have felt some compulsion toward the apparent simplicity and uniformity of the binomial, it seems certain that the general botanist would have found no more inconvenience in the use of trinomials than the zoologist, had he been given the opportunity.

Failures of specific segregation.—The segregation of species has practically all the disadvantages of generic segregation, and in addition some that are peculiar to it. Subjectively, it suffers critically from the inevitable lack of proper and adequate material, owing to its being confined to the herbarium. Even more serious is the fact that segregation is merely a matter of personal judgment, and makes use of none of the objective checks, such as statistics and experiment. As already indicated, there is a successive shifting of the standards for criteria, with the result that these always become lower in quantitative terms, and never higher. Not only do the standards differ from individual to individual, but sometimes they also change rapidly in the case of the same individual. This is unavoidable as long as personal judgment is the only process involved, and the continuance of this as the sole test will complete the existing chaos in another decade.

From the standpoint of one who must make use of the results, the greatest harm done by segregation arises from its treatment of all forms as species, and hence as equivalent. This is inconvenient enough in ordinary use, but it becomes fatal in all those cases where relationship is of more importance than the mere name. These constitute practically all the scientific and practical uses of plants, in which genetic relationship arising out of evolution is a matter of primary concern. In short, segregation is unscientific because it is unnatural and impracticable as to results, on account of its ignoring relationship. The second great disadvantage of segregation lies in the practical impossibility of recognizing most segregates in the field. This is a fatal difficulty in the case of all students of vegetation, whether ecologists or practical scientists, such as foresters, grazing experts, etc. The determination of the great majority of segregates can be made only in the herbarium, if at all, and frequently fails of application in the midst of the wealth of material in the field.

In the enormous increase of unrelated forms treated as species, segregation constantly destroys existing knowledge and fails to add anything new scientifically. Of the thousands who make use of systematic botany, not even the specialist has the time or ability to adjust his knowledge to each new segregation, and the general botanist or

practical scientist will not attempt it. The steady disappearance of recognized and recognizable species removes all their landmarks, and they come to look upon descriptive botany as hopeless. Their unanimously expressed opinions of it would doubtless be salutary, if these could only reach the ears for which they are intended. Meanwhile, the gap between the systematists and those they should serve widens, and it can only be bridged by a type of botany that frankly regards the needs of the latter as paramount. These needs are the very ones that arise out of evolution and relationship.

The nature of the grievance felt by those who would use taxonomy against the method of segregation may be readily understood by reference to tables 1 and 2. In the Rocky Mountain region the number of species has increased from 1,905 to 5,100 in 30 years, and these are now to be sought among 950 genera in place of 551. The species of 91 representative large genera have grown from 962 to 3,576, or almost fourfold. This is reflected in the average number of species per genus, which was 10 in 1885 and 39 in 1917. In the largest genera the increase is often greater; for example, *Eriogonum* has grown from 27 species to 122, *Salix* from 16 to 76, *Phacelia* from 6 to 44, *Krynitzkia* from 11 to 68, *Potentilla* from 16 to 99, *Lupinus* from 13 to 80, *Aster* from 40 to 139, *Senecio* from 21 to 114, and *Poa* from 12 to 67. *Aconitum* with 1 species in 1885 now has 11, *Dodecatheon* has increased from 1 to 18, *Frasera* from 1 to 11, *Gutierrezia* from 1 to 11, and *Chrysopsis* from 1 to 27. In the case of *Pentstemon* with an increase from 27 to 98 species, a further segregation (Pennell, 1920) has resulted in a total of 125 species, and this can be maintained as long as new personal judgments are brought to the task. This is fully confirmed by the fact that the species of 1909 are regularly intermediate in number between those of 1885 and 1917. This total represents only a 43 per cent increase, however, while the number for 1917 constitutes a further increase of 124 per cent.

When definite ecological investigation was begun in the Rocky Mountains in 1899, much enthusiasm was felt for the recently segregated units, as it was supposed that the contention that a finer analysis would be helpful to the ecologist was correct. For 6 or 8 years an endeavor was made to utilize the increasing crop of segregates in ecological studies, both in vegetation and in experimental evolution. Gradually it became evident that the so-called new species were herbarium-made, and could not be expected to fit the facts in the field, while it was quickly realized that they ignored relationships instead of suggesting them. In short, when they existed outside the herbarium, they made correlation difficult or impossible instead of aiding it. As a consequence of this attempt to make use of segregates, it was realized that the ecologist could work only with more objective units, checked by statistics and experiment, and based to the fullest degree upon evolutionary relationship. The outcome was "Rocky Mountain Flowers" (Clements and Clements, 1913), in which a definite endeavor was made to relate the myriad forms to definite specific stocks. This was done purely from the ecological and evolutionary viewpoints, and without any reference to previous treatments, with the exception that a few generic segregates were retained for practical reasons. In fact, the earlier treatment of Coulter, which followed closely that of Gray, was completely lost to view, and was not taken into account until the preparation of tables 1 and 2

TABLE 1.—Number of genera and species in Rocky Mountain manuals.

	Coulter, 1885.	Coulter and Nelson, 1909.	Rydberg, 1917.	Clements, 1913.
Genera.....	551	649	950	605
Species.....	1,905	2,733	5,100	1,878
Varieties.....	331	189	0

¹ Extra-regional units excluded.

in 1920. These at once revealed a striking similarity between the traditional treatment of the species as exemplified by Linnaeus, Bentham, Gray, and others and the ecological treatment based upon the fullest recognition of evolutionary processes. This was not merely evident in the total number of species, but with rare exceptions the numbers were also in close agreement for the 91 genera considered. While the evidence can not, in the nature of the case, be regarded as conclusive, it is strongly suggestive of the fact that the traditional concept and the ecological concept of the species are based upon the same phylogenetic unit and are essentially identical.

The scientific basis of species.—The basic essentials of the evolutionary treatment of species are a fixed species concept and their determination primarily in the field. In spite of occasional exceptions, the traditional species concept, crystallized by Linnaeus,

TABLE 2.—Number of species in representative genera.

	Coulter, 1885.	Coulter and Nelson, 1909.	Rydberg, 1917.	Clements, 1913.		Coulter, 1885.	Coulter and Nelson, 1909.	Rydberg, 1917.	Clements, 1913.
Ranunculus	22	24	66	20	Ribes	13	13	28	11
Aquilegia	7	9	19	5	Quercus	2	7	17	4
Delphinium	5	15	36	4	Epilobium	9	13	38	7
Aconitum	1	4	11	1	Oenothera	18	31	72	17
Draba	12	19	50	10	Mentzelia	9	12	30	6
Arabis	8	26	50	4	Opuntia	6	11	19	10
Lepidium	4	13	29	7	Ligusticum	4	5	9	4
Erysimum	4	7	16	5	Lomatium	8	10	29	9
Lesquerella	4	11	21	4	Galium	6	9	18	8
Roripa	4	7	18	6	Valeriana	3	4	13	2
Viola	8	18	28	9	Gutierrezia	1	5	11	1
Geranium	5	8	19	2	Grindelia	2	9	17	2
Arenaria	11	11	36	8	Chrysopsis	1	12	27	1
Claytonia	5	8	22	7	Haplopappus	17	30	61	16
Polygonum	16	28	38	21	Chrysothamnus	12	18	42	9
Eriogonum	27	34	122	26	Solidago	14	16	34	11
Chenopodium	8	14	23	10	Aster	40	52	139	31
Atriplex	10	15	37	10	Townsendia	13	15	21	11
Salix	16	34	76	17	Erigeron	31	41	102	19
Euphorbia	15	17	30	14	Antennaria	7	21	43	7
Dodecatheon	1	6	18	1	Helianthus	9	8	15	7
Polemonium	5	10	19	4	Hymenopappus	3	5	11	1
Phlox	8	17	26	7	Actinella	7	16	28	6
Gilia	22	23	73	23	Artemisia	23	26	72	17
Gentiana	14	13	31	10	Arnica	7	16	40	5
Fraseria	1	1	11	1	Senecio	21	41	114	26
Phacelia	6	14	44	5	Carduus	12	15	58	10
Lithospermum	5	6	12	7	Crepis	7	11	20	6
Krynitzkia	11	29	68	11	Agoseris	4	10	33	3
Mertensia	5	14	48	4	Tradescantia	1	2	5	1
Lappula	3	12	24	4	Allium	13	9	35	8
Pentstemon	27	48	98	26	Zygadenus	4	4	11	4
Mimulus	7	8	20	8	Sisyrinchium	2	4	11	1
Castilleja	9	23	61	9	Juncus	17	22	37	21
Pedicularis	8	11	20	9	Carex	87	72	162	47
Monarda	3	3	6	2	Agrostis	5	9	20	6
Rosa	7	8	30	4	Aristida	3	2	7	3
Potentilla	16	46	99	14	Stipa	6	14	21	9
Fragaria	2	4	12	2	Poa	12	25	67	14
Geum	5	6	15	4	Festuca	4	9	26	8
Lupinus	13	27	80	7	Bromus	3	10	24	10
Astragalus	64	76	196	60	Agropyrum	5	11	23	6
Aragalus	11	18	34	11	Elymus	4	12	42	6
Vicia	3	3	9	2					
Lathyrus	4	7	21	3	Total	962	1,481	3,576	866
Trifolium	12	16	47	10	Average No. of species per genus	10	16	39	9
Saxifraga	17	15	37	11					
Heuchera	6	8	18	6					

gave fairly uniform and thoroughly usable results in the hands of many workers for more than a century and a half. Even though supported chiefly by tradition, it has provided a stable basis for species that was quickly lost when segregation became the usual practice. However, preliminary statistical and experimental studies indicate that the traditional concept was in essential agreement with the evolution of specific stocks, while the concept used in segregation yielded only minor and recent modifications of this stock. With respect to convenience and usability, the traditional concept has everything in its favor, in that it builds upon existing knowledge, permits the recognition of few new species in well-known floras, assigns definite limits characterized as a rule by actual gaps in evolution, and affords the opportunity to relate minor variations to the major stock. As already indicated, the concept applied in segregation enormously increases the number of species, overwhelms specific stocks in a flood of segregates of all possible values, and thus destroys or obscures the main body of taxonomic knowledge. Consequently, if taxonomy is to be either stable or usable, it must still rest upon the species concept of Linnaeus and the practice of eminent taxonomists from his time to the present. No change of concept can be made on scientific grounds until the species so founded have been tested by statistics and experiment, and the evidence at present available indicates that these methods will confirm rather than modify the traditional and the evolutionary view of the species (cf. Clausen, 1922).

The thesis that species can be recognized only in the field would seem to require no argument, were it not for the fact that they are seldom made there. It is probable that few taxonomists would take exception to this statement, but many would question the practicability of the field method, and would incline to regard occasional collecting trips as a fair substitute. Moreover, custom itself furnishes a strong argument in favor of the herbarium as the place for recognizing species. These have always been "made" in the herbarium; why not continue to make them there? Reasons of convenience tell most strongly in favor of continuing this practice. The field is often distant, and the expense of field work heavy if not prohibitive. The field is available for work but a small part of the year in many regions, and personal convenience, as well as such duties as teaching, is often a deciding factor. Moreover, one works much faster by the herbarium method, and results accumulate much more rapidly. An even more cogent reason is the fact that types are available only in herbaria, and it is natural to feel that critical work can be done only in contact with them. However, the most compelling reason is that of tradition and custom, combined with the fact that no field method has heretofore been developed for the study of species. With this available, it is confidently to be expected that taxonomy, like other scientific subjects, will turn to the field as the one place in which material and process are fully available, and in which results will meet the most critical requirements as to scientific quality and permanence.

From the above, it follows that evolutionary taxonomy must regard the segregates of the last 25 years chiefly in the light of tentative proposals as to the course of evolution. It is imperative to reestablish species on the basis of the traditional concept as exemplified in America by Gray and those that have worked in a similar manner since. The fact is not ignored that all the master taxonomists recognized some forms that were not species according to their own concept (Chase, 1921), but this was exceptional and had no appreciable effect on the body of their species. The application of statistics and experiment to certain species of the "Synoptical Flora" has shown that a relatively small number are to be treated as variads. It is significant of Gray's concept and the basis of relationship behind it that in nearly every doubtful case he pointed out the inadequacy of the form as a species. These are the first of which the validity requires statistical test, in order that a coherent and uniform body of species that meet the evolutionary demands may be established. Even before this is completed, however, it is possible and desirable

to begin the evolutionary analysis of valid species, and to take existing segregates into account in doing this, as in the present monograph. For the immediate present, it must suffice to treat all primary modifications of the specific stock as subspecies, though it is known that these are not equal in rank or identical in origin, a subject that is further discussed on page 23.

In this connection it is becoming clearer that the herbarium type is always an inadequate and often a misleading representative of its species. It is merely an accident if it happens to represent the species as found in the field, and in one undergoing active evolution it can only suggest one variety out of many. In statistical and experimental studies of the species, the herbarium type will retain historical value alone, and the actual type will consist of a statistical expression drawn from hundreds if not thousands of individuals, and hence available to workers all over the world.

NOMENCLATURE.

Purpose and value.—A uniform and stable nomenclature has been the goal of systematic botanists for more than a half-century, and especially since the appearance of Kuntze's "Revisio Generum Plantarum" in 1891. Uniformity has been less sought than stability, and the latter has come to be linked generally with priority. It is beside the purpose of the present discussion to deal with the various proposals for securing stability and their divergent results, though the fact can not be ignored that all of these have signally failed of their purpose. It now appears certain that priority, attractive as it seems in the abstract, has failed finally to obtain recognition as the absolute rule of nomenclature, and it may confidently be expected that nomenclature will pay increasing attention to other matters, quite as important as a stereotyped stability. In fact, it seems never to have been realized that stability was destroyed more rapidly by the method of segregation than it could be established by the rules of nomenclature.

The primary purpose of nomenclature is to provide an accurate and convenient way of designating genera and species, as well as varieties and their forms. In the past, the emphasis has been placed upon accuracy with little thought of convenience, probably because stability has been a fetish before which all other considerations disappeared. The phrase, "A name's a name" has been used to justify the position that the botanist need concern himself no further than to apply any name he chose, regardless of all considerations except that of previous use. This has been one of the most unfortunate features of the usual attitude of specialists, and is largely responsible for the feeling of most scientists and practically all laymen toward the subject. To them it is merely a mass of hard names, with but a slight appreciation of the needs of those who would like to know plants. This lack of vision and sympathy has been one of the greatest handicaps of the systematist, and it is the chief reason why nomenclature requires modification and improvement. Here, no more than in the recognition of species can personal judgment or the lack of it be regarded as the final arbiter in the matter of names. Thousands of names have no further justification than the caprice of the describer, and hundreds of them are completely lacking in every canon of convenience and good taste. Indeed, taxonomy is the only field of science in which the blunders and banalities of the indifferent and incompetent are respected and perpetuated.

Future rôle.—It is as inevitable as it is unfortunate that the names of plants should be made by systematists for systematists. Since the latter possess all possible degrees of competence and good taste, it is natural that the standard for names should be low and that these should need the protection of codes to maintain themselves. The final stage in this respect is reached when it is provided that the blunders of the printer are to be corrected, but those of the author are not! Such rules seem futile, since increasingly high standards of scientific performance and scientific service in the future will cause

them to be more and more ignored. There are several cogent reasons why nomenclature should concern itself less with a fugitive stability derived from rules and give much more attention to one based upon excellence and usability. In the first place, it seems clear that the rights of thousands of users outweigh those of the scores of systematists, and that usability and attractiveness must rank with stability as primary qualities of a nomenclature. This is strikingly true when the future is weighed against the present, and it is realized that the codes of to-day would fix existing conditions for all time. While there seems little danger of this to one who believes that the methods and results of each generation of scientists will show an advance upon those of the preceding, it is unfortunate that many systematists appear to feel that nomenclature is a thing apart from science, and that progress in it can be prevented by codes.

Essentials of stability.—Those who hoped that application of the rule of priority would lead to a stable and universal nomenclature in a few years have been greatly disappointed and have come to realize that strict priority affords a less practicable basis than usage. The outcome for the flowering plants is still in doubt, but it is suggested by practically all the proposals for securing stability among the cryptogams, which agree in selecting starting-points that will disturb usage little or not at all. In the very nature of the case, greater stability is obtained by taking advantage of usage than by going counter to it. While to many, priority has seemed to have some special virtue as a basis for nomenclature, its merit must be measured by its practicability, and by this test it is little if any better than usage. This is best shown by the fact that even the most thoroughgoing priority, that dating from the "Species Plantarum," is based upon usage in that it ignores all previous work.

To some systematists stability has seemed to be achieved when the adherents of a particular code were in essential agreement as to its concrete application, a condition not always met. As an actual fact, however, stability exists only when a particular code of rules has universal sanction and gives the same results in application. Such a condition seems distant at present, and for many reasons it is to be hoped that it will not come about until systematists have a wider vision and truer perspective in matters of nomenclature. A further reason why stability is a will-o-the-wisp lies in the effect of segregation, for it must be recognized that stability consists as much in having the same unit for a name as in having the same name for a unit. It lies also in respecting existing landmarks and in relating all new knowledge to these. This in itself involves a thorough change in the current practice, at least in America, and demands that the trinomial be brought into regular use for segregates of valid species. The binomial should be restricted to the species as including all of its subspecies, and the trinomial would always serve to distinguish the subspecies and to relate it to its proper specific stock (cf. Clausen, 1922). Finally, it seems impossible to think that blundering, meaningless, or excessively long names can be stabilized. They detract from the value and usability of taxonomy, as well as its attractiveness, and true stability can be obtained only by correcting or ignoring them.

Practical nomenclature.—If the names of plants are to meet the needs of all those that use taxonomy or would use it, they should be brief, significant, well-constructed, and euphonic. In the present series of monographs an endeavor is made to secure maximum currency for the names used by taking into account the needs of the amateur and the general scientist as well as those of the specialist. This is achieved in the first place by retaining the traditional species, under which the segregates are assembled, while the names of the latter are retained in so far as their quality permits. Even while much latitude in regard to varietal and subspecific names is allowed by both codes, continuity is the essence of stability, and this can be secured only by retaining names whenever possible. Because of its greater emphasis upon usage, the International Code has

been followed in the main, wherever it is consistent with the principles adopted here. However, there has been no hesitation in selecting names from those valid under the American Code when these are preferable, and no compunction has been felt in using names sanctioned by neither code when this has been found to be in the interests of usefulness. To the conservative adherents of either code this may seem reprehensible, but there are many indications that it will be welcomed by the vast majority of non-specialists, who are much more interested in short significant names than they are in validity as determined by codes. It should be added, however, that in the present monographs it has been found necessary to depart from the rules of the International Code in but few cases and that the number of names not in agreement with either code does not exceed two or three. All departures from the International Code are clearly indicated in the text.

Invalid and corrected names.—Undesirable practices in nomenclature have been discussed at length by Clements (1902), and here it will suffice to point out those that are regarded as rendering names invalid or subject to correction. The number of undesirable names is relatively small, and their correction is based upon the contention that usability and uniformity are the first considerations. Furthermore, corrections should not be a matter of individual judgment, but should be in harmony with current good usage. Thus, in the matter of transliteration, it is probable that 99 per cent of all Greek names are properly transliterated into Latin, and there is no valid reason for not changing the others to correspond. Similarly, all incorrect spellings should be changed to conform to the best usage, and it is contended that an author has no more right to spell improperly than has a printer. Names of great length, which are fittingly termed sesquipedalian, should be shortened when more than six syllables long. Specific names ending in *-folia* are especial offenders in this respect, and are readily shortened without violence by dropping the last term.

The most serious offenses against good usage are found in hybrid and vernacular names, and in anagrams. To mention such names as *Henningsocarpum*, *Radlkofertoma*, and *Schweinfurthafra* is to condemn them. They can have no standing with those who believe that the rights of the many are paramount to those of the few, and that usability and good taste are at least as important as priority. The cost of the latter is also well illustrated by such doublets as *Symphoricarpus symphoricarpus* and *Grossularia grossularia*, which are rejected by one code but supported by another.

Essentials of usability.—It has repeatedly been emphasized that a nomenclature must be judged by its value to its users rather than to its makers. From this standpoint brevity and significance are the very essence of nomenclature, though structure, euphony, and uniformity are not to be ignored. Five syllables should constitute the maximum length for generic or specific names, and three or four should be the optimum. No name should be regarded as desirable that does not bear a direct application to the structure, habit, or behavior of the plant or some part of it. It is idle to cavil at such names as *canadensis*, *caroliniana*, etc., for species that occur throughout the Middle West, since they were geographically applicable at the time given. However, they prove the undesirability of geographical names, which, like personal ones, should be avoided. This applies equally to vernacular terms, though in all these cases existing names should be retained, except when seriously at fault. As to structure and euphony, future practice should adhere closely to general good usage, while existing names should be corrected when necessary. When there is a choice between a good name and one distinctly bad, no one should hesitate to use the former, notwithstanding the rule of priority. Euphony and brevity are most frequently ignored in the case of personal and vernacular names, such as *Krashevinnikoviana*, *Niedzwetzkyana*, *Turczaninowiana*, *Wosnessenskia*, and *Zaluzianskya*, and the ultimate rejection of such handicaps to taxonomy seems inevitable.

Finally, the user of names has the right to expect them to be as uniform and simple as possible. Initial *h* should never be lost, as frequently occurs in *Haplopappus*, *Heleocharis*, etc., and in the case of permissible alternatives, as in the genitive, the simpler form is always preferred, e. g., *nuttalli*, *parishi*, etc.

A binomial system of common names.—The realization of the fact that the vast majority of people make their contacts with plants only through the common names seems to render a more adequate system imperative. Most of the so-called common names of the manuals are not vernacular names at all, but mere translations of the technical name. They possess no currency, and lack the qualities to secure it. A few of the actual vernacular names are excellent, but most of them are either local, misapplied, or entirely without significance. When significant common names are in general use, they should be worked into a comprehensive system wherever possible. The most serious failures of vernacular names are in failing to show relationship and to make specific distinctions. In endeavoring to secure these values, it quickly became evident that the binomial was as indispensable for common names as for technical ones. In constructing a binomial system, the current name for the genus or one of its most important species was taken as the basis, and the specific term was used in a compound or as a modifier. The one case is illustrated by *Atriplex*, in which the generic term, scale, was derived from shadscale, the current name for *A. confertifolia*, and similar names made for the other important species, e. g., wingscale for *A. canescens*, lenscale for *A. lentiformis*, allscale for *A. polycarpa*, etc. The other is exemplified by *Artemisia*, in which the current name for the genus, sagebrush, is modified by a specific epithet in the case of all the shrubby species but *A. tridentata*, e. g., hoary sagebrush for *A. cana*, sand sagebrush for *A. filifolia*, coast sagebrush for *A. californica*, etc. The term sagewort is applied to the herbaceous species in a similar manner, e. g., dragon sagewort for *A. dracunculus*, field sagewort for *A. campestris*, etc.

METHODS AND RESULTS IN EVOLUTIONARY TAXONOMY.

Methods.—The conviction has been repeatedly expressed that taxonomy to be phylogenetic and permanent must be based upon the field as the primary seat of investigation. It is conceivable that hundreds of individuals representing the whole range of variation and adaptation might be specially collected and made use of in the herbarium, but this is beyond the bounds of practicability. This does not mean that the actual measurements involved in statistical studies will not be made indoors, but the specific analysis that precedes this is preeminently a field process. The field here is conceived in no narrow sense, but it includes greenhouse, garden, field inclosure, and in fact all habitats, natural or artificial, in which the evolutionary behavior of living plants can be studied. The complete field method demands a knowledge of the variation of the species concerned throughout its climatic area and of its adaptation as it enters diverse habitats adjacent to the normal one. It further requires statistical studies of the species and its variads in the whole range of natural conditions, and experimental analysis in controlled natural habitats as well as in garden and greenhouse. It is obviously a method that demands much and yields much in return. It needs field laboratories and transplant stations, and is impossible of use in collecting trips and reconnoissance. As a consequence, it is little adapted to the preliminary organization of the flora of new or little-known countries, but it is indispensable in testing and refining such results to the point where they accurately represent the facts of evolution and relationship.

Statistics.—The statistical study of the degree of modification, as shown by the individuals of a species or a variad, yields results of the most fundamental importance, an importance surpassed only by those obtained from experiment. The first of these is a far more exact expression of the stage of evolution attained collectively than the most

accurate judgment is capable of, together with a clear indication of the relation to adjacent units as revealed by the bases of the curve. Of equal importance is the evidence furnished by the modes as to the direction of evolutionary movement. This is true not only of the species or variad, but also of the criteria themselves, and one of the most significant services of the statistical method is the opportunity it affords of scrutinizing criteria as they occur in nature. This constitutes an invaluable service at this time, when experiment is still too rare to provide the results desired. The testing of criteria should be the first task of quantitative studies, were it not for the fact that this can be done at the same time that the modes and limits of species and variads are determined.

The methods of statistical analysis can be applied equally well to species and their variants as they exist in nature, to results of such outstanding natural experiments as ecads, and to the forms obtained by experiments under control. However, the chief value at present lies in the application to the study of variation as it occurs in nature, owing to the enormous mass of material demanding analysis. In this it is of the greatest value in determining whether a segregate represents an actual fact of evolution and in confirming its suggested relationship to the species as well as the nearest variads. While the statistical method applies only to characters that can be measured or counted, or to sequences, these are found to include practically all characters of importance in species and variads. It demands a large amount of material to insure the most accurate and comprehensive results, and the selection of this is of the first consequence. Random selection is without value for careful analysis, and gives usable results only where it is wished to obtain merely the total range of variation in a particular area or locality. A preliminary examination is indispensable to permit the recognition of variants and ecads, and to insure that the analysis runs parallel with these instead of cutting across them. While analysis on the spot is always desirable, owing to the abundance of material or the opportunity of checking, both as to forms and habitat factors, this is possible only at field laboratories and substations. In the case of regions remote from these, material must be collected with the maximum discrimination, and with especial reference to the object sought. This may be the range of variation of any character or any organ with respect to the individual, community, species, or variad. The use of fresh material is always preferable, but often impossible, and the question of the use of dried or preserved material depends somewhat upon the plant and part concerned, as well as upon facilities. The chief precaution necessary is to measure while living a few of the parts to be studied, in order to check out any alteration of size due to the method of preservation. As statistical methods come more into use in evolutionary taxonomy, the results will be regularly expressed in biometrical form, but at present tabulations and simple graphs furnish all the facts required.

Experiment.—The rôle of experiment in evolutionary taxonomy is even more fundamental than that of statistics, though in the beginning it rather supplements the latter, owing to the time involved in complete experiments. Its unique importance lies partly in the control possible throughout the entire process, but it arises chiefly from the fact that it alone yields conclusive evidence as to descent. The exact use of statistical methods affords practical certainty as to the origin and relationship of variads, for example, but the actual origin has already occurred, and its nature and causes can only be inferred. To bridge this gap, experiment is indispensable, and hence it must be the final arbiter in all questions of origin and descent. In actual practice, experiment is begun with the statistical studies or as soon after as possible, and the two are carried forward hand in hand, so that each may profit from the other.

As a matter of convenience, experiments may be designated as natural and artificial, though the line between them is slight. Natural experiments are those in which various migration agents have carried migrants into adjacent habitats and the individuals have

undergone definite adaptation to the controlling factor and have become ecads. In cases where the migration is interrupted, the question of descent lacks the final degree of certainty where more than one parent species may be concerned. In mountain regions where the topography is rugged and rapidly changing, habitats are so fragmented that they recur again and again in the same relation to each other. This offers ideal conditions for the invasion of new habitats, and the ecads of plastic species occur repeatedly. In many cases, gravity is the migration agent, and in others the annual extension of root-stock or runner brings about invasion. In both instances there is not only complete continuity in space, but often also in time, so that the question of the specific stock from which the ecad has sprung is as certain as in experiments started artificially.

Artificial experiments differ from natural ones chiefly in that the question of origin is always a matter of certainty. They differ also in being carried on necessarily under control, owing to the fact that the number of individuals is limited, and no chances can be taken with their loss. In nature there may be a hundred or a thousand individuals of an ecad in one spot, and this may occur repeatedly in a restricted mountain region. Thus, while it is sometimes desirable to protect a particular group from rodents, for example, it is rarely necessary. In artificial experiments, control and natural conditions are often antagonistic, and the decision between them must be made upon the basis of the results desired. In the case of hybridization this difficulty does not exist, since physical factors are not taken into account, and investigations of this process are especially adapted to garden and greenhouse. On the other hand, the origin and differentiation of existing species and ecads can best be studied in the field, as garden and greenhouse conditions can only be made to approximate natural habitats at the best. However, the plasticity of species and their reaction to known factors furnish admirable subjects for study under complete control, and certain aspects of mutation are also best studied in this manner.

In experiments at the Alpine Laboratory, where the chance of disturbance by man is slight, the degree of control has varied. Grasses and cacti require little protection in a region without grazing, and the garden of plains species has not been fenced. In the case of reciprocal transplants, it has not seemed practicable to protect each scattered individual with wire netting. With alpine plants, however, their early appearance and succulence, as well as the labor involved in transplanting, has made it necessary to fence the gardens against rodents from the first. This involves practically no change of the physical factors, if plants are kept away from the sides of the fence toward the sun, and the experience of several years indicates that all transplants and other field experiments can well be fenced, except in the case of natural experiments involving many individuals. The hazards of weather, such as hail and flood, alone work sufficient damage, and against these there is no protection that does not change conditions. The fencing of reciprocal transplants requires especial care to see that the plant is at no times shaded by the netting or harmed by the wind. Finally, adequate control in the case of transplants requires the reduction or elimination of competition where they are planted into other communities, since this involves a factor not readily measured.

Method of experiment—The primary methods of experiment in the field are transplanting, planting, seeding, and modification of the habitat. The details of these methods belong in another place, and it will suffice here to point out their differences and values. Transplanting consists in transferring the adult plant from one climate, habitat, or situation to another. It is reciprocal when two related species, a species and its variad, or two related variads are concerned. Climatic transplants are those in which a species is transferred from one climate or subclimate to another or to more than one, as when alpine species are moved to the montane and plains region, or a dominant of the true prairie to the mixed prairie and the bunch-grass prairie. Habitat or edaphic transplants

deal primarily with the transfer within the habitats of the same climax, i. e., between the climax and one or more seral habitats, or the latter alone. Such transplants are especially advantageous, as they are made with the minimum of labor, and usually give the most striking results in the form of ecads. Planting seedlings from the greenhouse or nursery, or sowing seeds under proper precautions, takes advantage of the fact that the seedling is usually more plastic than the adult, but it is subject to many more dangers during ecesis. Consequently, while they are standard methods in experimental vegetation, they are little used as yet in experimental evolution. The modification of the habitat is one of the best of methods, chiefly because it permits the modification of a whole group of individuals in position. It is further valuable in furnishing a check upon the behavior of related individuals transplanted to conditions similar to those produced by the modification. Its one disadvantage lies in the labor sometimes involved in bringing about an effective change of conditions, especially in forests. In such cases, however, Nature frequently steps in and brings about the desired result by the fall of a tree, by fire, or wind-throw. In woodland, scrub, grassland, or herbaceous communities it is often an easy task to change effectively the light intensity, water-content, air-content, etc.

In the case of reciprocal transplants, it is fairly certain that conditions will not be too extreme for either plant, but with climatic and edaphic transplants there is no definite assurance, at least in the beginning. To obviate this, a transplant sequence is used, by which plants are transferred to one or more intermediate zones or habitats. If conditions are too extreme in the last situation of the series and the plants are lost, those of the next less extreme habitat will serve to show the limits of adaptation. When plants are not plastic, however, extreme conditions furnish the only method of breaking the structural habit and thus permitting adaptation (cf. Turesson, 1922).

As already indicated, a certain amount of control can be exerted over physical factors in the case of field experiments. With respect to the primary factor, this is secured when the water-content of an area is increased or diminished, or the light intensity changed by clearing or shading, especially when part of the group or community is left under the original conditions to serve as a check. In a sense, moreover, a kind of control is assured when plants are transferred from sun to shade or from wet to dry. Garden experiments resemble those in the field in the extent to which factors can be controlled or manipulated, and in both complete measurements of all the major factors are indispensable. In the greenhouse, the opportunities for control and manipulation are much greater, and studies of adaptation to definite amounts of factor stimuli can be carried on with much greater convenience and certainty, especially where a sequence of intensities is desired. The greenhouse makes it possible to equalize in large degree all the factors except the one to be studied, and thus permits the more exact causal analysis of results obtained in the field. For this, measurement of the factors is as indispensable as in the field, since this alone permits the correlation of definite quantities of response with equally definite amounts of the controlling factor.

Objectives.—The first great object of the experimental method is to determine the relationship by descent of the species and variads already in existence. In doing this it necessarily deals with the production of new variads under known conditions, and this leads to the study of the whole question of the causes and methods by which new forms arise. The latter opens up the fundamental problems of the origin and transmission of new characters, the solution of which is possible only through the widest range of experiments under measured conditions. In close relation to the origin of forms stands the experimental study of the criteria employed to distinguish variads, species, and genera. This is of particular value to existing taxonomy, and hence is one of the first as well as one of the easiest points of attack. In this the correlation that exists

between organs or parts offers one of the most promising of objectives and one that may serve to explain structures whose origin is now entirely obscure. It seems probable that the correlation between parts is at bottom chiefly a question of competition for food, and, if this be true, the widest experimental vista is opened. While any of these problems may serve as the entry to experimental evolution, they are all so interrelated that a comprehensive attack upon them alone promises to yield adequate results in a reasonable time.

Variads.—The ecological attack upon the problems of evolution has led to the emphasis of three fundamental points, namely, origin, fixation, and differentiation. It proceeds upon the certain knowledge that new forms of plants are constantly being produced by the impact of environment, and hence its first task is to analyze the various methods of origin (Clements, 1907, 1908). Further studies of origin at the Alpine Laboratory have confirmed the hypothesis that direct adaptation to the habitat has there produced the largest number of new forms of plastic species. Mutation now seems less important than it did 15 years ago, but this is partly due to the increasing difficulty of distinguishing mutants from variants, and sometimes even from ecads. Much of variation is undoubtedly response to the gradual change of an efficient factor, or to minute habitats of varying intensity. Further search has not increased the small number of probable hybrids, and it has become necessary to attempt the direct production of hybrids in nature. In spite of the changing importance of the methods of origin, it still appears certain that adaptation, mutation, variation, and hybridization comprise the four processes of evolution, though it now seems evident that adaptation and hybridization constitute the two basic modes. The resulting differentiations of the species are distinguished as ecads, mutants, variants, and hybrids, and are included under the general term *variad*. As to fixation of these, evidence is slowly accumulating to show that this may be cumulative, and that even ecads may run the whole gamut of constancy from the most inconstant to the most fixed. Moreover, one character, such as form, may become fixed, while another arising from the same factor, such as the time of blooming, may be unstable. Finally, it seems clear to the ecologist that degree of differentiation must come to play a more definite rôle in the question of species and *variads*, and that this can be attained only through objective measurement.

METHODS OF TREATMENT.

General plan.—On the basis of the principles discussed above, a series of monographs is planned to comprise a large number of the most important genera and families of North America. For a number of reasons the interest centers in the West, chiefly because this still affords the fullest opportunity for the application of statistical and experimental methods on a large scale. It provides a much greater range of climatic and edaphic conditions, and to this appears to be related a correspondingly greater evolutionary activity. A further reason of the greatest importance lies in the fact that the four bases for ecological research, namely, Pike's Peak, Tucson, Berkeley, and Lincoln, afford unique opportunity for applying the phylogenetic method in the midst of the great climates and climaxes of the West. Finally, the vegetation of the West is not only of the first importance in relation to forestry, grazing, agriculture, land classification, and utilization, but it probably also furnishes the best opportunity in the world for the comprehensive and fundamental development of the science of vegetation itself in relation to climate and soil.

The three genera treated in this monograph were selected because of their taxonomic and ecologic interest. They have been objects of the most active evolution, with which has gone the widest distribution, both as to climate and soil. Ecologically, they are unsurpassed in the number of dominants and subdominants they furnish to the vegeta-

tion. As a consequence, they constitute indicators of great value, especially with reference to alkaline soils. Economically, the chief importance of *Artemisia* and *Atriplex* is as browse plants, while *Chrysothamnus* is interesting as a source of native rubber. All three genera have yielded a large number of segregates, and hence afford a good test of the phylogenetic method in taxonomy and of its value in actual use. Consequently, while the treatment has been made as thorough and consistent as possible, much thought has been given to rendering the results of the greatest usefulness to the non-specialist, ranging from the botanist and forester at one end to the physician and plant-lover at the other.

Field work.—As already indicated, taxonomic studies can be prosecuted to the best advantage in places where the plants grow under natural conditions. It is only by this means that a sufficiently large number of individuals can be passed in review, their variations noted, and the proper correlations made with environmental conditions. Other methods have certain advantages; for example, garden cultures permit of the assembling of forms for comparison and experimentation, but the time is past when any considerable number of North American or European plants should be described as new or opinions ventured as to their proper classification without a first-hand knowledge of their behavior in the field. The value of careful studies in garden and herbarium should not be minimized. In the case of a few rare species no other method is at present available, but the comparatively small number of specimens that can be assembled even in the largest establishments renders the results of such work necessarily incomplete. It seems, therefore, that greater efforts should be made by taxonomists to carry more of their work into the field and that much better facilities should be provided for such investigations.

With this importance of direct field studies in mind, much time has been given to them in the preparation of the present monographs. A general ecologic and taxonomic interest in the genera here treated had resulted in the assembling of a considerable number of data before intensive work was begun. The earliest field trip with these groups especially in mind was in 1917. In August of that year, Hall made collections and studies of *Chrysothamnus* in Colorado, Wyoming, and Nevada and spent the remaining months of the year largely upon this genus, about six weeks being given to field studies in eastern California and Nevada. These were continued in January and February of 1918, during which months much distributional and ecologic information was obtained in the desert area. In May, 1918, Clements prosecuted field studies on all three genera as they occur between Tucson, Arizona, and Berkeley, California, and was joined by Hall in June for similar investigations on a motor trip extending into Oregon and thence to Colorado. In the late summer, Clements worked south to Texas and west to Arizona, while Hall studied in western Colorado, Utah, and Nevada. The latter also visited eastern California, and in December worked from Reno, Nevada, to San Diego, the interest centering chiefly on *Chrysothamnus*. General field studies were combined with experimental activities in Mono County, California. Some of the results, especially those bearing upon the possibilities of this genus as a source of rubber and a classification of the forms of *C. nauseosus*, together with data secured in Utah by M. E. Jones and in Oregon, California, and Nevada by E. C. McCarty and J. R. Bruff, have been published by Hall and Goodspeed (1919).

The summer of 1919 was again spent by both authors at the Alpine Laboratory on Pike's Peak, Colorado, and collections were made from adjacent districts. At the close of the summer's work, field studies were prosecuted in unison during an automobile trip from the Laboratory to Wyoming and across Utah and Idaho to Oregon and California, Clements continuing the work to Tucson, Arizona. In 1920, Clements worked along a different route between Tucson and Berkeley and made a trip from Arizona to

Nebraska and Colorado, where the summer was spent at the Alpine Laboratory, except for an ecologic and taxonomic excursion into the Bad Lands of Wyoming, South Dakota, and Nebraska. In the meantime, Hall prosecuted studies, especially on *Atriplex*, in the alkaline districts of Utah, Colorado, and neighboring States. In the late summer a joint motor trip, with numerous stops and short sidetrips, extended across southern Colorado and northern New Mexico to Arizona, Hall continuing to the borders of Lower California.

In 1921, Clements again motored from Arizona to Nebraska and the Alpine Laboratory, continuing in August to the Pacific Coast. Hall spent a month in August and September in the mountainous portions of Idaho, Montana, and Washington, and then joined Clements for field work in eastern Oregon, western Nevada, and eastern California, going as far south as Mono County. Later in the year studies were made on the *Artemisias* of the coastal slope of California and on the *Atriplexes* of the San Joaquin Valley, the latter in connection with Dr. H. H. Severin, whose intimate acquaintance with these plants rendered the trip especially valuable.

Frequent short trips were made in addition to those outlined above, these being mostly confined to Arizona, California, and Colorado. Short stops were also made at numerous railroad stations when traveling by train. Most of these were between the Pacific Coast and Colorado, but a few were on the Atlantic seaboard. Because of the interest in phylogeny, an endeavor was made to reach all stations in the West where the genera occurred in abundance and where information regarding variations and intermediate forms could be obtained. Type localities were also visited as far as possible and data secured with a view to determining the degree of constancy in the characters used as a basis for species and varieties previously proposed by others. It is with deep regret that, because of lack of time and facilities, it has been found impossible to carry the field work into Canada and the Arctic regions on the one hand and into Mexico on the other.

Results of statistical studies and experiments.—Taxonomic botany is sadly in need of more exact methods of investigation. Far too many opinions have been expressed, too many species proposed, and too many descriptions drawn after a casual examination of only a few specimens, and sometimes without subjecting these to accurate measurements. During the present studies much time and thought has been given to an attempt to remedy this condition. Consequently, all criteria used have been subjected to the quantitative test as far as possible. Sometimes the results are expressed in tabular form, since this affords a concise method for the presentation of the evidence upon which conclusions are based, but in many cases it has been considered sufficient to preserve the data only in the herbarium and thus conserve space. It has been discovered by the use of these methods that many criteria heretofore supposed to be valid break down completely, whereas others commonly overlooked are shown to possess real merit. A notable example of this latter condition is the case of relation of length of stylar appendage to total length of style-branch in *Chrysothamnus*. By reference to table 23 it will be seen that this character is too variable for use in separating most of the subspecies of *C. nauseosus*, but, on the other hand, that two of these are set off from the others and brought near to each other on the basis of this trait. The results are useful not only for diagnostic purposes, but, what is of more importance, as indicating the relationships of the forms involved.

The next step in the application of the statistical method will be the expression of results by the use of graphs, as is commonly done by biometricians. This seems unnecessary in the present work, since the results can be read directly from the tables with almost as great ease as when expressed graphically. The importance of quantitative methods and the use of graphs has been emphasized recently by MacLeod (1919).

The value of all quantitative studies depends upon the accuracy of the methods employed. All measurements and counts tabulated in this paper were made either by one of the authors or by a trained assistant. In the latter case a portion of the results indicated for each form were carefully checked and all doubtful or extreme results were either verified or eliminated. The examinations were carried out with the aid of binocular dissecting microscopes equipped with micrometer disks ruled to 0.1 mm. Larger measurements, such as dimensions of the larger involucres, were made by using fine-pointed calipers with a set-screw attachment. The dimensions are for material preserved in liquid, or, when this was not available, for dried material which had been boiled after the usual manner. It is believed that the only serious source of error is in the number of disk-flowers reported for the *Artemisias*. In these plants the central flowers sometimes mature and drop out in the process of pressing. Therefore counts made from herbarium specimens may be too low in some instances. Wherever this was suspected the space in the table was left blank. The importance of boiling before taking measurements of dried organs should be emphasized when a high degree of accuracy is desired. In the *Compositae* the heads increase their diameter on pressing by as high as 25 per cent in some cases and the flowers are sometimes appreciably shortened by drying and wrinkling. The original shape and size are almost exactly regained by immersing in boiling water for a few seconds.

A series of experiments has been instituted for the purpose of testing the nature of some of the criteria used in the classification of the genera here treated. Since the plants are nearly all perennial, the results now available are limited. Transplants of *Chrysothamnus* have been carried from the desert area and established in coastal districts, while others have been moved into different habitats in the Great Basin, with the result that some definite information has been secured as to the constancy of certain forms. Experiments in pruning and in the cutting of roots at different depths have supplied data as to the ecologic behavior of this genus of plants. Reciprocal transplants of perennial *Artemisias* in Colorado have demonstrated the constancy of such characters as amount of pubescence for a period of three years in some cases, but it is still too early to predict final results. Some of the annual *Atriplexes* have been grown at Berkeley, where they could be kept under observation, with the result that certain characters of young plants, particularly leaf position, have been found to be so different from those described by earlier students of the genus that fundamental changes in the classification have been necessary. The final results of the experimental studies will be reported subsequently.

Illustrations.—All of the accepted species and many of the subspecies and minor forms are illustrated in the plates which accompany this memoir. This is entirely the work of Miss Ruth Jeannette Powell, to whom the authors are under lasting obligations for the exercise of much patience as well as artistic ability. Extensive scientific training has given her an insight into the methods and aims of botanical research which has greatly added to the accuracy of the results and to the clearness of their expression.

A majority of the plates were prepared from fresh specimens sent directly from the field. When it was found necessary to resort to dried or herbarium material, this was first restored to its natural form by immersing in boiling water for a few seconds, or at least a small portion was so treated to secure a correct idea of the size, shape, and relative position of the various parts. In some *Artemisias* the difference between fresh and dried heads amounts to as much as 10 per cent, but this varies with the amount of shrinking and wrinkling. All drawings made from dry specimens are indicated in the explanations accompanying the plates, and all such were prepared from boiled material. The amount of enlargement or reduction of each drawing is also indicated. It will be noted that this has been kept constant for each structure throughout a genus, thus enabling one

to make direct comparisons between the different forms without resorting to computations. The only features not drawn to scale are the thumb sketches sometimes inserted to indicate habit. These were prepared for some species after studies had been made by the artist in the field; most of them, however, were constructed from photographs of living plants taken for the purpose.

All of the drawings, with the exception of the thumb sketches just mentioned, are believed to be accurate as to shape and size. The smaller details were drawn as they appear under the binocular dissecting microscope, and measurements were made with the aid of a micrometer disk. In all cases a subsequent examination was made to be certain that the dimensions adopted represented the average of the material in hand.

Phylogenetic charts.—Since one of the main objects of the present monographs is to present a classification based upon phylogeny, it has been thought desirable to give a graphic presentation of the relationships between the numerous forms. A number of charts has been prepared to accompany the discussions of phylogeny. There is no thought of finality in the diagrams as here presented. Their purpose is to express the results of evolution as now understood, and it is fully appreciated that the evidence for certain phyletic lines is still far from conclusive. However, the importance of natural groupings and their expression in a readily intelligible form is so great that the charts are here presented as a contribution to the general subject of phylogeny. Moreover, in some groups the relationships are so well understood that only slight modifications will be necessary as the result of further studies.

Many of the charts are to be looked upon as expressions of degree of relationship rather than as illustrating definite lines of evolution. This is because it is sometimes easier to make out the relationships of biologic forms than it is to demonstrate the lines along which they have evolved. This is particularly true as regards the *direction* of evolution. For example, in many of the charts the relationships of certain groups are pretty well understood, but it is at present impossible to determine which one represents the original stock. Therefore, it may be necessary in some cases to start with one of the forms here placed fairly well up in the scheme, proceed thence towards the lower ones, and then around to other branches leading to the most highly developed of all.

Even though the exact lines of evolution can not always be indicated with certainty, the bringing together of related forms into increasingly larger and larger natural groups should be undertaken wherever possible, for this is the basis of taxonomy. The graphic representation of such relationships, if carried to all groups of plants, would doubtless be of much value to geneticists, breeders, and others who need to know the related forms of plants with which they are working. Furthermore, if properly prepared, phylogenetic charts may replace, to some extent at least, the analytical keys now in vogue. Largely with this use in mind, the differentiating characters as well as the names of the groups themselves have been inserted on the charts here presented.

Citation of authors, synonyms, and specimens.—The almost universal custom of following the specific, subspecific, and varietal name by that of the author who first used it is followed throughout this monograph. It is hoped, however, that as names and combinations of names become established, this practice will be deemed unnecessary, since its object is accuracy in the application of terms rather than credit to the author. When new combinations are made for the first time in this work, the first author of the final term is cited in parenthesis. There is no important reason why this should be followed by the name of the author of the new combination, but as a concession to custom this is done when such combination has been made prior to the issuance of this volume. It therefore follows that the present authors are responsible for all those combinations in which the parenthesis is not followed by the name of some other worker. In the case of a few trinomials the combination itself is not new, but the rank has been

changed, usually from that of variety to that of subspecies. In these instances the carrying over of the author of the variety as the author also of the subspecies is considered not justifiable.

An attempt has been made to give a complete synonymy under each of the species, except when the synonym applies only to foreign variations, when its application to North American forms can not be made with certainty, or when it results from such remote transfers as that of *Chrysothamnus* from *Aster*.

The citation of specimens examined is given for two principal purposes: (1) to indicate the distribution, and (2) to enable workers at the various herbaria to gain a clear notion of the authors' concepts of the species, subspecies, and minor variations. Specimens fairly representative of the group under consideration and from different portions of the area of distribution have therefore been chosen for citation, or if not representative, the variation is then indicated in parenthesis. A complete citation of *all* specimens examined is given only when the group is rare or otherwise of special interest. Initials and titles of collectors are seldom given, since it is believed that their omission will not lead to confusion when looking up the specimens in herbaria. The names of certain collectors have become so closely associated with botanical work in special regions that their initials seem superfluous. When collections by another with the same surname are cited, the initials of this latter botanist are given. Thus, "Jones" refers to Marcus E. Jones, for plants gathered anywhere in the West, the few collections by W. W. Jones being so cited; "Nelson" refers to Aven Nelson when Rocky Mountain plants are indicated, but to "E. W. Nelson" in the case of Mexican specimens, collections by Elias Nelson being cited in full.

The names of the herbaria in which the cited specimens were seen are indicated by abbreviations in parenthesis following the name of the collector. The abbreviations adopted are the following:

- CI, Unmounted specimens provisionally retained by the authors as part of the working collection of the Carnegie Institution.
 DS, Dudley Herbarium of Stanford University.
 Gr, Gray Herbarium of Harvard University.
 NY, Herbarium of the New York Botanical Garden, including the Torrey and other herbaria of Columbia University, there on deposit.
 Phila, Herbarium of the Academy of Natural Sciences of Philadelphia.
 R, Rocky Mountain Herbarium of the University of Wyoming.
 SF, Herbarium of the California Academy of Sciences, San Francisco.
 UC, Herbarium of the University of California, including the Brandegee Herbarium.
 US, United States National Herbarium, including that of the United States Department of Agriculture.

Herbaria studied and acknowledgments.—The detailed herbarium and statistical studies necessary as supplementing the field work have been carried out for the most part at the University of California. Here every facility was freely available, including the use of the herbarium and botanical library, and grateful acknowledgment is made to the University authorities and especially to the Department of Botany. Other California herbaria studied include those of the California Academy of Sciences, the Dudley Herbarium of Stanford University, and the C. F. Baker Herbarium of Pomona College. The Rocky Mountain Herbarium, at the University of Wyoming, was visited a number of times and found to be extremely helpful, especially because of the large amount of critical material brought together by President Aven Nelson and his staff. Professor Marcus E. Jones, of Salt Lake City, courteously aided in the study of types and other critical material in his collection, and the herbaria at the Universities of Nevada and Arizona were frequently consulted. All of the material belonging to the three genera here treated was examined by both authors in the winter of 1920-21 at three leading herbaria on the Atlantic Coast, namely, the Gray Herbarium of Harvard University, especially rich in types and in specimens gathered on the early surveys and expeditions

and well supplemented by more recent collections, especially by Professor Merritt L. Fernald and his colleagues from the northeast coast; the Herbarium of the New York Botanical Garden, where a splendid collection of *Artemisias* has been assembled, largely through the efforts of Dr. P. A. Rydberg during the preparation of his account of this genus for the North American Flora, and where the Torrey and other herbaria of Columbia University are deposited; and the United States National Herbarium, where the series of *Atriplex* is especially noteworthy, the original collection having been much enlarged by Mr. Paul C. Standley during his preparation of a revision of the species for the North American Flora. The Academy of Natural Sciences of Philadelphia was visited with special reference to the types of Nuttall's species. Critical studies were made at the E. L. Greene Herbarium, now at the University of Notre Dame, South Bend, Indiana, and photographs taken of many of the type specimens. The herbarium of the Missouri Botanical Garden was consulted in regard to certain types and duplicate types there deposited, but time did not permit of a complete examination of all the specimens in this rich collection.

It has been found desirable in a few cases to borrow material for critical study at Berkeley. Thus, a considerable collection of *Chrysothamnus* was received on loan from the Rocky Mountain Herbarium through the courtesy of President Aven Nelson, and Dr. B. L. Robinson has kindly sent specimens of *Atriplex* and *Artemisia* from the Gray Herbarium of Harvard University. An authentic specimen of *Artemisia domingensis* was contributed by the Botanical Garden and Museum of Berlin, Germany, at the suggestion of Dr. I. Urban. Photographs of types have proved exceedingly useful, especially when accompanied by fragments of the specimens themselves. Such photographs were secured in large numbers from the United States National Herbarium, the New York Botanical Garden, the Gray Herbarium, and the Greene Herbarium. These prints, together with the fragments which usually accompanied them, were obtained in part as an exchange with the University of California, where they now form a part of the botanical collection.

Grateful acknowledgment is here made to the curators of the various herbaria mentioned above, both for the privilege of examining specimens under their care and for valuable suggestions and critical opinions given during the progress of the work. In this latter connection should be mentioned also the large number of botanists, foresters, and others who have been consulted from time to time on certain matters with which they were especially familiar.

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GENUS ARTEMISIA.

RELATIONSHIPS AND GENERIC LIMITS.

Artemisia is a member of the *Anthemideae* or mayweed tribe of the *Compositae*. Its nearest ally is *Tanacetum*, from which it differs by only one constant technical character, namely, the type of inflorescence, although several other characters are so nearly constant as to remove any thought of uniting the two.

The inflorescence of the heads in *Artemisia* is always of the paniculate type. Sometimes the panicle is reduced to a single raceme, but never or rarely to a single head, and nowhere in the genus do we find any approach to a cymose inflorescence. *Tanacetum*, on the other hand, has a distinctly cymose arrangement of the heads, and even when the head is solitary, as sometimes occurs in *T. huronense*, *T. bipinnatum*, *T. compactum*, and other species, this is evidently the result of reduction from the cymose type as indicated in most cases by the presence of cymes in other individuals of the same species.

A second character useful in the recognition of *Artemisia* as distinct from *Tanacetum* is found in the shape of the anther-tips. In the former genus these are always lanceolate or subulate and pointed; in *Tanacetum* they are broadly lanceolate to ovate and more or less obtuse, with the single exception of the recently discovered *T. compactum*, of western Nevada, in which species the tips are subulate and acute.

Although *Artemisia* and *Tanacetum* constitute two rather well-defined and natural genera, various attempts have been made in the literature to establish additional ones by the process of taxonomic segregation. One of the earliest of these attempts was by Tournefort, who in 1700 recognized *Artemisia*, *Abrotanum*, and *Absinthium* (Inst. Rei Herb. 1:457-460). These proposed genera were based in part upon floral characters and hence they still serve as subgenera or sections in many modern treatments, but their full generic recognition is without practical value, since each contains at least a few species which, in all but purely technical characters, very closely resemble certain species in one of the other groups. The other attempts to establish genera within *Artemisia* and *Tanacetum* have been based upon characters of slight importance, and therefore the generic standing of the resulting segregates is very insecure. The latest treatment of the North American forms is by Rydberg (N. Am. Fl. 34 : 242-285, 1916). Since this author is inclined to the acceptance of genera on less important characters than those demanded by most botanists, it is not surprising to find that all of the earlier proposed segregates, except those of Tournefort, are here treated as genera and three new ones added. A list of these, with a tabulation of the principal characters used in their differentiation is given in table 3, at bottom of next page.

The following key has been prepared in order to bring out the contrasting characters fully. It differs in some details from the key given by Rydberg. According to the treatment preferred here, the first four "genera" fall into *Tanacetum*, the fifth stands as *Crossostephium* but confined to a single Old World species, and the last two are referred back to *Artemisia*.

Inflorescence cymose, the cyme occasionally reduced to a single head.	
Anther-tips lanceolate or ovate, more or less obtuse.	
Corollas of the marginal flowers oblique; pappus coroniform	1. <i>Tanacetum</i> .
Corollas of marginal flowers not oblique; pappus none.	
Achenes swelling and becoming gelatinous in water; receptacle pubescent	2. <i>Vesicarpa</i> .
Achenes neither swelling nor becoming gelatinous in water; receptacle glabrous	3. <i>Sphaeromeria</i> .
Anther-tips subulate, acute	4. <i>Chamartemisia</i> .
Inflorescence racemose-paniculate.	
Receptacle glabrous or pubescent but never chaffy-bracted.	
Achenes and corollas glabrous to arachnoid, but not villous.	
Pappus a lacerate crown; ray-flowers in 2 rows	5. <i>Crossostephium</i> .
Pappus wanting; ray-flowers in 1 row or wanting	6. <i>Artemisia</i> .
Achenes and corollas arachnoid-villous	7. <i>Picrothamnus</i> .
Receptacle chaffy-bracted	8. <i>Artemisiastrum</i> .

Although a discussion of *Tanacetum* and its three segregates does not fall within the province of this paper, *Chamartemisia* is so near *Artemisia* that its generic position should be here considered. This proposed segregate of *Tanacetum* has the subulate anther-tips of *Artemisia*, but in habit, inflorescence, receptacle, and corollas it agrees with the *Sphaeromeria* section of *Tanacetum*. There is, to be sure, no other *Sphaeromeria* with a pappus, but the genuine species of *Tanacetum* have a coroniform pappus. The species of *Artemisia* are universally devoid of pappus, and moreover, the presence or absence of pappus can not be accepted as of generic value in this case. It seems, therefore, that *Chamartemisia* is much more closely related to *Tanacetum* than it is to this genus, and that it may be referred to *Tanacetum*, section *Sphaeromeria*, or a new section established for it, since its distinguishing characters are not sufficient to sustain a new genus. The inflorescence in the few specimens thus far collected is so reduced that one can not say with certainty whether it is of the paniculate or of the cymose type, but the assemblage of other characters perhaps warrants the conclusion that it is the former.

Crossostephium, as here delimited, consists of but a single species, namely *C. artemisioides* Lessing, based upon *Artemisia chinensis* Vahl, not Linnaeus, a species of the Philippine Islands and China. Gray had suggested that this be reduced to *Artemisia* and that it stand next to *A. australis* Lessing, of the Hawaiian Islands, and *A. californica* Lessing, of western North America (Syn. Fl. 1²: 370, 1884). Rydberg has taken the same view of this relationship, but refers all three of the species just mentioned to the genus *Crossostephium*. It seems that both treatments are erroneous, and that it is better to restrict *Crossostephium* to *C. artemisioides* alone. This belief is based upon a careful examination of material, by which it is found that the American and Hawaiian species referred to *Crossostephium* are lacking in the two essential features of that genus, namely, the coroniform pappus and the double row of ray-flowers. A more detailed statement is given in the discussion of the relationships of *A. californica* (p. 54).

The two remaining segregates of *Artemisia* indicated in the preceding key are based each upon a single character. *Picrothamnus*, with but one species, *A. spinescens*, is an *Artemisia* of the section *Dracunculus*. It was established by Nuttall (Trans. Am.

TABLE 3.—Characters of *Artemisia*, related genera, and segregates.

	Anther-tips.	Inflorescence.	Pappus.	Corolla of marginal flowers.	Receptacle.
<i>Tanacetum</i> Linnaeus.....	Ovate, obtuse	Cymose or solitary by reduction.	Coroniform.	Oblique, somewhat ligulate.	Naked.
<i>Vesicarpa</i> Rydberg ¹	Ovate-lanceolate.	Cymose.	Wanting.	Nearly tubular.	Pubescent.
<i>Sphaeromeria</i> Nuttall.....	Ovate, "obtusish."	Cymose or solitary.	Wanting.	Nearly tubular, slightly if at all oblique.	Naked.
<i>Chamartemisia</i> Rydberg ² ...	Subulate.	Solitary or two, probably reduced from a cyme.	Coroniform.	Nearly tubular; no ligules.	Naked.
<i>Crossostephium</i> Lessing ³	Subulate.	Panicled.	Coroniform.	Nearly tubular; no ligules; in 2 rows.	Essentially naked.
<i>Picrothamnus</i> Nuttall ⁴	Subulate.	Racemose.	Wanting.	Short, 2-cleft.	Naked.
<i>Artemisia</i> Linnaeus.....	Lanceolate or subulate.	Panicled or the panicle reduced and raceme-like or spike-like.	Wanting.	Tubular, often oblique	Naked or pubescent.
<i>Artemisiastrum</i> Rydberg....	Subulate.	Panicled.	Wanting.	Tubular.	Chaffy.

¹ Differs from all the others in the somewhat utricular achenes, the surface of which becomes gelatinous in water.

² *Chamartemisia* has pappus of *Tanacetum*, corolla of *Sphaeromeria*, and anther-tips of some *Artemisias*.

³ *Crossostephium* as originally described has only one species; extended by Rydberg to include *Artemisia californica* with ray-flowers in a single row and no pappus (see page 54).

⁴ *Picrothamnus* was separated from *Artemisia* on spiny habit, villous achenes, and villous corollas (achenes and corollas glabrous to rarely pubescent in *Artemisia*).

Phil. Soc. II. 7:417, 1841) and reduced to *Artemisia*, section *Dracunculus*, by D. C. Eaton (Watson, Bot. King's Expl. 180, 1871), which reduction was accepted by Bentham and Hooker, Gray, Hoffmann (in Engler and Prantl's *Natürlichenpflanzenfamilien*), and by others. Recently it has been revived by Rydberg and others, but without additional substantiating characters. Its most striking feature is the villous pubescence of the achenes and corollas. This can not be considered of generic or even of sectional value, since, aside from the fact that such characters are never of prime importance, the recognition of *Picrothamnus* would lead to claims for generic rank for such species as *A. parishi*, in which the achenes are arachnoid-pubescent, while the corollas remain glabrous, and which is also of such close natural relationship to *Artemisia tridentata* that it is here taken as a subspecies. The spinescent habit is not exactly duplicated elsewhere in the genus, but it is approached in *A. rigida* and in some forms of the Asiatic *A. persica* Besser, one of which, described as variety *subspinescens* (Besser, Fl. Orient. 3:374, 1873), has similarly rigid branches that are persistent and indurated after anthesis. This does not belong to the same section as *spinescens*, but its tendency to become subspinose indicates that the habit need not exclude a form from the genus. Another feature of *spinescens* is found in the completely fused style-branches. Since this frequently occurs also in several species of the section *Dracunculus*, as discussed under the heading of Criteria, it seems to be an additional bond between *Picrothamnus* and *Artemisia*, especially when the high evolutionary position of *Dracunculus* is considered. Any other arrangement would necessitate the assumption that the fused character of the style-branches was developed independently in two widely separated groups.

Finally, *Artemisiastrum*, which has been proposed as a new genus to include *A. palmeri* alone, is an evident recognition of the importance of receptacular bracts. While the presence or absence of these structures is of much value in the classification of the *Compositae*, their occasional occurrence in a genus whose species are almost universally devoid of them may be looked upon as a possible case of reversion rather than as the basis for a new genus. In fact, it is not uncommon for certain of the *Helenieae* to exhibit chaff on the receptacle of species in which it is usually naked, yet there is no thought of separating these aberrant forms even as species (*Baeria chrysostoma*, *Chaenactis carphoclinia*, etc.). Since the other characters of *Artemisiastrum* are not fundamentally different from those of other species of the section *Seriphidium*, the presence of receptacular chaff may be considered of not more than specific value in this case. An attempt to assign the same value to a character wherever it appears, for the sake of consistency or otherwise, would lead to the creation even of new tribes for *A. palmeri* and for the occasional forms of *Baeria* and *Chaenactis* just mentioned, on the plea that this character is used elsewhere in the *Compositae* for the differentiation of tribes.

From the considerations just presented it seems impossible that *Picrothamnus* and *Artemisiastrum* are other than offshoots from the main line of *Artemisia*, and furthermore that each has arisen at a different point. There is no evidence to indicate that either was developed before the differentiation of other *Artemisias* took place; in other words, that they represent phylogenetic lines distinct from *Artemisia*. Their defense must rest, therefore, upon the plea that their differentiating characters are such as are used elsewhere for generic distinction, but such treatment leads neither to stability nor to an expression of the facts of evolution and relationship as they are now understood. For these reasons, these proposed segregates are here again referred to *Artemisia*. *Crossostephium* is an entirely different case. When restricted to its single original species it represents a definite phylogenetic line distinct from *Artemisia*. After the elimination of the American species recently referred to it, but which belong to *Artemisia*, *Crossostephium* has good characters as a natural monotypic genus.

ORIGIN AND DEVELOPMENT OF THE SECTIONS.

The first attempt at a systematic arrangement of species now referred to *Artemisia* was that of Tournefort in the latter part of the eighteenth century. This early botanist pointed out certain characters of some importance, such as the pubescence or the lack of it on the receptacle, and published a synopsis of the forms known at that time (Inst. Rei Herb., 457-460, 1700). These were arranged under three genera, namely, *Absinthium*, *Abrotanum*, and *Artemisia*. Since Tournefort's system was based largely upon gross external characters, and especially upon aspect, it led to unnatural groupings, which were abandoned by later workers in the *Compositae*, although his generic names have been retained for certain of the sections.¹

Linnaeus, in the Species Plantarum, united Tournefort's three genera under the one name of *Artemisia*, thus establishing the genus as now generally accepted. He made only specific use of the receptacular character indicated by Tournefort and based his divisions of the genus, which were not indicated by section names, upon the unimportant characters of habit, inflorescence, and foliage.

A notable advance was made when Cassini established the genus *Oligosporus* in 1817 to accommodate those *Artemisias* in which the flowers in each head are of two sorts, i. e., marginal pistillate flowers and central perfect ones, the latter with abortive or at least sterile achenes. This group corresponds to the present section *Dracunculus*. The other species were all assigned to the genus *Artemisia*, *Absinthium* not being recognized. Cassini's treatment was adopted by Lessing (Synopsis Gen. Comp., 264, 1832), who also recognized three subgenera of *Artemisia*, based upon features which had in the meantime been emphasized by Besser.

While all of the above workers made certain contributions toward a natural arrangement of the species, it was more than a hundred years after the publication of Tournefort's studies before a rational and comprehensive natural system was proposed. This was by the Russian botanist Besser, who published his results in various papers, including the first part of what was designed to be an extensive and fully illustrated monograph of the genus.²

The monograph projected by Besser was never completed, because of his death in 1842, but a masterly summary of his studies is presented in DeCandolle's Prodrômus (6:93-127, 1837). The subdivisions of the genus as established by Besser, together with the characters assigned are as follows:

- SECTION I. *Dracunculus*. Heads heterogamous; marginal flowers pistillate (and fertile); central flowers perfect but sterile; receptacle glabrous.
 SECTION II. *Seriphidium*. Heads homogamous (flowers all perfect and fertile); receptacle glabrous.
 SECTION III. *Abrotanum*. Heads heterogamous; marginal flowers pistillate (and fertile); central flowers perfect and fertile; receptacle glabrous.
 SECTION IV. *Absinthium*. Heads heterogamous; marginal flowers pistillate (and fertile); central flowers perfect and fertile; receptacle hairy.

Although Besser apparently missed the evolutionary significance of his classification, it has the decided virtue of being natural. It is based primarily upon fundamental differences in floral structure, and therefore always will be used as the basis for any

¹ Gaertner, Meyer, and Scherbius (Fl. Wetterau 3 : 196, 1801) retain the Tournefortian genus "*Absynthium*" with one species, namely *A. vulgarius* Bauhin, that is, *A. absinthium* Linnaeus.

² BESSER, W. S. 1829. Synopsis Absinthiorum. Bull. Soc. Imp. Mosc. 1 : 219-265.
 ———. 1831. de Seriphidiis seu de sectione IIIa Artemisiarum Linnaei. Bull. Soc. Imp. Mosc. 7 : 1-46.
 ———. 1834. Tentamen pe Abrotanis seu de sectione IIda Artemisiarum Linnaei. Nouv. Mem. Soc. Mosc. 3 : 1-92.
 ———. 1835. Dracunculi seu de sectione IVta et ultima Artemisiarum Linnaei. Bull. Soc. Imp. Mosc. 8 : 1-95.
 ———. 1836. Supplementum ad synopsis Absynthiorum tentamen de Abrotanis, dissertationem de Seriphidiis atque de Dracunculis. Ib. 9 : 1-115.
 ———. 1841. Revisio Artemisiarum Musei Regii Berolinensis, cuius partem constituit Herb. Wildenovianum instituta. Linnaea 15 : 83-111.
 ———. 1845. Monographae Artemisiarum, Section I. *Dracunculi frutescentes*. Mem. Sav. Etr. St. Petersb. 5 : 1-44.

scheme that aims at a representation of relationships. It will be readily seen, however, that the four sections are not of equal rank, the third and fourth differing from each other only by the absence or presence of hairs on the receptacle. This was noticed by Gray, for in his Synoptical Flora we find *Abrotanum* and *Absinthium* united into what is called *Euartemisia*, the other two sections of Besser being retained with the same limits as in the Prodrromus. The logic of this reduction is sound, but for practical purposes it seems better to retain *Absinthium* and *Abrotanum* as sections.

Up to the present time students of *Artemisia* seem to have contented themselves with its subdivision into more or less natural sections, but have not been much concerned with the phyletic arrangement of these sections. In even the latest treatments the section *Dracunculus* is still found at the beginning, although there is abundant evidence that this is a more highly specialized type than *Abrotanum*, and that, with the possible exception of *Seriphidium*, it is the most highly developed of all of the groups. A considerable rearrangement is therefore necessary in order to bring the sequence into harmony with well-established principles of phylogeny. The various groups, their distinguishing characteristics, and their probable relationships are indicated in the accompanying chart (fig. 1) and may be expressed in key form as follows:

- Heads heterogamous, the marginal flowers pistillate.
 Central flowers fertile, with normally developed achenes.
 Receptacle not hairy 1. *Abrotanum*.
 Receptacle long-hairy 2. *Absinthium*.
 Central flowers sterile, their achenes aborted. 3. *Dracunculus*.
 Heads homogamous, the marginal flowers wanting. 4. *Seriphidium*.

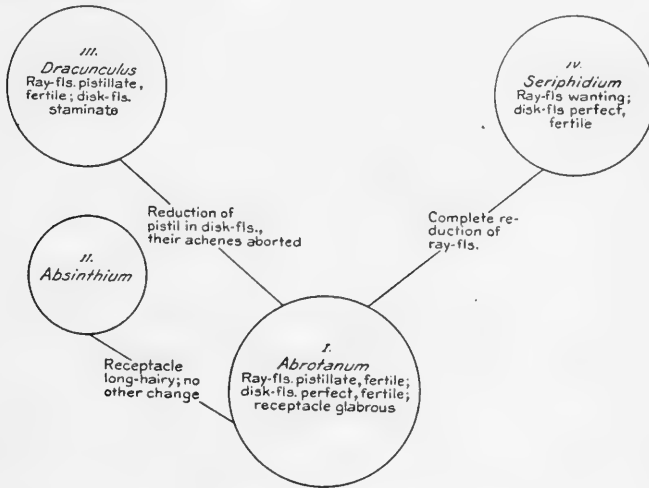


FIG. 1.—Phylogenetic chart of the sections of *Artemisia*.

This arrangement is based on the assumption that *Artemisia* is derived from an ancestor resembling *Chrysanthemum* or *Tanacetum*, in which the ray-flowers are present and pistillate and the disk-flowers perfect and fertile. In the genus *Tanacetum* section *Sphaeromeria* there is an evident reduction in the ligule of the ray-flowers, proceeding in some cases to its complete elimination, when the corolla closely approximates that of *Abrotanum* in structure and shape.

The most primitive of the sections is *Abrotanum*. This seems certain from the consideration that all others exhibit very marked peculiarities which could come about only through the modification of an *Abrotanum*-like ancestor. Thus, forms without ray-flowers or with aborted disk-flowers certainly were derived from a form in which both ray-flowers and disk-flowers were present and fertile. The evident connection of certain species of *Abrotanum* with the still more primitive *Crossostephium* is additional evidence pointing in the same direction. *Abrotanum* is by far the largest of the sections and is widely distributed in both the New and the Old World. The species are mostly perennial herbs, the best known of which is the common mugwort, or sagewort (*A. vulgaris*.)

Absinthium is an assemblage of European and northern herbaceous perennials. It differs from *Abrotanum* solely in the presence of a copious villous pubescence on the receptacle. Since this character does not reappear elsewhere in the genus,¹ the group is considered as a derivative or subdivision of *Abrotanum* which has not led to any decided development. Its distinguishing character is not such as to warrant its recognition as a separate section, yet it is continued because of usage and practicability.

The two remaining sections of *Artemisia* have been evolved by the same process of reduction as that exhibited in the development of the genus itself. The loss of the pappus and of fully functional ray-flowers has been followed by the progressive reduction of the flowers of the head. This appears to arise in consequence of the fact that the ray-flowers and disk-flowers had come to have essentially the same function, and hence to compete with one another for the food-supply brought to each head. A demand for food in excess of the supply would inevitably bring about the reduction and loss of the less important parts. This might operate in either of two directions, namely, to eliminate the unnecessary pistils in the disk-flowers or to effect the loss of the ray-flowers, already much reduced in functional value. Both of these specializations resulted in economy of material and increase of parental care, and have actually been carried out in the respective sections, *Dracunculus* and *Seriphidium*.

The section *Dracunculus*, which comprises herbs and low shrubs of both hemispheres, is here taken as a development from *Abrotanum*. It is considered as a farther advance, for not only are the calyx-limb and stamens of the marginal flowers wanting as in that section, but the pistil of the central flowers ceases to function, so that the central achenes are uniformly sterile and in most cases entirely aborted. There is thus a complete division of labor between the two sorts of flowers, the marginal ones functioning exclusively as pistillate, the others as staminate.

Seriphidium is a comparatively small group in this country, where the representatives are all shrubs or at least woody perennials, commonly known as sagebrush (*A. tridentata*, etc.). In the Old World there are many herbaceous as well as shrubby species, but it is not certain that these are of the same phylogenetic stock as the American ones. It is possible that the characters of the section have been developed independently on the two continents. If this is the case, then *Seriphidium* as now accepted is not a natural subdivision. Whether of one origin or of two, this section, like *Dracunculus*, is probably a derivative of *Abrotanum*, but its evolution has proceeded along quite different lines. Instead of the central flowers becoming essentially staminate, they have remained perfect and the achenes are fertile, but the marginal flowers have entirely disappeared, thus rendering the head homogamous through reduction. This may be viewed as the result of competition between the central and the marginal flowers of the head, the former having succeeded in drawing food away from the latter, which in consequence have failed to function and have finally disappeared from the heads. This is an advantage

¹ The receptacle in *A. californica* is sometimes puberulent, but never long-hairy.

so far as the species as a whole are concerned, as is indicated by the fact that although the average number of flowers in the head is much less in *Seriphidium* than in any other section, the species are abundant in individuals and widely distributed. An intermediate stage between *Abrotanum* and *Seriphidium* is indicated by *A. bigelovi*, a low shrub with the aspect of certain forms of *A. tridentata*. Here the ray-flowers, recognized by their peculiar 2-toothed corollas, are usually present, although reduced in number to only one or two, but occasionally entirely suppressed, the head then consisting of only two or three flowers with regular 5-toothed corollas. Perhaps this species represents the beginning of the *Seriphidium* line, where the evolution of homogamous from heterogamous heads is still in progress.

In accordance with this discussion of the relationships of the various sections of *Artemisia* to one another, the sequence in the following treatment conforms to the diagram and key here presented, and hence departs quite radically from that found in any preceding monograph. While this may at first seem somewhat confusing, it is believed that the phylogenetic basis on which it rests is ample justification for its adoption.

CRITERIA FOR THE RECOGNITION OF SPECIES AND SUBSPECIES.

It is obvious that the best criteria are those which have to do with the structure and development of the flowers and particularly those of the fruits. Such differences in character are not wanting in *Artemisia*, but they are extremely few. It is not surprising, therefore, to find that these are of such importance that they are used as a basis for the sections of the genus. Thus, the suppression of the ray-flowers in some cases and the complete disappearance of the disk-achenes in others are both recognized as sectional characters, as already discussed in the preceding chapter. Other characters, such as minor modifications in floral structure, and especially that of the involucre and the more vegetative parts of the plant, will now be taken up in detail.

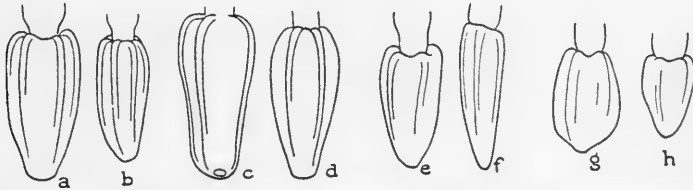


Fig. 2.—Achenes of *Artemisia*: a, b, from a single plant of *A. tridentata typica* (73923 UC); c, d, from another plant of *A. tridentata typica* (71705 UC); e, f, from a single plant of *A. cana* (Hall 11673); g, h, from another plant of *A. cana* (Hall 11690). All of the achenes are more or less granular-glanduliferous. All $\times 16$.

Achene.—The shape of the achene in *Artemisia* apparently is a modification of the prism. In some species it is still essentially prismatic, with four faces, but there always is a more or less evident narrowing toward the base and the summit is truly truncate in only a few cases. The nearest approach to the prism is seen in the achenes of some of the subspecies of *A. norvegica*, *A. tridentata*, and *A. cana*, as shown on the respective plates. The variation within a species, and even on a single plant, is greater than would be expected. This variation is seen especially in the extent of incurving at the summit and in the prominence of the angles, these latter often being reduced to ribs or nerves, or in some cases they are quite obsolete. Something of this is shown in the accompanying figures, where it will be seen that very unlike achenes occur in some of the species.

Differences in shape and especially in size are often due merely to differences in maturity. This is so evident, and fully ripe achenes are so seldom represented in herbaria that a statement of size in a diagnosis is rarely of value. On the contrary, it is often positively misleading. For these reasons the size is not indicated in the descriptions in the present paper.

Notwithstanding the considerable fluctuation within even a single species, achenial characters serve somewhat as a guide in the matter of natural groupings. Thus, for example, in the section *Abrotanum* the achenes are comparatively short and tend toward the formation of a border or crown at the broad summit. This border fits loosely around the base of the corolla-tube. It is most noticeable in *A. pontica*, *A. abrotanum*, and *A. californica*, all of which seem to be primitive in most of their other characters. The crown-like summit is here perhaps a remnant of the disk which bore the pappus in those forms precedent to *Artemisia* in the line of evolutionary development. A similar but less definite crown persists also in section *Seriphidium*, but here it is usually associated with more elongated achenes, often with four or five raised longitudinal ribs or angles.

Style-branches.—The usual condition of the style is 2-cleft at maturity, as in most *Compositae*. In the ray-flowers the branches are either acute or thickened and somewhat obtuse, while in the disk-flowers the branches are almost uniformly truncate at apex and more or less distinctly fimbriate or at least penicillate. In some cases, however, the style in the disk-flowers is undivided and capped by a disk with a roughened or fimbriate border. This is certainly a development from the 2-cleft style, brought about by the fusion of the branches. It obtains only in certain species of the section *Dracunculus*. This character of the peltate stigmas has sometimes been used for the purpose of distinguishing the *dracunculus-campestris* group, in which the style is said to be undivided, from the *filifolia-pedatifida* group, in which the style is described as usually more or less 2-cleft. An examination of seven collections of *A. dracunculus* from widely separated localities discloses the fact that in all of these the style is cleft into two lobes, which are erect, or nearly so, as in *A. filifolia*. Frequently the branches stand so close together that they appear to be united, yet when lightly pressed with a needle they spring apart or even recurve. No instance of complete fusion was encountered in this species, although the condition doubtless exists. Fusion is apparently more common in *A. campestris*, 5 subspecies of which were studied, with 42 as the total number of flowers examined. In 30 of these the style-branches were completely fused, while in the remaining 12 they were separate at least along one margin. Completely fused branches and fully cleft styles are frequently found in the same head. In some cases the fusion is evident only along one side, the result being a cylinder split down for a short distance along a single line.

Passing to *A. filifolia*, it was found that both conditions always obtained on the same plant as far as examined, a small majority of the styles having fused branches. A similar condition prevails in *A. pedatifida*, and in this species the various degrees of fusion are especially well represented (e. g., Nelson's 7058, from Sweetwater County, Wyoming.) Two of the stages are shown on plate 16. In *A. spinescens* the branches are always completely united, as far as has been observed.

The fused character of the styles is thus seen to be a variable trait, occurring irregularly in one section of the genus and hence of little specific and of no sectional or sub-generic value.

Corolla.—The size of the disk-corollas is sometimes of very definite value as a specific and subspecific character. Certain species, notably *A. parryi*, *A. stelleriana*, *A. pattersoni*, and *A. pedatifida*, stand off very sharply in this feature from their nearest allies. The

shape differs slightly between the species, but this can not be expressed with sufficient definiteness to render the character of much descriptive value. The central flowers are always regularly 5-lobed. The marginal corollas, on the other hand, are so highly modified and there is so much variation even in plants which are otherwise almost identical, that their use is of but slight importance in taxonomic work.

The color of the flowers is sometimes used as the sole criterion for the recognition of so-called species, quite contrary to usage in connection with other flowering plants. At the best, color can be looked upon only as indicating strains or races when forms are found to differ by this feature alone. In some cases color is associated with the amount and quality of the light. Thus, *A. californica* normally has yellowish or brownish flowers, but along the desert borders they are commonly red. Similarly, the flowers of *A. norvegica* are pale yellow in the Rocky Mountains, but Arctic forms are frequently pink or red. Rydberg has made use of color in retaining *A. purshiana* as distinct from *A. gnaphalodes* (N. Am. Fl. 34:273, 1916) and numerous observations confirm his statement that the latter form, with dark-brown or purplish corollas, occurs only to the east of the Rocky Mountains. West of this area only the yellow-flowered "*purshiana*" is found, but unfortunately for the correlation with geographic distribution, this occurs also at times within the area assigned to the purple-flowered form (see further on, p. 86).

The futility of attempting to use flower-color as a specific or even a subspecific criterion in the field is evidenced by studies made on Coal Creek, in the Teton Mountains of Wyoming (samples preserved at herbarium, University of California, 11444, 11445). Here, at 2,500 meters altitude, there grows an abundance of *A. vulgaris floydmani*, the plants forming colonies of considerable extent. In one of these the corollas were all pure greenish-yellow or at the most edged with pale purple, but neighboring colonies were all deep purple. While this difference was not great, it was positive and each plant could be placed, on close examination, in either the yellow or the purple group. Therefore, if this character is to be used for the separation of species in one part of the genus, it should be applied throughout, and this would result in breaking up *floydmani*, already too close to *discolor*, into two subspecies and assigning these to identical habitats. A similar division would presumably be necessary for many other species and subspecies. Such procedure, while possibly desirable after a close genetic analysis and after a method has been devised for classifying these minor forms, is neither necessary nor advisable at the present time. The pubescence of the corolla will be referred to later (p. 43).

Number and reduction of flowers in the head.—The reduction or complete suppression of certain types of flowers in the head was used by Besser as the chief basis for his classification into sections, and it is still the most important character available for this purpose. All species of *Artemisia* may be classed as either heterogamous or homogamous. In the former the head consists of an outer circle of ray-flowers and an inner one of disk-flowers, these two kinds of flowers being rather easily distinguished by reference to the plates. Homogamy has been brought about through a complete elimination of ray-flowers. This is regularly the case in the section *Seriphidium*. That the reverse has not been the direction of evolution—that is, that heterogamy has not arisen from homogamy—is evidenced by a consideration of the fact that such an assumption would necessitate the corollary of the development of ray-flowers in *Artemisia*. This in turn would lead either to the assumption that the Artemisias were the progenitors of all of the radiate *Compositae* or to the polygenetic origin of this character. If further evidence is needed it is seen in the nature of the ray-corolla when this is present. It is always an apparently functionless structure with an irregular orifice and is plainly a vestige of the regular corolla and not so modified as to give evidence of being an incipient ligulate corolla. A connection between heterogamy and homogamy is apparently found

in *A. bigelovi*, a species which has ray-flowers, but these are very few in number and even entirely wanting in some heads, while in all of its other characters it is similar to the uniformly homogamous *A. tridentata*.

The number of ray-flowers and of disk-flowers in a head is often of specific value. These numbers are therefore always stated in descriptions and are used to some extent in keys. The extent of variation is again indicated in the tables.

The abortion of pistils of the disk-flowers was also used by Besser as a basis for sectional classification. This abortion consists in the almost complete reduction of the ovary and consequently of the achene, and in a considerable modification of the style. The stigma in these aborted pistils is of course functionless. All of the species showing this remarkable modification were placed by Besser in his section *Dracunculus*, and there is no apparent reason for assuming that the section is other than a natural one. The character is obviously to be looked upon as one indicating a high order of development, and *Dracunculus* is therefore accepted as one of the two most highly specialized sections of the genus.

Involucre.—The structure of the involucre and the bracts often furnishes important specific criteria in the *Compositae*. In *Artemisia*, however, the involucre, while yielding some characters of value, is on the whole quite disappointing. The size of the involucre is used to a very considerable extent, but it should be understood that this is usually associated with the number of flowers in the head. In stating the size it is found that the height is much more useful than the breadth. This is simply because the height is a dimension which can be measured with definiteness, whereas the breadth depends not only upon the state of maturity, but, in the case of herbarium specimens, upon the pressure which has been applied in their preparation. The largest heads in the species found in America occur in *A. stelleriana*. The heads are here so large that the species may always be distinguished by this character alone, except for an occasional very large head of *A. vulgaris tilesi*. In *A. vulgaris* there is a very considerable range of size, as indicated by the tables, but it is noteworthy that one subspecies, namely, *litoralis*, has an involucre regularly so narrow that its dimensions never overlap those of any other. The fluctuations both in height and breadth within subspecies and within species is indicated in a number of the tables.

The relative length of bracts within a single involucre has been used in many instances by Rydberg in his treatment of the genus in the North American Flora. It is true that the outer bracts are sometimes so differently set off from the inner that this character of relative length becomes of importance, but it is impossible to detect the sharp differences that one is led to assume from his descriptions. The absence of differences where they are supposed to exist is indicated in the figures on pages 124 and 149. The outer bracts are usually shorter than the inner and sometimes they have their own peculiar shape, but the gradation is so slight and the external bracts undergo so many modifications that such criteria must be used with exceeding caution. Even the inner bracts are not constant in the shape of the exposed portions. The number is sometimes helpful, and this is brought out together with the extent of the variation in the tables, where actual counts of large series are indicated.

Inflorescence.—By far the most common type of inflorescence is the panicle. All others are modifications of this. When the panicle is narrow and much simplified, it may be either racemose or spicate. When it is much shortened and condensed the panicle becomes capitate. These various forms of inflorescence are modifications of the paniculate type, as seen from the frequent series of intergradations that can be found almost anywhere. They are also derived forms as evidenced by the fact that the panicle is by far the most abundant and that it occurs in forms which are primitive in their other features. In only one case does the modified type of inflorescence run

parallel with specific characters. This is in *A. senjavinensis*, in which the heads are always in a dense terminal cluster, as far as known. It should be noted, however, that this type of inflorescence also occurs in certain subspecies of the very closely related *A. norvegica*.

Leaves.—The leaves in *Artemisia* are always alternate and simple, but in almost all other respects they run through long series of variations. They are evidently plastic structures. They range from entire to twice-pinnatifid, even in a single species. Terete leaves occur among the American species only when this condition has been brought about by the folding of the margins, as in *abrotanum*, *filifolia*, etc. It seems that these tightly revolute leaves can be changed back to plane leaves by a change in the environment. For example, in *A. californica* the leaves and their lobes are usually revolute and terete, yet in vigorous young growth the lobes flatten out and become 1.5 to 2 mm. broad. This is seen even in the northerly part of the range of the species, while to the south, and especially on some of the islands off the coast of southern California, it is very pronounced. Somewhat different seems to be the case of a very narrow-leaved form of *Artemisia cana*. This species usually has leaves 2 to 4 mm. wide. It sometimes happens that the plants growing with the normal form have leaves only 1 mm. wide, and no intermediate forms appear. The exact reason for this is not known, but possibly the narrow-leaved type is a mutation from the broader-leaved one. The venation of the leaf is sometimes very prominent and is then an aid in the recognition of the species. This is particularly true in the case of *A. rigida*.



FIG. 3.—Leaves of *Artemisia vulgaris heterophylla*, to show variation in outline: a, leaf from plant growing on a moist northerly slope (most leaves on this plant were of this type, with long, spreading lobes); b, leaf from plant of loose soil fairly moist (the moderately spreading lobes are characteristic of the plant); c, d, e, f, g, common types of leaves on southerly exposure. All from the Oakland Hills, California. All $\times 0.4$. See also fig. 7, p. 74.

The extent and nature of the lobing of leaves furnish useful criteria in a few cases. Thus, in certain species the blade is uniformly divided into filiform lobes, in others a unique type of dentation, confined to the summit of the leaf, furnishes a useful clue as to relationships. In most species, however, the variation is so extensive that leaf-characters fail almost entirely, even for the recognition of subspecies and varieties. All students of the genus have attempted to use them, but those most familiar with the plants in the field are the least inclined to attach importance to cut of leaf. Thus, Piper, in speaking of species here referred to *A. vulgaris*, expresses the opinion that leaf contour is worthless as a character and that its use leads to an artificial disposition of species and subspecies (*Contr. U. S. Nat. Herb.* 11:588-589, 1906). Evidence of a similar nature is recorded very incompletely in figure 3, where seven different cuts of

leaf are shown, all from plants growing in a small range of hills in California. Many intermediate forms could also be shown. While field studies are necessary fully to comprehend the extent of this variation, some attempts have been made to bring the evidence into herbaria. Thus, for example, at the United States National Herbarium is a series of 13 sheets of a form of *A. vulgaris*, filed under *A. atomifera* Piper, showing gradations in leaf from entire or merely 3-toothed to divided with 3 spreading lobes on each side, these lobes separate nearly to the midrib (*Piper 6466*). A still more extensive series has been collected near Spokane, Washington, by Miss Evelyn Moore. These are now on file at the University of California under *A. vulgaris candicans*.

An attempt has been made to correlate these leaf-forms with ecologic conditions, and some success has resulted at least as regards leaf-area. Thus, wide leaves are most frequent in the north and along the Pacific Coast, whereas narrower leaves and lobes become more abundant as a species extends its range to the south and especially to the arid and more strongly illuminated portions of the southwest. The leaves shown in figure 12 (p. 95) suggest an edaphic effect of environment, since all were from the same climatic area. It will be noted from the explanation that the broader and more deeply cut leaves are from the better and moister soil, while the narrower, entire ones are from stony arid slopes. Nature and extent of lobing can not always be correlated with environmental conditions, as shown by the frequent occurrence of very unlike foliage on plants growing under apparently identical conditions. Leaves like those labeled *c* to *f* of figure 3 are found on plants growing side by side. Much experimental work will be necessary before the significance of such variations will be understood.

The illustrations thus far referred to are mostly of the polymorphous *A. vulgaris*, but similar conditions are found in other species. Variations are illustrated to a limited extent in the plates, particularly in those of *A. tridentata*, and additional examples are shown in figures 21 and 22 (pp. 144, 145).

Stipule-like appendages have been noted in a few of the species and are illustrated in figure 10. These are in reality lobes which have become isolated from the body of the leaf and taken up positions near the base of the petiole, as is evident from their lack of constancy in number, position, and size. Sometimes they grade insensibly into the more conspicuous lobes of the blade. They supply a valuable character for the recognition of *A. procera*, especially. As to *A. vulgaris*, they are almost uniformly present in subspecies *typica*, very common but sometimes wanting in *arctica*, only occasionally present in *candicans* and *heterophylla*, and almost entirely absent from the other American subspecies. These facts are of much value as corroborative evidence in working out the phylogeny of these forms.

Stem and bark.—Among the herbaceous species it is found that certain minor characters have been used to some extent as criteria. The reddening of the stems with age is very noticeable in some cases and is at least a tendency which is helpful in the detection of certain subspecies. The amount of pigment formed is known in other genera to be so often dependent upon the amount of light that it is doubtful if the color is of more than suggestive importance in *Artemisia*. The striation of the stem is quite marked in some species, while others have smooth stems. This is again of minor significance, especially as the striation is often masked by the pubescence. The character seems to be of some value in distinguishing *A. tridentata*, in which the striæ are present, but which often requires the removal of the tomentum for their detection, from the very similar but botanically distinct *A. bigelovi*, in which the striations are entirely wanting. The bark is different in different species, but it requires considerable field experience to make use of this character. In *cana*, *rigida*, and *pygmaea* the bark is dark and fibrous. In *tridentata* it is more shreddy and peels off in narrow strips, while in *bigelovi* it is sheathing on the older parts of the stem and peels off in sheets rather than strips.

Roots.—The true roots, as contrasted with the rootstocks and caudex mentioned above, have not been used for purposes of classification. The root system of *A. filifolia* has been described and mapped by Weaver (Carnegie Inst. Wash. Pub. 286:73, fig. 25, 1919).

Pubescence.—As in other botanical groups, this character is a misleading one to use, if only its relative abundance and the accompanying effect on the general appearance of the plant are taken into account. Thus, all gradations in the amount of pubescence on different parts of the plant, and consequently in the appearance of the plant itself, are well known in the numerous variads of *A. vulgaris*. More important is the persistence of the pubescence when this is present. For example, the behavior of tomentum in the subspecies of *vulgaris* is exceedingly variable, and yet certain ones exhibit a strong tendency to retain the tomentum, while others have an equally strong tendency to drop it as the parts mature. Even more important is the nature of pubescence itself. This difference in the character of the trichomes and the direction they take in regard to the surface of the epidermis is especially helpful in separating *norvegica* and its associates from the *vulgaris* group of species. In the former the pubescence, when present, is spreading, or villous, while in the latter it is more or less appressed, tangled, and therefore tomentose. Yet even here it is possible to select forms of the two different groups that are so much alike in this character that their separation becomes exceedingly perplexing.

The pubescence of the receptacle is a matter of great importance. It occurs only in one section of the genus, namely, *Absinthium*. This criterion separates a natural group of the species, although it is probably not of sufficient importance to be rated as a sectional character. The fact that the pubescence is easily determined, and that in this section it is very long and copious, while it is entirely wanting throughout the rest of the genus, leads to the retention of *Absinthium* largely because of practical considerations. The corollas and achenes are all long-pubescent in *spinescens*, and this character here seems to attain specific importance. However, in one subspecies of *A. tridentata*, namely, *parishi*, the achene is long-pubescent, although no other characters can be found which run parallel with this one. A suggested explanation is that *parishi* has arisen through mutation in this single character. Aside from the rather pronounced pubescence just under consideration, there are sometimes a few prominent hairs on the upper part of the corolla. These are frequently described in species of the Old World, but their presence or absence seldom runs parallel with other characters. Such hairs are occasionally found in American plants, especially in forms of *A. norvegica* and in *A. pattersoni*. They furnish a nearly but not quite constant criterion for the recognition of the latter species as distinct from *A. scopulorum*. In *A. norvegica saxatilis* the corollatube is perhaps always long-hairy.

Resins, oils, and odors.—Resins are not copiously developed in *Artemisia* and no species is marked by impressed resin-dots of the foliage. There is, however, a prominent exudation of resin on some parts, particularly on the flowers and achenes. These resin-dots harden and become somewhat granular. Since they are more noticeable in some species than in others, it may be that their presence affords contributory evidence as to the standing of certain forms, but their use would require much more detailed studies than have as yet been given to them. The oils are abundant in some species and give quite characteristic odors to the herbage in these cases. For this reason, the odor of the herbage in each of the species is mentioned in the present monograph, although it is recognized that such descriptions do not carry a clear conception of actual conditions. It is only by extended observation in the field that one can come to recognize the different sorts by odor alone.

Habit.—All degrees of duration are found in the genus, from annual herbs to arborescent, tree-like perennials. The annual and biennial plants have a definite taproot, but

the transition from annual to biennial habit is so often dependent upon ecologic conditions that this character is of but slight importance. There are certain places in the genus, however, where only annual and biennial species are found, while in other sections plants of short duration are not known to occur. A great majority of the American species are perennial herbs, growing either from rootstocks or from a caudex that supports a number of stems. The underground structures have not been examined in detail and their characters have been used but slightly in classification. The caudex habit is often an extreme form, derived from a rootstock, the stock becoming much shortened and the stems growing in close proximity. It often happens that within a single species some forms will have extensively creeping rootstocks, while others will have a short caudex, the latter usually belonging to more northerly habitats. In almost all cases when the plant is an herb the stem is simple up to the inflorescence.

The shrubby habit has been developed at three different places in the genus, or at least this follows if the present classification into sections is a natural one. However, the largest shrubs, as well as the largest number of shrubby species, are found in the section *Seriphidium*. These shrubs show considerable variation in habit, and hence the differences are not sharp enough to permit of their use as specific criteria. The size is sometimes helpful, but it is not always dependable. For example, the largest shrub of all is *A. tridentata*, the most common of the sagebrushes, yet even in subspecies *typica* of this are found forms sometimes less than 1 dm. high. Such reduced forms are often easily accounted for by field studies in that they are due to unfavorable environmental conditions, usually to competition, especially with perennial grasses, or to continuous browsing, to fire, to poor soil, or to a combination of all of these factors. One of the American species of shrubs stands out very sharply from all the rest by its decidedly spiny habit. This is *A. spinescens*, a species which is well set off also by important floral characters.

RELATIVE PLASTICITY OF THE SPECIES.

The genus *Artemisia* includes species representing nearly all degrees of plasticity. Some are in a state of constant and extensive variation, and by means of their numerous forms are enabled to occupy very unlike habitats. Such species come naturally to have a wide geographic distribution and also a wide altitudinal range in mountainous districts. While their forms are difficult to treat taxonomically, because of this large number and the striking dissimilarity of the extremes, the determination of the evolutionary lines is rendered fairly certain because of the presence of intermediate forms and the comparative ease of manipulation in experimental studies. The most notable species of this class is *A. vulgaris*. This ranges almost throughout the temperate and subarctic portions of the Northern Hemisphere and comprises an almost endless series of variations, some 65 of which have been described as distinct species by various authors. It seems quite probable that some are now fixed in their principal characters and that they are limited to particular habitats in consequence, but that many are still in a state of flux, at least in some portion of their range.

Other species which are represented by more than the average number of forms are *norvegica*, *campestris*, *dracunculus*, and *tridentata*. These do not possess the high plasticity of *vulgaris*, but each is represented by 15 or more named variands in addition to many minor forms. All are of wide distribution and have also a large altitudinal range.

Of the less plastic species, only *A. frigida* is of wide distribution. It has but few named variations in America, but a considerable number of them in Asia. A few introduced species are not here taken into account, since in each case the American plants have in all probability descended from one genetic strain. The remaining species, such as *spinescens*, *parryi*, *franserioides*, *pedatifida*, etc., are all rare or local, or confined to

peculiar habitats. In these, experiment alone can determine whether their stability is germinal or due to constant environic relations.

In reviewing these lists it will be noted that the mobile species are not confined to any one section, but that they are well distributed throughout the genus. It is apparent that in each section one or two species have assumed the lead and by reason of their high plasticity have been able so to accommodate themselves to a wide variety of environmental impacts that related species have been largely excluded from extensive areas. Whether favorable initial conditions have led to greater variation in some species than in others, or whether the difference in the number of forms produced by various species is due to an inherent difference in their plasticity, is an interesting problem that scarcely falls within the scope of the present paper.

GENERIC DIAGNOSIS.

ARTEMISIA LINNAEUS, Sp. Pl. 845, 1753.

Annual and perennial herbs and shrubs, usually aromatic and bitter. Roots fibrous, the annual species with a taproot, the perennial herbs often with rootstocks or caudex. Leaves alternate, entire to variously lobed or dissected. Heads small, nodding or erect, commonly panicle but the panicle sometimes much reduced and then raceme-like, spike-like or globoid, apparently discoid but the marginal flowers with irregular corollas except in one section where the flowers have been suppressed. Involucre ovoid to campanulate or hemispheric; bracts imbricated in 2 to 4 series, dry, at least the inner ones scarious or with scarious margins. Receptacle plane, convex or hemispheric, naked or hairy or rarely chaffy. Ray-flowers pistillate and fertile or wanting; corollas narrowly tubular, usually tapering upwards, with 2, 3, or 4 teeth, commonly oblique at orifice; stamens wanting; style more or less exserted, 2-cleft, the branches terete to oblong and somewhat flattened. Disk-flowers hermaphrodite, fertile or sterile; corollas campanulate, funnelform or trumpet-shaped, regular, 5-toothed; anthers longer than the filaments, obtuse or subcordate at base, the connective produced into a lanceolate or subulate tip; style exserted or sometimes included, cleft into 2 more or less recurved branches which are flat, truncate, and erose or fimbriate at the end, or the branches more or less fused into a slender column surmounted by an erose or fimbriate disk or cup. Achenes in both ray and disk ellipsoid or obovoid to nearly prismatic, with 2 to 5 angles or ribs or with numerous faint striæ, or smooth, usually glabrous, rounded at summit to an epigynous disk, or truncate, or crowned with a very short annulus. Pappus none.

Key to the Sections of Artemisia.

- Heads heterogamous, marginal flowers pistillate, disk-flowers hermaphrodite; receptacle glabrous or pubescent.
- Disk-flowers fertile, ovary normal. SECTION I. *Abrotanum* (p. 46).
 Receptacle not hairy. SECTION II. *Absinthium* (p. 46).
 Receptacle beset with numerous long hairs between disk-flowers. SECTION III. *Dracunculus* (p. 47).
 Disk-flowers sterile, ovary abortive; receptacle glabrous. SECTION III. *Dracunculus* (p. 47).
 Heads homogamous by complete reduction of ray-flowers, disk-flowers all hermaphrodite and fertile; receptacle glabrous. SECTION IV. *Scriphidium* (p. 47).

Key to the North American Species of Artemisia.

SECTION I. ABROTANUM.

(Ray-flowers present, disk-flowers present and fertile, receptacle glabrous.)

- Heads with more than 10 flowers; leaves never cuneate and 3-toothed at apex, although sometimes spatulate and 3-cleft or 3-lobed. Herbs and shrubs.
- Stems woody (decidedly so in the only native species, less woody in the 2 introduced ones); leaves mostly dissected into filiform lobes; achenes angled, broad and truncate at summit.
- Principal leaves 2 or 3 times pinnatifid. Introduced species.
- Leaves 3 to 6 cm. long, lobes slender, ascending; petiole naked. 1. *A. abrotanum* (p. 49).
 Leaves 1 to 3 cm. long, lobes short, spreading; petiole auricled at base. 2. *A. pontica* (p. 52).
 Principal leaves mostly once pinnatifid. Native species. 3. *A. californica* (p. 53).
- Stems herbaceous, sometimes a little woody at base; leaves entire or variously cut but seldom with truly filiform lobes; achenes smooth or ribbed but scarcely angled, mostly with slight incurving at summit.
- Plant perennial, stems from a rootstock or caudex; leaves various.
- Foliage not tomentose beneath but silvery-canescens, villous, or glabrous; stems 6 dm. or less high. Subalpine and Arctic plants with dissected leaves.
- Disk-corollas 2.5 to 3.5 mm. long (smaller in some forms of No. 4); heads 5 to 9 mm. broad, except in *senjavinensis* and *norvegica glomerata*.
- Segments of leaves strongly divergent, primary divisions at right-angles to rachis. 4. *A. macrobotrys* (p. 56).
- Segments of leaves pointing forward
- Leaf-lobes longer than their hairs, or leaves glabrous; lower leaves usually 2 or 3 times cleft or divided. 5. *A. norvegica* (p. 57).
 Leaf-lobes exceeded and nearly concealed by their long villous pubescence; all leaves simply cleft or entire. 6. *A. senjavinensis* (p. 65).
- Disk-corollas 2 mm. or less long; heads 4 to 5 mm. broad. Southern Rocky Mountains. 7. *A. parryi* (p. 66).
- Foliage more or less tomentose beneath, usually densely so; stems 3 to 30 dm. high.
- Disk-corollas 3.5 to 4 mm. long; involucre 6 to 7 mm. high. A white-tomentose herb with very large heads and thick obtuse leaf-lobes. 8. *A. stelleriana* (p. 67).
- Disk-corollas 1.5 to 3 mm. long; involucre 2.5 to 5 mm. high.
- Leaves (except the uppermost) twice dissected and lobes obtuse; disk-flowers 45 to 90.
- Heads not secund; leaf-lobes linear; involucre 5 mm. high. 9. *A. alaskana* (p. 68).
 Heads decidedly secund; leaf-lobes elliptic or oblanceolate; involucre 2.5 to 3 mm. high. 10. *A. franserioides* (p. 69).
 Leaves variously cut or entire but lobes always acute; disk-flowers 3 to 40 or rarely 50. 11. *A. vulgaris* (p. 71).
- Plant annual or biennial, with taproot; stem erect; leaves 2 or 3 times pinnately parted or divided.
- Leaves green; divisions not filiform.
- Involucre 2 to 3 mm. high; inflorescence a dense compound spike; heads crowded, erect. 12. *A. biennis* (p. 101).
 Involucre 1 to 1.5 mm. high; inflorescence a loose panicle; heads loose, often nodding. 13. *A. annua* (p. 102).
 Leaves white-tomentose; divisions filiform. Mexican species with dense panicles. 14. *A. klotzschiana* (p. 103).
- Heads with only 2 to 4 flowers; leaves at least in part cuneate and 3-toothed at summit. Low shrub. 15. *A. bigelovi* (p. 104).

SECTION II. ABSINTHIUM.

(Ray-flowers present, disk-flowers present and fertile; receptacle villous.)

- Stem 4 to 10 dm. high; divisions of leaves oblong or oblanceolate, ultimate segments 1.5 to 4 mm. wide. 16. *A. absinthium* (p. 106).
- Stem 1 to 4 dm. high; divisions of leaves linear, ultimate segments about 1 mm. wide.
- Plant woody and mat-like at base; stems very leafy; heads usually in panicles. 17. *A. frigida* (p. 108).
 Plant not woody and mat-like at base; stems sparsely leafy; heads in racemes or solitary.
- Heads 5 to 25, 4 to 6 mm. broad; disk-flowers 15 to 30; leaves mostly twice pinnatifid. 18. *A. scopulorum* (p. 110).
 Heads 1 to 5, 5 to 7 mm. broad; disk-flowers 30 to 120; leaves once pinnately divided or cleft. 19. *A. pattersoni* (p. 112).

Key to the North American Species of *Artemisia*—Continued.

SECTION III. DRACUNCULUS.

(Ray-flowers present, disk-flowers present but sterile, their achenes aborted; receptacle glabrous.)

- Plant herbaceous, stems sometimes a little woody at base; heads more than 15-flowered (including both ray- and disk-flowers).
 Leaves mostly entire but occasionally with an irregular lobe or lower leaves sometimes 3- to 5-cleft. 20. *A. dracunculus* (p. 115).
 Leaves pinnatifid, bipinnatifid, or dissected, except the uppermost.
 Disk-corollas campanulate, 1.5 to 3 mm. long; lower leaves 2 to 10 cm. long including petiole; inflorescence 1 to 10 cm. broad. 21. *A. campestris* (p. 120).
 Disk-corollas tubular-funnelform, 3 to 3.5 mm. long; lower leaves rarely over 2 cm. long including petiole; inflorescence about 0.5 cm. broad. 23. *A. pedatifida* (p. 131).
 Plant shrubby but sometimes dwarfed; heads less than 15-flowered.
 Achenes and corollas glabrous or only minutely pubescent; plant not spinescent.
 Inflorescence loosely paniculate; involucre about 1.5 to 2 mm. high; disk-corollas 2 mm. or less long; shrub normally 3 to 10 dm. high. 22. *A. filifolia* (p. 130).
 Inflorescence spike-like; involucre about 3 mm. high; disk-corollas 3 to 3.5 mm. long; shrub dwarf (1.5 dm. or less high). 23. *A. pedatifida* (p. 131).
 Achenes and corollas cobwebby with long hairs; plant spinescent. 24. *A. spinescens* (p. 132).

SECTION IV. SERIPHIDIUM.

(Ray-flowers wanting, disk-flowers present and fertile; receptacle glabrous.)

- Receptacle not chaffy; leaves tomentose on both sides, except in *pygmaea* and one subspecies of *tridentata*.
 Leaves gray, wholly covered with a canescent or silvery tomentum, either entire or palmately toothed, cleft, or parted.
 Heads in spikes or panicles, at least the upper ones longer than their subtending bracts.
 Leaves (except the uppermost entire ones) cuneate to spatulate-linear in outline, mostly toothed or parted. 25. *A. tridentata* (p. 135).
 Leaves linear, somewhat tapering to each end, all entire or rarely with a few teeth or lobes, silvery-canescens. 26. *A. cana* (p. 150).
 Heads sessile in axils, all much exceeded by their subtending leaves; divisions of leaves linear, mostly 5 to 15 mm. long, silvery. 27. *A. rigida* (p. 153).
 Leaves green, glandular-puberulent, lower pinnatifid with 5 to 7 lobes. 28. *A. pygmaea* (p. 154).
 Receptacle chaffy with scarious bracts which subtend most of the flowers; leaves green above, tomentose beneath. 29. *A. palmeri* (p. 155).

Artificial Key to the North American Species of *Artemisia*.

- Plant an herb, stems often thickened and perennial at base but never decidedly woody.
 Duration annual or biennial; plant with a taproot.
 Inflorescence¹ spike-like but in reality composed of a series of short spikes. 12. *A. biennis* (p. 101).
 Inflorescence a panicle.
 Leaves gray, densely hairy, lobes thread-like. Mexico. 14. **A. klotzschiana* (p. 103).
 Leaves green, glabrous or sparsely hairy when mature, plane.
 Achenes all well formed and fertile. 13. *A. annua* (p. 102).
 Achenes of central flowers aborted and sterile (subspecies *caudata* of). 21. *A. campestris* (p. 120).
 Duration perennial; plant with branching crown or with rootstocks.
 Segments of leaves mostly 2 mm. or more wide, linear to lanceolate or ovate, or leaves entire and over 2 mm. wide.
 Lobes of leaves obtuse.
 Involucre 6 to 7 mm. high; corolla of disk-flowers 3.5 to 4 mm. long. 8. *A. stelleriana* (p. 67).
 Involucre 2.5 to 5 mm. high; corolla of disk-flowers 1.5 to 2.5 mm. long.
 Receptacle without hairs between flowers. Native.
 Heads growing from both sides of branch (not secund). Alaskan species. 9. *A. alaskana* (p. 68).
 Heads growing from only one side of branch (secund). Southwestern United States. 10. *A. franseriaoides* (p. 69).
 Receptacle densely long-hairy between flowers. Introduced. 16. *A. absinthium* (p. 106).
 Lobes of leaves acute, or leaf itself acute if not lobed.
 Leaves with a dense tomentose or woolly pubescence, at least beneath. 11. *A. vulgaris* (p. 71).
 Leaves with silky or spreading pubescence or glabrous.
 Central flowers with normal achenes; leaves mostly pinnatifid or cleft. 5. *A. norvegica* (p. 57).
 Central flowers without achenes; leaves mostly entire or with few lobes. 20. *A. dracunculus* (p. 115).
 Segments of leaves mostly 1 mm. or less wide, linear or filiform, rarely elliptic or ovate in dwarf plants, or leaves entire and less than 2 mm. wide.
 Receptacle not evidently hairy between flowers.
 Leaves mostly entire, a few cleft into 2 or 3 short ascending lobes, green. 20. *A. dracunculus* (p. 115).
 Leaves pinnatifid into 5 to 10 or more spreading divisions.
 Achenes present only in marginal flowers, those of central flowers wanting. 21. *A. campestris* (p. 120).
 Achenes present in all flowers.
 Foliage tomentose or woolly, especially beneath; leaf-lobes linear-filiform (mostly subspecies *wrightii* of). 11. *A. vulgaris* (p. 71).

¹ Throughout this key the term inflorescence is used to indicate the assemblage of heads. Strictly speaking, each head is an inflorescence in itself.

Artificial Key to the North American Species of Artemisia—Continued.

- Foliage silky-pubescent to glabrous, never woolly or tomentose; leaf-lobes lanceolate or elliptic.
- Disk-corollas 2.5 mm. or more long (rarely shorter in the Alaskan *macrobotrys*).
- Segments of leaves strongly divergent. 4. *A. macrobotrys* (p. 56).
- Segments of leaves pointing forward.
- Leaf-lobes not concealed by their hairs. 5. *A. norvegica* (p. 57).
- Leaf-lobes entirely hidden among their long villous hairs. 6. *A. senjannensis* (p. 65).
- Disk-corollas 2 mm. or less long. Southern Rocky Mountains. 7. *A. parryi* (p. 66).
- Receptacle densely long-hairy between the flowers.
- Stems very leafy; heads usually in panicles. Middle and lower altitudes. 17. *A. frigida* (p. 108).
- Stems sparsely leafy; heads in racemes or solitary. Alpine and subalpine.
- Heads 5 to 25; leaves mostly twice pinnatifid. 18. *A. scopulorum* (p. 110).
- Heads 1 to 4; leaves only once pinnatifid or cleft. 19. *A. patersoni* (p. 112).
- Plant a shrub, sometimes low but always decidedly woody at base.
- Leaves (except sometimes the uppermost ones) pinnately lobed or pinnatifid, ultimate divisions mostly linear.
- Lobes of at least most of leaves again divided or dissected.
- Receptacle not hairy.
- Inflorescence a panicle; leaves twice pinnatifid. Introduced.
- Leaves green above. 1. *A. abrotanum* (p. 49).
- Leaves white on both sides. 2. *A. pontica* (p. 52).
- Inflorescence raceme-like; leaf-divisions ternately cleft. Alaskan. 9. *A. alaskana* (p. 68).
- Receptacle thickly beset with long woolly hairs between flowers.
- Plant 5 to 10 dm. high; divisions of leaves lanceolate. Introduced. 16. *A. absinthium* (p. 106).
- Plant 1 to 4 dm. high; divisions of leaves narrowly linear. Native. 17. *A. frigida* (p. 108).
- Lobes of leaves mostly entire.
- Central flowers without subtending bracts.
- Foliage gray with a close pubescence. Coastal shrub 5 to 25 dm. high. 3. *A. californica* (p. 53).
- Foliage green, glandular; dwarf plant of the Great Basin. 28. *A. pygmaea* (p. 154).
- Central flowers mostly subtended by conspicuous bracts of receptacle. Large, coastal plant. 29. *A. palmeri* (p. 155).
- Leaves either entire or palmately toothed or cleft from summit.
- Shrub very spiny; corollas copiously long-hairy. 24. *A. spinescens* (p. 132).
- Shrub not spiny; corollas not hairy.
- Principal leaves entire or rarely with a few teeth or lobes, linear, somewhat tapering to each end. 26. *A. cana* (p. 150).
- Principal leaves (that is, all but uppermost entire ones) toothed or cleft or parted at summit (often spatulate or filiform).
- Lobes or teeth of leaf plane, not filiform or thread-like.
- Inflorescence a spike, raceme, or panicle with at least upper heads longer than their subtending bracts.
- Heads in panicles; shrub 1 to 20 dm. high; leaves toothed or cleft but never more than halfway down.
- Panicles loosely branched; flowers all alike in the head. 25. *A. tridentata* (p. 135).
- Panicles closely branched, heads glomerate; corollas of outer flowers much reduced and without stamens. Southern Rocky Mountains. 15. *A. bigelovi* (p. 104).
- Heads in racemes; shrub 0.5 to 1.5 dm. high; leaves divided nearly to base into usually 3 lobes. 23. *A. pedatifida* (p. 131).
- Inflorescence consisting of solitary heads sessile in the axils, all much exceeded by their subtending bracts or leaves. 27. *A. rigida* (p. 153).
- Lobes of the leaf filiform (thread-like).
- Achenes narrow at summit; heads 3- to 9-flowered. Nebraska and Texas to Chihuahua and Nevada. 22. *A. filifolia* (p. 130).
- Achenes broad at summit; heads 20- to 50-flowered. Coast of California and Lower California. 3. *A. californica* (p. 53).

SECTION I. ABROTANUM.

PHYLOGENY OF THE SPECIES.

There are two native North American species in this section which are so isolated phylogenetically from the others that they are represented on the chart by divergent lines from the base. One of these is *A. californica*. This is similar to two Old World species now introduced into the United States, *A. abrotanum* and *A. pontica*, but since the connections may be rather remote these are indicated by broken lines. The other isolated native species is *A. bigelovi*, which may have arisen from *A. californica*, but is probably of more ancient lineage. The remaining species fall into three natural assemblages, conveniently referred to as the *norvegica*, *vulgaris*, and *biennis* groups.

The *norvegica* group, that is, those species inclosed in a major circle at the left, is certainly of boreal origin, *norvegica* itself having a more or less continuous distribution in the circumpolar regions of Eurasia and North America, with a southward extension into the Rocky Mountains. The center of distribution was probably in Siberia, the American forms coming by way of Alaska and thence down the continent. *A. parryi* is a stranded species of high mountains near the southern limits of the group, while *macrobotrys* and *senjavinensis* are boreal developments that do not extend far southward.

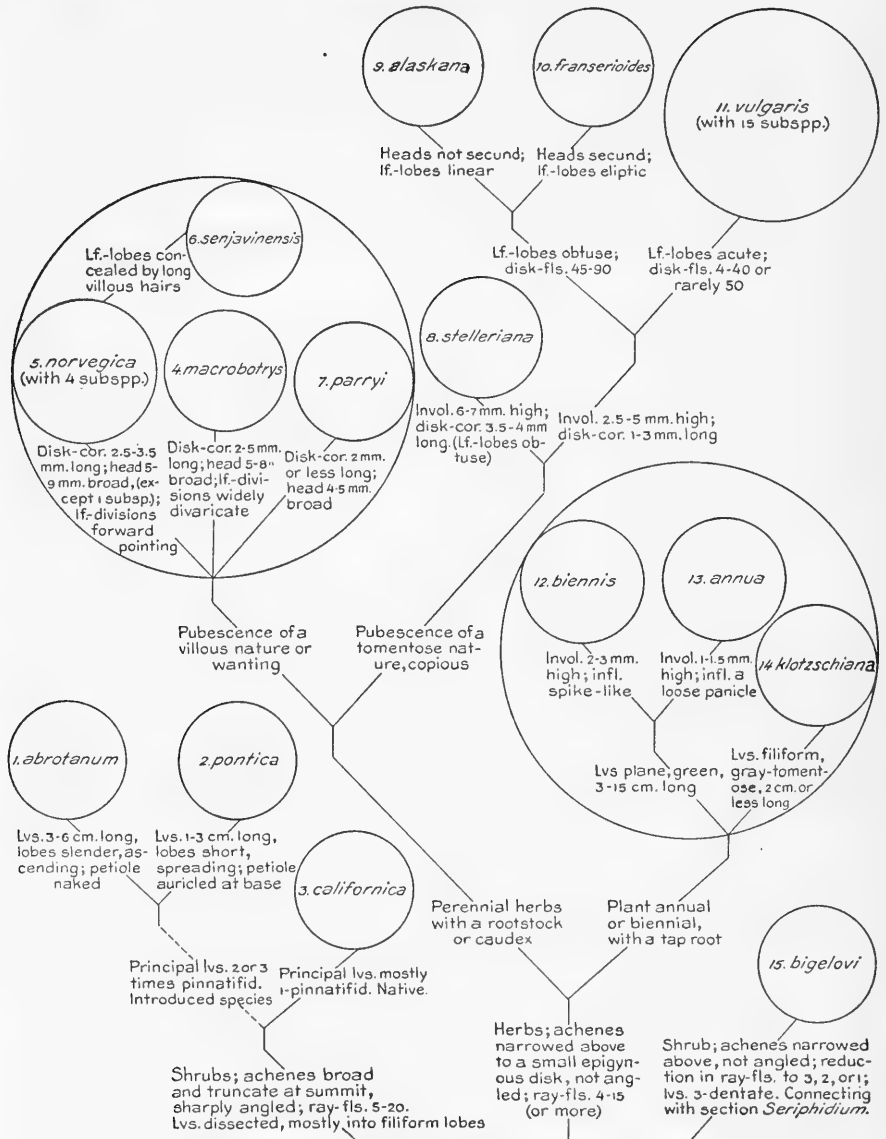
The *vulgaris* group is not inclosed in a major circle on the chart because the species are not so closely related to one another as are those of the other two groups. *A. vulgaris* itself is of wide distribution on both continents, has its center of distribution in northern Asia, and has a fan-like distribution in North America, the area of widest extent east and west being in the United States. In the course of its migrations this species has adapted itself to an extensive series of conditions, and an enormous number of minor variations and subspecies has resulted. The northern broad-leaved, large-headed *tilesi* undoubtedly represents the most primitive of these, since the others exhibit increasingly specialized structures when arranged in the order of their southerly and easterly distribution. The other species of the *vulgaris* group are *stelleriana*, which is of wide distribution but restricted to sandy beaches; *alaskana*, a little-known species of the far north; and *franserioides*, which apparently is a relict stranded in the southern Rocky Mountains.

The *biennis* group comprises three species, all closely related and characterized by their annual or at most biennial habit. Two of the species are represented also in Europe, and since none of them occur in Arctic regions, it seems probable that they have reached America by way of the North Atlantic, where land connections may have been more recent than across the Pacific, or it may be that the introduction was even more direct. Whatever the route, the connection is an old one, since time must be allowed for the later evolution of the peculiar Mexican *A. klotzschiana*.

The evidence upon which this sketch is based is indicated in detail in the paragraphs on the relationships of the several species.

1. ARTEMISIA ABROTANUM Linnaeus, Sp. Pl. 845, 1753. Plate 1. GARDEN SAGEBRUSH.

A shrub, 5 to 20 dm. high, pleasantly scented; stems much branched, erect or somewhat spreading, forming rounded bushes, the twigs erect, prominently striate, glabrous, often red or reddish tinged; principal leaves numerous, petioled (petiole naked at base), 3 to 6 cm. long, 2 or 3 times pinnately dissected into ascending linear-filiform divisions with revolute margins, green, glabrous or sparsely puberulent above, lightly tomentulose beneath; upper leaves similar but smaller and some only once pinnatifid or 3-cleft or entire; inflorescence an elongated terminal panicle, leafy below, 15 to 40 cm. long, 4 to 15 cm. broad; heads heterogamous, short-peduncled, nodding; involucre hemispheric or subglobose, about 2 to 2.5 mm. high, 2.5 to 3 mm. broad (involucres somewhat larger according to some descriptions, but only small-headed forms thus far seen); bracts 8 to

FIG. 4.—Phylogenetic chart of the species of *Artemisia* section *Abrotanum*.

18, the outer ones linear-lanceolate, nearly equaling the inner ones, with herbaceous medial line and broad scarios margins, canescent or somewhat tomentose, the rest broadly elliptic, mostly scarios and less pubescent; receptacle naked; ray-flowers 5 to 15, corolla about 1.5 mm. long, narrowed upwards; disk-flowers 10 to 20, fertile, corolla campanulate, 1.5 to perhaps 2 mm. long, 5-toothed, glabrous; style-branches of disk-flowers flat, truncate, erose at summit; achenes nearly oblong but broadest at the truncate summit, 4- or 5-angled, glabrous.

Southern Europe and the Orient; occasionally escapes from gardens in North America. Type locality, Syria. Collections: McDonough, New York, July, 1886, *Coville* (US); Washington Island, Wisconsin, September 13, 1889, *Schuette* (Gr); Benson County, North Dakota, August 3, 1913, *Lunell* (US); Indian Head, Assiniboia, *Macoun 10986* (NY).

MINOR VARIATIONS.

Artemisia procera Willdenow, Sp. Pl. 3: 1818, 1804. European and Asiatic botanists have almost universally treated this as a species distinct from *A. abrotanum*, but the two are so closely similar in all essential characters that its reduction to subspecific rank would better express their botanical relationship. It is less shrubby than this species, the stems are said to be more decidedly erect, and the leaves are more finely dissected. The involucre is described as only subcanescent or even glabrous (Willdenow) as contrasted with the densely cinereous or even tomentose involucre of *abrotanum*, but apparently all degrees of density of pubescence occur. *A. procera* was collected many years ago at Buffalo, New York, by Clinton, and was said then to be established in two or three places as a garden escape. A number of varieties are recognized in the Old World, and similar forms may be expected in *abrotanum*. These are based upon such characters as the shape and size of the head, the presence or absence of pubescence on the corollas, and the amount of odor. Eight of these varieties are described by Besser (in De Candolle, Prodr. 6: 108, 1837).

RELATIONSHIPS.

This common Old World plant has given its name to the section *Abrotanum* and with scarcely a doubt is one of the most primitive species of the genus. This conclusion is based upon the theory that the other sections arose from this one, as outlined in the chapter on subgenera and sections, and also upon the shape and ribbing of the achenes. These achenial characters ally *abrotanum* with *pontica* and *californica*, as is set forth under the latter species where reasons are also given for considering this the most primitive group of the section.

The size of the heads and flowers and the number of the latter are all somewhat smaller as given in the above description than those of Rydberg in the North American Flora. Our figures are based upon 10 sheets, about half of which are of introduced plants, the remainder being European.

ECOLOGY AND USES.

The life-form of *Artemisia abrotanum* is that of the shrub or bush, resembling *A. californica*. Its rôle in vegetation appears to have received no attention in its native area. In America the species is cultivated and has escaped into waste places.

In old English gardens especially, but also in American gardens, the southernwood, or old man, as this species is commonly called, is much grown as an ornamental shrub. Its value for this purpose lies in its strong bushy growth and in the pleasant odor of the herbage. At the Canada experimental farms it is considered as the best shrub for wind-breaks, while in Colorado it has been used as a nurse crop in reforestation, although it there kills down in winter and so is of only temporary use. The plants are easily grown, both from seeds and from cuttings taken in early summer, and thrive in any ordinary garden soil. They are somewhat tender as regards cold, but are grown as far north as the Canadian boundary on both sides of the continent. The leaves have a pleasant taste and were formerly much used for the preparation of a decoction employed as a tonic and anthelmintic.

2. ARTEMISIA PONTICA Linnaeus, Sp. Pl. 847, 1753. Plate 1. ROMAN WORMWOOD.

A perennial herb with a slightly woody base and creeping rootstock, 3 to 10 dm. high, the herbage fragrant; stems unbranched for most of their length, erect, striate, lightly puberulent, glabrate and then commonly reddish; principal leaves crowded, petioled (the petiole with stipule-like often lobed auricles at base), 1 to 3 cm. long, twice pinnatifid into short divergent linear divisions, these often toothed, the margins obscurely revolute, tomentulose but sometimes glabrate above, densely tomentulose beneath; upper leaves similar but smaller, the uppermost sessile and less divided or only ternately cleft or entire; inflorescence a terminal panicle, leafy below, 10 to 25 cm. long, 2 to 4 cm. broad; heads heterogamous, short-peduncled, nodding or at least spreading on the raceme-like branches; involucre hemispheric, about 2 to 3 mm. high, 3 to 4 mm. broad; bracts 12 to 18, the outermost ones lanceolate, herbaceous, densely tomentulose, slightly shorter than the others, the inner ones obovate or broadly elliptic, mostly scarious, tomentulose only where exposed; receptacle naked; ray-flowers 10 to 15 or 18, corolla about 1 mm. long, narrowly tubular, rather deeply toothed; disk-flowers 25 to 45, fertile, corolla campanulate, 1 to 1.5 mm. long, 5-toothed, glabrous; style-branches of disk-flowers flat, truncate, erose at summit; achenes somewhat turbinate, with broad truncate shoulder-like summit which often forms a narrow raised border, 4- or 5-angled, glabrous.

Eastern Europe and adjacent Asia; escaped from cultivation in southern Canada and at various points from Maine to Pennsylvania and Ohio. Type locality, Hungary. Collections: Portland, Maine, *Fernald 2213* (Gr); Walpole, New Hampshire, *Fernald 509* (SF); Southington, Connecticut, September 15, 1908, *Bissell* (Gr); Point Edward, Ontario, *Dodge 24* (US); Gouverneur, New York, *Phelps 1218* (Gr); Luzerne County, Pennsylvania, September 20, 1890, *Small and Heller* (US); Milan, Erie County, Ohio, August 20, 1914, *MacDaniels* (Gr).

RELATIONSHIPS.

The closest allies of *A. pontica* are Old World species. One of these, namely *A. abrotanum*, occurs also in America as an introduced plant. The evidence of the close relationship of these two species is found chiefly in the achenes, which are almost identical in shape and angles and very unlike those of most other species. The evidence at hand indicates that *pontica* is the more highly developed of the two, as is seen in its more specialized leaves and reduced inflorescence. It is not unlikely that a close study of Old World species will reveal others more closely allied to *pontica*. The nearest American relative, and the only one with similar achenial characters, is *A. californica*, under which is given a full discussion of the probable origin of this group.

The only *Artemisia* with which *pontica* could be confused in this country is *A. abrotanum*. From this it differs in its herbaceous habit, and especially in the shorter leaves with very short divergent segments and with a pair of conspicuous divided lobes at the base of the petiole. The young foliage is quite gray or almost white as compared with the green foliage of *abrotanum*, and the flowers are smaller.

ECOLOGY AND USES.

Artemisia pontica is a perennial herb with creeping rootstock and slightly woody base, which forms open societies on hillsides and open places in central and southeastern Europe. In America it is an infrequent escape in waste places.

The gray and finely dissected leaves give to this plant a very pleasing appearance, and it is therefore in some use as a garden ornamental. In France it is sometimes preferred to *A. absinthium* in the preparation of absinthe, but it is not much used for this purpose. It has also found some use as a substitute for southernwood (*A. abrotanum*) for medical purposes, but it is said to be less efficacious.

3. ARTEMISIA CALIFORNICA Lessing, *Linnaea* 6 : 523, 1831. Plate 2. COAST
SAGEBRUSH.

A rounded shrub with a definite woody trunk, 5 to 15 or rarely 25 dm. high, with a strong pungent odor; stems several or numerous, freely branched, the older parts with a brown fibrous bark, the twigs mostly erect, stout, striate, gray or nearly white with a close canescent pubescence; principal leaves sessile or at least with no distinction between blade and petiole, 2 to 5 or rarely 10 cm. long, 0.5 to 1 mm. wide below the lobes or 1 to 3 mm. wide in insular forms, ternately or pinnately or rarely bipinnately divided into long segments not wider than the rachis, commonly with fascicled ones in their axils, minutely but densely cinereous or canescent; upper and fascicled leaves gradually reduced in size upwards, less divided or entire, pubescent like the lower; inflorescence racemose-paniculate, leafy-bracteate throughout, 10 to 30 cm. long, 1 to 10 cm. broad; heads heterogamous, peduncled, nodding; involucre hemispheric, 2.5 to 4 mm. high, 3 to 5 mm. broad; bracts 12 to 20, the outer ones short, thick, and herbaceous, the inner ones with thick backs and broad scarious margins, oblong or rhomboidal, obtuse, all canescent on the exposed parts; receptacle conic, glabrous (or barely pubescent); ray-flowers 6 to 10, or up to 15 in insular forms, corolla tubular, nearly regular, about 4-toothed, 1 mm. long; disk-flowers 15 to 30, or 30 to 40 in insular forms, corolla campanulate, 5-toothed, 1.5 to 2 mm. long, glandular-granuliferous; style of ray-flowers 2-cleft, well exerted, of disk-flowers 2-cleft, barely exerted, the branches truncate; achenes of both ray- and disk-flowers oblong-turbinate, broad and truncate at summit, with a slightly raised, often undulate rim, 5-angled, resinous-granuliferous.

Abundant on exposed slopes of low hills and ranges in California from the north side of San Francisco Bay and Mount Diablo to San Pedro Martir in Lower California; also on the adjacent islands and east in southern California to the borders of the Colorado Desert. Type locality, California. Collections (all in California and Lower California): Hills just east of Vallejo, north side of San Pablo Bay, *Hall*; Mare Island, north side of San Francisco Bay, September 22, 1874, *Greene* (Gr); type collection, San Francisco, *Chamisso* (Gr); San Antonio Cañon, Black Mountain, Santa Cruz Mountains, *Abrams* 8 (US, minor variation 4, *A. foliosa* Nuttall); Pacific Grove, *Heller* 7198 (DS, Gr, NY, UC, US); near Santa Barbara, *Eastwood* 145 (Gr, NY, UC, US); Avalon, Santa Catalina Island, January 1901, *Trask* (NY, US, minor variation 4, *A. foliosa* Nuttall); Pot's Trail, San Clemente Island, *Trask* 286 (NY, US, type collection of *Crossostephium insulare* Rydberg, minor variation 7); San Nicholas Island, *Trask* 71 silvery and 71a dun-colored (NY, US, same variation); Cabezon, westerly edge of Colorado Desert, October 15, 1904, and October 24, 1907, *Bailey* (UC, minor variation 4, *A. foliosa* Nuttall); Las Huevitas, near San Rosario, Lower California, May 1889, *Brandegee* (UC); Guadalupe Island, *Franceschi* 11 (UC).

MINOR VARIATIONS AND SYNONYMS.

This species is fairly constant in its botanical characters, due in part to an almost continuous distribution throughout its range and perhaps also to its isolation phylogenetically from its nearest allies. The only variation of more than passing interest is No. 7 of the following list.

1. ARTEMISIA ABROTANOIDES Nuttall, *Trans. Am. Phil. Soc.* II. 7 : 399, 1841. Described from specimens collected near Santa Barbara with no reference to the earlier *californica*, for which it is an exact synonym.

2. A. FISCHERIANA Besser, *Nouv. Mem. Soc. Nat. Mosc.* 3 : 21, 1834. Same as *A. californica*. Type locality, San Francisco Bay.

3. A. FISCHERIANA VEGETIOR Besser, l. c. 88, is *A. californica*.

4. A. FOLIOSA Nuttall, l. c. 397. Recently revived by Rydberg, who separates it on the basis of its silvery-white pubescence and the mostly ternately cleft leaves with very narrow segments. These distinctions are impossible to apply in the field because of the presence of all grades of pubescence and type of leaf, often on the same or closely neighboring plants. Dwarfed individuals in which the leaves are shortened and the inflorescence reduced are most likely to exhibit the characters of *foliosa*. While the twigs and foliage grade insensibly in color from the common gray type to the silvery-white of *foliosa* in the coastal districts, according to Vernon Bailey these two color-forms grow together at Cabezon, on the edge of the Colorado Desert, and intermediate

are there absent. The extreme development of the white form, with the leaves nearly all reduced to the trifid type and with numerous gray, brittle twigs, is found at the most easterly known station for the species, namely 7 km. southeast from Palm Springs (February 1921, *Jaeger*). All of these characters are in line with the general tendency in desert vegetation. The ternately cleft nature of the foliage is derived from the pinnate type, as indicated by specimens in which the leaves are 3-lobed, but with one lobe attached lower down than the others (130825 UC); in the typical form some of the leaves are often only ternately cleft or bifid at the summit (29665 UC and 91195 UC), while others are irregularly pinnatifid. Some of these leaf-forms are shown on the accompanying plate. The type of *foliosa* came from around Monterey.

5. *CROSSOSTEPHIUM CALIFORNICUM* Rydberg, N. Am. Fl. 34 : 243, 1916. *A. californica*.

6. *C. FOLIOSUM* Rydberg, l. c. *A. californica*, the form, or state, referred to under No. 4.

7. *C. INSULARE* Rydberg, l. c. 244. A robust, insular variation of *A. californica* with leaf-segments 1 to 3 mm. wide and not revolute. Thus far it is known only from San Clemente and San Nicholas Islands, off the coast of southern California. The typical form also grows on at least one of these (San Clemente Island, March 25, 1918, *Evermann*, Calif. Acad. Sci.). On neighboring islands are found forms intermediate between the type of *californica* and the one listed above as *foliosa*. The remarkable width of the leaf-segments and rachis in *insulare* is the result of the failure of the margins to become closely revolute, as in the other variations. This condition is approached in specimens from near Santa Monica, on the mainland nearly opposite the islands on which *insulare* grows. In these the leaf-margins are revolute but do not meet. The largest leaf-segments are 1.5 mm. wide (near Santa Monica Experiment Station, *Barber 284*, UC). Segments up to 1.8 mm. wide occur on vigorous shoots from as far north as the Oakland Hills. Two color-forms occur on the islands, both with the wide leaf-lobes, so that if *foliosa* is accepted as a species, or variety, it will be necessary similarly to recognize these forms. The type of *insulare* came from along Pot's Trail, San Clemente Island.

RELATIONSHIPS.

There has been a wide divergence of opinion as to the relationships of this species. Both Gray and Rydberg have assumed a close connection with *Crossostephium artemisioides* Lessing (*Artemisia chinensis* Vahl, not Linnaeus), a species of the Philippine Islands and China. The former author would therefore unite the genus *Crossostephium* with *Artemisia* (Syn. Fl. N. Am. 1:370, 1884), while Rydberg would refer *californica*, together with 2 minor segregates, to the genus *Crossostephium* (N. Am. Fl. 34:243, 1916). The bases for this assumed relationship were (1) a distinct ribbing of the disk-achenes and (2) the supposed presence of a coroniform pappus, two characters not otherwise known at that time in the genus, except in the Hawaiian *A. australis* Lessing. There can be no question as to the ribbing of the achenes in *A. californica*. In mature fruits these ribs take the form of 5 sharp angles; 3 and 4 ribs are included in descriptions but a careful examination of numerous collections indicates that 5 is perhaps the universal number. The presence of these angles suggests a remote connection, through forms now extinct, with true *Crossostephium* of southeastern Asia, but further evidence is needed in support of the hypothesis. This evidence is not to be found in the presence of a pappus or in any other character thus far pointed out. As a result of detailed studies on a large series of specimens, the conclusion is reached that the Californian species never shows any evidence of a true pappus. The summit of the achene is broad and the edges commonly curve upward to form a shallow cup or rim about the base of the corolla-tube, as indicated in the detailed drawings of plate 2. But there is no reason to interpret this as a pappus-crown, and, in fact, it is no more prominent than in some species universally accepted as genuine Artemisias, for example, *A. pontica* and *A. tridentata* (plates 1 and 18). There is never any splitting of this rim nor the presence of distinct paleae as in the case of true *Crossostephium*. Furthermore, this monotypic genus differs decidedly from our American plants in the presence of 2 rows of ray-flowers, a character apparently overlooked both by Gray and by Rydberg. Although *A. californica* and *A. australis* were described by Lessing in the same volume as his genus *Crossostephium*, he made no comparisons with this last and presumably had no thought of their relationship. His treatment, which considers *Crossostephium* as a monotypic genus and refers *californica* and *australis* to *Artemisia*, was followed by Bentham and Hooker and by Hoffman in Engler and Prantl's Pflanzenfamilien and is the one which

still seems the most reasonable. Whether or not the angular achenes signify a remote connection with *Crossostephium*, it is very certain that nothing is gained by throwing *californica* and *australis* into this genus on the basis of a single character and in the face of decided differences in other important features.

Much more direct is the connection between *A. californica* and two Old World species, namely *A. pontica* and *A. abrotanum*. These are in agreement as to all essential features, even down to the angled turbinate disk-achenes with broad shoulder-like summits, as is shown in the accompanying plates. Angled achenes are encountered at a number of places in the genus. Sometimes these angles are reduced to ribs which pass through all degrees of depression until in some cases the surface seems to be perfectly smooth (p. 37). Since the characters of strongly angled and crowned achenes are approximated also in true *Crossostephium*, which because of its pappus and two rows of ray-flowers may be accepted as still more primitive, *A. pontica*, *A. abrotanum*, and *A. californica* (together with *A. australis*) may well represent the early stock from which the other *Artemisia* have been derived. There is no reason to assume, however, that the other species have arisen from these as they now exist, for although primitive in most of their characters, each exhibits special development along certain lines and all are shrubby in habit. This demonstration of the phylogenetic connections of *californica* and similarities between it and the Hawaiian *A. australis* render more plausible the theory that it has had some geographic connection, perhaps through Asia, with the primitive Old World stock, as now represented by *pontica* and its allies. How *californica* came to be stranded on the Pacific coast of North America is a problem that can not now be solved, but it apparently resulted from the general circumpolar migration of the genus.

Among the native American representatives of the section *Abrotanum*, *Artemisia californica* stands alone. It is the only species, except for the anomalous *A. bigelovi*, which is shrubby in habit. For these reasons it is assigned to a divergent line on the phylogenetic chart. Whether it has arisen from a *Crossostephium*-like ancestor, or whether of some other origin, its early segregation seems certain, in view of the absence of direct connection with existing species. In aspect it is most like *A. filifolia*, which it also represents ecologically on the Pacific Coast. While it is not impossible that these two are connected phylogenetically, the difference in nearly all technical characters seems to render this improbable.

The available evidence therefore points to the tentative conclusion that *A. californica* is not directly related to any other American species, but that its connections are with the Hawaiian *A. australis* and with certain Old World species, especially *A. pontica* and *A. abrotanum*. Furthermore, these four species best represent the early stock of *Artemisia* and hence the connection with the genus *Crossostephium*.

ECOLOGY.

In life-form *Artemisia californica* is a bush, which resembles both *A. filifolia* and *A. tridentata*. It is the most important dominant of the Coastal sagebrush association, extending from San Francisco Bay to the Mojave and Colorado Deserts, and blooming through the summer. Typically, it is a climax dominant, but it is often subclimax to the chaparral association in the habitat of the latter. It comes in contact with the true sagebrush of the Great Basin at various places from Tehachapi Pass south to Lower California, and the two not infrequently mingle on equal terms. Its lower contact is with the *Stipa* bunch-grass prairie along the coast and in the interior savannah, and with *Larrea* scrub at the desert's edge. Above it lies the *Adenostoma-Ceanothus* chaparral, with *Adenostoma* and *Artemisia* in particular mingling over a narrow ecotone.

The chief associates of the coast sagebrush are *Salvia mellifera*, *S. apiana*, *S. nivea*, *Eriogonum fasciculatum*, *Rhus integrifolia*, *Eriodictyum tomentosum*, and *Lotus glaber*.

Where it forms low savannah it mixes with *Stipa eminens* and *S. setigera* especially, or with the annuals, such as *Avena fatua*, *Bromus maximus*, etc., that have replaced the native bunch-grasses. In its relation to water, it stands just below *Adenostoma* and just above its climax associates. It is essentially a xerophyte, ranging from a rainfall of 25 to 10 inches. As an indicator, it denotes a climate slightly moister than that of the bunch-grass prairie and drier than that of the chaparral. In the chaparral climax it indicates disturbance of the soil, usually associated with alluvial or colluvial deposits.

USES.

The Spanish-Californians and other early settlers made some use of this plant for medicinal purposes, employing it for almost every ill. According to Torrey (Bot. Mex. Bound. 17, 1859), it was used by the Mexican immigrants as a popular remedy against cholera, under the name of "*estafiat*." The Americans usually call it "old man." The foliage is not regularly browsed by cattle, because of the strong odor and bitter taste, and although browsed by sheep and goats, this is done only in the absence of more palatable food. As a result the hillsides of western California are in many places covered with a dense stand of this brush where more desirable species are destroyed by sheep, goats, and donkeys. Because of its abundance and lightness the pollen is a frequent cause of hay-fever, as has been determined by skin-reaction tests. This has led to the use of an extract prepared from the pollen as a desensitizing agent for the relief of certain types of hay-fever on the Pacific Coast. Beneficial results are secured only in those cases where positive reactions are first obtained with the pollen extract.

4. ARTEMISIA MACROBOTRYS Ledebour, Fl. Alt. 4:73, 1833. Plate 4.

A perennial herb with a rootstock, 2 to 4 dm. high, probably nearly inodorous; stems several from a slender crown, simple below, erect, glabrous or sparingly pilose, plainly striate, yellowish-green; basal and lower leaves crowded, petioled, 4 to 8 cm. long including petiole, pinnately divided into several pairs of segments which spread nearly at right angles, these parted into lanceolate very acute lobes which are sometimes again cleft, copiously long-pilose or glabrate; upper leaves similar; inflorescence an elongated terminal raceme or this somewhat branched and subpaniculate, 10 to 20 cm. long, 1 to 3 cm. broad; heads heterogamous, peduncled (peduncles 1 to 5 mm. long), mostly nodding; involucre hemispheric, 3 to 4 mm. high, 6 to 7 mm. broad (much smaller at least in some Siberian forms), bracts 14 to 18, elliptic or the outer ovate, obtuse, brown and scarious on the margins, sparingly villous; ray-flowers about 9 to 12, fertile, corolla tapering upwards, about 2 mm. long; disk-flowers about 30 to 50, fertile, corolla funnellform, 2 to 3 mm. long or only 1.5 in small-headed Siberian forms, mostly glabrous; style-branches of ray-flowers acute to emarginate, of disk-flowers truncate and erose at summit; achenes elliptic-turbinate, 4- or 5-ribbed, glabrous.

Western Yukon to Siberia. Credited to Alaska by Rydberg (N. Am. Fl. 34:264, 1916), but apparently rare there; widely distributed in Siberia. Type locality, dry plains of the Kerlyk River, Siberia. Collections: The only specimen seen from America is one from above Fort Selkirk, Yukon Territory, July 14, 1899, *Tarleton 111* (NY).

MINOR VARIATIONS AND SYNONYMS.

This plant is so little known in America that nothing can be said as to its possible variations. The extent of variation in Siberian forms is mentioned under the heading of Relationships.

1. *ARTEMISIA LACINIATA* β Willdenow, Sp. Pl. 3:1843, 1804.—The original name under which *A. macrobotrys* was described. Cited by Ledebour as a synonym of his *A. macrobotrys*.

2. *ARTEMISIA TANACETIFOLIA* Linnaeus, Sp. Pl. 848, 1753.—A synonym as far as the reference to Siberia is concerned. At least some portions of the description, such as "*foliis bipinnatis subtus tomentositis nitidis*," refer to some other plant, probably *A. nana* Gaudin. Therefore the name *A. tanacetifolia* can not be taken up for the present species, notwithstanding its early date of publication.

RELATIONSHIPS.

The relation of *A. macrobotrys* to *A. parryi*, its nearest ally, has been discussed under the latter, since it is the derived form. The only other American species with which it is connected is *A. norvegica*, but the connection is not very close. The most striking difference between the two is in the foliage. In *macrobotrys* the primary divisions of the leaves spread nearly at right-angles to the rachis, while in *norvegica* they point forward, and the shape of these divisions is different, as shown in the illustrations. The heads, and especially the disk-corollas, of the former are much smaller than in any variety of *norvegica*, except a few which are otherwise very different.

A much closer ally is found in *A. laciniata* Willdenow (Sp. Pl. 3:1843, 1804), a species of similar distribution in Siberia, but not known in America. There is a striking similarity in habit and foliage and especially in the strongly divergent primary divisions of the leaves. Ledebour (Fl. Rossica, 2:582, 1844-46) states that in *laciniata* these segments are all reflexed-divaricate, and uses this as one of his distinguishing features. It may be expected, however, that more copious material will show all degrees of divergence. It is even possible that *macrobotrys* will eventually again become a variety of *laciniata*, as Willdenow once treated it (Sp. Pl. 3: 1843, 1804, as *A. laciniata* β), but the evidence at hand does not justify this. The distinguishing characters, as far as indicated by available collections, may be set forth as follows:

<i>Artemisia laciniata</i> Willdenow.	<i>Artemisia macrobotrys</i> Ledebour.
Primary divisions of the leaves mostly reflexed divaricate.	Primary divisions of the leaves widely divaricate but never reflexed.
Petiole wide and plainly canaliculate.	Petiole slender and obscurely if at all canaliculate.
Involucre 3 mm. high, 4 mm. broad.	Involucre 3 to 4 mm. high, 6 to 7 mm. broad.
Disk-flowers 25 to 30.	Disk-flowers 30 to 50.
Disk-corollas 1.5 to 2 mm. long.	Disk-corollas 2 to 3 mm. long.

While additional collections will certainly necessitate modifications of the above diagnoses, it is hoped that the differences here tabulated will serve to distinguish these two closely related species. Both of them exhibit much variation in minor characters. Thus, in writing of *macrobotrys* as it occurs in Siberia, Ledebour (l. c.) says:

"Variat foliis glabriusculis et plus minus pilosis; laciniis latioribus et angustioribus, longioribus et brevioribus remotioribus et approximatis; rachi plus minus late alata et dentata; corollis pilosiusculis et nudis."

Similar variations may be expected among American plants, but since the area of distribution is here much smaller than in Asia, it is probable these are not so marked. Detailed descriptions of *macrobotrys* are given by Ledebour in connection with the original description and the species is figured by him (Ic. Fl. Ross., pl. 467).

From the above considerations it seems fairly certain that *macrobotrys*, *laciniata*, and *parryi* form a close natural group, and that *norvegica* is a related species less closely connected. Of these, *macrobotrys* is perhaps the most primitive. The characters of *laciniata*, especially the extreme development of the tendency toward reflexed leaf-divisions and the reductions in heads and flowers, indicate this as a derived species. Similarly, *parryi* may be regarded as a derivative from *macrobotrys* with reduced heads and flowers. Its geographic position at outlying stations would support this view, but the tendency of its leaf-segments to point forward in some specimens indicates that it may have separated from the parent stock before the character of divergence had become thoroughly fixed.

ECOLOGY AND USES.

Nothing is known of the ecology or uses of this species.

5. ARTEMISIA NORVEGICA Fries, Novit. Fl. Suec. ed. 1:56, 1817. Plate 3.
BOREAL SAGEWORT.

A perennial herb with a caespitose caudex or short rootstock, 1 to 5 dm. high or much reduced in Arctic forms, mildly fragrant; stems densely clustered, simple up to the

inflorescence, erect, striate, densely villous to glabrous, often reddish tinged; basal leaves crowded, petioled, 1 to 15 cm. long including the petiole, 1 to 3 times pinnately divided or parted into lanceolate or rarely linear or spatulate lobes, varying from silvery-silky to glabrous; upper leaves less dissected; inflorescence normally an elongated terminal panicle, 10 to 4 cm. long and 1 to 5 cm. broad but in some forms much reduced and raceme-like, spike-like, or head-like; heads heterogamous, peduncled or sessile, commonly nodding; involucre hemispheric, 4 to 6 mm. high, 4 to 7 mm. broad (up to 8 mm. broad in the original European form); bracts 9 to 20, broadly elliptic, obtuse, with greenish medial portion and broad brown-scarious margins, villous to glabrous; ray-flowers 6 to 20, corolla narrowed upwards, 2 to 2.5 mm. long, obliquely toothed, villous or glabrous; disk-flowers about 15 to 73, or even up to 120 in the typical form and in subspecies *globularia*, fertile, corolla funnelliform, 2.5 to 3.5 mm. long, 5-toothed, villous to glabrous or granular; style-branches truncate, those of the disk-flowers commonly dilated and arose at summit; achenes nearly cylindrical but with mostly raised ribs, truncate or with a slight rim at summit, glabrous but usually granulariferous.

Widely distributed in northern and mountainous regions, Arctic shores of North America (at least as far east as Camden Bay) to the Rocky and Sierra Nevada Mountains, northwest to Bering Sea and Siberia; also in Scandinavia.

SUBSPECIES.

There is a very considerable range of variation in the size of the plant, the branching of the inflorescence, and the amount of pubescence. The number of recognizable variations is not so great, however, as the long list of described segregates would seem to indicate. This is because the latter have been too often based upon pubescence and other characters which are strongly fluctuating, even over small geographic areas. The more striking variations in North America are the following:

Key to the Subspecies of *Artemisia norvegica*.

- Heads in elongated spikes, racemes, or panicles.
 Inflorescence open-paniculate or loosely racemose; plants mostly 2 to 5 dm. high; pubescence villous or wanting.
 Leaf-blades mostly less than 4 cm. long, short-oblong or roundish in outline; involucre 5 to 6 mm. high. (Not American; included for comparison only). Typical *A. norvegica*.
 Leaf-blades mostly over 4 cm. long, elongated-oblong in outline; involucre 4 to 5.2 mm. high. (a) *saxatilis* (p. 58).
 Inflorescence a narrow raceme or somewhat spike-like; plants mostly 2 dm. or less high; pubescence usually canescent or appressed silvery-silky. (b) *heterophylla* (p. 59).
 Heads in a dense globoid terminal cluster. Northern dwarf forms sometimes simulated by reduced plants of *heterophylla*.
 Lower leaf-blades simply or only 2 times divided; petiole broad, involucre more than 5 mm. broad. (c) *globularia* (p. 59).
 Lower leaf-blades 2 or 3 times divided; petiole narrow, involucre mostly less than 5 mm. broad. (d) *glomerata* (p. 60).

5a. *ARTEMISIA NORVEGICA SAXATILIS* (Besser).—Stems 1.5 to 5 dm. high; foliage varying from merely somewhat pilose (as in the original *A. norvegica*) to copiously villous (*A. saxicola* Rydberg, minor variation 9) or, on the other hand, to perfectly glabrous (*A. levigata* Standley, minor variation 5); lower leaves 5 to 15 cm. long, the blade usually elongated-elliptic or oblong in outline and 2 to 8 cm. long (usually over 4 cm. long), much divided into linear-lanceolate acute lobes; inflorescence openly paniculate, 10 to 30 cm. long, sometimes narrow and racemose, especially in Alaskan forms; heads large, the involucre 4 to 5.2 mm. high; disk-flowers 33 to 75, their corollas 2.5 to 3.5 mm. long. (*A. chamissoniana saxatilis* Besser; Hooker, Fl. Bor. Am. 1:324, 1833). Alberta (and probably farther to the northeast), to the high mountains of southern Colorado, the Sierra Nevada of California, and north through Washington and Alaska

¹ Typical *A. norvegica* should perhaps be admitted to the North American flora. Wille records the species from Greenland (Engler's Bot. Jahrb. 36, beiblatt 81:58, 1905), but he did not distinguish between the typical and the American subspecies.

to eastern Siberia. Type locality, Rocky Mountains. Collections: Union Peak, Wyoming, *Nelson 397* (Gr); high mountains about Empire, Colorado, *Patterson 218* (Gr); Ethel Peak, Larimer County, Colorado, *Goodding 1891* (Gr, NY, UC, US); near Mineral King, southern Sierra Nevada Mountains, California, *Hall and Babcock 5659* (DS, UC); mountains above Bear Valley, near Lake Tahoe, California, July 29, 1889, *Sonne* (UC); Horse Shoe Basin, Okanogan County, Washington, *Elmer 705* (NY, nearly glabrous, minor variation 1, *A. arctica* Lessing); Olympic Mountains, Washington, *Elmer 2618* (DS, NY, moderately pubescent, intermediate to minor variation 1, *A. arctica* Lessing); head of Smoky River, Alberta, *Riley 30* (US, glabrous form, type of *A. levigata* Standley, minor variation 9); Fisk Creek, Selkirk Mountains, British Columbia, *Butlers and Holway 436a* (Gr, minor variation 1, *A. arctica* Lessing); Glacier River, Unalaska, *Van Dyke 73* (Gr, minor variation 1, *A. arctica* Lessing, green and nearly glabrous); St. Paul Island, Bering Sea, *Macoun 94013*, very pubescent (NY), and *94014*, green and nearly glabrous (Gr).

5b. *ARTEMISIA NORVEGICA HETEROPHYLLA* (Besser).—Stems 0.5 to 2 dm. high; foliage silvery-canescens or silky, usually densely so (least so or even glabrate in *A. comata* Rydberg, minor variation 2), somewhat villous with spreading hairs (in *A. richardsoniana* Besser, minor variation 12); lower leaves 1 to 6 cm. long, the blade roundish in outline and 1 to 3 cm. long, 1 to 3 times dissected into linear barely acute divisions; inflorescence spike-like, 4 to 10 cm. long, congested toward the summit but often open and raceme-like below; heads small, the involucre 3.5 to 4.5 mm. high; disk-flowers 10 to 25 or more, their corollas 3 to 3.5 mm. long. (*A. heterophylla* Besser, *Nouv. Mem. Soc. Nat. Mosc.* 3:74, 1834.) Eastern Siberia and Arctic shores of North America to Great Slave Lake and the high mountains of Washington. Type locality, St. Lawrence Bay, Bering Strait, eastern Siberia. Collections: Arctic Coast of Canada, *Richardson* (US, type collection of *A. richardsoniana* Besser, minor variation 12); Camden Bay, Alaska, on gravel tundra, *Johansen 122* (NY, type collection of *A. comata* Rydberg, minor variation 3); sandspit at Martin Point, Alaska, *Johansen 134* (NY, minor variation 3, *A. comata* Rydberg); Bernard Harbor, northern Canada, in gravel tundra, *Johansen 337* (NY, form with villous pubescence, *A. richardsoniana* Besser, minor variation 12); Bernard Harbor, northern Canada, on sandy slopes and sand dunes, *Johansen 304 and 304a* (NY, form with silvery pubescence and dark-margined bracts, minor variation 8, *A. hyperborea* Rydberg, of which Johansen's 304 is the type number); Copper Island, September 3, 1891, *Macoun* (Gr, form near minor variation 8, *A. hyperborea* Rydberg); vicinity of Norton Sound, Alaska, 1900, *Macgregor*; Mount Rainier, Washington, August 27, 1896, *Flett* (US, type of *A. tacomensis* Rydberg, minor variation 14).

5c. *ARTEMISIA NORVEGICA GLOBULARIA* (Chamisso).—Stems 0.4 to 1 dm. high; foliage gray with a dense silky-villous pubescence, varying to sparsely pubescent and green; lower leaves 1 to 3 cm. long, the blade flabelliform or obovate in outline and less than 1 cm. long, once or twice ternately divided into broadly linear or elliptic acute divisions, the petiole wide and flat; inflorescence a single terminal globoid cluster of heads, 1 to 2 cm. across; heads rather large, the involucre 4 to 6 mm. high; disk-flowers about 50 to 120, their corollas 3 to 4 mm. long. (*A. globularia* Chamisso; Besser, *Nouv. Mem. Soc. Nat. Mosc.* 3:64, 1834.) Western Alaska and eastern Siberia. Type locality, St. Lawrence Bay, Siberia. Collections: St. George Island, Bering Sea, July 31, 1891, *Macoun* (Gr); St. George Island, Bering Sea, June 29, 1920, *Johnston* (SF, densely pubescent, gray); same, but on cliffs, August 13, 1920, *Johnston* (SF, sparsely pubescent, green); St. Paul Island, Bering Sea, August, 1920, *Hanna* (SF); St. Paul Island, Bering Sea, *Macoun 94015* (Gr, NY); St. Paul Island, Bering Sea, August 15, 1897, *Kincaid* (UC); St. Matthew Island, Bering Sea, *Macoun 87* (NY); type collection (Gr, ex-herb. Acad. Petrop.).

5d. *ARTEMISIA NORVEGICA GLOMERATA* (Ledebour).—Stems 0.4 to 1.2 dm. high; foliage gray with a dense silky-villous pubescence; lower leaves 0.8 to 2 cm. long, the blade flabelliform or orbicular in outline and less than 1 cm. long, 2 or 3 times ternately divided into linear acute divisions, the petiole slender; inflorescence a single dense terminal globose cluster of heads, 1 to 2 cm. across; heads small, the involucre 3.5 to 5 mm. high; disk-flowers 16 or more, their corollas about 2.5 mm. long. (*A. glomerata* Ledebour, Mem. Acad. St. Petersb. 5:564, 1815.) Western Alaska to eastern Siberia and the Kurile Islands. Type locality, St. Lawrence Bay, Siberia. Collections: Cape Thompson, Alaska, *Muir 80* (Gr); Arakamtchetchene Island, Bering Straits, 1853–56, *Wright* (Gr); St. Lawrence Bay, eastern Siberia, July 24, 1895, *Sharp* (Phila.); St. Lawrence Bay, *Eschscholtz* (Gr, ex-herb. Ledebour).

MINOR VARIATIONS AND SYNONYMS.

1. *A. ARCTICA* Lessing, *Linnaea* 6:213, 1831.—The nearly glabrous form of *A. norvegica saxatilis*. Most common in the far Northwest, but specimens which are almost entirely glabrous come from as far south as the southern Sierra Nevada of California (*Purpus* 1635, UC), and all degrees of pubescence are found in different collections. It seems quite unlikely that the amount of pubescence is other than a response to ecologic conditions. It is therefore not surprising to find that in the far Northwest the plants are mostly, although not all, of the nearly glabrous type, and that in the arid Rocky Mountain districts they are strongly pubescent, while in the Cascades and Sierra Nevada occur both sorts with numerous intermediate forms. *A. arctica* also differs, according to Rydberg, in the inner bracts, which are said to be "ovate, obtuse, or rarely acutish, with a broadly lanceolate green center," while those of true *saxatilis* (*A. saxicola* Rydberg) are said to be "ovate, acute, with a narrowly lanceolate green center." There is, to be sure, some variation in the bracts, but these run parallel neither with the variations in pubescence nor with geographic distribution, as is shown by the series of 12 bracts represented in figure 5. Various forms referred to *A. arctica* by Besser, Gray, and others belong partly to subspecies *saxatilis* and partly to subspecies *heterophylla*. The type locality of *arctica* is Unalaska.

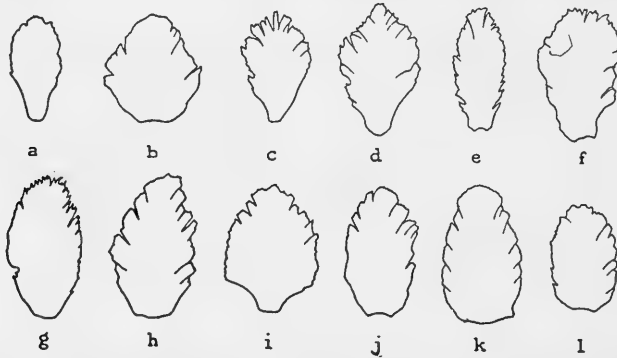


FIG. 5.—Inner bracts of *Artemisia norvegica saxatilis*: a to f, inner bracts from plants referable to true *saxatilis* because of the strong pubescence on stems and foliage; g to l, inner bracts from plants referable to minor variation 1 (*A. arctica* Lessing) because of the nearly glabrous stems and foliage. a, from Colorado (69460 UC); b, from Colorado (489332 US); c, from Colorado (29773 UC); d, from California (91243 UC); e, from California (193585 UC); f, from California (63517 UC); g, from Alaska (204365 UC); h, from Alaska (204501 UC); i, from Alaska (91242 UC); j, from California (29703 UC); k, from California (40555 UC); l, from California (91240 UC). All $\times 6$.

2. *A. CHAMISSONIANA SAXATILIS* Besser, in *Hooker Fl. Bor. Am.* 1:324, 1833.—*A. norvegica saxatilis*.

3. *A. COMATA* Rydberg, *N. Am. Fl.* 34:263, 1916.—A form combining the greenish herbage and elongated leaf-blades of *A. norvegica saxatilis* with the reduced stature (1. to 1.5 dm.) and narrow, racemose inflorescence of *heterophylla*. Although the stems and foliage are nearly glabrous, the rachis of the inflorescence and the peduncles are notably white-villous. The involucre is very dark and nearly glabrous. Type locality, Collinson Point, Camden Bay, Alaska. (Illustration in Macoun and Holm, Rep. Canadian Arctic Exped. 5:plate 13. figs. 3 and 6.)

4. *A. COOLEYAE* Rydberg, l. c. 265.—Placed next to *A. parryi* in the North American Flora because of its small heads, glabrous herbage, and "light brown" margins to the involucrel bracts. The inflorescence, too, has the long, ascending branches of *parryi*, but this, as also the small size of the heads, may be the result of a deformity. On the whole, the plant seems more like an aberrant specimen of *A. norvegica saxatilis*. The leaves with slender, attenuate, forward-pointing lobes are almost identical with those of some forms of *saxatilis*; for example, Howell's plant from Yes Bay, Alaska (August 21, 1895, NY) or Elmer's plant from Washington (*Elmer 705*, NY). The glabrous character also occurs in *saxatilis* of the *levigata* form. The distinction between light brown and fuscous, as applied to the color of bract-margins, is too subtle for use as a distinguishing character. The final disposal of *A. cooleyae* may await the assembling of copious material in perfect condition. Type locality, above Silver Bow Basin, Juneau, Alaska.

5. *A. GLOBULARIA* Chamisso, Besser, Nouv. Mem. Soc. Nat. Mosc. 3:64, 1834.—*A. norvegica globularia*.

* 6. *A. GLOMERATA* Ledebour, Mem. Acad. St. Petersb. 5:564, 1815.—*A. norvegica glomerata*.

7. *A. HETEROPHYLLA* Besser, l. c., 74, 1834.—*A. norvegica heterophylla*.

8. *A. HYPERBOREA* Rydberg l. c., 262.—*A. norvegica heterophylla*. The pubescence in the type specimen is dense, closely appressed, and silvery, even in the inflorescence, and the bracts are conspicuously dark-margined. Type locality, sand dunes at Bernard Harbor, Northwest Territory. (Illustrated in Macoun and Holm, Rep. Can. Arctic Exped. 5: Plate 13, figs. 2 and 4.)

9. *A. LEVIGATA* Standley, Smiths. Misc. Coll. 56²²:2, 1912.—The perfectly glabrous form of *A. norvegica saxatilis*. As already indicated under *A. arctica*, of this list, the amount of pubescence is exceedingly variable and can not be correlated with other characters. The type of *levigata* came from the Smoky River, Alberta, and absolutely glabrous plants are known also from the middle Sierra Nevada of California (*Brewer 2129*, UC). The original specimen of *A. arctica* is a comparatively low plant (3 dm.?) with a racemose inflorescence, but paniculate forms also are sometimes essentially glabrous (*Walker 932*, from Alaska) while the racemose forms are commonly pubescent (*Walker 770* and *Funston 93*, both from western Alaska). It is thus evident that the use of such criteria would necessitate the acceptance of several more species than have as yet been proposed.

10. *A. MINUTA* Rydberg, l. c., 261.—Provisionally placed by its author between forms here referred to *A. norvegica heterophylla*; also keyed with *A. pedatifida* because of the somewhat woody stems. "Flowers unknown and therefore its place in the genus uncertain." The type specimen, which came from Medicine Hat, Alberta, is not identifiable.

11. *A. NORVEGICA PACIFICA* Gray, Syn. Fl. N. Am. 1^o:371, 1884.—*A. norvegica saxatilis*. The relation of this form to the original *saxatilis* is discussed under *A. arctica*, of which variety *pacifica* is an exact synonym.

12. *A. RICHARDSONIANA* Besser, Bull. Soc. Nat. Mosc. 9:64, 1836.—Here referred to *A. norvegica heterophylla*, although further collections and field study may furnish characters entitling it to separate rank. The only distinguishing feature thus far assigned to it is the variable one of its more spreading villous pubescence. Type locality, Arctic Coast of Canada. (Illustrated by Macoun and Holm, Rep. Can. Arctic Exped. 5: plate 13, figs. 1 and 5, 1921.)

13. *A. SAXICOLA* Rydberg, Bull. Torr. Club 32:128, 1905.—*A. norvegica saxatilis*. In raising the original *A. chamissoniana saxatilis* Besser to specific rank, Rydberg changed the name to *saxicola* because of the earlier *A. saxatilis* Waldstein and Kitaibel, 1804. This last is generally regarded as a synonym of *A. camphorata* Villar, a European species.

14. *A. TACOMENSIS* Rydberg, N. Am. Fl. 34:262, 1916.—*A. norvegica heterophylla*. According to Rydberg, the stems are less than 1 dm. high, the basal leaves 1 to 1.5 cm. long, the herbage silvery-canescant, and the involucre densely white-villous, whereas in the original *heterophylla* the stems are 1 to 2 dm. high, the basal leaves 3 to 6 cm. long, the herbage silky-villous, and the involucre densely villous. The type of *tacomensis*, which came from Mount Rainier, Washington, substantiates these distinctions, but other specimens from Mount Rainier (August 20, 1889, *Greene*, UC) which must be taken as expressions of the same form, have stems 1.2 to 1.6 dm. high, basal leaves 1.5 to 5 cm. long, and involucre densely lanate as originally described for *heterophylla*. In view of these facts, *A. tacomensis* can not be accepted as more than a form of *heterophylla* with marginally smooth and silvery foliage. The involucrel bracts of these southern plants are quite pale along the margins as contrasted with the usually dark-margined bracts in forms from the far north.

15. *A. TYRRELLI* Rydberg, l. c., 262.—A rare plant known only from an incomplete specimen gathered in northern British Columbia. Probably best referred to *A. norvegica heterophylla* but robust, the stems 2 to 3 dm. high. The herbage is silky-canescant or silvery.

RELATIONSHIPS.

Artemisia norvegica is not of American origin. This is clear from a consideration of the fact that all of the species on this continent to which it is most closely related possess certain specialized features wanting in *norvegica*. This indicates either that they are themselves derivatives of *norvegica*, or have come down from some more ancient ancestral stock. The species here referred to are *A. senjavinensis*, *A. macrobotrys*, and *A. parryi*.

The relationship of each of these to *norvegica* will be discussed under the respective species. The exact place of origin of *norvegica* probably will never be determined, but from the facts of distribution it seems to have been somewhere near the central portion of Eurasia. After its migration toward the north, the species spread west and east along the Arctic shores and seems to have broken up into two principal stocks, one resulting in the form represented by the present nomenclatorial type, the other yielding a group of forms centering around subspecies *saxatilis*. The former is of northwestern distribution, being most abundant in Scandinavia; the latter belongs to extreme north-eastern Asia and America. No specimens are at hand from the intervening area, that is, northern Siberia, and it seems from the literature that no forms of the species are

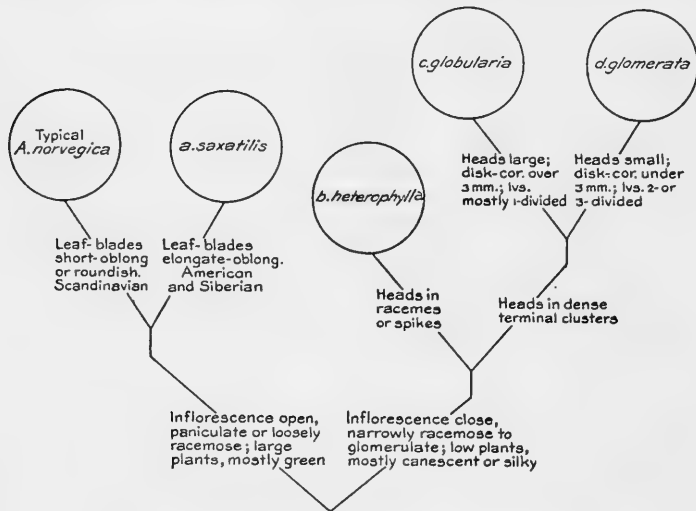


FIG. 6.—Phylogenetic chart of the subspecies of *Artemisia norvegica*.

there present. If further exploration proves this to be the case, then the close similarity between Scandinavian and American forms will be most remarkable. It is quite possible, however, that the species has reached America through a route extending westerly from Scandinavia, since Wille reports it in Greenland (Engler's Bot. Jahrb. 36, beiblatt 81:58, 1905). The Old World and Rocky Mountain types are so nearly alike in most of their characters that W. J. Hooker was unable to see any differences whatever between certain specimens from Norway and others from the Rocky Mountains (Hooker, Fl. Bor. Am. 1:325, 1833). But a careful comparison of large series from both regions establishes certain decided tendencies which render their subspecific separation highly desirable, while at the same time the overlapping in all essentials makes their specific segregation impossible. Typical *norvegica*, as it grows in Scandinavia, is a plant with leaf-blades often as broad as long through the congestion of the segments near the end of the rachis; the heads average larger than in any American variety (see table 4), and the peduncles are usually longer. In all of these characters, however, it is sometimes matched by forms of subspecies *saxatilis*. Although the two are widely separated geographically, there are some specimens of each that can not be positively identified

on morphological characters alone. The degree of difference in the size of the head and the amount of overlapping is indicated in table 4, where these features are brought out in the columns headed "Involucre." The size of the head is also proportional to the number of flowers. While this number will not serve to differentiate the two forms, because of the amount of variation, a decided tendency towards the higher numbers is seen in the specimens from the Old World.

While the Scandinavian plants exhibit but little variation among themselves, the American branch yields a considerable number of minor derivatives, a majority of which are ecologic, at least in origin. These differ from one another principally in habit, type of inflorescence, size of heads, and especially in the amount of pubescence. Some have been given specific names, and these are here treated under the heading "Minor variations."

In addition to the two subspecies already discussed, there are three which are alike in that all have undergone a reduction in the inflorescence. This has been accompanied by a dwarfing in the plant itself and the pubescence usually is not only more copious, but has taken on a close, canescent, often silky character. The subspecies are *heterophylla*, *globularia*, and *glomerata*. They are restricted to northern North America and the extreme easterly part of Siberia. This group (fig. 6) is indicated as having been evolved before the segregation of *saxatilis*, but there is no evidence other than that obtained from the leaves to substantiate this arrangement. On the basis of geographic distribution, it is simpler to assume that the branch is an offshoot from *saxatilis*, in which the leaf-blades have retained the short, rounded outline sometimes found in that subspecies. The least amount of modification has taken place in subspecies *heterophylla*. In this the inflorescence has been reduced from the usual open panicle to a spike, and when this is much shortened it becomes almost capituliform, as in some of the specimens of the type collection of *A. richardsoniana*, here referred to *heterophylla*. The subspecies is widely distributed in northwestern America, which accounts for the presence of several intergrading forms.

The final stage in the reduction of the inflorescence is reached by *globularia* and *glomerata*. Here the heads are always in dense terminal clusters. In these northern derivatives the foliage, as well as the stem and inflorescence, fails to reach full development and the pubescence is not so white, appressed, and silvery as in *heterophylla*. While probably of ecologic origin, either from this or from some similar subspecies, their best characters seem now to be fixed, as indicated by the absence of a completely intergrading series. Much more copious collections from the far north are needed before such points can be finally determined. The subspecies *globularia* and *glomerata* are closer in general aspect than any other pair within the species, but on the basis of the statistics presented in table 4 they are the most distinct. The total absence of overlapping in some of the characters tabulated might seem good evidence of their specific segregation. However, it should be pointed out that the differences are all of one order, namely, the smaller number of flowers and their smaller size in *glomerata*, with the inevitable result of a reduction in the size of the involucre. This character, even when taken in connection with the tendency towards a more simply cut foliage, can scarcely be of specific value, especially when so few collections are available for study. Moreover, *heterophylla* is also to be taken into account. By injecting its measurements into the series a nearly complete gradation is obtained, even from the small number of specimens tabulated. The additional criterion of pubescent corollas in *glomerata* as contrasted with glabrous or only glandular-granuliferous ones in *globularia* has been used by Besser (DeCandolle, Prodr. 6:116, 1837) and others, but the unreliability of this character, which has been demonstrated in the discussion on criteria, is here evidenced by the nearly entire absence of hairs on the corollas of the three collections of *glomerata*

cited in table 4, as well as of all the *globularia* material available. Ledebour (Fl. Ross. 2:588, 1844-46) describes both as having pilose corollas. The shape of the disk-corollas is perhaps of greater significance. There seems to be a tendency in all of these dwarf subspecies towards a sudden enlargement of the throat, as shown in plate 3, this

TABLE 4.—Variation in the subspecies of *Artemisia norvegica*.

	Herbarium.	Involucre.			No. of ray-flowers.	No. of disk-flowers. ¹	Total no. of flowers. ¹	Length of disk-corollas.
		Height.	Breadth.	No. of bracts.				
		mm.	mm.					
<i>Typical A. norvegica:</i>								
Kongs vold, Norway.....	Gr	5.6	7.8	16	22	121 (1)	143	3.5
Dovre, Norway.....	Gr	6.0	7.2	25	11	71	82	3.6
Do.....	Gr	5.3	7.3	17	12	95	109	3.4
Ahlberg, Norway.....	13388 US	6.2	7.3	18	10	45	55	3.2
Doorenses, Norway.....	US	5.8	7.5	16	13	92	105	3.5
Average.....		5.7	7.4	18	13	84	98	3.4
<i>Subspecies saxatilis:</i>								
Disenchantment Bay, Alaska..	91242 UC	4.5	7.3	17	9	44	55	3.2
Nome, Alaska.....	91245 UC	4.7	7.0	15	9	45	56	3.1
Silver Bow Basin, Alaska.....	29727 UC	4.6	7.0	12	8	46	54	3.2
White Pass, Yukon, Alaska.....	SF	4.2	7.0	18	8	53	61	3.0
Vixen Inlet, Alaska.....	204365 UC	5.2	7.4	12	6	33	39	3.1
Kuiu Island, Alaska.....	204501 UC	4.2	7.1	15	7	35	42	3.5
Short Bay, Alaska.....	91241 UC	4.0	7.3	18	6	38	44	3.3
Upper Truckee, Calif.....	193585 UC	5.2	7.3	17	10	53	63	2.8
Do.....	91244 UC	5.0	6.8	16	8	36	44	3.0
Yosemite Park, Calif.....	29704 UC	5.2	7.3	12	6	73 (1)	79	2.8
Mineral King, Calif.....	91243 UC	4.4	7.0	13	10	73	83	2.5
Farewell Gap, Calif.....	63517 UC	5.2	7.1	12	8	34	42	3.0
Little Kern, Calif.....	91240 UC	4.0	6.8	16	6	46	52	3.0
Clear Creek, Colo.....	29773 UC	5.1	7.4	15	8	64	72	3.1
Ethel Peak, Colo.....	69460 UC	5.0	6.9	19	10	56	66	2.5
Average.....		4.6	7.1	15	8	45	56	3.0
<i>Subspecies heterophylla:</i>								
Bernard Harbor, Can.....	NY	4.0	5.3	12	5	24	29	3.1
Do.....	NY	3.3	5.1	10	10	10	20	3.5
Sarauna, Bering Island.....	US	4.1	5.5	14	7	15	22	3.3
Mount Rainier, Washington.....	29776 UC	4.8	6.0	10	8	16	24	2.8
Average.....		4.0	5.4	11	7	15	23	3.1
<i>Subspecies globularia:</i>								
St. George Island, Bering Sea.....	Gr	4.5	19	14	3.8
St. Matthews Is., Bering Sea.....	Gr	4.0	5.5	11	8	3.4
Do.....	NY	4.6	19	17	3.2
Do.....	Gr	5.0	6.2	11	7	3.1
Do.....	73910 UC	5.8	8.0	13	13	3.3
St. George Island, Alaska.....	SF	5.2	7.5	16	10	25	35	3.8
Do.....	SF	4.9	7.3	13	10	22	32	3.6
St. Paul Island, Alaska.....	SF	5.1	7.1	17	11	32	43	3.9
Average.....		4.8	6.9	14	11	26	36	3.5
<i>Subspecies glomerata:</i>								
St. Lawrence Bay.....	Gr	5.0	4.3	9	7	2.5
Do.....	Phila	4.0	4.0	7	8	2.5
Bering Strait.....	Gr	5.0	5.2	9	8	2.6
Average.....		4.7	4.6	8	7	2.5

¹ The disk-flowers often fall out of the involucre in dried specimens. For this reason the lower numbers are not reliable. This applies especially to the last two subspecies, of which the material is rather poor.

being most noticeable in *glomerata*. But the meager material at hand scarcely justifies the taxonomic use of this feature at present. The probable explanation as to the phylogeny of the last three subspecies is that each represents a distinct evolutionary line which has become fixed through isolation.

ECOLOGY AND USES.

Artemisia norvegica is a perennial herb with caudex or short rootstock, which blooms from early July to October. It forms clans in alpine and Arctic meadows and subalpine forests, and sometimes becomes a consociate on stony slopes or in burned areas. It usually indicates moist areas in forests, where it is often associated with *Carex*, *Juncus*, *Erigeron*, *Mimulus*, etc. No uses are known for this species.

6. ARTEMISIA SENJAVINENSIS Besser, Nouv. Mem. Soc. Mosc. 3:65, 1834.

Plate 4.

A perennial herb with a thick multicapital caudex, about 0.5 to 1 dm. high, the odor not known; stems numerous, forming dense tufts, simple above the basal branches, the central ones erect, the outer ones spreading, densely villous with long shaggy white or tawny hairs; basal leaves densely crowded, sessile, less than 1.5 cm. long, simply 3- to 5-cleft into ovate, acute lobes, very densely silky-villous like the stems, the hairs longer than the lobes and nearly concealing the leaf; upper leaves 1 to 2 cm. long, cleft less than halfway into elliptic rather obtuse lobes, similarly silky-hirsute; inflorescence a congested globose terminal spike, 1 to 2 cm. long and of equal breadth; heads heterogamous, sessile, erect; involucre campanulate, about 4 mm. high and 4 to 5 mm. broad; bracts about 8, elliptic, denticulate, obtuse, with brown scarious margins, densely long-villous; ray-flowers 5 to 8, fertile, corolla tubular, about 2 to 2.4 mm. long, lobed, granular; disk-flowers 10 to 20, fertile, corolla funnelform, about 2.5 to 3 mm. long, 5-toothed, granular; style-branches of ray-flowers ligulate, truncate, entire, of disk-flowers dilated, rounded and erose at summit; achenes nearly cylindrical, with about 5 vertical ribs or nerves, glabrous.

Western Alaska and eastern Siberia. Type locality, Senjavin Sound, Siberia. Collections: Kotzebue Sound, western Alaska, "*Beechey*" (Gr, ex-herb. Hooker); same locality, "*Arnbitt*" (NY); Arakamtchetchene Island, Bering Straits, 1853-56, *Wright* (NY, US). Siberian collections as far as known include only the following: Type collection, *Mertens* (Gr, ex-herb. Acad. Petrop.); Fretum Senjavin, *Bongard* (NY, other species also have been distributed with these data); Terra Tschuktschorum, St. Lawrence Bay, *Eschscholtz* (according to Ledebour, Fl. Ross. 2:589, 1844-46).

SYNONYMS.

1. *ARTEMISIA ANDROSACEA* Seeman, Botany Voy. Herald 34, 1852.—The excellent plate accompanying the original description leaves no doubt that this is exactly *A. senjavinensis*. Type locality, Kotzebue Sound, Alaska.

2. *A. SEMAVINENSIS* Besser, Nouv. Mem. Soc. Mosc. 3:65, 1834.—The original spelling of the specific name; corrected to *senjavinensis* by Besser (Bull. Soc. Nat. Mosc. 9:64, 1836).

RELATIONSHIPS.

There is considerable evidence to support the view that this is a reduced far-northern derivative either of *A. macrobotrys* or *A. norvegica*. The small size of the heads might seem to indicate the former, but the very dense and persistent pubescence is more like that of certain forms of the latter, which also includes a small-headed subspecies *glomerata*. Both *senjavinensis* and *glomerata* exhibit an extreme reduction in habit, as a result of the arctic conditions under which they grow, so that they are closely similar in aspect, but they are not sufficiently close in other features to justify their inclusion in one collective species. The former is unique in the extreme development of the long and dense villous pubescence, and is especially distinct from *glomerata* in the cut of the leaf,

as shown in the plates. Their occupation of the same general region (both grow around Kotzebue Bay), without any evident tendency towards intergradation, also indicates that they are not directly connected, although undoubtedly of the *norvegica-macrobotrys-lacinata* stock.

ECOLOGY AND USES.

Artemisia senjavinensis is a dwarf mat-former produced by extreme Arctic conditions, as indicated by the short branches and coating of long hairs. No uses are known for it.

7. ARTEMISIA PARRYI Gray, Proc. Am. Acad. 7:361, 1868. Plate 4.

A perennial herb with a rootstock, 1 to 4 dm. high, probably without strong odor; stems usually in groups, simple below, erect, glabrous, faintly striate, seldom if ever reddish tinged; basal and lower leaves much crowded, petioled, 4 to 8 cm. long including petiole, twice pinnately divided into linear elongated lobes, the divisions either widely spreading or ascending, sparingly pilose especially on the back or glabrous; upper leaves smaller and less dissected but with similar elongated linear lobes and similar pubescence; inflorescence an elongated terminal raceme or branching and subpaniculate, 10 to 30 cm. long, 0.5 to 5 cm. broad, when compound the branches ascending; heads heterogamous, peduncled (peduncles 1 to 5 mm. long), mostly nodding; involucre hemispheric, 3 mm. high, 4 to 5 mm. broad; bracts 14 to 18, elliptic, obtuse, brown and scarious on the margins, glabrous or rarely a little villous; ray-flowers about 8, fertile, corolla tapering upwards, about 1.5 mm. long, pubescent or glabrous; disk-flowers about 30 to 50, fertile, corolla funnelform, about 2 mm. long, 5-toothed, pubescent or glabrous; style-branches of ray-flowers acutish, of disk-flowers truncate or rounded and erose at summit; achenes nearly cylindrical but narrowed below, truncate or slightly rounded at summit, faintly 4- or 5-ribbed, smooth or granuliferous.

Known only from the high mountains of southern Colorado and southeastern Utah. Type locality, Huerfano Mountains, Colorado (erroneously stated by Gray to be in New Mexico). Collections: Type, September, 1867, *Parry* (Gr); Colorado: Sangre de Cristo Pass, 1867, *Parry* (Gr); Crestones, Sangre de Cristo Mountains, at 3,700 m. altitude, *Brandegee* (Gr, UC 173290, very similar to the type); Cottonwood Lake, *Shear 3802* (NY); La Sal Mountains, near Mount Peal, southeastern Utah, *Rydberg* and *Garrett 9003* (NY).

SYNONYMS.

1. ARTEMISIA SAXICOLA PARRYI Nelson; Coulter and Nelson, Man. Rocky Mt. 568, 1909.—Based upon *A. parryi* Gray.

RELATIONSHIPS.

It is difficult to determine the exact position of this species in the phylogenetic scheme of the Artemisias. This is due to its scarcity, its local distribution, and the absence of variations. It is very certain, however, that it belongs to the group of *macrobotrys* and *norvegica*, and although not heretofore associated taxonomically with the former, it seems to be a far southern representative of that Siberian and Alaskan species. The heads and flowers are smaller than in *macrobotrys*, but aside from this and a certain leaf-character there are no essential differences. The principal reason for associating these two is that both exhibit a unique divergence of the primary divisions of the leaf. In *macrobotrys* the divisions, at least of the lower leaves, stand at about a right angle to the rachis. An equally great divergence occurs in some specimens of *parryi*, for example, *Brandegee's* plant from Crestones, Colorado (Univ. Calif. Herb. 173290), while in others the divisions are directed forward. In shape, the segments are quite different. Those of *macrobotrys* are lanceolate and very acute, while those of the present species are

strictly linear, the sides being nearly parallel, and the apex is often obtuse or only barely acute. If the assumption is correct that *A. parryi* is an offshoot from a *macrobotrys*-like ancestor, then it is widely separated geographically from its nearest relatives. It is apparently an isolated species that became stranded on the higher peaks of the southern Rocky Mountains, perhaps during one of the migrations of the glacial period, and has there developed its unique characters. More copious collections are much needed and especially a fuller exploration of the northern Rocky Mountains in order to discover forms connecting this with *macrobotrys*, if such forms exist.

The relationship with *A. norvegica* is less close. It is difficult to prepare a key that will separate *parryi* from all of the variations of this species, but each of the subspecies differs in essential characters. The only one that inhabits the same general region is *saxatilis*, and this is so different in its large heads, with numerous large flowers, as well as in the foliage, that any direct phylogenetic connection is out of the question.

Rydberg has recently described as *A. cooleyae* a new species which he places next to *parryi*, apparently considering it a segregate from this. It is discussed in the present paper among the minor variations of *A. norvegica*.

ECOLOGY AND USES.

Artemisia parryi is a rootstock perennial, forming clans in the subalpine zone in southern Colorado and western Utah. It is too infrequent to be of use.

8. ARTEMISIA STELLERIANA Besser, Nouv. Mem. Soc. Mosc. 3:79, 1834. Plate 5. BEACH SAGEWORT.

A stout perennial herb, from a creeping cespitose somewhat woody rootstock, 3 to 5 dm. high, inodorous; stems crowded, erect or the base decumbent, simple up to the inflorescence, densely white-tomentose or white-floccose, striate; basal leaves crowded, petioled, 3 to 8 cm. long, 0.7 to 3 cm. wide, obovate or spatulate, with a few coarse obtuse lobes or teeth near the summit, densely white-tomentose on both sides; principal and upper leaves sessile or subsessile, 2 to 6 cm. long, 1.5 to 4 cm. wide, obovate or broadly oblanceolate in outline, pinnately lobed, the lobes 3 to 9, elliptic and very obtuse, the whole leaf densely white-tomentose on both sides; inflorescence a dense panicle, 10 to 20 cm. long, 2 to 4 cm. broad, sometimes almost raceme-like; heads heterogamous, erect or nodding, on peduncles 2 mm. or less long, often subsessile; involucre hemispheric, 6 to 7 mm. high, 6 to 9 mm. broad; bracts 9 to 12, in 3 series, the outer ones broadly lanceolate and acute, the middle ones about one-half longer and obtuse, the innermost about as long as the middle series, elliptic, largely scarious, and acute, all densely tomentose on exposed parts; ray-flowers 7 to 12, fertile, corolla subcylindric, obscurely 2-toothed or merely erose around the orifice, 2 to 2.5 mm. long, graniferous; disk-flowers 25 to 40, fertile, corolla trumpet-shaped, 3.5 to 4 mm. long, deeply 5-toothed, resinous-granuliferous; style-branches truncate, erose across the summit; achenes nearly terete but narrowed at base and slightly rounded to the summit, glabrous.

Sandy shores along the coast from Quebec to New Jersey, and also inland from Ontario to New York, Wisconsin, and perhaps elsewhere; also in eastern Asia and in some parts of Europe. Type locality, Port of Petropaulovski, Kamchatka. Collections: Strand west of Riviere Blanche, Quebec, *Fernald* and *Collins 762* (Gr); sandy seashore, Falmouth, Massachusetts, July 2, 1895, *Deane* (Gr); sandy shore, Middletown, Rhode Island, July 4, 1909, *Williams* (Gr); New London, Connecticut, June 24, 1892, *Learned* (Gr); sand dunes, Five-mile Beach, New Jersey, *MacElwee 1441* (NY); sandy shore, Oneida Lake, New York, *Haberer 2311* (Gr); Sandy Hook, New Jersey, June 19, 1900, *Williams* (Gr); lake-shore sands, near Port Huron, Michigan, *Dodge 5* (NY).

RELATIONSHIPS.

The large, heterogamous heads with numerous flowers, the fertile achenes in both ray and disk, and the absence of specialized features indicate that this is one of the most primitive of Artemisias. It occurs native in eastern Siberia and is apparently not far removed phylogenetically from *A. vulgaris*, some large-headed forms of which occupy the same phytogeographic area. The American species which it most closely resembles is *A. franserioides* of the southern Rocky Mountains, and since this species has no close relatives in America it seems not impossible that it is an offshoot from the *stelleriana* stock. The agreement between the two in essential characters and somewhat in the cut of the leaf is quite close, although the dissection has been carried much farther in *franserioides* and the individual flowers are reduced in size. *A. stelleriana* appears to be a non-plastic species, since no varieties or forms have been described, as far as we have been able to learn.

ECOLOGY AND USES.

Artemisia stelleriana is a perennial herb with creeping rootstocks, which forms consocieties on sandy shores and on dunes, often covering extensive areas as a pure community. It has generally been assumed to be an escape from cultivation, in all its European and American stations (Fernald, *Rhodora* 2:38, 1900), but it is a puzzling fact that it has always escaped into the sands of seashores and lake-shores, and apparently never into roadsides and waste places.

The remarkably white herbage gives to this species a certain value as an ornamental plant. It is therefore grown to a limited extent both in American and European gardens, more especially for borders. Beyond this it is of no economic value.

9. ARTEMISIA ALASKANA Rydberg, N. Am. Fl. 34:281, 1916. Plate 5.

A perennial herb or perhaps shrubby at base, the lower portions not present on the single specimen thus far collected, 4 dm. or more high, the odor not known; stems apparently crowded at the base to form a tussock or close clump, mostly erect, simple except below and in the inflorescence, striate, sparingly tomentulose; lower leaves crowded, petioled, 3 to 5 cm. long, 1.5 to 4 cm. wide across the lobes, twice dissected, first pinnate into 3 to 5 divisions, each of which is irregularly again cleft, or some leaves twice ternate, the ultimate segments oblong or linear, obtuse, 0.4 to 2 cm. long, 2 mm. or less wide, the whole leaf appressed silvery-tomentose on both sides; upper leaves 5 to 6 cm. long, mostly with 1 or 2 linear lateral lobes and a 3-cleft terminal one, or simply ternate, the lobes linear and obtuse, silvery-tomentose like the lower, the leaves of the inflorescence ternately cleft to entire and scarcely reduced in length; inflorescence a very open raceme, or subpaniculate below, leafy throughout, 25 to 30 cm. long, 4 to 6 cm. broad; heads heterogamous, on peduncles 1 to 7 cm. long, erect or nodding; involucre hemispheric, 4.5 to 5 mm. high, 6 to 7 mm. broad; bracts about 15 to 20 in addition to a few linear subtending bracts of the peduncle, elliptic or ovate, obtuse, with broad scarious erose margins, villous-tomentose; ray-flowers 7 to 16, fertile, corolla tubular, 1.5 to 2 mm. long; disk-flowers about 50 to 60, fertile, corolla funneliform, 5-toothed, 2 to 2.5 mm. long, glandular-granuliferous below; style of ray-flowers linear, obtuse, of disk-flowers flat, strongly recurved, penicillate at the truncate apex; achenes nearly prismatic, truncate at summit, faintly angled, glabrous.

Known only from the type collection, between Nulata and Nowikakat, on the Yukon River, west-central Alaska, July 23 to 27, 1889, *Russell* (US).

RELATIONSHIPS.

The close relationship between this form and the Siberian *A. turczaninoviana* Besser was suggested by Rydberg in connection with his original diagnosis. The similarity

between the two is so close that future collections in the intervening territory will probably demonstrate the presence of intermediate forms. The chief differences, as far as indicated by the scant material at hand, are the following:

<p style="text-align: center;"><i>Artemisia turczaninoviana.</i></p> <p>Leaves of the inflorescence reduced, 1 cm. or less long.</p> <p>Peduncles less than 1 cm. long, all simple.</p> <p>Involucre 3 mm. or less high.</p>	<p style="text-align: center;"><i>Artemisia alaskana.</i></p> <p>Leaves of the inflorescence elongated, mostly 2 to 6 cm. long.</p> <p>Peduncles 1 to 7 cm. long, the lower ones branched.</p> <p>Involucre about 5 mm. high.</p>
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While the differences here indicated will serve to distinguish the two forms as now represented in herbaria, it will be noticed that they are all based upon characters which in other groups are found to undergo a wide range of variation when a large series of specimens is available for study. There are no constant differences in size or number of flowers in the head. A serious objection to the reduction of *alaskana* to a subspecies of *turczaninoviana* is the relation of the latter to the still older *A. rutaefolia* Stephani and its variation *A. kruhsiana* Besser, both natives of Siberia. These are supposed to differ in their ternate instead of pinnatifid leaves, but this is a variable feature. Besser's plate of *turczaninoviana* (Besser, *Nouv. Mem. Soc. Imp. Nat. Mosc.* 3: plate 1, 1834), as also nearly all authentic specimens at hand, has some leaves which are once or twice ternate, while on the same stems some are first pinnate and with the primary divisions with 2 or 3 lobes. Probably more important are the circumscription of the entire leaf and the shape of the segments. The ultimate divisions are obovate-lanceolate in *rutaefolia*, cuneate in *kruhsiana*, narrowly oblong to linear in *turczaninoviana* and *alaskana*. It is probable that a complete series will ultimately be found. In the meantime, it seems less likely to lead to confusion to retain *alaskana* as a distinct species, while indicating its close relationship to these Siberian forms. It is not directly connected with any other American *Artemisia*.

ECOLOGY AND USES.

Nothing is known of the ecology or uses of this rare species.

10. ARTEMISIA FRANSERIOIDES Greene, *Bull. Torr. Club* 10: 42, 1883. Plate 6. FOREST SAGEWORT.

A perennial herb from short creeping rootstocks, 3 to 10 dm. high, pleasantly fragrant with a sweet heavy odor; stems clustered, erect, simple up to the inflorescence, conspicuously grooved, tomentulose when young but glabrate except towards the summit, reddish tinged at maturity; basal leaves at first forming rosettes but not crowded, petioled (the petioles 1 to 5 cm. long), the blade 4 to 7 cm. long, 3 to 6 cm. wide, suborbicular or ovate in outline, pinnately divided into 5 to 9 elliptic or oblanceolate divisions which are again cleft or divided into oblong or oblanceolate entire or toothed obtuse divisions, glabrous or minutely puberulent above, finely but densely gray-tomentulose beneath; principal and upper leaves like the lower, but becoming gradually smaller, less dissected, and shorter petioled; inflorescence a lax narrow panicle, 15 to 40 cm. long, 1 to 4 cm. broad, the heads notably secund on the branches, rarely reduced and raceme-like; heads heterogamous, nodding, on peduncles 1 to 4 mm. long; involucre hemispheric, 2.5 to 3 mm. high, about 5 mm. broad; bracts 9 to 15, nearly equal, narrowly to broadly elliptic or oblong, very obtuse, brownish or greenish yellow, with a narrow erose scarious border, finely tomentulose, sometimes glabrate; ray-flowers 6 to 13, fertile, corolla narrowly tubular, about 1.5 mm. long, the orifice contracted and scarcely toothed, granulariferous; disk-flowers 45 to 90, fertile, corolla narrowly campanulate, 1.5 to 2 mm. long, 5-toothed, resinous-granulariferous; style-branches truncate, erose at the summit; achenes nearly cylindrical, truncate and with a raised border at the broad summit, faintly nerved, glabrous.

Southern Rocky Mountains at more than middle altitudes (chiefly in the Canadian Zone): Colorado, New Mexico, Arizona, and Chihuahua. Type locality, in deep shady woods of *Pseudotsuga* near the summits of the Pinos Altos Mountains, New Mexico. Collections: Colorado, Rio La Plata, near Parrott City, September, 1875, *Brandegee* (UC); Lake Creek, Sangre de Cristo Range, at 2,750 m. altitude, August, 1874, *Brandegee* (UC); near Pagosa Peak, *Baker 632* (Gr, NY); San Juan Mountains, on both sides of Wolf Creek Pass, *Clements and Hall 11106* and *11114* (UC); Roubadeaux Pass, Rocky Mountains, *Kreuerfeldt* in Gunnison's Expedition 37 (Gr); White Mountains, New Mexico, at 2,300 m. altitude, *Wooton 347* (Gr, NY, UC); type collection, September 15, 1880, *Greene* (Gr, UC, the latter labeled October 14, 1880); Huachuca Mountains, Arizona, *Gooding 855* (NY); Mount Graham, southern Arizona, September, 1874, *Rothrock 753* (Gr); Sierre Madre, Chihuahua, at 3,000 m. altitude, *Pringle 2013* (UC, NY).

RELATIONSHIPS.

In gross aspect *Artemisia franserioides* is more like certain forms of *A. vulgaris* than any other American species. It differs from all of these, however, in the bipinnately divided foliage with obtuse lobes and in the remarkably secund inflorescence, this latter a unique feature in this section of the genus. Its connection with *vulgaris* would naturally be sought through one of the southern subspecies (it has been several times mistaken for *A. vulgaris discolor*), but these all differ in having undergone a considerable reduction in the number of disk-flowers, none having more than about 20 in a head, while *franserioides* has 47 to 90 or more. Since its other characters are also at considerable variance with all of the subspecies of the main branch of *vulgaris*, as diagrammed in figure 9, it is not desirable to invoke reversion to account for this large number. It is more likely that *franserioides* is a descendant from a more primitive type than any of the forms just mentioned. Perhaps this ancestor is not represented by existing species, but it is interesting to note the similarity between *franserioides* and *stelleriana*, as has been already mentioned under the latter species. These two are so closely similar in technical characters and in the obtuse nature of the leaf-lobes that their derivation from the same stock seems quite likely. *A. stelleriana* is native in eastern Siberia where other similar species occur, such as *turczanoviiana* and *rutaefolia*. In any case, the parent form of *A. franserioides* was undoubtedly an inhabitant of the far north, and *franserioides* is therefore to be looked upon as a remnant stranded on the high mountains of the southern United States and northern Mexico.

This species is fairly constant in vegetative characters and in those of the involucre and flowers, as is shown in table 5 (page 72). This is in agreement with most other species of limited distribution and at the same time well separated phylogenetically.

ECOLOGY AND USES.

Artemisia franserioides is a rootstock-perennial, which forms clans in shady openings in forest of aspen or Douglas spruce, where it is associated with *Epilobium spicatum*, *Berberis aquifolium*, *Thalictrum fendleri*, *Fragaria vesca*, *Geranium caespitosum*, and *Artemisia dracunculus*. The flowers bloom from August to late September. No uses are known for this species.

11. ARTEMISIA VULGARIS Linnaeus, Sp. Pl. 848, 1753. Plates 6 to 9. SAGEWORT; MUGWORT.

A perennial herb, sometimes suffruticose at base, from a creeping rootstock, 3 to 20 dm. high, with a peculiar pungent odor; stems either scattered or more commonly growing in close formation, sometimes clustered on short caudex-like rootstocks, erect, simple up to the inflorescence, striate or shallowly grooved, cinereous-tomentose to glabrous, often reddish tinged in age; basal leaves not crowded, petioled, 6 cm. or less long, from shallowly toothed near the summit to twice pinnately dissected, white-tomentose at least beneath; principal and upper leaves exceedingly various in outline and lobing,

from entire to twice dissected, the upper surface glabrous to densely and permanently white-tomentose, the lower surface always white-tomentose; inflorescence paniculate, 10 to 40 cm. long, usually 2 to 8 cm. broad but sometimes reduced to a spike only 1 cm. broad or again with spreading branches and then up to 15 or 20 cm. broad; heads heterogamous, short-peduncled or sessile, nodding or erect; involucre campanulate to ovoid, 3 to 5 mm. high, 2 to 8 mm. broad; bracts 7 to 16, ovate or broadly elliptic, obtuse, with pale or light-brown scarious margins, densely tomentose to glabrous; ray-flowers 4 to 10, fertile, corolla narrowed and irregularly toothed above, 1.5 to 2 mm. long, glabrous or resinous-granuliferous; disk-flowers 3 to 50, fertile, corolla funnelform, 1.5 to 3 mm. long, 5-toothed, glabrous or only resinous-granuliferous; style-branches truncate or obtuse, those of the disk-flowers dilated and erose at summit; achenes ellipsoid, not nerved or angled, glabrous but often resinous-glandular.

Almost throughout North America; common also in the Old World.

SUBSPECIES.

No other *Artemisia* has such a multitude of variations as *A. vulgaris*. Many of these result from environmental influences; in others, individual variation is so great that a taxonomic analysis becomes impossible. The American forms may be assembled into 15 subspecies, as follows:

Key to the Subspecies of Artemisia vulgaris.

- Involucre 4 to 5 mm. high, 4 to 8 mm. broad; disk-flowers 20 to 50. Northwestern forms. Foliage green above, densely white-tomentose beneath; involucre sparsely tomentose, greenish. (a) *tilesi* (p. 72).
- Foliage white-tomentose on both sides, sometimes less densely so above; involucre densely tomentose. (b) *candicans* (p. 73).
- Involucre 3 to 4 mm. high, 2 to 4 mm. broad; disk-flowers 3 to 20, or occasionally to 25 (in *heterophylla* and *longifolia*, and even to 50 in *discolor*, which connects through large-headed forms with *tilesi*).
- Divisions of lower leaves again toothed cleft or lobed; divisions of middle stem-leaves also usually toothed or cleft.
- Leaves green and nearly glabrous above, white-tomentose beneath.
- Primary divisions of leaves 5 to 15 mm. wide, directed forward. (c) *typica* (p. 73).
- Primary divisions of leaves less than 5 mm. wide, spreading.
- Panicle 5 cm. or less broad, compact; heads mostly 20- to 50-flowered. (d) *discolor* (p. 74).
- Panicle 10 to 15 cm. broad, with spreading leafy branches; heads 15- to 20-flowered. (e) *redolens* (p. 75).
- Leaves white-tomentose on both sides. (f) *flodmani* (p. 75).
- Divisions of all the leaves entire or nearly so or leaves themselves entire.
- Leaves ample, principal ones 1 to 2.5 cm. or more wide, with a few prominent lanceolate lobes, varying to entire, upper surface green; involucre 3 to 4 mm. high.
- Disk-flowers 9 to 23; involucre campanulate, 2.5 to 3.5 mm. broad, densely tomentose. (g) *heterophylla* (p. 76).
- Disk-flowers 3 to 7; involucre ovoid, 2 to 2.5 mm. broad, nearly glabrous. (h) *litoralis* (p. 76).
- Leaves narrow, 1 cm. or less wide exclusive of lobes when present, divisions also narrow, upper surface either green or gray-tomentose; involucre rarely over 3 mm. high except in subspecies *gnaphalodes* and *longifolia*.
- Principal leaves entire or variously toothed, cleft, or rarely divided but the lobes not slender and elongated (except in a rare form of *longifolia*, with lobes caudate-attenuate).
- Inflorescence plainly paniculate, 1.5 cm. or more broad.
- Margins of leaves not evenly serrate.
- Upper surface of leaves more thinly tomentose than lower or at length glabrate and green. (i) *ludoviciana* (p. 76).
- Upper surface of leaves densely white-tomentose like lower, tomentum usually persistent (exceptions in *longifolia* are recognized by the caudate leaves).
- Involucre 3 to 3.5 mm. high; leaves not very slender, entire or with comparatively short lobes. (j) *gnaphalodes* (p. 77).
- Involucre about 4 mm. high; leaves slender and elongated, often caudate-attenuate, entire or divided into similarly elongated lobes. (k) *longifolia* (p. 78).
- Margins of leaves evenly serrate. (l) *serrata* (p. 79).
- Inflorescence a narrow spike-like panicle 1 cm. or less broad. A low plant, often woody below, with narrow leaves inclined to be entire or only slightly lobed. (m) *lindleyana* (p. 79).
- Principal leaves mostly divided into slender elongated or linear-filiform lobes 4 mm. or less wide.
- Leaf-lobes mostly 2 to 4 mm. wide. (n) *mexicana* (p. 80).
- Leaf-lobes 0.5 to 1 mm. wide. (o) *wrightii* (p. 80).

11a. *ARTEMISIA VULGARIS TILESII* (Ledebour).—Stems 2 to 6 dm. high, from rootstocks; lower leaves ovate in outline, cut nearly to the midrib into unequal lobes, these often again cleft or toothed; principal leaves ovate or broadly elliptic in outline, 7 to 17 cm. long, 3 to 7 cm. wide, cleft more than half-way to the midrib into unequal segments which are either entire or with a few lobes or teeth, both primary and secondary lobes all pointing forward and acute or acuminate (except in an occasional plant, as in *A. tilesii arctica* Besser, minor variation 84, in which the lobes are broad and obtuse), the leaves of the inflorescence less cut or often entire, all leaves green and glabrous or only puberulent above, densely and permanently white-tomentose beneath, the margins narrowly revolute; inflorescence in the original form dense, spike-like, 0.5 dm. or less long by about 2 cm. broad, commonly overtopped by the leaves, but in the more common form (minor variation 85, *A. tilesii elatior* Torrey and Gray) the inflorescence an elongated panicle 1 to 3 dm. long by 2 to 6 cm. broad and much exceeding the leaves; involucre hemispheric, 4 to 5 mm. high, 5 to 8 mm. broad, glabrous and green or yellowish to puberulent and more or less canescent, or reddish, mostly 30- to 70-flowered. (*A. tilesii* Ledebour, Mem. Acad. St. Petersb. 5: 568, 1805.)

TABLE 5.—Variation in *Artemisia franserioides*.

	Herbarium.	Involucre.		No. of bracts.	Ray-flowers.	Disk-flowers.	Length of disk-corollas.
		Height.	Breadth.				
		mm.	mm.				mm.
Rio La Plata, Southwestern Colo.	172715 UC	3.0	5.0	9 11	6 7	50 54	1.8
Sengre de Cristo Range, Colo.	173319 UC	2.5	4.5	11 9	8 12	60 50	1.8
White Mountains, N. Mex.	135385 UC	3.0	5.0	14 11	8 9	65 48	1.5
Sierra Madre, Chihuahua.	34329 UC	3.0	5.0	14 13	9 6	55 47	1.8
Same collection.	91232 UC	3.2	5.0	11 12	6 6	48 53	2.0
San Juan Mountains, Colo.	205741 UC	3.0	5.0	15 13	13 8	91 61	2.0
Do.	205740 UC	3.0	5.0	14 12	10 11	58 60	1.8
Pinos Altos Mountains, N. Mex. (type collection).....	172707 UC	2.8	5.0	11 12	8 9	59 83	2.0
Average.....		2.9	5.0	11	8	58	1.8

Eastern Siberia and arctic North America east at least to Hudson Bay, south to Montana, northeastern Nevada, and Oregon. Type locality, Kamchatka. Collections: King Point, Arctic America, June 28, 1906, *Lindstrom* (NY); Arctic shore between Mackenzie and Coppermine Rivers, *Richardson* (NY, variation 84 with short, obtuse leaf-lobes, *A. tilesii arctica* Besser); vicinity of Norton Sound, Alaska, 1899, *Rhodes*, *Newhall*, and *Giacomini* (UC); vicinity of Norton Sound, Alaska, 1900, *MacGregor* (UC, typical); St. Paul Island, Bering Sea, *Macoun 94006* (Gr); St. Lawrence Island, Bering Sea, August 15, 1891, *Macoun* (Gr); Arakamtchetchene Island, Bering Straits, 1853-56, *Wright* (Gr); Unalaska, Bering Sea, *Macoun 20625* (NY, type collection of *A. unalaskensis* Rydberg, minor variation 87); Lake Iliamna Region, Alaska, *Gorman 281* (Gr, NY, US, type collection of *A. gormanii* Rydberg, minor variation 24); White Pass, Yukon, *Eastwood 899* (SF); Skaguay, Alaska, *Eastwood 772* (SF); Nome, Alaska, *Blaisdell 80* (NY, UC, minor variation 24, *A. gormanii* Rydberg); Dawson, Canada, *Eastwood 455* (SF); Churchill, Hudson Bay, *Macoun 79263* (Gr, with small heads and narrow inflorescence of minor variation 85, *A. tilesii elatior* Torrey and Gray, but the inflorescence leafy); Chilliwack Valley, British Columbia, *Spreadbrough* (Geological Survey of Canada 76930, NY); Stehekin, eastern Washington, *Griffiths 195* (NY, minor variation 85, *A. tilesii elatior* Torrey and Gray); Chiwankum Lake, Wenatchee Forest, Washington, *Eggleston 13597*

(US); Cascade Mountains, 49° N. lat., Oregon, 1859, *Lyall* (Gr, minor variation 85, *A. tilesi elatior* Torrey and Gray); Wallowa Mountains, Oregon, *Piper 2491* (Gr, same variation); Martin Creek, Elko County, Nevada, *Kennedy 4274* (UC, same variation); Bozeman Cañon, Montana, *Rydberg 2943* (NY, same variation).

11b. *ARTEMISIA VULGARIS CANDICANS* (Rydberg).—Stems 5 to 15 dm. high, leafy, from strong rootstocks, forming small bush-like clumps or thickets; lower leaves obovate or broadly oblong, from deeply cut into spreading lanceolate lobes which are typically again lobed or toothed to shallowly and obtusely few-lobed; principal leaves obovate or oblanceolate or broadly elliptic in outline, 4 to 10 cm. long, 1.5 to 4 cm. wide, pinnatifid or divided into oblong or lanceolate often again cleft segments, these more or less divergent or in some forms the leaves with only a few short coarse teeth or shallow lobes and some nearly entire (minor variation 61, *A. platyphylla* Rydberg), those of the inflorescence less lobed to entire, all leaves densely white-tomentose on both sides, but especially beneath, the margins very narrowly revolute; inflorescence a cylindrical panicle, sometimes divided into short, dense glomerules (the typical form) or more open by the elongation of the peduncles (minor variation 19, *A. floccosa* Rydberg), 2 to 4 cm. broad; involucre hemispheric, about 4 to 5 mm. high, 4 to 7 mm. broad, tomentose, 20- to 50-flowered (*A. candicans* Rydberg, Bull. Torr. Club 24:296, 1897). Montana to western Wyoming, Idaho and eastern Oregon and Washington. Type locality, Little Belt Mountains, Montana. Collections: Type collection, August 18, 1896, *Flodman 882* (NY, US); Lima, Montana, *Rydberg 2942* (NY, US, type of *A. floccosa* Rydberg, minor variation 19); Cliff Creek, Wyoming, August, 1900, *Curtis* (NY); Yellowstone Lake, Wyoming, *Nelson 6612* (R, type of *A. gracilentia* Nelson, minor variation 25); Gilmore, in the Lemhi Range of eastern Idaho, *Hall 11548* (UC); near Prineville, Oregon, *Leiberg 801* (NY); Spokane River at Spokane, Washington, *Elmer 867* (NY, type collection of *A. platyphylla* Rydberg, minor variation 61); same locality, September and October, 1921, *Moore* (UC, a large series of leaf-variations connecting *candicans* and *platyphylla*).

11c. *ARTEMISIA VULGARIS TYPICA*.—Stems erect, 5 to 15 dm. high, from shallow rootstocks, often growing in small clumps; lower leaves obovate, cut nearly to the midrib into unequal lobes with toothed or incised margins; principal leaves obovate, broadly elliptic or oblanceolate in outline, 5 to 10 cm. long, 3 to 7 cm. wide, cleft nearly to the midrib into unequal segments (the terminal much the largest) which are again irregularly toothed or more deeply cleft, the lobes and teeth all pointing forwards and approximate, the leaves of the inflorescence simply pinnatifid to entire, all leaves smooth, green and glabrous or nearly so above, densely and permanently white-tomentose beneath, the margins obscurely revolute; inflorescence an ample branching leafy panicle with ascending branches along which the heads are disposed in glomerules, 4 to 20 cm. broad (occasionally reduced to a single compact panicle about 3 cm. broad); involucre campanulate, 3.5 to 4 mm. high, 2.5 to 3.5 mm. broad, cinerous-tomentose, 15- to 25-flowered. (*A. vulgaris* Linnaeus, Sp. Pl., 848, 1753.) Widely distributed in the Old World; probably introduced in America, where it now grows at many places from Newfoundland to Georgia, Alabama, Wisconsin, Manitoba, and Ontario; also in British Columbia and on Martinique. Type locality: Europe. Collections: Prince County, Prince Edward Island, *Fernald, Long, and St. John 8231* (Gr); Nova Scotia, *Howe and Lang 157* (NY); Birchy Cove, western Newfoundland, on rubbish heaps, *Fernald and Wiegand 4167* (Gr); Yarmouth, St. John River, at St. Francis, Maine, *Fernald 70* (Gr, NY, UC, US); Point Edward, Lake Huron, Ontario, *Macoun 26353* (US); New Haven, Connecticut, September 28, 1886, *Setchell* (UC); near Andover, New Jersey, September 26, 1887, *Britton* (UC); Rochester, New York, August 16, 1917, *House* (Gr); Detroit, Michigan, September 1, 1915, *Chandler* (US); Lake Vadnais, Ramsey County, Minnesota,

Sandberg 711 (US); Brunswick, Glynn County, Georgia, *Harper 1527* (Gr, NY, US); Linnton, Oregon, *J. C. Nelson 837* (Gr); flood plain of the Columbia River, British Columbia, *Shaw 1170* (US); vicinity of St. Pierre, Martinique, *Père Duss 1737, 4075* (US).

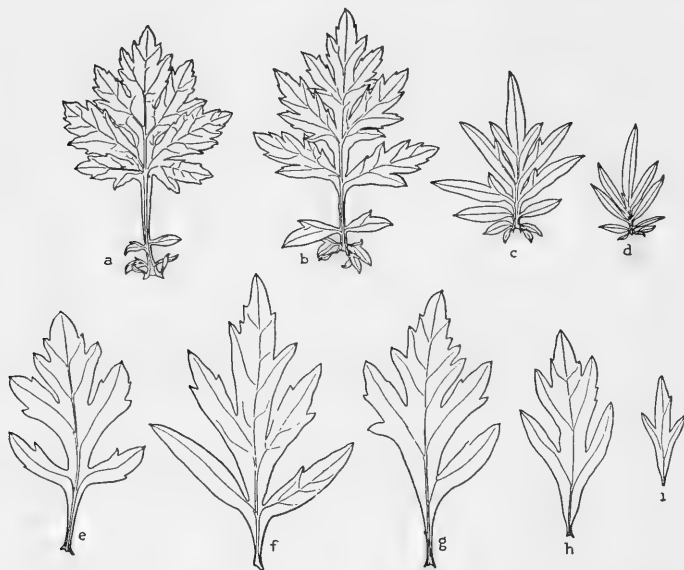


FIG. 7.—A comparison of leaf-outlines of *Artemisia vulgaris typica* and *A. v. heterophylla*: a, b, c, d, leaves of *typica* from one plant in the Botanical Garden of the University of California; e, f, g, h, i, leaves of *heterophylla* from one plant in the Oakland Hills, California. All $\times 0.5$

11d. *ARTEMISIA VULGARIS DISCOLOR* (Douglas).—Stems erect, 2 to 8 dm. high, from horizontal sometimes suffrutescent rootstocks; lower leaves obovate or oblanceolate, cut nearly to the midrib into spreading divisions which are again toothed or more deeply lobed; principal leaves obovate or broadly elliptic in outline, 2 to 8 cm. long, 1 to 4 cm. wide, dissected nearly to the midrib into linear or lanceolate lobes, these either entire, toothed, or lobed, the leaves toward the inflorescence simply cleft or entire, all green and glabrous or glabrate above, densely to sparsely white-tomentose beneath, the margins commonly revolute; inflorescence a compact panicle, sometimes raceme-like, 1 to 3 cm. broad or much broader when composed of racemiform branches; involucre campanulate, 3.5 to 4 mm. high, 2 to 4 mm. broad, very sparsely tomentose and glabrate or glabrous from the beginning, yellowish-green, somewhat shining, 20- to 50-flowered. (*A. discolor* Douglas in Hooker, Fl. Bor. Am. 1: 322, as synonym, 1833; Besser, Bull. Soc. Nat. Mosc. 9: 46, 1836.) The three most notable variations under this subspecies are diagnosed under *A. michauxiana*, page 84, and specimens belonging to them are indicated in the following citations. Saskatchewan and Montana to Colorado, the Sierra Nevada of California, and British Columbia. Type locality, near Spokane and Kettle Falls, Washington. Collections: Lake Louise region, Alberta, *Rosendahl 1097* (NY, minor variation 53, *A. michauxiana* Besser); Bridger Mountains, Montana, August 21, 1902, *W. W. Jones* (DS, UC, US, genuine); Long Baldy, Little Belt Mountains, Montana,

Flodman 881 (NY, US, type collection of *A. graveolens* Rydberg, minor variation 26); Emigrant Gulch, Montana, *Rydberg* and *Bessey 5201* (NY, US, type collection of *A. tenuis* Rydberg, minor variation 80); same locality and collectors, *5201a* (NY, US, type collection of *A. tenuis integerrima* Rydberg, minor variation 81); same locality and collectors, *5203* (Gr, NY, minor variation 30, *A. incompta*, Nuttall); Thornberg's Pass, southern Idaho, *Nuttall* (Gr, Phila, type collection of *A. incompta* Nuttall); Mackay, Idaho, *Nelson* and *Macbride 1521* (DS, Gr, US, minor variation 26, *A. graveolens* Rydberg); Doyle Creek, Wyoming, *Goodding 385* (NY, UC, US, similar variation); Anita Peak, northwestern Colorado, *Goodding 1753* (Gr, NY, minor variation 30, *A. incompta* Nuttall); head of Bullion Creek, Marysvale, Utah, *Jones 5873* (UC, genuine); Humboldt Cañon, West Humboldt Mountains, Nevada, *Heller 10625* (DS, Gr, NY, UC, minor variation 26, *A. graveolens* Rydberg); trail to Mount Whitney, California, *Culbertson 4341* (UC, genuine); near Summit, Placer County, California, *Heller 12898* (SF, UC, minor variation 30, *A. incompta* Nuttall); base of Steins Mountains, Oregon, *Cusick 1990* (UC, form with inflorescence as in genuine *discolor* but foliage as in minor variation 53, *A. michauxiana* Besser; specimens of this and the next in other herbaria are not as here indicated); Steins Mountains, Oregon, *Cusick 1991* (UC, *A. michauxiana* Besser, both as to foliage and inflorescence); fissures of dry rocks near the Kettle Falls and sources of the Columbia River, 1826, *Douglas* (NY, from type of *A. michauxiana* Besser, minor variation 53); type collection, *Douglas* (NY, tracing and fragment from the type); west of Skagit River, British Columbia, *Macoun 769245* (NY, minor variation 53, *A. michauxiana* Besser).

11e. *ARTEMISIA VULGARIS REDOLENS* (Gray).—Stems erect, 4 to 8 dm. high, from rootstocks; lower leaves oblanceolate or obovate, twice pinnately dissected; principal leaves obovate or broadly elliptic in outline, 3 to 5 cm. long, nearly as wide, dissected to the midrib into spreading lobes, these commonly parted into linear spreading lobes or at least toothed, the leaves of the inflorescence simply parted or entire, all sparsely tomentulose or glabrate above and moderately white-tomentose beneath, the margins narrowly revolute; inflorescence an open leafy panicle with ascending branches, 10 to 15 cm. broad; involucre campanulate, 3 to 3.5 mm. high, 3 mm. broad, sparingly silky-tomentose, 15- to 20-flowered (*A. redolens* Gray, Proc. Am. Acad. 21:393, 1886). Chihuahua, Durango, and probably in other of the States of northern Mexico. Type locality, near Chihuahua City, on cool slopes under cliffs. Collections: Type collection, *Pringle 296* (Gr, NY); same locality, *Pringle 1059* (NY, UC); barranca below Sandia Station, Durango, *Pringle 13535* (Gr, US).

11f. *ARTEMISIA VULGARIS FLODMANI* (Rydberg).—Stems erect, 3 to 5 dm. high, from branched rootstocks; lower leaves obovate or oblanceolate, deeply cut into spreading divisions which are again toothed or lobed; principal leaves (as far as known) obovate in outline, 3 to 7 cm. long, 2 to 4 cm. wide, dissected nearly to the midrib into lanceolate lobes, these mostly again cleft, the uppermost leaves entire or simply cleft, all with a persistent tomentum on both faces, but this denser and whiter beneath, the margins revolute; inflorescence a rather dense leafy panicle 1 to 2 cm. broad (broader in one of the type specimens, but this due to injury to the central axis); involucre campanulate, about 3 mm. high and broad, gray with a loose persistent tomentum, about 20- to 30-flowered. (*A. flodmani* Rydberg, N. Am. Fl. 34:276, 1916.) Mountains of Montana, Idaho, and western Wyoming, doubtful specimens also from northeastern Utah and eastern Oregon; rare. Type locality, Little Belt Mountains, Montana, 9 miles east of Barker. Collections: Type collection, *Flodman 883* (NY); Coal Creek, Teton Mountains, Wyoming, near timber-line, *Hall 11444* and *11445* (UC); same, but at 2,250 m. altitude, in the lodgepole forest, *Hall 11438* (UC); Twilight Gulch, Owyhee County, Idaho, *Macbride 486* (UC).

11g. *ARTEMISIA VULGARIS HETEROPHYLLA* (Nuttall).—Stems 3 to 15 or even 20 dm. high, from horizontal rootstocks, often in thicket formation on good soil, or scattered; lower leaves oblanceolate or obovate, coarsely few-lobed; principal leaves oblanceolate or broadly elliptic in outline, often somewhat spatulate, long-acute, 7 to 15 cm. long, 1.5 to 5 or 10 cm. wide, saliently cut-toothed or cleft, the lobes few, lanceolate, acute, and forward-pointing, or sometimes the leaves mostly entire (variations illustrated on p. 41), and those of the inflorescence usually so and much reduced, all sparsely tomentulose and green above, densely white-tomentose beneath, the margins obscurely revolute or plane; inflorescence an elongated pyramidal panicle, 2 to 8 cm. broad; involucre campanulate, 3 to 4 mm. high, 2.5 to 3.5 mm. broad, gray-tomentose, 15- to 30-flowered (*A. heterophylla* Nuttall, Trans. Am. Phil. Soc. II, 400, 1841). Saskatchewan and Idaho to the Pacific Coast from British Columbia to Lower California; the most abundant subspecies in Oregon and California. Type locality, "Rocky Mountains by streams." Collections: Type collection, *Nuttall* (Gr); near Red Lodge, Montana, *Rose 664* (US); Lake Pend d'Oreille, northern Idaho, *Sandberg 822* (US); Tamarack, Washington County, Idaho, *Clark 227* (UC); West Klickitat County, Washington, *Suksdorf 871* (UC); Wawawai, Snake River Cañon, Washington, *Piper 6466* (US, type of *A. atomifera* Piper, minor variation 4); Grants Pass, Oregon, July 14, 1887, *Howell* (UC); damp land near Yreka, northern California, *Butler 1798* (UC); valley of the Van Duzen River, California, *Tracy 3976* (UC); Chico, California, *Heller 11135* (Gr, NY, UC, US); Red Clover Valley, northern Sierra Nevada Mountains, California, *Heller and Kennedy 8876* (UC, NY, US, a form common in the mountains, with thin and rather narrow leaves; intermediate to subspecies *ludoviciana*); Pacific Grove, Monterey County, California, *Heller 7195* (DS, UC); Clear Creek Cañon, western Nevada, *Baker 1458* (Gr, NY, UC); near Mesmer, Los Angeles County, California, *Abrams 2955* (DS, Gr, NY, UC, US); Avalon, Santa Catalina Island, September 1897, *Trask* (US).

11h. *ARTEMISIA VULGARIS LITORALIS* (Suksdorf).—Stems 6 to 15 dm. high (or more), from large sometimes suffrutescent rootstocks; lower leaves oblanceolate or obovate, coarsely few-toothed or few-lobed; principal leaves broadly lanceolate or broadly elliptic in outline, sometimes nearly oblanceolate, gradually acute, 7 to 15 cm. long, 1.5 to 3 cm. wide, with a few prominent teeth or short lobes, these lanceolate acute and forward-pointing, some of the leaves commonly entire, especially the narrow elongated ones of the inflorescence, all very sparsely tomentulose and green above, densely white-tomentose beneath, the margins very narrowly revolute or plane; inflorescence an elongated leafy panicle, 3 to 9 cm. broad; involucre ovoid, 3 to 4 mm. high, 2 to 2.5 mm. broad, obscurely tomentulose or apparently glabrous, yellowish-green and shining, 8- to 12-flowered. (*A. vulgaris* var. *litoralis* Suksdorf, Deut. Bot. Monats. 18:98, 1900.) Along the Pacific Coast from British Columbia to Cape Mendocino, California; common on the bluffs of Puget Sound. Type locality, stony sea-beaches near Fairhaven, Washington. Collections: Chilliwack Valley, British Columbia, *Macoun 26352* (Gr); Vancouver Island, June 28, 1887, *Macoun* (US); Chuckanut Bay, Washington, July 5, 1890, *Suksdorf 980* (NY, UC, US, apparently the type collection); Fairhaven, Washington, *Piper 2808* (Gr); east of Scenic, Washington, *Otis 804* (SF); Quiniault Valley, Washington, *Conard 260* (Gr); mouth of the Umpqua River, Oregon, June, 1887, *Howell* (NY, UC, US); Shelter Cove, Humboldt County, California, *Bolander 6482* (Gr); near Scotia, Humboldt County, California, *Davy and Blasdale 5544* (UC); Cape Mendocino, California, *Tracy 4973* (UC).

11i. *ARTEMISIA VULGARIS LUDOVICIANA* (Nuttall).—Stems erect, 3 to 10 dm. high, often crowded on the rootstocks or scattered; lower leaves oblanceolate, lobed or entire; principal leaves linear or oblanceolate in outline, 3 to 9 cm. long, 0.5 to 2 cm. wide,

mostly cleft into few divergent linear-lanceolate acute lobes, sometimes mostly entire or only dentate, the uppermost entire, all gray and loosely floccose or green and nearly glabrous above, white-tomentose beneath (see note under citation of type specimen); inflorescence an elongated narrow compact panicle, 1.5 to 3 cm. broad or sometimes leafy, more branched, and then up to 10 cm. broad; involucre campanulate, about 3 mm. high, 2.5 to 3 mm. broad, more or less tomentose (green and nearly glabrous in form known as *A. potens*), 12- to 20-flowered. (*A. ludoviciana* Nuttall, Genera 2:143, 1818.) Abundant and widely distributed in western North America: Montana, and perhaps farther north, to Wisconsin, Kansas, Texas, Chihuahua, California, Washington, and Idaho; introduced in New England (Collins, Rhodora 1:47, 1899; Fernald and Wiegand, Rhodora 12:144, 1910). Type locality, on the banks of the Mississippi River near St. Louis. Collections (mostly with leaves much greener above than in the type): Wild Horse Island, Montana, *Butler 469* (NY); Fort Howard, Wisconsin, September 15, 1878, *Schuette* (UC, intermediate to subspecies *gnaphalodes*); Woods Creek, Wyoming, *Nelson 8045* (UC); McIntyre Creek, Larimer County, Colorado, *Osterhout 2242* (Osterhout Hb, R, NY, type collection of *A. silvicola* Osterhout, minor variation 76); Idaho Springs, Colorado, *Shear 4617* (NY, type of *A. cuneata* Rydberg, minor variation 10); near Ouray, Colorado, *Underwood and Selby 74* (NY, type of *A. underwoodi* Rydberg, minor variation 88); Riley County, Kansas, *Norton 300* (NY); Courtney, Missouri, *Bush 6509* (Gr, NY); type collection, "St. Louis," *Nuttall* (Phila., leaves more tomentose above than in most specimens here cited, but the tomentum much less dense than on the under surface where it is closely felted and white); Ottawa, Oklahoma, *Stevens 2500* (Gr); Weatherford, Texas, *Tracy 8135* (NY); near Colonia Garcia, Chihuahua, *Townsend and Barber 326* (NY); Cananea, Sonora, *Donnelley 44* (UC); near Pecos, San Miguel County, New Mexico, *Standley 5118* (NY); Fort Lowell, Arizona, *Thorner 50* (UC, NY); Bear Valley, San Bernardino Mountains, California, *Abrams 2823* (Gr, NY); trail to Mount Whitney, California, *Culbertson 4341* (NY, minor variation 62, *A. potens* Nelson); Charleston Mountains, Nevada, *Heller 11086* (NY, same variation); Marysvale, Utah, *Jones 5846* (UC, NY); Columbia River, Washington, *Suksdorf 1610* (UC).

11j. ARTEMISIA VULGARIS GNAPHALODES (Nuttall).—Stems erect, 3 to 10 dm. high, from creeping rootstocks; lower leaves oblanceolate or somewhat cuneate to linear, entire or often with a few teeth or even pinnately cleft into lanceolate lobes; principal leaves linear to broadly elliptic in outline, 3 to 10 cm. long, 0.5 to 3 cm. wide, mostly entire in the typical form but varying to dentate, cleft, or even divided into several linear-lanceolate acute ascending lobes, those of the inflorescence chiefly entire and narrow, all leaves densely permanently and equally white-tomentose on both sides, the margins essentially plane (connects with subspecies *longifolia* through forms with leaves entire and broad but glabrate and through others with leaves narrow but permanently tomentose, while the form with prominent short and broad leaf-lobes is *A. brittoni* Rydberg, minor variation 6); inflorescence an elongated panicle, dense, 2 to 5 cm. broad; involucre campanulate, 3 to 3.5 mm. high, about 3 mm. broad, densely tomentose, 15- to 30-flowered (lower counts probably due to the falling out of some of the flowers). (*A. gnaphalodes* Nuttall, Genera 2:143, 1818.) Ontario and Michigan to Missouri, Texas, Coahuila, California, British Columbia, and Saskatchewan; introduced in Pennsylvania and along the Atlantic Coast from Quebec to Massachusetts. Type locality, dry savannahs about Green Bay, Lake Michigan. Collections: Newbury, Massachusetts, introduced, August 7, 1899, *Williams* (Gr); Point Edward, Lake Huron, Ontario, *Macoun 2635* (NY, US); Lake Mendota, Madison, Wisconsin, August 24, 1893, *Sudworth* (NY, US); Oregon, Ogle County, Illinois, September 2, 1886, *Waite* (US); Moscow, Iowa, *Somes 3707* (US); near Thedford, central Nebraska, *Rydberg 1725* (Gr, US); Black Hills Forest, South Dakota, *Murdoch 4305* (Gr); Centennial, Wyoming,

Gooding 2119 (Gr, NY, UC, US); Red Desert near Creston, Wyoming, *Nelson 4426* (R, type of *A. rhizomata pabularis* Nelson, minor variation 73); Laramie, Wyoming, *Nelson 6896* (UC, minor variation 72, *A. rhizomata* Nelson); Golden, Colorado, September 6, 1919, *Hall* (Cl, includes several forms of leaves, some representing *A. brittoni* Rydberg, see fig. 12, p. 95); Gunnison, Colorado, *Baker 573* (UC, Gr, NY, minor variation 65, *A. pudica* Rydberg); McPherson, Kansas, September 5, 1890, *Kellerman* (US); Courtney, Missouri (introduced?), *Bush 5858* (Gr, NY, US); Woods County, Oklahoma, *Stevens 2869* (Gr); Colorado, Texas, *Tracy 8141* (Gr, NY, type collection of *A. texana* Rydberg, minor variation 82); vicinity of Saltillo, Coahuila, *Palmer 286* (Gr, NY, UC, US, minor



FIG. 8.

Portions of the type specimens of *Artemisia vulgaris ludoviciana* and *A. v. gnaphalodes*: a to e, from tracings of the type of *ludoviciana*; f, from a tracing of the type of *gnaphalodes*; both types in the Herbarium of the Academy of Natural Sciences of Philadelphia. The foliage of a to e is slightly greener above than below, that of f is equally white-tomentose on both faces. All $\times 1$.

variation 6, *A. brittoni* Rydberg, so determined by Rydberg); Doña Ana County, New Mexico, *Wooton 504* (NY, US, type collection of *A. albula* Wooton, minor variation 1); Humboldt County, Nevada, *Torrey 249* (Gr); Tantillas Cañon, San Diego County, California, 1875, *Palmer* (Gr, minor variation 1, *A. albula* Wooton); San Jacinto Cañon, southern California, *Johnston 1847* (NY); Davis Creek, northeastern California, July, 1895, *Austin* (UC); Spokane, Washington, *Sandberg 900* (NY, minor variation 67, *A. purshiana* Besser); Columbia River, Washington, *Scouler 234* (NY, type of *A. obtusa* Rydberg, minor variation 58); Nampa, Idaho, *Nelson* and *Macbride 1081* (DS, Gr, NY, UC, minor variation 67, *A. purshiana* Besser); Beavermouth, British Columbia, *Shaw 1153* (Gr); Bozeman, Montana, *Blankinship 255* (US); Indian Head, Assiniboia, *Macoun 10984* (US); Sarcee Reserve, Alberta, *Goddard 492* (UC).

11k. *ARTEMISIA VULGARIS LONGIFOLIA* (Nuttall).—Stems erect, 3 to 10 dm. high, often clustered on a strong woody rootstock; lower leaves narrowly lanceolate or slightly oblanceolate, sometimes with a few prominent teeth or lobes; principal leaves linear or very narrowly lanceolate, commonly caudate-attenuate, 5 to 15 cm. long, 0.2 to 0.5 cm. wide, entire (apparently a form with slender lobes grows on gumbo soil, see minor variation 13, *A. falcata* Rydberg), those of the inflorescence linear-attenuate and much reduced, all leaves loosely floccose and glabrate above (in the typical form), white-tomentose beneath, the margins strongly revolute; inflorescence a strict panicle, 1 to 8 cm. broad; involucre

campanulate, about 4 mm. high, 3 to 4 mm. broad, densely tomentose, sometimes a little glabrate, 20- to 30-flowered. (*A. longifolia* Nuttall, Genera 2:142, 1818.) South-central Canada to Nebraska, Colorado, Wyoming, and Montana; also west to Oregon and Washington, according to North American Flora. Type locality, rocky situations on the banks of the Missouri River. Collections: Saskatchewan, 1858, *Bourgeau* (Gr, a form with leaves green above and a very open inflorescence); vicinity of Rosedale, Alberta, *Moodie 1097* (DS, Gr, SF, NY); Fort Pierre, Nebraska, July, 1853, *Hayden Survey* (NY); Lake De Smet, Wyoming, *Nelson 8545* (UC, NY, US); Washington County, South Dakota, August, 1886, *Hatcher* (UC); plains, Colgate, near Glendive, eastern Montana, *Sandberg 1011, 1014* (Gr, NY, SF, US).

11l. ARTEMISIA VULGARIS SERRATA (Nuttall).—Stems strictly erect, 10 to 30 dm. high, from rootstocks; lower leaves lanceolate, closely and rather evenly serrate (for deviations see fig. 13); principal leaves lanceolate or linear-lanceolate, acuminate, 7 to 15 cm. long, 1 to 2.5 cm. wide, serrate like the lower, only the very tip and about 1 cm. near the base entire, the teeth 2 mm. or less long, those of the inflorescence gradually reduced, narrower and mostly entire, all of the leaves green and glabrous above, white-tomentose beneath, the margins sometimes obscurely revolute; inflorescence a leafy panicle, 5 to 15 cm. broad; involucre narrowly campanulate, 2.7 to 3 mm. high, about 2 mm. broad, more or less floccose, 12- to 20-flowered. (*A. serrata* Nuttall, Genera 2:142, 1818.) Restricted to the central and northern portions of the Mississippi Valley, except as naturalized further east, as in northern New York; Wisconsin to northern Illinois, Kansas (?), Iowa, North Dakota, and Minnesota. Type locality, near the Prairie du Chien, on the banks of the Mississippi River. Collections: Upper Louisiana, *Nuttall* (Phila, one of the type collections); Taylors Falls, Minnesota, August, 1892, *Taylor* (DS, NY, UC, US); Glenwood, Minnesota, August, 1891, *Taylor* (UC, typical in every detail except that the leaves are entire); Dane County, Wisconsin, *Wibbe* (US); prairies of Winnebago County, Illinois, August, 1859, *Bebb* (Gr); Fayette County, Iowa, *Fink 404* (US).

11m. ARTEMISIA VULGARIS LINDLEYANA (Besser).—Stems erect, 1.5 to 4 dm. high, usually several from a woody rootstock; lower leaves oblanceolate, toothed or lobed; principal leaves linear or oblanceolate in outline, 2 to 5 cm. long, 0.4 to 1.5 cm. wide, sharply toothed or cleft into short divergent lanceolate lobes, the upper ones mostly entire, loosely floccose or green and glabrate above, white-tomentose beneath; inflorescence a short and narrow raceme-like panicle (sometimes completely racemose, sometimes with a few erect racemiform branches), 0.5 to 2 cm. broad; involucre campanulate, 3 to 4 mm. high, 2 to 3 mm. broad, tomentose, but the tomentum often thin and partly deciduous; heads 18- to 30-flowered. (*A. lindleyana* Besser, in Hooker, Fl. Bor. Am. 1:322, 1833.) West of the Rocky Mountains from Montana to Utah, Arizona, eastern California, Washington, and Idaho. Type locality, northwest coast of America. Collections: Type collections, northwest America, *Douglas* (Gr, ex-herb. Lindley, fragments of *legitima*, *brevifolia*, *subdentata*, *coronopus*, leaves entire to once-cleft, minor variations 38 to 41); Lewis River, Rocky Mountains, *Nuttall* (Gr, Phila, type of *A. pumila* Nuttall, minor variation 66); head of dry wash, Abajo Mountains, southeastern Utah, *Rydberg* and *Garrett 9615* (NY); Holbrook, Arizona, October 9, 1897, *Zuck* (NY, inflorescence racemose-spicate but otherwise like minor variation 76, *A. silvicola* Osterhout); Sequoia National Park, southern Sierra Nevada, California, *Davidson 2057* (UC); Fish Hook Ferry, eastern Oregon, *Leiberg 935* (NY, type of *A. leibergeri* Rydberg, minor variation 35); banks of the Columbia River, Washington, *Suksdorf 1611* (UC, Gr, NY); Clarks Fork Valley, Idaho, *Leiberg 1567* (UC); near Thompson Mountain, northern Idaho, *Leiberg 1610* (NY, inflorescence inclined to branch).

11n. *ARTEMISIA VULGARIS MEXICANA* (Willdenow).—Stems erect, 3 to 8 dm. high, from slender herbaceous rootstocks, more densely leafy than in most other varieties; lower leaves narrowly oblanceolate, cleft into several very slender lobes; principal leaves linear or the outline often oblanceolate because of the divergent lobes, 3 to 10 cm. long, only 0.2 to 0.4 cm. wide when entire but up to 5 cm. wide across the spreading lobes when these are present, typically cleft nearly to the midrib into elongated linear acute lobes 2 to 4 mm. wide, those of the inflorescence chiefly entire, all leaves green and lightly tomentose or glabrate above, densely white-tomentose beneath, the margins narrowly revolute; inflorescence a leafy panicle, 3 to 8 cm. broad; involucre campanulate, 2.5 to 3 mm. high, about 3 mm. broad, or 4 mm. high and broad in form known as *A. ghiesbreghtii* Rydberg, gray-tomentose, perhaps sometimes only sparingly so, 15- to 30-flowered. (*A. mexicana* Willdenow; Sprengel, Syst. 3:490, 1826.) Dry plains from Missouri, southern Colorado, and Texas to New Mexico and probably Arizona, thence south and apparently common to San Luis Potosi, Durango, Jalisco, Vera Cruz, Yucatan (according to Millspaugh, Field Mus. Nat. Hist. Bot. 1:323, 1896), Chiapas, and probably into Guatemala. Type locality, Mexico. Collections: Greenwood, Missouri, *Bush 412* (Gr, NY, US, minor variation 36, *A. lindheimeriana* Scheele); Wichita, Kansas, *Poole 1300* (US, same variation); foot of Spanish Peaks, Colorado, September 3, 1873, *Greene* (Gr); Naturita, southwestern Colorado, *Payson 590* (Gr); White Mountains, New Mexico, *Wooton 344* (Gr, UC, US); Black Range, New Mexico, *Metcalfe 1248* (NY, type of *A. neomezicana* Greene, minor variation 57); Weatherford, Texas, *Tracy 8135* (Gr); near Chihuahua City, Chihuahua, *Pringle 290* (NY, type of *A. revoluta* Rydberg); near San Julian, Chihuahua, *Nelson 4939* (Gr, US); Sierra des Parras, Coahuila, *Purpus 4659* (UC, condensed form with short leaves and narrow inflorescence; perhaps nearer subspecies *ludoviciana*); near Durango, *Palmer 907* (Gr, UC, US); Alvarez, San Luis Potosi, *Palmer 59* (Gr, UC, US); Tula, Hidalgo, *Pringle 9848* (Gr, NY, US); slopes of barranca of Guadalajara, 1,380 m., Jalisco, *Pringle 8765* (Gr, UC, US); Eslava, Federal District, Mexico, *Pringle 11820* (Gr, US, heads exceptionally large, minor variation 21, *A. ghiesbreghtii* Rydberg); Esperanza, Puebla, *Arsene 2113* (US); Orizaba, *Mueller 1868* (NY, type of *A. muelleri* Rydberg, minor variation 55).

11o. *ARTEMISIA VULGARIS WRIGHTII* (Gray).—Stems erect, 3 to 6 dm. high, from short creeping rootstocks; lower leaves of sterile shoots elliptic or lanceolate, entire, densely white-tomentose on both sides; lower leaves of flowering stems usually cleft or divided into linear-filiform lobes; principal leaves oblanceolate in outline, 1 to 5 cm. long, 0.5 to 1 cm. wide including spread of the lobes, some of upper ones entire but mostly cleft or divided into linear-filiform acute lobes, these 0.5 to 1 mm. wide, those of the inflorescence reduced but similar, all leaves white-tomentose on both sides (minor variation 8, *A. carruthi* Wood), or greener and glabrate above (typical), those of the inflorescence reduced but similar, the margins closely revolute; inflorescence a close panicle, 1 to 3 cm. broad, or the individual panicles so arranged as to form a more compound and much broader inflorescence, or sometimes reduced to a nearly simple raceme; involucre campanulate, 3 to 3.3 mm. high, 2 to 2.5 mm. broad (larger in forms known as *A. pringlei* and *A. prescottiana*), pale, tomentulose, 10- to 35-flowered. (*A. wrightii* Gray, Proc. Am. Acad. 19:48, 1883.) Kansas to western Texas, Chihuahua, Arizona, Utah, and central Colorado; an aberrant type reported from the Columbia River (minor variation 63, *A. prescottiana* Besser); introduced into Missouri and Rhode Island. Type locality, Santa Rita del Cobre, New Mexico, according to Rydberg. Collections (many are the form known as *A. carruthi* Wood, i. e., minor variation 8); Pawtucket, Rhode Island, on wastes, October, 1898, *McCudden* (Gr); Lane County, Kansas, *Hitchcock 302* (Gr, NY, US, apparently the type collection of *A. kansana* Britton, minor variation 33); Amarillo,

Texas, *Ball 1141* (US); near Dulce, New Mexico, *Standley 8270* (US); type collection, *Wright 1279* (NY); plains near the City of Chihuahua, Chihuahua, *Pringle 625* (Gr, type of *A. pringlei* Greenman, minor variation 64); Chiricahua Mountains, Arizona, *Blumer 1794* (DS, Gr, NY, US); Flagstaff, Arizona, September 2, 1889, *Sheldon* (UC); along San Juan River, southeastern Utah, *Rydberg* and *Garrett 10006* (NY, UC); Marshall Pass, Colorado, *Baker 879* (NY, UC, US); Black Cañon, Colorado, *Baker 698* (Gr, UC, US, minor variation 5, *A. bakeri* Greene).

MINOR VARIATIONS AND SYNONYMS.

1. *ARTEMISIA ALBULA* Wooton, Contr. U. S. Nat. Herb. 16:193, 1913.—A form of arid situations in the southern Rocky Mountain States and northern Mexico, here included under *A. vulgaris gnaphalodes*, but with distinctive habit, very narrow leaves, widely branched inflorescence, and exceptionally small heads, the involucre 3 mm. high. The following collections belong here: Organ Mountains, Doña Ana County, New Mexico, at 1,400 meters altitude, *Wooton 504* (NY, US, type collection); near Fort Huachuca, Arizona, *Lemmon 2783*½ (Gr); Limestone Hill, Cochise County, Arizona, *Eggleston 10966* (Gr); Tantillas Cañon, San Diego County, California, 1875, *Palmer* (Gr); Sierra en Media, Chihuahua, *Nelson 6488* (Gr).

2. *A. ARACHNOIDEA* Sheldon, Bull. Torr. Club, 30:310, 1903.—A variation intermediate between *A. vulgaris tilesi* and *A. v. heterophylla*, with heads about 4 mm. high and with 25 to 35 flowers. Originally distinguished from *tilesi* by the "subsecund loose inflorescence and peculiar involucre bracts." The involucre is subtended by a few minute bracts, as is common in *A. vulgaris*, and is arachnoid-pubescent as occurs also in *tilesi*. The lower leaves are mostly wanting in the specimens distributed under the type number, but the remaining ones show deep lobes suggestive of both *tilesi* and *heterophylla*. Type locality, sandy banks of the Columbia River, 1 mile west of Vancouver, Washington.

3. *A. ARGOPHYLLA* Rydberg, N. Am. Fl. 34:274, 1916.—Intermediate between *A. vulgaris gnaphalodes* and *A. v. candicans*. The type specimen is like the former, but very robust and with large heads, the involucre fully 4 mm. high. Type locality, near Long's Peak, Colorado. Specimens referred here come also from as far west as northern California and eastern Washington.

4. *A. ATOMIFERA* Piper, Contr. U. S. Nat. Herb. 11:588, 1906.—A form or race of *A. vulgaris heterophylla*, but the upper surface of the leaves, as also the involucre, speckled with numerous white resinous atoms. A series of specimens gathered with the type exhibit a wide variation in the leaves from entire to pinnately divided. Type locality, Wawawai, Washington.

5. *A. BAKERI* Greene, Pl. Baker 3:31, 1901.—Perhaps best referred to *A. vulgaris wrighti* because of the very narrow leaf-lobes, none of which reach 2mm. in breadth, but intermediate to subspecies *ludoviciana* through its wider-leaved forms. The foliage is green and glabrate above, greener than in typical *A. wrighti*, from which it also differs in the mostly nodding and slightly larger heads. The position assumed by the heads is not considered important. Plants with gray foliage and all other characters of the *carruthi* form of subspecies *wrighti* sometimes have heads as uniformly nodding as in *bakeri*, for example, Pagosa Springs, southern Colorado, *Baker 749* (UC). The type was collected by Greene in the cañon of the Gunnison, near Cimarron, Colorado. This has not been seen, but the above notes are based upon other specimens cited by Greene, namely, Black Cañon, Gunnison Watershed, Colorado, *Baker 698* (Gr, UC, US).

6. *A. BRITTONI* Rydberg, Bull. Torr. Club 32:129, 1905.—A form of *A. vulgaris gnaphalodes* in which the heavily tomentose leaves are parted into 3 to 5 short and rather broad divergent lobes. This is one of the extreme types of lobing and therefore appears very distinct when compared with normal *gnaphalodes*. A gradation in the character as it occurs at Golden, Colorado, the type locality, is shown in figure 12, page 95. (See also under *A. diversifolia* in this list.)

7. *A. CANDICANS* Rydberg, Bull. Torr. Club 24:296, 1897.—*A. vulgaris candicans*.

8. *A. CARRUTHI* Wood, in Carruth, Trans. Kans. Acad. Sci. 5:51, 1877.—The oldest name for *A. vulgaris wrighti*, but not well established. *A. carruthi* is the state or form in which the leaves are about equally tomentose on the two sides. In habit, width of leaf and lobes, inflorescence, and size of heads and flowers the two are exactly alike. The difference in the amount of tomentum on the upper surface of the leaves is not so significant as the difference between certain other pairs of forms here given subspecific rank, for example, *gnaphalodes* and *ludoviciana*, not only because the leaves are narrower and the difference therefore less noticeable, but also because of the presence of all degrees of variation in plants growing very near each other. This intergradation has been noted at a considerable number of stations, especially in southern Colorado and northern New Mexico. At some places the amount of tomentum almost certainly depends upon ecologic conditions. Leaves which are perfectly glabrous on the upper surface have not yet been found. Those of sterile shoots are always densely white-tomentose on both surfaces, entirely regardless of the amount of tomentum on the foliage of flowering stems. Thus, there is often an abrupt transition from the white foliage on the short innovations clustered about the base of the plant to the gray or greenish foliage of the middle and upper portions. It should be noted

that when Gray proposed his *A. wrightii* he did not intend to establish a species distinct from *A. carruthi*, the earlier publication of which he apparently overlooked. The type of *A. carruthi* came from Kansas.

9. *A. COLORADENSIS* Osterhout, Bull. Torr. Club 27:506, 1900.—*A. vulgaris wrightii*. The leaf-segments are unusually wide and revolute-margined. If flattened out they would be about 3 mm. wide, thus much resembling those of some forms of subspecies *ludoviciana*, although more densely gray-tomentose on the upper surface. Grows in dry, rocky places, which suggests that it may be only a xerophytic ead of the cut-leaved form of *ludoviciana* or of *gnaphalodes*. Type locality, near Dale Creek, Larimer County, Colorado.

10. *A. CUNEATA* Rydberg, N. Am. Fl. 34:269, 1916.—A striking foliage-form of *A. vulgaris ludoviciana*. The principal leaves are cuneate-obovate, 2 to 4 cm. long, about 1 cm. wide, and with a few salient teeth around the wide summit. Type locality, Idaho Springs, Colorado. Rare, but known from as far west as Fishhook Ferry, Franklin County, Oregon, *Leiberg 937* (Gr.).

11. *A. CUNEIFOLIA* Scheele, Linnaea, 22:162, 1849.—Not *A. cuneifolia* De Candolle, 1837. The types not seen. Apparently a tall, very erect, and rigid small-headed form of *A. vulgaris mexicana*. Type locality, high places on the prairie near New Braunfels, Texas.

12. *A. DISCOLOR* Douglas, in Hooker, Fl. Bor. Am. 1:322, as synonym, 1833; Besser, Bull. Soc. Nat. Mosc. 9:46, 1836.—*A. vulgaris discolor*.

13. *A. DISCOLOR INCOMPTA* Gray, Syn. Fl. 1²:373, 1884.—Based upon *A. incompta* Nuttall, here considered as a trivial form of *A. vulgaris discolor*. (See *incompta* of this list.)

14. *A. DIVERSIFOLIA* Rydberg, Bull. Torr. Club 28:20, 1901.—When restricted to the form originally described, this is the same as *A. vulgaris gnaphalodes*, except that the lower leaves are pinnately cleft into 3 to 5 narrowly lanceolate acuminate lobes which are directed forward. While probably of *gnaphalodes* origin, it may be compared with *ludoviciana*, of which it is possibly an expression with both faces of the leaves about equally tomentose. In the North American Flora (34:275, 1916) Rydberg extends the description to include anything in the way of leaves from pinnately cleft to "the upper or rarely all entire." Thus "*A. diversifolia*" becomes a convenient receptacle for a considerable number of leaf-forms, all of which are here assigned to subspecies *gnaphalodes*. Some of these come very close to the minor variation called *A. brittoni* Rydberg. If one is to use the cut of leaf as a specific character, as is sometimes done for segregates of both *gnaphalodes* and *ludoviciana*, consistency would demand that it be applied also in connection with these forms conveniently assembled under *diversifolia*. This, however, is an extreme to which no one, apparently, is willing to go. Variations in cut of leaf on plants from the same area are shown in the figures on page 95. Type locality, Priest River, Idaho.

15. *A. DOMINGENSIS* Urban, Symb. Ant. 7:430, 1912.—A form of *A. vulgaris* perhaps nearest to *typica*. The type specimen has not been seen, but Doctor Urban has kindly sent a fragment from the Herbarium of Krug and Urban (No. 1534) which he considers to be the same. This was collected in the mountains of Haiti, November, 1896. The leaves are small and apparently without stipule-like lobes at base, but otherwise as in *typica*, as far as the scant material indicates. The involucre is 2 mm. high, 2.6 mm. broad, and of about 15 bracts. The only head dissected had 28 ray-flowers and 15 disk-flowers. The large number of the former is remarkable. The type locality is near Constanza, Santo Domingo.

16. *A. DOUGLASIANA* Besser, in Hooker, Fl. Bor. Am. 1:323, 1833.—*A. vulgaris heterophylla*. The form with nearly entire leaves. Type locality, Northwest America. (See discussion under *A. hookeriana* of this list.)

17. *A. ELATIOR* Rydberg, Mem. N. Y. Bot. Gard. 1:430, 1900.—Based upon *A. tilesii elatior*. (See under this name in the present list.)

18. *A. FALCATA* Rydberg, N. Am. Fl. 34:271, 1916.—In every respect the same as *A. vulgaris longifolia*, except that many of the very narrow, elongated leaves have salient spreading lobes. An almost exact match for the type except for this lobing is found in undoubted *longifolia* specimens, for example, Boiler Rapid, Athabasca River, *Preble* and *Cary 131* (US). The foliage resembles that of *mexicana*, but the large heads serve to distinguish it and the distribution is very different. Apparently confined to gumbo soils and known only from South Dakota to Saskatchewan within the general area occupied by *longifolia*. Type locality, Fort Pierre, South Dakota.

19. *A. FLOCCOSA* Rydberg, Bull. Torr. Club 24:297, 1897.—*A. vulgaris candicans*. Separated on the basis of the inflorescence, the heads all erect and on peduncles 1 to 12 mm. long instead of sessile in glomerules; also on having the leaves equally tomentose on both sides. In considering a series of collections, like those at the New York Botanical Garden, some will fall plainly into one or the other if the inflorescence alone is considered, but some specimens have both sessile and peduncled heads and the length of the peduncle varies to such an extent that no two people would separate all of the material in the same way. The density of the tomentum also shows much intergradation and does not vary parallel with the inflorescence characters. Even in the type of *candicans* the difference between the upper and lower surfaces of some leaves is not noticeable. At the type locality of *floccosa*, namely Lima, Montana, some plants have the small heads of *gnaphalodes*, the involucre only 2.5 cm. high, while others have involucre 4 mm. high, as in *candicans*. These extremes were collected under *Hall 11570*, and other forms and intermediates under *Hall 11563* and *11567*, all from near Lima.

20. *A. FLODMANI* Rydberg, N. Am. Fl. 34:276, 1916.—*A. vulgaris flodmani*.
21. *A. GHIESBREGHTI* Rydberg, l. c., 271, 1916.—Taken to be an exceptionally large-headed form of *A. vulgaris mexicana*, the involucre 4 to 5 mm. high, but perhaps better treated as a distinct variety related to *mexicana*. Known from only a few collections from Chiapas, which is the type locality, and the Federal District of Mexico.
22. *A. GNAPHALODES* Nuttall, Genera 2:143, 1818.—*A. vulgaris gnaphalodes*.
23. *A. GNAPHALODES DIVERSIFOLIA* Nelson; Coulter and Nelson, Man. Rocky Mt. 569, 1909.—Based upon *A. diversifolia* Rydberg, which see.
24. *A. GORMANI* Rydberg, N. Am. Fl. 34:267, 1916.—This is exactly the *etiator* form of *A. vulgaris tilesi* with rather narrow leaf-lobes, some of which are again toothed or divided, and only about 10 disk-flowers. The subspecies *tilesi* must be taken to include some forms with entire leaf-lobes and some with toothed or cleft lobes, as called for by Rydberg's description in the North American Flora. The narrow leaf-lobes of *gormanii* can scarcely be admitted as a character of subspecific importance in a species where the foliage is so variable, and the smaller number of disk-flowers is perhaps due to the age of the type specimens, the heads of which look as though some flowers had been lost. Type locality, Lake Iliamna region, Alaska.
25. *A. GRACILENTA* Nelson, Bull. Torr. Club 27:35, 1900.—*A. vulgaris candicans*. Heads either sessile and glomerate or short-pedicelled; leaves equally white-tomentose on both sides. Type locality, sandy beaches and banks of Yellowstone Lake.
26. *A. GRAVEOLENS* Rydberg, Bull. Torr. Club 24:296, 1897.—*A. vulgaris discolor*, but with greener leaves than in the type and these with slightly broader segments as in the form once called *A. incompta* Nuttall. (See under *A. michauxiana* of this list.) The type came from Long Baldy, Little Belt Mountains, Montana, but green plants of this form occur from the northern Rocky Mountains nearly to the Pacific Coast.
27. *A. HERRIOTTI* Rydberg, l. c., 37:455, 1910.—*A. vulgaris heterophylla*. Separated from the *douglasiana* form of this subspecies on the basis of its erect heads with only 5 to 15 flowers and the oblong involucre. A more recent examination of one head from the type reveals a total of 18 flowers (7 ray and 11 disk) which brings the number well within the limits for *heterophylla*, as indicated in table 6. Type locality, Edmonton, Alberta.
28. *A. HETEROPHYLLA* Nuttall, Trans. Am. Phil. Soc. II, 400, 1841. Not *A. heterophylla* Besser, 1834.—*A. vulgaris heterophylla*. The original description is so drawn as to include both this and subspecies *litoralis*. The heads are given as "cylindric-ovate and small," which applies better to *litoralis*, but the type locality is given as "Rocky Mountains by stream," whereas *litoralis* is closely confined to a narrow coastal strip. A specimen at the herbarium of the Philadelphia Academy of Sciences labeled by Nuttall as from the Columbia Plains and as a type of his *heterophylla*, is plainly *litoralis*. Another, in the Gray Herbarium, labeled by Nuttall as from the Rocky Mountains by streams and also as a type of his *heterophylla*, is just as plainly the more inland form here treated as *A. vulgaris heterophylla*. The Philadelphia specimen has small, ovoid, glabrous heads; the one at the Gray Herbarium has larger, hemispheric, tomentose heads. Since the locality as given on the Gray Herbarium label agrees with that stated by Nuttall in connection with his description, this specimen is taken as the type. (See also under *A. hookeriana* and *A. douglasiana* of this list.)
29. *A. HOOKERIANA* Besser, in Hooker, Fl. Bor. Am. 1:322, 1833.—Not positively identified. The original description as well as fragments and tracings at the Gray Herbarium, apparently of the type, indicate a form close to *A. vulgaris heterophylla*, with heads of maximum size for this subspecies and white stems. The leaf is deeply pinnatifid with acute lobes. The type was collected by Drummond in the Rocky Mountains and therefore, even though it might be accepted as belonging to the same subspecies as the Pacific Coast *heterophylla*, it represents an outlying form far removed from the center of distribution. It is largely because of these doubts and the facts of distribution that *hookeriana* is not here taken up as the subspecific name of the common mugwort, which ranges from British Columbia to Lower California and has commonly passed as *A. vulgaris* var. *californica* Besser and *A. heterophylla* Nuttall. *A. douglasiana* Besser is another trivial variation of subspecies *heterophylla*. In the North American Flora *hookeriana* and *douglasiana* are both recognized as species and distinguished from each other on the lobing of the leaf, the former having lower leaves deeply divided into more or less falcate divisions, the latter having lower leaves with shorter lobes or teeth directed forward. In that work *hookeriana* was stated to occur from Saskatchewan to Oregon, *douglasiana* from Idaho and southern Washington to southern California. The utter unreliability of leaf-characters in this group has been already demonstrated (p. 41). They do not run parallel with distribution, as is indicated by the presence as far north as Oregon of plants with nearly entire or few-lobed leaves (Grant's Pass, Oregon, July 14, 1887, *Howell*), while in the south there are plants in which the leaves are deeply cut into spreading lobes (Laton, Kings County, California, October 25, 1919, *Hall*, and many collections from around San Francisco and Monterey bays), and throughout middle and northern California both forms are common. It is not unusual to find all gradations in leaf-lobing on plants growing close together (see text-figs. 3, 7, and 12). It is true, however, that in southern California, except along the coast, the general tendency is towards entire or short-lobed leaves. The original description of *A. douglasiana* calls for entire leaves, but this was probably due to the collector having taken only the tops of the plants.

30. *A. INCOMPTA* Nuttall, Trans. Am. Phil. Soc. II, 7:400, 1841.—*A. vulgaris discolor*. A robust form with broad segments to the leaves. (See diagnosis under *A. michauxiana* of this list.)
31. *A. INDICA CANADENSIS* Besser; Hooker, Fl. Bor. Am. 1:323, 1833.—*A. vulgaris typica*, from description.
32. *A. INDICA MEXICANA* Besser, Nouv. Mem. Soc. Nat. Mosc. 3:56, 1834.—*A. vulgaris mexicana*.
33. *A. KANSANA* Britton, in Britton and Brown, Ill. Fl. 3:466, 1898.—A form of *A. vulgaris wrightii* equivalent to *A. carruthi* of this list. The type, which came from the plains of Lane County, Kansas (*Hitchcock 302*, NY), is the common form in Kansas and western Missouri. There is little doubt that it is identical with *carruthi*, a name apparently overlooked by Britton.
34. *A. KENNEDYI* Nelson, Proc. Biol. Soc. Wash. 18:175, 1905.—*A. vulgaris heterophylla*. Type locality, Verdi, Washoe County, Nevada. Well separated by its author from *A. suksdorfii* Piper, that is, from *A. vulgaris litoralis*, but not compared with true *heterophylla*, which was assumed to be identical with *suksdorfii*. Even if *heterophylla* were so identified, there are other names, notably *hookeriana* and *douglasiana*, which would have precedence for this subspecies with broader gray involucre and more numerous flowered heads. (See further under *hookeriana* of this list and in Hall, Univ. Calif. Publ. Bot. 3:218, 1907.)
35. *A. LEIBERGI* Rydberg, N. Am. Fl. 34:267, 1916.—This is a variation of *A. vulgaris lindleyana* with rather large heads and perhaps more nearly hemispheric involucre. The size of the heads is frequently equaled on plants referred without hesitation to this variety and the shape of the involucre is scarcely if at all different. The type specimen of *leibergi* came from Fish Hook Ferry, Oregon, in a region where *lindleyana* is common, especially on stony stream-banks which are flooded at seasons of high water.
36. *A. LINDHEIMERIANA* Scheele, Linnaea, 22:163, 1849.—A variation of *A. vulgaris mexicana* approaching *A. v. ludoviciana*; stems rigid and almost woody; involucre only about 2 mm. broad. Type locality, dry streamway of the Cibolo River, 15 miles westerly from New Braunfels, Texas.
37. *A. LINDLEYANA* Besser; Hooker, Fl. Bor. Am. 1:322, 1833.—*A. vulgaris lindleyana*.
38. *A. LINDLEYANA BREVIFOLIA* Besser, l. c.—*A. vulgaris lindleyana*, a late form with short fascicled leaves.
39. *A. LINDLEYANA CORONOPUS* Besser, l. c.—*A. vulgaris lindleyana* with the leaves sinuately cleft.
40. *A. LINDLEYANA LEGITIMA* Besser, l. c.—Typical *A. vulgaris lindleyana*.
41. *A. LINDLEYANA SUBIDENTATA* Besser, l. c.—*A. vulgaris lindleyana* with leaves 2 to 5 cm. long, 2 to 4 mm. wide, irregularly dentate.
42. *A. LONGIFOLIA* Nuttall, Genera 2:142, 1818.—*A. vulgaris longifolia*.
43. *A. LUDOVICIANA* Nuttall, Genera 2:143, 1818.—*A. vulgaris ludoviciana*.
44. *A. LUDOVICIANA DOUGLASIANA* Eaton, in Watson, Bot. King. Expl. 183, 1871.—*A. vulgaris douglasiana*, as to synonymy.
45. *A. LUDOVICIANA GNAPHALODES* Torrey and Gray, Fl. N. Am. 2:420, 1843.—Based upon *A. gnaphalodes* Nuttall, here treated as *A. vulgaris* subsp. *gnaphalodes*.
46. *A. LUDOVICIANA INTEGRIFOLIA* Nelson, First. Rep. Fl. Wyo. 13S, 1896.—*A. vulgaris longifolia*.
47. *A. LUDOVICIANA LATIFOLIA* Torrey and Gray, l. c.—*A. vulgaris gnaphalodes*. Based upon *A. purshiana latifolia* Besser.
48. *A. LUDOVICIANA LATILOBA* Nuttall, Trans. Am. Phil. Soc. II, 7:400, 1841.—The type not seen and the description indefinite. According to Rydberg it is the same as his *A. platyphylla*, here reduced to *A. vulgaris candicans*.
49. *A. LUDOVICIANA SERRATA* Torrey and Gray, l. c.—Based upon *A. serrata* Nuttall, here reduced to *A. vulgaris serrata*.
50. *A. MEXICANA* Willdenow in Sprengel, Syst. 3:490, 1826.—*A. vulgaris mexicana*.
51. *A. MEXICANA BAKERI* Nelson; Coult. and Nelson, Man. Rocky Mt. 569, 1909.—Based upon *A. bakeri* Greene, which see.
52. *A. MEXICANA SILVICOLA* Nelson, l. c.—Based upon *A. silvicola* Osterhout, which see.
53. *A. MICHAUXIANA* Besser; Hooker, Fl. Bor. Am. 1:324, 1833.—The oldest name for the group of forms here assembled under *A. vulgaris discolor*, this varietal name selected because of its brevity and long usage as a species in most of the standard floras. This *discolor* group is exceedingly variable in habit, foliage, and color, thus giving rise to several so-called species. Specimens representing these are indicated in the citations under *discolor*. The three most divergent forms may be diagnosed as follows:
- Genuine *discolor*. Plant rather large, usually 3 to 5 dm. high, leaves mostly 4 to 8 cm. long, deeply cleft into long attenuate segments, these mostly 1 to 4 mm. wide; inflorescence loose and broad. Quite certainly the ecologic response to lower altitude and better soil conditions than those obtaining where the next form grows. Found along rivers and creeks or in copses. Common at high altitudes in the Sierra Nevada, but always in moist sandy places.
- A. michauxiana* Besser. Plant low, 1 to 3 or sometimes 4 dm. high; leaves only 1 to 4 cm. long, cleft into short lanceolate lobes, these 1 to 4 mm. wide; inflorescence rather compact, narrow, spike-like. The common reduced form of high altitudes which has commonly passed as *A. discolor*. Type locality, Rocky Mountains. Intermediate between this and true *discolor*, both as to foliage and inflorescence, are specimens from British Columbia, *Macoun 14591*, *14593*, and *76926* (NY), and many others.

The form occurs south through the Cascade Mountains to Oregon, but apparently does not reach California.

A. incompta Nuttall. Plant robust, 3 to 9 dm. high; leaves 4 to 8 cm. long, cleft into long or sometimes short but always comparatively broad lanceolate segments, these commonly 3 to 5 mm. wide; inflorescence loose and open, decidedly paniculate. Scarcely distinguishable from genuine *discolor*, except by the wider leaf-segments. Belongs to moderate altitudes, both in the Rocky Mountains and in the Sierra Nevada.

Other but still less important forms are indicated in the present list under *A. graveolens*, *A. potens*, *A. tenuis*, and *A. tenuis* var. *integerrima*.

54. *A. MICROCEPHALA* Wooton, Bull. Torr. Club 25:455, 1898.—Because of the earlier *A. microcephala* Hildebrand, this name was changed by Wooton to *A. albula*, which see.

55. *A. MUELLERI* Rydberg, N. Am. Fl. 34:270, 1916.—A form of *A. vulgaris mexicana* with the upper leaves inclined to be wider (5 to 15 mm. wide) and usually entire. The type specimen has only upper leaves, but others of the same form in the Columbia University Herbarium have leaves well below the inflorescence and none of these are cut. However, Pringle's 9848, from Hidalgo, as represented at New York, is almost identical with the type of *muelleri*, except that lower leaves are present, and these are cut nearly to the base into 3 long linear-attenuate lobes, as in typical *mexicana*. Evidently here as elsewhere in the species the use of leaf-lobing as a criterion would result in much confusion. The leaves of *muelleri* are strongly veined beneath. Type locality, Orizaba.

56. *A. NATRONENSIS* Nelson, Bull. Torr. Club 26:485, 1899.—*A. vulgaris longifolia*. Type locality, Willow Creek, Wyoming.

57. *A. NEOMEXICANA* Greene; Rydberg, N. Am. Fl. 34:279, 1916.—A narrow-leaved form of *A. vulgaris mexicana*, therefore intermediate to subspecies *wrightii*. The leaves, which are green and glabrate above, are up to 4 mm. wide below the divisions and the lobes themselves are 1 to 2 mm. wide. The inflorescence is more condensed than usual in *mexicana*, the main portion only about 2 cm. broad, but in one of the types the basal portion is more branched and 4 cm. broad. Type locality, Hillsboro Peak, Black Range, New Mexico.

58. *A. OBTUSA* Rydberg, l. c., 274, 1916.—A leaf-form of *A. vulgaris gnaphalodes*, in which the lower leaves are pinnately parted into 3 to 7 divisions. Although these divisions are described as oblong and obtuse, they of course narrow more or less towards the summit and are mostly mucronate, so that they approach too closely the shape of the divisions in other forms of *gnaphalodes*, especially *A. diversifolia*. Type locality, Columbia River, Washington.

59. *A. PABULARIS* Rydberg, Bull. Torr. Club 33:157, 1906.—Based upon *A. rhizomata* variety *pabularis*, which see.

60. *A. PAUCICEPHALA* Nelson, Bull. Torr. Club 27:35, 1900.—A variation of *A. vulgaris* intermediate between the subspecies *candicans* and *ludoviciana*. The large heads with involucre 4 mm. high and the 3 mm. long disk-corollas seem to ally it more closely with the former, but the tomentum is as sparse as in the latter. Said to be distinguished by its tufted cespitose habit and its low erect stems. Nelson found 40 to 60 flowers in a head; recent counts of 2 heads of type material indicated totals of 23 and 27 flowers respectively. Type locality, near Yellowstone Lake, on the banks of a tributary creek.

61. *A. PLATYPHYLLA* Rydberg, N. Am. Fl. 34:275, 1916.—A foliage variation of *A. vulgaris candicans*, the lower and middle leaves cuneate-obovate and with a few short wide lobes or teeth above the middle. Very striking in its extreme development, but thoroughly intergrading with typical *candicans* at the type locality, namely, Spokane, Washington, and in the surrounding country, as evidenced by an extensive series of specimens collected by Miss Evelyn Moore (Herb. Univ. Calif.).

62. *A. POTENS* Nelson, Bot. Gaz. 54:418, 1912.—*A. vulgaris discolor*. This is very close to the original *discolor* form and is not at all of the *michauxiana* type, so often taken as typical *discolor* (see under *michauxiana* of this list). The lower leaves are mostly wanting from specimens of the type collection, but a few withered ones have lobes again toothed and in earlier leaves the foliage is probably twice-cut. According to Nelson, *potens* is herbaceous to the ground and grows on dry saline-gravelly clays of the plains. Type locality, Mackay, Idaho.

63. *A. PRESCOTTIANA* Besser; Hooker, Fl. Bor. Am. 1:324, 1833.—Apparently known only from plants collected by Douglas in northwest America. At the herbarium of the New York Botanical Garden is a drawing and fragment from a plant at Kew collected by Douglas near the Grand Rapids of the Columbia in 1825. These are said to correspond exactly with the type in the Lindley Herbarium. From this material and the description it seems that *prescottiana* is very close to *A. vulgaris wrightii*, but differs in the strictly racemose arrangement of the heads. This character suggests subspecies *lindleyana*, but the foliage is very different, the leaves and their lobes being almost filiform and revolute. The involucre is 3.5 mm. high and nearly 5 mm. broad. Further collections are needed before the exact placing of this form can be made.

64. *A. PRINGLEI* Greenman, Proc. Am. Acad. 40:50, 1904.—A Mexican variation of *A. vulgaris wrightii*. The large heads are arranged in a racemiform panicle, the number of heads reduced, and the number of flowers in each head increased. In the type specimen the involucre is 3 mm. high and broad, this being about

the average for *wrightii*, but in other plants from near the type locality (Eulalia Plains, September 29, 1885, Wilkinson, US 227800), the height and breadth are 4.0 and 3.8 mm., respectively. As is seen from table 6, the total number of flowers is about the maximum for subspecies *wrightii*, while the number of ray-flowers is considerably higher than in any other collection examined. In the Eulalia Plains specimens, however, the proportion between the number of flowers in ray and disk is about normal, but the total is astonishingly high, there being 10 to 14 in the ray and 24 to 28 in the disk. This is so exceptional that the counts have not been entered in the table. The type is from plains near the city of Chihuahua, Pringle 625 (Gr).

65. *A. PUDICA* Rydberg, Bull. Torr. Club 32:130, 1905.—*A. vulgaris gnaphalodes*. A form with thinish leaves, loosely branched inflorescence, and nodding heads, such as to be expected in moist shady places. The most striking character lies in the inflorescence, which is composed of many long, erect racemiform branches. But this may be due in some cases to injury to the growing tip of the central axis, thus causing an exceptional development of the branches. Such injury is plainly evident in some specimens on the type sheet, as also among duplicates of the type, while other specimens of the same collection show no evident injury. Type locality, Gunnison, Colorado.

66. *A. PUMILA* Nuttall, Trans. Am. Phil. Soc. II, 7:399, 1841.—Not *A. pumila* Link 1822. A reduced form of *A. vulgaris lindleyana* only 1 to 1.5 dm. high. Type locality, in the Rocky Mountains, Lewis River, by ponds or in depressions.

67. *A. PURSHIANA* Besser, in Hooker, Fl. Bor. Am. 1:323, 1833.—*A. vulgaris gnaphalodes*. The leaves are supposedly broader, but since the types of *gnaphalodes* are wanting all but the upper leaves, this can not be verified and, indeed, is of no importance in view of the wide range of variation in leaf-width. According to Rydberg (N. Am. Fl. 34:273, 1916), the flowers over the range assigned to *purshiana* are light-brown or yellowish, while true *gnaphalodes*, which is assigned only to districts from the Rocky Mountains east, has dark-brown or purplish corollas. But even according to this discriminating authority, *purshiana* sometimes occurs as far east as Nebraska. While it seems to be true that the corolla-color is usually lighter in plants from west of the Rocky Mountains, there is much variation in the shade and the criterion is difficult of application, especially to dried specimens (see under Criteria, p. 39). The type locality of *A. purshiana* is plains of the Saskatchewan.

68. *A. PURSHIANA ANGUSTIFOLIA* Besser, l. c.—Probably a very narrow-leaved form of *A. vulgaris longifolia*. Type locality, Red River.

69. *A. PURSHIANA LATIFOLIA* Besser, l. c.—*A. vulgaris gnaphalodes*, from the description. (See *A. purshiana* of this list.)

70. *A. REDOLENS* Gray, Proc. Am. Acad. 21:393, 1886.—*A. vulgaris redolens*.

71. *A. REVOLUTA* Rydberg N. Am. Fl. 34:272, 1916.—*A. vulgaris mexicana*. The leaves are divided into very narrow lobes (2 to 4 mm. wide) and the margins of these are more noticeably revolute than in most specimens. Apparently a response to strongly xerophytic conditions. Type locality, near the city of Chihuahua.

72. *A. RHIZOMATA* Nelson, Bull. Torr. Club 27:34, 1900.—A variation of *A. vulgaris gnaphalodes* with interrupted inflorescence, semiwoody rhizomes, and usually narrow leaves. Found on low saline flats adjacent to streams. Type locality, Sweetwater River, Wyoming.

73. *A. RHIZOMATA PABULARIS* Nelson, l. c., 1900.—A slender competition-form of *A. vulgaris gnaphalodes*, the types from saline draws of the Red Desert of Wyoming, growing with grasses. Leaves only 2 to 5 mm. wide. According to Rydberg (N. Am. Fl. 34:273, 1916), the corollas are light-brown as contrasted with the dark-brown corollas of *gnaphalodes*, but those on the type sheets appear dark-brown or nearly purplish.

74. *A. SELGENSIS* Turczaninow; Besser, Nouv. Mem. Soc. Nat. Mosc. 3:50, 1834.—This Eurasian species has been accredited to North America by Rydberg (N. Am. Fl. 34:266, 1916) on the basis of supposedly introduced plants collected at Lower Albina, near Portland, Oregon (*Sheldon 1115*, NY, US). There is good reason to believe, however, that these plants represent one of the many forms of *A. vulgaris heterophylla*, which is common in Oregon. The lower leaves are wanting, so that there is no evidence of the double lobing of true *selgensis*. The upper leaves can be almost duplicated in native west-American forms (see, for example, the figures on p. 41). The heads are small for *heterophylla*, but they are immature and not smaller than on many native plants at the same stage. When compared with European material of true *selgensis*, these Oregon plants are seen to possess the same general appearance, and especially the remarkably smooth upper surface of the leaves. But that species, or rather form, for it is often considered a minor variation of typical *A. vulgaris*, has characteristics not found in these, especially the presence of 1 or 2 pairs of stipule-like lobes on the lower part of the petiole. These structures are almost universally absent from *heterophylla*. The petiole in the Oregon plants referred to *selgensis* is devoid of lobes, although there are a few reduced leaves in the axils which may easily be mistaken for lobes. Even if *selgensis* can be demonstrated to be distinct from *A. vulgaris typica*, its admission to the North American flora may await further evidence.

75. *A. SERRATA* Nuttall, Genera 2:142, 1818.—*A. vulgaris serrata*.

76. *A. SILVICOLA* Osterhout, Bull. Torr. Club 28:645, 1901.—Best referred to *A. vulgaris ludoviciana*, but the leaves mostly entire, very green above, and the heads rather large. Reduced to a variety of *mexicana* by Nelson, but lacks the long and narrow leaf-lobes which furnish the only distinguishing feature of that subspecies. Rather common in partial shade in Colorado. Type locality, MacIntyre Creek, Colorado.

77. *A. SUBGLABRA* Nelson, Bull. Torr. Club 27:36, 1900.—A green variation from *A. vulgaris discolor*. The same as *A. graveolens* of this list. Type locality, stony banks of Yellowstone River, near Yancey's, Yellowstone Park.

78. *A. SUKSDORFI* Piper, Bull. Torr. Club 28:42, 1901.—*A. vulgaris litoralis*. The type collection of both is the same.

79. *A. SULCATA* Rydberg, N. Am. Fl. 34:270, 1916.—*A. vulgaris mexicana*. Separated chiefly because of the grooved stems and shining glabrate involucre. The stems are nearly always more or less grooved in *mexicana* and the pubescence of the involucre is too variable to furnish a good criterion. Type locality, Casas Grandes, Chihuahua.

80. *A. TENUIS* Rydberg, Mem. N. Y. Bot. Gard. 1:431, 1900.—Referred to *A. vulgaris discolor*. A slender, small-headed form of *A. graveolens*, which in turn is only a green variation of *discolor*. The heads are erect. Originally compared with *A. lindleyana*, but the paniculate inflorescence and the double lobing of at least some of the leaves will serve to distinguish it. Type locality, Emigrant Gulch, Montana.

81. *A. TENUIS INTEGERRIMA* Rydberg, l. c., 432, 1900.—Probably a chance variation of the preceding, with which the type and only specimen was collected. Lower leaves wanting, but the upper ones remarkably entire. Type locality, Emigrant Gulch, Montana.

82. *A. TEXANA* Rydberg, N. Am. Fl. 34:274, 1916.—A leaf form of *A. vulgaris gnaphalodes*, differing from the type only in the more deeply cleft foliage. The heads are of minimum size, about 3 mm. high; otherwise very close to the form called *A. diversifolia* Rydberg. Type locality, Colorado, Texas.

83. *A. TILESII* Ledebour, Mem. Acad. St. Petersb. 5:568, 1805.—*A. vulgaris tilesii*.

84. *A. TILESII ARCTICA* Besser, Hooker, Fl. Bor. Am. 1:324, 1831.—A form of *A. vulgaris tilesii* with entire, short, and obtuse leaf-lobes. From the arctic littoral of North America.

85. *A. TILESII ELATIOR* Torrey and Gray, Fl. N. Am. 2:422, 1843.—A form of *A. vulgaris tilesii* with the panicle more developed and far exceeding the leaves. Apparently the only form from Montana and Oregon to British Columbia, whereas typical *tilesii* belongs to regions farther north and especially around Bering Sea. But the elongated inflorescence of typical *elatiore* also occurs in the north, for example: *Walker 1077* from Chilkat Valley; 1891 *Turner*, from Porcupine River; and *Blaisdell 80*, from Nome. Intermediate forms and specific localities are indicated in the collections cited of subspecies *tilesii*. Type locality, subarctic America.

86. *A. TILESII UNALASKENSIS* Besser, Linnaea 15:106, 1841.—One of the many foliage variations of *A. vulgaris tilesii*. The main leaves are described as deeply trifid, the lanceolate, acute lobes sparsely and unequally dentate. Type locality, Island of Unalaska.

87. *A. UNALASKENSIS* Rydberg, N. Am. Fl. 34:266, 1916.—A form of *A. vulgaris tilesii*; the stems tall and heads in a loose elongated panicle, therefore closely resembling the form here listed as *elatiore*. But it differs from all others in having the lower leaves with approximate divisions and therefore appearing almost palmate, and the leaves exhibit the extreme of dissection. The type is from the island of Unalaska, *Macoun* (Herb. Geol. Surv. Canada, 20625). The writers have seen only a photograph and piece of the type deposited at the New York Botanical Garden Herbarium.

88. *A. UNDERWOODII* Rydberg, Bull. Torr. Club 32:129, 1905.—*A. vulgaris ludoviciana*. This is a foliage-form, the leaves rather narrower than the average and pinnately parted. Such forms occur throughout most of the range of *ludoviciana*, but especially in the arid mountains and foothills of Nevada, California, and the Southwest. Some Californian plants referred here by Rydberg are narrow-leaved forms of *A. v. heterophylla*. Type locality, Ouray, Colo.

89. *A. VULGARIS AMERICANA* Besser, Linnaea 15:105, 1841.—Two subspecies of *A. vulgaris* are included in the original description. The former of these, judging from the description and distribution, is equivalent to subspecies *tilesii* (the form known as *elatiore*); the other is subspecies *mexicana*, as indicated by a portion of the original specimen collected by Engelmann.

90. *A. VULGARIS VAR. CALIFORNICA* Besser, Linnaea 15:91, 1841.—*A. vulgaris heterophylla*. Besser's name gives the first correct combination according to the International Code, if treated as a variety. Type locality, San Francisco.

91. *A. VULGARIS DOUGLASIANA* Rydberg, N. Am. Fl. 34:268, 1916.—As synonym. This is an evident slip for *A. ludoviciana* var. *douglasiana*, since the former combination does not appear in the publication referred to by Rydberg.

92. *A. VULGARIS VAR. GNAPHALODES* O. Kuntze, Revisio, 309, 1891.—*A. vulgaris* subspecies *gnaphalodes*.

93. *A. VULGARIS VAR. LITORALIS* Suksdorf, Deuts. Bot. Monats. 18:98, 1900.—*A. vulgaris* subspecies *litoralis*.

94. *A. VULGARIS VAR. LUDOVICIANA* O. Kuntze, l. c., 309, 1891.—*A. vulgaris ludoviciana*.

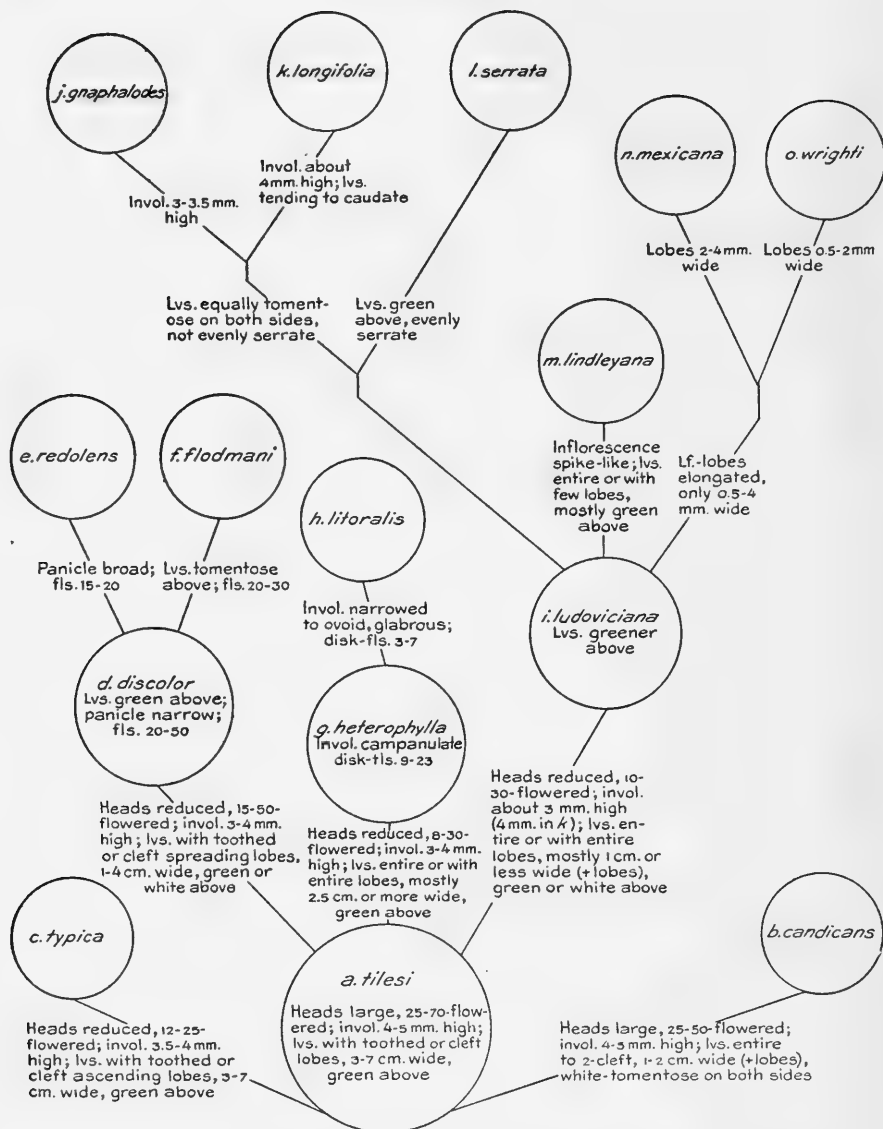
95. *A. VULGARIS VAR. MEXICANA* Torrey and Gray, Fl. N. Am. 2:421, 1843.—*A. vulgaris* subspecies *mexicana*.

96. *A. VULGARIS TILESII* Ledebour, Fl. Rossica 2:586, 1846. *A. vulgaris* subspecies *tilesii*.

97. *A. VULGARIS VULGATISSIMA* Besser in Hooker, Fl. Bor. Am. 1:322, 1883.—Type specimen not seen; probably to be identified with one of the forms of *A. vulgaris tilesii*. Type locality, Northwest America.

98. *A. WRIGHTII* Gray, Proc. Am. Acad. 19:48, 1883.—*A. vulgaris wrightii*.

99. *OLIGOSPORUS MEXICANUS* Lessing, Syn. Gen. Compos. 264, 1832.—Based upon *A. mexicana* Willdenow, that is, *A. vulgaris mexicana*.

FIG. 9.—Phylogenetic chart of the subspecies of *Artemisia vulgaris*.

RELATIONSHIPS.

The species of *Artemisia* most closely related to *A. vulgaris* are indicated on the chart (fig. 9). *A. alaskana*, *A. franserioides*, and *A. stelleriana*, although assembled close to *vulgaris* in the diagram, are believed not to be directly concerned with its origin, since these species represent divergent phylogenetic lines. None of them indicate any tendency towards intergradation with the forms now under consideration. On the other hand, the group consisting of *A. parryi*, *A. macrobotrys*, *A. norvegica*, and *A. senjavinensis* seems to have had an origin very close to that of *vulgaris*. It is not necessary here to discuss in detail the relationship of this assemblage to *vulgaris*, since this has been done elsewhere. It should here be noted, however, that in considering this group as a whole, certain forms of *vulgaris* come the nearest to representing the original primitive stock. This is because each of the others possesses certain features indicative of an extreme development along one or more lines. Therefore none of them can be considered as primitive. It seems either that the earlier evolutionary stages have entirely disappeared, or that they have not as yet been discovered by botanical collectors. Although this dropping out of the earlier forms has resulted in the production of some 5 rather sharply defined and non-overlapping species—or more if Asiatic forms are taken into account—it is not to be assumed that these are widely separated phylogenetically, or that all can be defined with absolute certainty. On the contrary, some of them differ from certain subspecies of *vulgaris* only by features so subtle that a close phylogenetic analysis is necessary in order to retain them in specific rank. Thus, for example, *A. parryi* closely simulates *A. vulgaris discolor* and *A. v. lindleyana*, yet from its geographic distribution and morphologic characters it is seen that its connection with *vulgaris* stock is not through these specialized varieties, but through more primitive forms probably now extinct. While the other enumerated species are of close kin to *vulgaris*, all can similarly be shown to belong to lines which diverged from the parent stock before the numerous subdivisions of this species began to differentiate.

Artemisia vulgaris is the most variable of all the *Artemisias*, at least as far as the American species are concerned. When the subspecies are arranged in what appears to be a natural phylogenetic sequence, as is attempted in the accompanying diagram, it is seen that, although the extremes are far apart, all are so closely held together by forms representing intermediate steps that no place is found where a line can be drawn that will separate the multitude of forms into well-defined species. This condition is not so remarkable, however, when it is noted that the variations are not in essential features but chiefly in characters of foliage, size of heads, number of flowers, and amount of pubescence. Some of the resultant variations are very unlike in appearance, but it is not difficult to see how all have had a common origin in no far distant past. As an aid to this it should be remembered that not all of the known forms are indicated on the chart, but only those which are sufficiently noteworthy to be ranked as subspecies. Between many of these, still smaller variations are known, most of which are enumerated in the text under the heading of "Minor variations." These represent the still shorter steps in the progress of evolution within the species. Nearly all of them, as well as all of the accepted subspecies, have at one time or another been classed as distinct species, so that in all some 80 described units, as well as many more undescribed ones, are available for study. It is thus seen that *Artemisia vulgaris* offers one of the most promising fields for phylogenetic researches. In some portions of this field all intermediate stages are still available, so that even the direction of evolution can be worked out with a reasonable degree of certainty by means of field observations, mapping of distribution, and statistical analyses. In other places small gaps occur. In some instances these have been bridged through the production of the intermediate stages by experimental methods. In only a few places are the lines of descent so broken that they can not be satisfactorily

reconstructed. It should not be inferred from these remarks, however, that the accompanying chart is presented with confidence as to its accuracy. Rather is it to be looked upon as a first attempt to unravel the tangled skein of relationships in this complex species, and to arrange into some sort of natural sequence the numerous taxonomic units bequeathed by the descriptive botanists. Many changes in grouping, and especially in direction, will doubtless be found necessary as further evidence is brought to bear upon this problem.

The most primitive of all of the subspecies of *A. vulgaris* is probably *tilesi*. This has large heads with numerous flowers, a tendency towards twice-pinnatifid leaves, and a northern distribution. The cumulative evidence indicates that this group of American Artemisias had its origin far to the north and that the forms have been multiplied as the stock spread to the south. If the opposite were assumed, namely, that the southern forms are the older, while the northern ones are the derived strains, then serious difficulties would be encountered in interpreting the origin of the character differences. In the present case it seems fairly certain that the large-headed forms like *tilesi*, which occur only in the north, have given rise to the more southerly forms with fewer flowers to the head and with other reductions.

Assuming that the subspecies *tilesi* was early established in the north, it is not unlikely that it represents a still more primitive type which ranged far to the east and west in arctic and subarctic regions. One of the derivatives of this form, or perhaps of *tilesi* itself, is subspecies *typica*. This nomenclatorial type of the species is native in north-central Asia and is well known in Europe as an introduced plant. It differs from *tilesi* in the usually reduced size of the heads and in the reduced numbers of flowers in the individual head, as indicated in table 6, but it retains the character of twice-dissected leaves. At the base of the petiole are 2 stipule-like lobes, an almost unique feature in the genus, but these structures are occasionally found also in *tilesi* (Dutch Harbor, Unalaska, *Van Dyke 101, Gr*), as indicated in figure 10. Additional connecting forms may be expected as the flora of Siberia and Alaska become better known. There are also frequent suggestions of a connection between *typica* and some of the other West-American subspecies, notably *heterophylla*. The similarity in the foliage is indicated in figure 7, p. 74. Even the stipule-like basal lobes are sometimes present in specimens referable only to *heterophylla* (northern Idaho, *Sandberg 822, US*) and they are rather common in *A. v. discolor*.¹ It is believed, however, that these similarities are due to the persistence of ancestral traits rather than to any immediate phyletic connection. From these considerations it is concluded that *typica* is an offshoot from the original stock best represented by *tilesi* and that it is not directly connected with any other American form. It is thus a western divergence which has reached our territory only as an introduction by way of Europe, and for this reason it is indicated on the chart as lying entirely to one side of the other subspecies. It should be noted, however, that *typica* is sometimes considered as native in the Northeast, and that if introduced it reached America a long time ago (Fernald, *Rhodora* 2: 135, 1900). Notwithstanding its close connection with *tilesi*, as shown above, there is a wider phylogenetic gap between these two subspecies than is usually the case among series of forms as here set forth.

Another subspecies is conceived as diverging from *tilesi*, but in a different direction. This is *candicans*, of the northwestern United States and adjacent Canada, where its range meets that of *tilesi*. Apparently it has given rise to none of the others, although there is some evidence of a connection, especially with *gnaphalodes*. The subspecies *candicans* scarcely differs from *tilesi*, except in the presence of a copious white tomentum on the upper as well as on the lower surface of the leaves. This appearance of paired subspecies,

¹ The nature of the false stipules in *Artemisia vulgaris* and other plants has been investigated by Schiller (*Sitzb. Akad. Wiss. Wien*, 112: 793-819, 1903).

differing only in the tomentum, recurs at a number of places in the species, as, for example, between *ludoviciana* and *gnaphalodes* and also, but with the addition of other tendencies, between *discolor* and *flodmani*. When the former pair is reached in this discussion, evidence will be adduced for considering the heavily tomentose as the more advanced type.

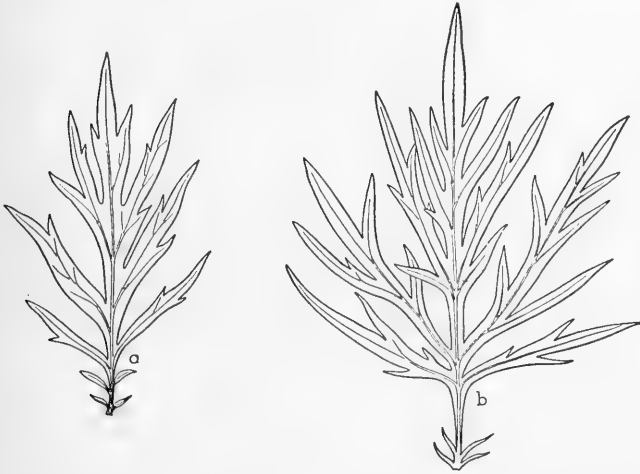


FIG. 10.
Leaves of *Artemisia vulgaris typica* and *A. v. tilesi*:
a, *typica* from Rochester,
New York, August 16,
1897. House (Gr); b, *tilesi*
from Dutch Harbor, Unalaska,
Van Dyke 101 (Gr).
Both $\times 0.5$.

Aside from *tilesi* itself, the subspecies thus far considered have not led to other well-marked variations, however numerous their minor forms may be. The remaining subspecies, on the other hand, may be grouped around three central ones, each of which has given rise to one or more groups of equal rank with itself. The first of these is *discolor*, a common subspecies in the western mountainous districts. This is widely separated from *tilesi* in most taxonomic treatments and is even placed in a separate section of the genus in the latest monographic account (Rydberg, N. Am. Fl. 34:245, 1916). Yet in all essential characters these two forms come very close to each other; both have short, twice-dissected leaves with the same peculiar cut to the lobes, the involucre is green in both, and the heads, although averaging smaller in *discolor*, exhibit a complete intergradation in this respect (see table 6). Thus the only characters left for the distinction of *discolor* are the usually smaller heads and the somewhat narrower lobes of the smaller leaves. The connection seems to be established by specimens in which the heads are large, but with all the other characteristics of *discolor* (Bear Cañon, Custer County, Idaho, Nelson and Macbride 1521). In the collection just cited the involucre is about 4 mm. high and 4.5 mm. broad and the number of disk-flowers varies from 23 to 29. For some unexplained reason, *A. v. discolor* often has been confused with *A. v. mexicana*, but this latter has exceptionally long leaves with slender, entire lobes and the heads are usually smaller and more tomentose. The inflorescence of *discolor* is sometimes very similar to that of *A. v. lindleyana* and the two are often confused in the absence of good foliage. This subspecies seems to intergrade or hybridize also with subspecies *gnaphalodes* and *ludoviciana*, as is indicated by a series of specimens gathered near Durant, in western Montana (Hall 11579 and 11580 UC).

Indicated on the chart as a derivative of *discolor*, but of doubtful origin is the subspecies *redolens*. If morphological characters alone were taken into account, the two could be

maintained as separate subspecies only with the greatest difficulty. The widely branching inflorescence and fewer-flowered heads make *redolens* an easily recognized unit, but these features may be only the result of the habitat, since it is thus far known only from the proximity of cliffs in northern Mexico. Because of this wide geographic separation from its nearest relatives, *redolens* may stand as a subspecies, at least until its ecology is better understood. It was referred by Gray to the section *Dracunculus*, an error which has been already pointed out by Rydberg (N. Am. Fl. 34:278, 1916). Another derivative of the *discolor* group is subspecies *floodmani*. This is a local form confined to western Montana and adjacent States. The upper surface of its leaves has taken on a heavy tomentum and the flowers in each head have been reduced in number.

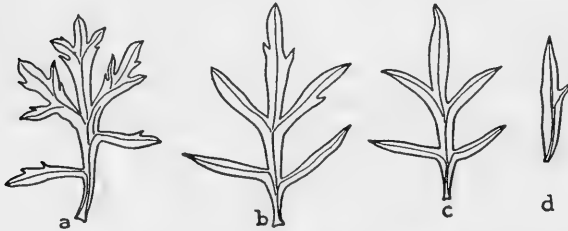


FIG. 11.
Leaves of *Artemisia vulgaris discolor*: a, from near the base of the stem; b, c, d, from toward the summit of the same plant. Yosemite National Park (73969 UC). This is the "incompta" form, also known as *A. underwoodii*. All $\times 0.8$.

In its early southward migration, the subspecies *tilesi*, which is here considered as the progenitor of all the other native American forms, underwent modification in a number of its characters. Thus, through a simplification in the cut of the leaf, together with some reduction in the leaf-size and in the size of the heads, there was evolved the more southerly subspecies *heterophylla*. This has been variously known as *A. hookeriana* Besser (1833), *A. douglasiana* Besser (1833), *A. vulgaris* var. *californica* Besser (1841), and *A. heterophylla* Nuttall (1841). The last is here chosen for the subspecific name as being the most descriptive and the one in most general use. Forms connecting *heterophylla* with *tilesi* are common where the geographical ranges of the two overlap in southern Canada and adjacent United States. In this area are found specimens of *tilesi* with leaves only once-pinnatifid and others in which the size of heads, foliage characters, and habit are such that they might be classed as either the one or the other. The overlapping in the size of the heads and in the number of flowers per head is brought out in table 6. The types of *heterophylla* came from somewhere in Canada and were probably low plants with pinnatifid leaves. It is unfortunate that the types were from near the border of the area of distribution, since they do not well represent the normal form so common farther south, especially from Washington to California. However, leaf-tracings and a single head taken from the types and preserved at the New York Botanical Garden can be easily duplicated in California.

Subspecies *heterophylla* is comparatively rare in the northern Rocky Mountain States and entirely wanting to the south of them, but to the west it swings across Washington nearly to the coast, is abundant in Oregon and California, and extends on southward into Lower California. Because of their more nearly entire leaves, these southern plants recently have been referred to "*A. douglasiana* Lindley," the type of which came from the Columbia River. This form, however, is scarcely distinguishable except in the herbarium, where specimens frequently exhibit only the upper leaves. Field studies indicate that the lower leaves are probably never entire. It must be said, however, that southern specimens are likely to have a larger number of entire or only toothed leaves

than northern ones. This does not apply to coastal plants, since in these the leaves are for the most part deeply pinnatifid. These facts are in accord with the general theory that as the species extends towards the south or away from the coast the foliage is reduced in size and simplified in its lobing. Even in those forms of *heterophylla* which have undergone the greatest amount of modification in foliage characters, the leaves are still ample as compared with those of *ludoviciana* and other varieties of dry, interior habitats. In this connection it should be noted that, while *heterophylla* often grows in warm, arid districts, it there occupies stream-banks, bottom-lands, and other places where there is a reasonable amount of soil moisture to draw upon. As to the nature of the lobing of the foliage, this varies through all degrees from deeply pinnatifid with widely spreading and narrow lobes to entire. Often a peculiar cut will be observed in all of the principal leaves of one clump of plants, while an entirely different type will be found on neighboring plants. This seems to indicate the presence of numerous strains, possibly with hybrids between them. Apparently the only rational way of organizing these leaf-forms is by the method of genetic analysis. Any attempt to classify them by usual taxonomic methods would lead only to confusion, and it is because of the recognition of this that the numerous so-called species of some recent works, based upon leaf-characters alone, are here relegated to the category of minor variations. A hint as to what may be expected in the way of leaf-forms is given in figure 3, p. 41, and figure 7, p. 74.

In strong contrast to the trivial variations just discussed is the subspecies *litoralis*, a form restricted to the vicinity of the coast from southern British Columbia to Mendocino County, California. It differs from subspecies *heterophylla*, of which it is a derivative, especially in the narrowed, shining involucre and in the reduced number of flowers. Although the collections have been numerous, no intermediate forms have been encountered. The absence of overlapping in the number of flowers is indicated in table 6, and the two may be distinguished without hesitation by an examination of the involucre alone.

The remaining subspecies differ from those thus far discussed in the usually smaller heads which have a reduced number of flowers. Their leaves are comparatively narrow and only once pinnatifid or toothed or often entire. This seems to be a natural group which has originated from the *tilesi* stock and, spreading out over a large area to the southeast of the range of that primitive form, has now come to occupy the Rocky Mountain region especially, but with extensions southward through Mexico, east to slightly beyond the Mississippi River, and west almost to the Pacific Coast. This westward extension, however, is much less important than the others, since the group is not strongly represented west of the Great Basin. During the course of its occupancy of this extensive area, and perhaps because of the wide range of conditions here encountered, the group broke up into an innumerable series of forms, many of which have been accorded specific rank by taxonomists. All of these so-called species are based upon highly variable characters, such as those of the foliage, inflorescence, pubescence, etc. Many of them are here mentioned only under minor variations, and some of the less important and unnamed ones are not mentioned at all, while those which seem to represent definite stages in the development of the species, or centers about which the minor variations may be grouped, are treated as subspecies. Even these accepted subspecies are sometimes so closely interlocking in their characters that the evolutionary lines can not be worked out with certainty at this time. This portion of the chart is therefore presented more for the purpose of indicating the characters used than to show phyletic lines.

The original form, which in turn gave rise to the others of this group, seems to have been something now included under the subspecies *ludoviciana*. The derivation of the others from this can be accounted for in accordance with the laws of phylogeny (see

Bessey's dicta, Mo. Bot. Gard. Annals 2:109, 1915), but if the sequence were reversed it would run counter to these laws. Examples of this will be given a little farther on. The subspecies *ludoviciana* is typically a form with small heads, the principal leaves with a few short lobes, as shown in tracings from the type (fig. 8), and an evident but light tomentum on the upper surface of the leaves, the lower surface heavily tomentose, as in all the subspecies of *A. vulgaris*. The concept is here extended, however, to include the more common form with the upper surface of the leaves nearly or quite glabrous; also forms in which the leaves are variously lobed or entire, since these characters have been demonstrated to be too subject to variation to be of taxonomic value. *Ludoviciana* is a derivative of *tilesi*, and not the other way around, as seems evident from its distribution and from the specialized nature of its characters, i. e. the reduced heads, each with a reduced number of flowers, the narrower and simply lobed leaves, and the tendency toward the development of a tomentum on the upper surface of the leaves.

A subspecies very close to *ludoviciana*, and united with it by Gray and others, is *gnaphalodes*. This differs in having leaves which are heavily tomentose on both sides, a character difference which ordinarily would not be considered as of much value, yet one which is here found to be the most constant of all those proposed for the breaking up of this complicated group of forms. Sometimes these two subspecies occupy adjacent habitats. Subspecies *ludoviciana* then occupies the more shaded or moist situations, the two forms thus standing somewhat in the relation of ecads to each other. At other times, however, one will occupy vast extents of territory to the complete exclusion of the other, as, for example, on much of the plains country east of the Rocky Mountains, where in some districts only *gnaphalodes* is found. Just as *ludoviciana* may be looked upon as a southeastern or Rocky Mountain development from *tilesi*, so *gnaphalodes* may be considered as the more xerophytic offshoot from *ludoviciana*, occupying in part the same geographic area but also extending farther towards the east. Various forms of leaves taken from plants growing on the same hillside are illustrated in figure 12.

In the northerly part of the Mississippi Valley the *gnaphalodes* stock has so modified the leaves that these have become elongated and drawn out at the apex into a more or less tail-like appendage, while at the same time the heads remain larger than usual. This is subspecies *longifolia*. It is easily recognized in its extreme development, but frequent intergrades reveal its undoubted connection with *gnaphalodes*. The leaves in *longifolia* are sometimes green on the upper surface. This is brought about by the shedding in age of the heavy tomentum and hence does not indicate a direct connection with *ludoviciana*. Various stages in this shedding process may be seen in specimens collected at Lake De Smet, Wyoming (Nelson 8545, UC).

The most striking of all of the subspecies of *Artemisia vulgaris* is *serrata*. This occurs only in the upper part of the Mississippi Valley, where it grows in good and rather moist soil. It is a larger plant than other subspecies of this region and bears much elongated panicles of rather small heads (see table 6). The principal distinguishing characters, however, lie in the leaves. These are remarkably constant in their lanceolate shape and in the distribution of the pubescence, the upper surface being always green and nearly or quite glabrous, the lower surface densely white-tomentose. The even serratures of the margins also are usually constant, but a few collections exhibit intermediate forms connecting with subspecies *ludoviciana* and *gnaphalodes*. Specimens referable to *gnaphalodes*, but with the leaves toothed somewhat as in *serrata* are: Spring Grove, Minnesota, Rosendahl 693 (Gr), and near Minneapolis, Minnesota, 1892, Aiton (Gr). Leaves with margins intermediate between these two subspecies are illustrated in figure 13. The shape of the leaf is sometimes exactly matched in plants identified as subspecies

ludoviciana, because of the entire margins and other characters (Glenwood, Minnesota, August, 1891, Taylor, UC). While the principal leaves of these are entire, the lower exhibit remote and irregular dentations not at all comparable to the even serratures of *serrata*. It seems, therefore, that, while this is an especially distinct form, and although

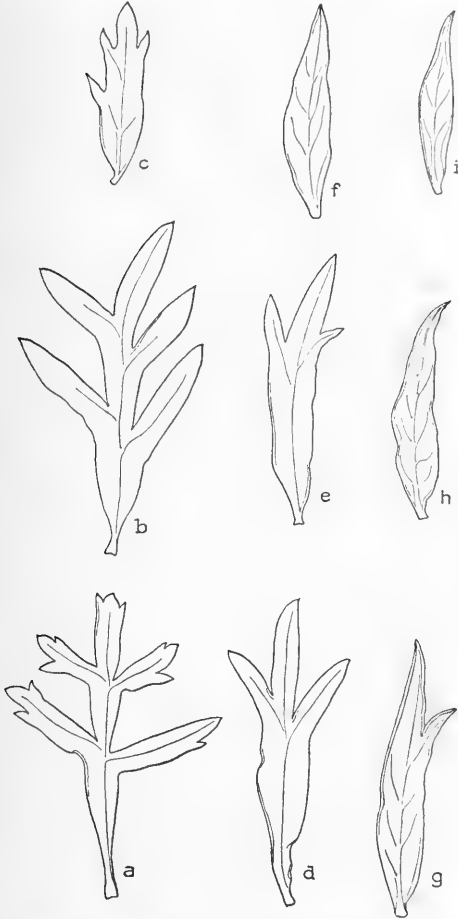


FIG. 12.

Variation in outline of leaves of *Artemisia vulgaris gnaphalodes*. The three leaves in each vertical row are from a single plant; the lowest leaf in each column is from near the base of the stem, the middle leaf from somewhat above midway of the stem, the highest leaf from the lower part of the inflorescence. All three plants were growing within 100 m. of one another near Golden, Colorado. The plant with leaves shown in first column was in loose soil with rank vegetation; the others on higher slopes, the soil hard and stony, the surrounding vegetation less rank. All of the leaves are densely tomentose beneath and scarcely less so above. Plant at left would be classed as *Artemisia brittoni* (minor variation 6) and plant at right as *A. gnaphalodes* by those who use leaf characters as specific criteria. All $\times 0.4$.

its exact origin can not now be traced, its connection with subspecies *ludoviciana* and *gnaphalodes* is sufficiently well established to justify its reduction to a subspecies of this group. (See fig. 13, p. 96.)

Close to *ludoviciana* but usually recognized by its more reduced, spike-like inflorescence, is subspecies *lindleyana*. The plants of this are often quite woody at the base. Here

also belongs subspecies *mexicana*, which is clearly a southern derivative of a *ludoviciana*-like ancestor but marked by a very leafy habit, the foliage continuing well up into the inflorescence, and by narrow leaves and lobes, these latter much elongated and with finely revolute margins. It appears to be an ecologic type, but it is so extreme and as far as known is so well restricted geographically that it perhaps has subspecific value. According to Rydberg, the leaves of the type are not revolute, and he therefore names the common form with revolute leaves as *A. revoluta* (see p. 86).

In the arid portions of the southern Rocky Mountains and northern Mexico and running out onto the plains to the southeast as far as Kansas is found yet another derivative of *ludoviciana*, namely, subspecies *wrightii*. This, also, is a more xerophytic type. Perhaps partly because of the more arid conditions under which it grows, and partly because of the increased light intensity, the foliage has reached the extreme in the matter of reduction of leaf surface. The leaves are small and divided into almost filiform seg-



FIG. 13.

Leaves of *Artemisia vulgaris gnaphalodes* and *A. v. serrata*: a, b, leaves of *gnaphalodes* from Spring Grove, Minnesota, *Rosendahl 693* (Gr); c, leaf of *serrata* from middle portion of stem, Fountaindale, Illinois, *Bebb* (Gr). All $\times 0.8$.

ments. Because of this notable narrowing of the lobes, the various forms here included under *wrightii* have been commonly treated as one or more distinct species, even by conservative systematists. But intermediate forms are so plentiful in all of the larger herbaria that they need not even be cited, and in the field it becomes impossible to draw any line between true *ludoviciana* and *wrightii*. However, the latter may stand as a subspecies to include these small and extremely narrow-lobed forms of the south. Within the subspecies *wrightii* may be detected several minor variations, as indicated on page 81. In some and perhaps in all of these, as well as in typical *wrightii*, the basal leaves on sterile shoots are floccose with a white tomentum on both surfaces, quite regardless of the nature of the pubescence on the upper leaves. Although this suggests a possible connection with some white-leaved ancestor, all of the other evidence points to *ludoviciana* as the source of this subspecies.

TABLE 6.—Variation in the subspecies of *Artemisia vulgaris*.

	Herbarium.	No. of bracts.	No. of ray-flowers.	No. of disk-flowers. ¹	Total flowers. ¹	Length of disk-corolla.
Subspecies <i>filisi</i>:						
Eastern Siberia.....	NY	9	9	21	30	mm. 2.5
Plover Bay, Siberia.....	Gr	10	10	16	26	2.7
Bering Sea.....	NY	10	13	35	48	2.5
St. Paul Island, Bering Sea.....	Gr	17 13	17 13	52 46	69 69	2.5
Dutch Harbor, Unalaska.....	Gr	12 12	10 7	30 15	40 22	3.5
Hushajak, Alaska.....	Gr	12	10	37	47	3.0
Dawson, Alaska.....	NY	12	14	35	59	3.0
British Columbia.....	NY	8 10	10 15	28 28	38 43	3.0
Wenatchee Forest, Wash.....	886446 US	11	13	46	59	2.6
Wallowa Mountains, Oreg.....	Gr	11 11	8 9	10 16	18 25	2.5
Bozeman Cañon, Mont.....	NY	9	8	17	25	2.0
Average.....		10	10	28	40	2.7
Subspecies <i>canadensis</i>:						
Spokane, Wash.....	Gr	13	7	18	25	2.5
Do.....	11621a CI	13	14 10	35 23	49 33	2.8
Do.....	11621b CI	12	10	19	29	2.6
Gilmore, Idaho.....	11548 CI	12	11	30	41	2.5
Near Sexton Glacier, Mont.....	1027299 US	13	12	30	42	2.5
Lima, Mont. ³	2942 NY	11	6	23	28	2.6
Near Belton, Mont.....	1027298 US	11	8	28	36	2.8
Little Belt Mountains, Mont. ⁴	NY	11	7	21	28	3.0
Yellowstone Lake ⁵	20753 R	14	10	28	38	3.0
Average.....		12	9	25	34	2.7
Subspecies <i>typica</i>:						
Upper Austria.....	29799 UC	10	8	9	17	2.4
Jarvikyla, Finland (980).....	UC	9 10	10 10	10 18	20 28	2.6
Thames River, Surrey, Eng.....	US	10 9	12 7	14 10	26 17	2.0
France.....	SF	9 10	6 7	5 8	11 15	2.7
Do.....	154861 UC	10 11	7 8	8 9	15 17	2.2
Italy.....	6495 Baker	9 10	7 6	9 12	16 18	2.0
Europe.....	29800 UC	9 10	6 7	9 10	15 17	2.8
Western Newfoundland.....	Gr	9 8	8 7	7 5	15 12	2.7
British Columbia.....	622063 US	10 9	8 7	8 5	16 12	2.3
St. John River, Me.....	29797 UC	16 12	9 7	9 7	18 14	2.6
Connecticut.....	29798 UC	9 10	7 7	8 8	15 15	2.5
Oswego, N. Y.....	193573 UC	12 16	8 7	15 14	23 21	2.6
Ulica, N. Y.....	29796 UC	10	9	9	18	2.1
Near Andover, N. J.....	29801 UC	13 18	8 9	9 8	17 17	2.1
Stepney, Conn.....	283798 US	10 10	10 8	17 15	27 23	2.6
Glynn County, Ga.....	431833 US	12	12	16	28	2.8
Detroit, Mich.....	983227 US	10 9	9 7	13 11	22 18	2.3
Ramsey County, Minn.....	US	12 14	8 10	12 10	20 20	2.4
Average.....		10	8	10	19	2.4
Subspecies <i>discolor</i>:						
Doyle Creek, Wyo.....	51519 UC	9	6	15	21	2.0
Sierra La Sal, Utah ¹	135408 UC	14	10	18	28	1.8
Stein Mountains, Oreg. ²	91235 UC	9	9	19	28	2.3
Mount Adams, Wash. ³	193455 UC	10	9	20	29	2.0
Durant, Mont. ⁴	11580a CI	9	8	16	24	2.2
Gilmore, Idaho.....	11552 CI	8	8	16	24	2.3
Inyo County, Calif.....	205772 UC	10	11	16	27	2.0
Average.....		9	8	17	25	2.0

TABLE 6.—Variation in the subspecies of *Artemisia vulgaris*—Continued.

	Herbarium.	No. of bracts.	No. of ray-flowers.	No. of disk-flowers. ¹	Total flowers. ¹	Length of disk-corolla.
Subspecies <i>heterophylla</i>:						
Edmonton, Alberta ²	NY	11 8	6 9	14 16	20 25	mm.
Wawawai, Wash. ²	NY	10	7	11	18	2.1
Klickitat County, Wash.....	29795 UC	9	7	15	22	2.7
Mount Puddo, Wash.....	Gr	8 8	9 8	20 15	29 23	3.0
Ketchum, Idaho.....	Gr	10 10	9 9	23 28	32 37	2.1
Grants Pass, Oreg.....	172631 UC	13 15	8 9	7 6	15 15	2.8
Do.....	29687 UC	10 11	6 8	9 15	15 23	2.3
Ormsby County, Nev.....	135381 UC	8 10	6 8	11 11	17 19	2.0
Butte County, Calif.....	171429 UC	8 10	6 6	7 11	13 17	3.0
Humboldt County, Calif.....	169318 UC	9 10	7 7	23 23	30 30	3.2
Princeton, Calif.....	71769 UC	8	5	10	15	2.5
Palo Alto, Calif.....	75361 UC	8 9	6 9	11 12	17 21	2.2
Verdugo Cañon, Calif.....	53973 UC	9 11	8 8	17 16	25 24	2.5
Los Angeles County, Calif.....	149246 UC	13 13	7 7	14 15	21 22	2.0
San Bernardino County, Calif.....	184750 UC	9 11	8 8	13 16	21 24	2.0
Average.....		10	7	14	21	2.5
Subspecies <i>litoralis</i>:						
Vancouver Island.....	NY	8 7	5 3	2 5	7 8	2.3
Montesano, Wash.....	NY	6 7	4 6	5 6	9 12	2.5
Whidbey Island, Wash.....	76560 UC	7 7	4	5	9	1.5
Chuckanut Bay, Wash.....	29802 UC	7 8	5 6	4 5	9 11	2.5
Chehalis County, Wash.....	173318 UC	7 8	6 7	3 4	9 11	2.7
Umpqua River, Oreg.....	29683 UC	7 6	4 5	4 4	8 9	2.5
Humboldt County, Calif.....	204825 UC	8	6 5	5 7	11 12	2.4
Scotia, Calif.....	127815 UC	7 9	4 5	3 3	7 8	1.5
Average.....		7	5	4	9	2.2
Subspecies <i>ludoviciana</i>:						
Albany County, Wyo.....	146529 UC	9 10	7 8	6 10	13 18	2.2
Rincon Mountains, Ariz.....	153811 UC	8 9	9 10	7 8	15 18	2.0
Marysvale, Utah.....	159142 UC	9 10	7 7	7 10	14 17	2.5
Klickitat County, Wash.....	130200 UC	7 8	6 6	9 12	15 18	2.3
Bluff Lake, Calif.....	149209 UC	7 9	7 6	7 6	14 12	2.8
Poison Spider Creek, Wyo.....	51764 UC	10	6	12	18	2.2
Carbon County, Wyo.....	69458 UC	10	7	15	22	2.4
Average.....		9	7	9	17	2.3
Subspecies <i>gnaphalodes</i>:						
Traverse County, Minn.....	194030 UC	8 8	5 6	5 5	10 11	2.0
Laramie, Wyo.....	51690 UC	10 13	7 10	15 20	22 30	2.5
Centennial, Wyo.....	70519 UC	10 11	10 10	13 17	23 27	2.5
Teton Forest, Wyo.....	91259 UC	10 12	7 7	12 16	19 23	1.9
Gunnison, Colo.....	34509 UC	10 12	9 9	19 20	28 29	2.5
Elko County, Nev.....	171417 UC	12 13	9 10	15 15	24 25	2.1
Modoc County, Calif.....	29669 UC	10 11	9 12	15 17	24 29	2.4
Oregon.....	91180 UC	9 11	7 8	13 14	20 22	2.7
Wallowa County, Oreg.....	170203 UC	10 12	7 8	21 21	28 29	2.0
Cañon County, Idaho.....	167954 UC	9 9	6 10	16 12	22 22	2.2
Montana.....	29764 UC	9 10	6 7	8 8	14 15	2.0
Sedan, Mont.....	166430 UC	11 12	7 8	12 17	19 25	2.5
Average.....		10	9	16	24	2.5
Subspecies <i>serrata</i>:						
Taylor Falls, Minn.....	29783 UC	9 9	8 8	7 10	15 18	1.6
Minnesota.....	67857 UC	12 13	8 7	5 4	13 11	2.0
Glenwood, Minn.....	29758 UC	11 12	6 7	12 11	18 18	2.0
Winona County, Minn.....	46282 UC	7 9	8 7	4 5	12 12	1.8
Northern Ill.....	193540 UC	9 7	9 7	5 5	14 12	2.0
Average.....		9	7	6	14	1.8

TABLE 6.—Variation in the subspecies of *Artemisia vulgaris*—Continued.

	Herbarium.	No. of bracts.	No. of ray-flowers.	No. of disk-flowers. ¹	Total flowers. ¹	Length of disk-corolla.
Subspecies mexicana:						
Durango, Mex.	91175 UC	11 13	8 9	15 18	23 27	mm. 2.4
Alvarez, Mex.	135371 UC	15	8	15	23
Chihuahua, Mex.	135375 UC	9 10	8 9	9 11	17 20	2.2
Jalisco, Mex.	135374 UC	10 11	7 8	9 10	16 18	2.0
Comanche Spring, Tex.	147496 UC	9 11	4 6	4 7	8 13	1.7
Lincoln County, N. Mex.	135373 UC	13	8 9	12 16	20 25	2.2
Socorro County, N. Mex.	135372 UC	11 13	7 8	13 13	20 21	2.5
Average.....		11	7	11	18	2.2
Subspecies wrightii:¹⁰						
Black Cañon, Colo. ¹¹	34510 UC	7 9	8 11	14 10	22 20	2.2
Marshall Pass, Colo.	34515 UC	10 13	11 9	16 11	27 20	2.0
Pagosa Spring, Colo.	34520 UC	12 8	7 6	8 6	15 12	2.0
Dale Creek, Colo. ¹²	Oster. 2010	11 11	8 8	9 10	17 18	2.2
Costilla County, Colo.	11092 CI	8 10	14 12	18 21	32 33	2.1
La Veta Pass, Colo.	11093 CI	9 10	16 13	17 14	33 27	2.0
Do.	11094 CI	10 9	10 9	15 14	25 23	2.2
San Juan Valley, Colo.	11122 CI	14 9	9 7	16 19	25 26	2.4
San Juan Mountains, Colo.	11104 CI	9 11	7 8	10 12	17 20	2.1
Southeastern Utah.	175395 UC	8 6	6 6	7 10	13 16	2.2
Do.	NY	9 9	6 5	7 6	13 11	2.3
Do.	NY	11 9	8 10	19 18	27 28	2.1
Desert Region.	91219 UC	9 7	7 7	8 4	15 11	2.0
San Francisco Mountain, Ariz.	135407 UC	6 9	4 5	5 6	9 11	1.8
Do.	11183 CI	8 10	14 12	16 16	30 28	2.0
Flagstaff, Ariz.	193609 UC	8 9	6 7	4 6	10 13	2.0
Chihuahua ¹⁴	Gr	14 13	18 16	16 18	34 34	1.9
Average.....		9	8	12	21	2.0

¹ The lower numbers sometimes are doubtless due to loss of flowers in pressing.

² Minor variation 61, same as *A. platyphylla* Rydberg.

³ Type of *A. floccosa* Rydberg, minor variation 19.

⁴ Type of subspecies *candicans* (Rydberg).

⁵ Type of *A. gracilentia* Nelson, minor variation 25.

⁶ Minor variation 53, *A. michauxiana* Besser.

⁷ Minor variation 30, *A. incompta* Nuttall.

⁸ Type of *A. herrioti* Rydberg, minor variation 27.

⁹ Duplicate type of *A. atomifera* Piper, minor variation 4.

¹⁰ Includes several specimens referable to minor variation 8, *A. carruthi* Wood.

¹¹ Minor variation 5, *A. bakeri* Greene.

¹² Type of *A. coloradensis* Osterhout, minor variation 9.

¹³ Type of *A. prinqueti* Greenman, minor variation 64.

ECOLOGY.

The subspecies of *Artemisia vulgaris* of the greatest ecological importance are *heterophylla*, *ludoviciana*, *gnaphalodes*, *mexicana*, and *wrightii*. These are all typically representative of the species in the presence of rootstocks, vigorous growth, and late blooming. As a consequence, they form societies in the late summer and autumn aspect of the climax grassland, and persist for a long time as relicts of this formation in cultivated regions. The similarity in their behavior is perhaps to be ascribed to their close relationship, and may explain their distribution, as they appear to be mutually exclusive to a high degree. They follow the grassland into the savannahs and parks of the foothill and montane zones, reaching the maximum elevation at about 9,000 feet in the Rocky Mountains.

Artemisia v. gnaphalodes is most characteristic of the true prairies, but is also an important society of the subclimax and mixed prairies. Like its relatives, it is strongly gregarious, owing to its stout rootstocks, and the society often has the appearance of many scattered clans. *Ludoviciana* is more typical of the foothill portions of the mixed prairie and runs high up in the great mountain parks, such as Estes Park. It tolerates considerable shade, and is an important feature of the ground-cover of yellow-pine woodland. The rootstocks are less stout than in *gnaphalodes*, and the plants make a more uniform society. In the mixed prairies of northern New Mexico and Arizona, *ludoviciana* is largely replaced by *mexicana* and especially *wrightii*, with essentially the same ecological

behavior. *Heterophylla* is the characteristic form in the bunch-grass prairies of California and Oregon, where it makes societies like those of *gnaphalodes*. In California especially it has largely disappeared with the native grasses, and is now found chiefly in the low savannah formed by the coast sagebrush. In Washington and British Columbia *heterophylla* is largely replaced by *tilesi*, which takes a similar rôle in the grassland.

In addition to the dominant grasses of the respective associations, these forms mix and alternate with a large number of subdominant herbs, especially the asters, goldenrods, sunflowers, and other species of the autumnal aspect. *Gnaphalodes*, *ludoviciana*, or *wrightii* is frequently associated with one or more of the other grassland species of *Artemisia*, namely, *dracunculus*, *campestris*, and *frigida*. On the Pacific Coast *heterophylla* is often found with *A. californica*, and in the interior with *A. tridentata*.

As indicators, all of the subspecies considered denote the climax association and climate, and hence are valuable in reconstructing grassland that has disappeared. This is particularly true in California, where the deep-rooted *heterophylla* persists long after the native bunch-grasses have been grazed out. In general, *gnaphalodes* and *ludoviciana* indicate greater moisture, as they are most abundant in the moister true prairies and foothills respectively. As a rule they are not good indicators of overgrazing and other disturbance, probably owing to their lack of mobility, and are in corresponding contrast to other grassland species, such as *A. frigida* and *campestris*.

USES.

This, the most abundant sagewort in western North America, forms an important part of the late fall and winter feed for all classes of stock, but especially for sheep. It is variously known on the ranges as sage-weed, white sage, and mugwort. The taste is so pungent that it is scarcely touched until after frost, but late in the season, when other feed is scarce, it is quite generally eaten. There seems to be no preference as to subspecies, since all of the common ones, particularly *discolor*, *ludoviciana*, and *gnaphalodes*, are reported upon favorably. It seems, therefore, that the inclusive name of *Artemisia vulgaris*, or sagewort, is the only one with which the grazing experts need to concern themselves when studying the value of these plants.

The medicinal properties of *Artemisia vulgaris* have led to its use for a great variety of diseases. This has been largely confined, however, to domestic practice, the plant being scarcely more than noticed in the pharmacopoeias. The subspecies *typica* is employed in Europe as an emmenagogue and for epilepsy and colds. In California subspecies *heterophylla* is used by the Indians as a remedy for colds, headache, fevers, stomach troubles, and rheumatism. The methods employed are described by Chesnut (Contr. U. S. Nat. Herb. 7:392, 1902). In France, typical *vulgaris* has been worked up into moxas, which are burned for purposes of cauterization. Since its value for this purpose depends chiefly upon the woolly tomentum, it seems that some of the more heavily tomentose American subspecies, such as *candicans* or *gnaphalodes*, would be better adapted to the purpose. The essential oils present have been studied by Rabak (Pharm. Rev. 24:324, 1906). By far the most important medical use of the plant is as a preventive of hay-fever in those cases which are caused by its own pollen. Some hay-fever sufferers are particularly sensitive to the pollen of this plant, as is indicated by skin-reaction tests. Such people find relief by taking at first injections of very dilute pollen solution (about 1:300,000) and gradually increasing the strength until no reaction is obtained. This desensitization enables the patient to pass through the hay-fever season without being subject to attacks, assuming that he is not suffering from the effect of other pollens as well. Preliminary studies indicate that the pollen of the different subspecies all react alike. Therefore, in testing and treating hay-fever cases, the specialist need pay no attention to the complicated series of subspecies and minor variations. (See further under *Atriplex rosea*, p. 260.)

12. ARTEMISIA BIENNIS Willdenow, Phytogr. 11, 1794. Plate 10. BIENNIAL SAGEWORT.

An annual or biennial herb from a taproot, 3 to 30 dm. high, nearly inodorous; stem simple up to the inflorescence, erect, striate, glabrous, often tinged with red; basal leaves crowded, widely petioled, 5 to 15 cm. long, twice pinnately parted or divided into lanceolate sharply toothed or cleft divisions, glabrous; upper leaves mostly larger, once pinnately parted into lanceolate toothed or entire divisions, glabrous; inflorescence a compound terminal spike, leafy throughout, 10 to 50 cm. long by 1 to 2 cm. broad or rarely the lower branches elongated and the inflorescence thus much broader, the short branches rigidly ascending; heads heterogamous, sessile, crowded, erect; involucre hemispheric, 2 to 3 mm. high, slightly broader; bracts 8 to 14, the outer ones narrow and green, the inner ones nearly orbicular and scarious except along the green midrib, all glabrous; ray-flowers 6 to 22 or perhaps more numerous, fertile, corolla oblique, slightly under 1 mm. long, granular; disk-flowers 15 to 40, fertile, corolla campanulate, about 1 mm. long, 3- or 4-toothed, granular; style-branches flat, truncate; achenes ellipsoid, longitudinally 4- or 5-nerved, glabrous.

Widely distributed in North America except in the southeast, presumably native only from the northern Rocky Mountains to British Columbia; Nova Scotia to New Jersey, Missouri, New Mexico, southern California, and British Columbia; also in Kamchatka. Type locality, said to be New Zealand, but this is erroneous. Collections: Gloucester County, New Brunswick, *Blake 5639* (Gr); Longueil, Quebec, *Brother Victorin 1054* (US); Naugatuck, Connecticut, August 30, 1903, *Bristol* (Gr); Canton, New York, *Phelps 1016* (Gr); Wayne County, Michigan, September 16, 1916, *Chandler* (US); Iowa City, Iowa, *Somes 3923* (US); Sheffield, Missouri, *Bush 3300* (Gr, NY, US); Castle Rock, Colfax County, New Mexico, August 28, 1913, *Wooton* (US); Palo Alto, California, *Baker 172* (DS, Gr, SF, US); Columbia River, in Klickitat County, Washington, September 29, 1883, *Suksdorf* (US); Beavermouth, British Columbia, *Shaw 1192* (Gr, NY); vicinity of Glacier Park Station, Montana, *Standley 17659* (US); Traverse County, Minnesota, September, 1893, *Sheldon* (US); Thomas Lake, Saskatchewan, *Macoun and Herriot 72834* (NY).

RELATIONSHIPS.

The close connection between this species and the two next following will be discussed under *A. annua*. It can not be separated from *annua* on the duration of the root, since this is variable and dependent upon local conditions. The most striking difference is the character of the inflorescence, but even this is untrustworthy in reduced forms in which the small heads closely simulate those of *annua*. The heads, however, are never nodding and never distinctly pedunculate, and the achenes are larger and more distinctly angled. Mature achenes are 1 mm. long, while those of related species are only 0.5 to 0.8 mm. long. Apparently there is a marked difference in the odor of the crushed herbage, but this requires verification by field examination of specimens from numerous widely separated localities. There is little to indicate which of these two species is the more primitive, but the larger heads with more numerous flowers seem to assign this position to *biennis*. *A. annua* then becomes a derivative that has undergone a reduction in the number of flowers at the same time that the inflorescence has become more freely branched and the heads smaller in size.

ECOLOGY AND USES.

Artemisia biennis is a biennial or annual with a taproot, blooming from August to December. It occasionally forms clans in the grassland formation, but it is typically a ruderal, growing along roadsides and in waste places. In these, as well as in burns, it sometimes makes a pure consociation, but it is usually associated with other weeds, such as *Medicago hispida*, *Madia sativa*, and *Centaurea melitensis*.

Although no practical value attaches to this plant, it is of economic interest because of its abundance as a weed in certain districts, especially in the Mississippi Valley from about the latitude of Missouri northward. Here it often completely occupies fallow fields and other waste places, reproducing abundantly from seed. It is easily held in check by cultivation or even by cutting, if the tops are destroyed before the seed ripens, but the cutting must extend over at least two seasons since the root is often of biennial duration.

Artemisia biennis is objectionable also because of its pollen, which, as determined by actual tests, is one of the causes of hay-fever in late summer and autumn. The pollen is spherical, spiculate, and produced in great abundance. Its use in pollen therapy is recommended for those patients who give a positive reaction to it in skin-tests.

13. ARTEMISIA ANNUA Linnaeus, Sp. Pl. 847, 1753. Plate 10. ANNUAL SAGEWORT.

An annual herb from a taproot, 3 to 30 dm. high, very sweet-scented; stem simple below, erect or weak and flexuous, striate, glabrous, rarely tinged with red; basal leaves crowded, petioled, 3 to 10 cm. long, once or twice pinnately parted or divided into lanceolate pinnatifid segments, glabrous; upper leaves very similar; inflorescence a wide and loose terminal panicle, leafy throughout, 10 to 50 cm. long, 3 to 20 cm. broad, the very slender branches (racemes) widely spreading or recurved; heads heterogamous, peduncled, not crowded, often nodding; involucre hemispheric, 1 to 1.5 mm. high, slightly broader; bracts 8 to 14, the outer ones narrow and green, the inner ones broader and scarious except along the green midrib, all glabrous; ray-flowers 5 to 9, fertile, corolla oblique, about 0.6 mm. long, granular; disk-flowers 5 to 20, probably fertile, corolla broadly cylindric, about 1 mm. long, toothed, granular; style-branches flat, truncate; achenes narrowly turbinate, apparently not nerved, glabrous.

Native of Asia, where widely distributed, except in the extreme south, and of eastern Europe, naturalized throughout the central and eastern part of the United States, to a limited extent in the West, and in eastern Canada. Type locality, Siberia. Collections: Charlottetown, Prince Edward Island, *Fernald 8236* (Gr); Kingston, Ontario, September 13, 1900, *Fowler* (Gr, US); Bridgeport, Connecticut, July 9, 1895, *Eames* (US); Campbell County, Virginia, *Fauntleroy 621* (US); Cooke County, Tennessee, *Kearney 793* (NY, US); Ralls County, Missouri, September 13, 1913, *Davis* (SF); Benton County, Arkansas, *Plank* (NY); Canton, northern New York, *Phelps 1768* (Gr, US); Riverton, Nebraska, *Bates 4752* (Gr); Los Angeles, California, 1908, *Arnold* (Gr).

RELATIONSHIPS.

This is one of three species of the section *Abrotanum* that form a close group or subsection, the other two being *biennis* and *klotzschiana*. They are all annuals or at the most biennials with a straight taproot and a terminal inflorescence, which begins well toward the base of the strict, erect stem. However, some doubt as to the close relationship between *annua* and the other two was introduced by J. D. Hooker who, in his *Flora of British India*, reported as follows (*Fl. Brit. Ind.* 3:323, 1881): "Though usually placed in the section *Abrotanum*, I find the ray-flowers to be always fertile and the disk-flowers sterile." In that work *annua* was transferred to the section *Dracunculus*. While the material now available is too young to permit of a definite statement as to the fertility of the disk-flowers, the achenes are well formed, and both these and the corollas are almost exactly like those of *A. biennis* at the same stage of development, except that they are somewhat smaller. In any event, the two are so close in all other essentials that their distribution into different sections seems scarcely advisable. The probable origin from *A. biennis* has been discussed under that species.

ECOLOGY AND USES.

Artemisia annua is an annual with a taproot, which occurs in America as a naturalized weed in waste places, and in fallow fields, where it forms a consociety of the secondary succession.

It is probable that this species is not sufficiently abundant at any place in America to be of much interest either as a weed or as a cause of hay-fever. It may be held in check by the methods described under *A. biennis*, but the process may be simplified because of the annual duration of the root.

14. ARTEMISIA KLOTZSCHIANA Besser, *Linnaea* 15:107, 1841. Plate 10.

An annual herb from a taproot, 5 to 10 dm. (or more?) high, the odor not known; stem simple below, strictly erect, striate, conspicuously canescent, reddish where the tomentum has been rubbed off; basal leaves crowded, short-petioled, less than 2 cm. long, bipinnately divided into filiform segments, canescent; upper leaves 1 to 2 cm. long, once or twice pinnately parted or divided into linear-filiform segments, gray with a dense somewhat villous tomentum; inflorescence a compound terminal spike nearly as long as the whole plant, short-leafy throughout, 20 to 50 cm. (or more?) long, about 2 cm. broad, or much broader when composed of ascending spike-like branches; heads heterogamous, sessile or subsessile, erect; involucre hemispheric, 2.5 to 3 mm. high and slightly broader; bracts 12 to 18, all elliptic, green beneath the canescent tomentum save for a narrow white-scarious border; ray-flowers 50 to 70 (?), fertile, corolla narrowed above, less than 1 mm. long, granular; disk-flowers 6 to 12, fertile, corolla campanulate, about 1 to 1.3 mm. long, 4- or 5-toothed, granular; style-branches of ray-flowers acute, of disk-flowers truncate at the penicillate summit; mature achenes not seen.

Mexico, from Coahuila and San Luis Potosi to Vera Cruz and Hidalgo; also in Ecuador. Type locality, plains of Perote, Vera Cruz. Collections: Saltillo, Coahuila, *Palmer 87* (Gr); San Luis Potosi, *Schaffner 706* (NY, US); city of Zacatecas, *Palmer 784* (Gr); near Zontecomate Station, Hidalgo, *Pringle 8918* (Gr, NY, UC, US); Pachuca, Hidalgo, *Purpus 1566* (NY, UC).

RELATIONSHIPS.

There is little doubt that this species is closely related to *A. biennis*, notwithstanding its very different appearance due to the remarkably dense gray pubescence. The leaves are much smaller in the present species, the involucre bracts are narrower and less scarious, and the achenes are slightly smaller and probably less distinctly angled. It is not impossible that the disk-achenes both in *klotzschiana* and *annua* are partly sterile, whereas they are normally all fertile in *biennis*, but this opinion requires more material before it can be verified. The exceptionally large number of ray-flowers, that is, 54 to 68 in the plants examined, is unique, but the number will doubtless be found to be more variable as further collections are studied.

There is a wide gap between the geographic area occupied by this species and that of *A. biennis*. It is not surprising, therefore, that a number of minor morphological differences can be found, as noted above, and that there are no intermediate forms as to pubescence. It is possible that *klotzschiana* is an offshoot from *A. vulgaris* through subspecies *wrightii*, which it much resembles in superficial appearance, but from which it differs in floral characters, the large number of ray-flowers, and especially in the very different root-system.

The extension of range of this species southward to Ecuador is on the basis of a single specimen at the New York Botanical Garden collected by Rose. Further field exploration will be necessary to determine whether it is a native so far south or whether it has been introduced from Mexico.

ECOLOGY AND USES.

Artemisia klotzschiana is an annual with taproot, which forms clans in the desert plains grassland at high altitudes in Mexico. So far as known, no use is made of this species.

15. ARTEMISIA BIGELOVI Gray, Pacif. R. R. Rep. 4:110, 1857. Plate 9. FLAT SAGEBRUSH.

A low shrub, commonly 2 to 4 dm. high, the odor faint, pleasant, not pungent; stems many, spreading below, the numerous flowering branches slender and erect, the bark apparently sheathing on the old parts, the twigs densely silvery-canescens, not striate; principal leaves sessile by a narrow base or apparently petioled, linear-cuneate, 1 to 2 cm. long, 2 to 4 mm. wide, sharply 3-toothed at the truncate apex or many entire, silvery-canescens; upper leaves linear-elliptic or linear-cuneate, mostly entire, acute or slightly obtuse, silvery-canescens; inflorescence an elongated narrow panicle with short recurved branches, sometimes nearly simple and spike-like, 8 to 20 cm. long, 1 to 4 cm. broad; heads heterogamous, or rarely homogamous on the same plant by reduction of the ray-flowers, sessile, several in each short recurved cluster; involucre turbinate, 2.5 to 3.5 mm. high, 2 to 2.5 mm. broad; bracts 8 to 12, the outer ones ovate, thick, and only half as long as the inner ones, these oblong and obtuse, all densely short-tomentose, the margins scarious; ray-flower usually solitary, sometimes 2, or wanting, corolla cylindric, 1 to 1.5 mm. long, narrowed above, obscurely toothed; disk-flowers 1 to 3 (usually 2), fertile, corolla broad-funnelform, 5-toothed, 2 to 3 mm. long, glabrous; style-branches of ray-flowers 2-cleft, exserted, of disk-flowers 2-cleft, the branches erose-truncate, included; achenes of both ray and disk ellipsoid, about 5-ribbed, glabrous.

Southern Rocky Mountains, from southern Colorado and southeastern Utah to northwestern Texas and western Arizona. Type locality, rocks and cañons on the Upper Canadian, Texas. Collections: Bluffs near Pueblo, Colorado, September, 1873, *Greene* (Gr); Soda Springs Ledge and Frank's Ranch, Cañon City, Colorado, *Brandegee* 996 (UC); southeastern Utah, *Rydberg* and *Garrett* 9876 and 9891 (NY, UC); type collection, 1853-54, *Bigelow* (Gr, NY "Rocky Dell, September 18, western border of Texas," according to label in Torrey Herb.); White Mountains, New Mexico, *Wootton* 502 (NY); Burro Mountains, New Mexico, *Rusby* 232, in part (UC); near Farmington, northwestern New Mexico, *Hall* 11141 (UC); Navajo Indian Reservation, Arizona, *Standley* 7355 (NY, type collection of *A. petrophila* Wootton and Standley, minor variation 1); Billings, Arizona, *Jones* 4571 (US); Grand Cañon, Arizona, *Hall* 11187 (CI).

SYNONYM.

1. ARTEMISIA PETROPHILA Wootton and Standley, Contr. U. S. Nat. Herb. 16:193, 1913.—Described as having homogamous heads, but in the type specimens the flowers are too immature for a positive determination of this point. In every other respect the specimens are exactly like *A. bigelovi*, which apparently was overlooked when the original diagnosis was prepared. The type came from near Farmington, New Mexico, where typical *bigelovi* is plentiful, especially on the low hills towards the south.

RELATIONSHIPS.

The habit, general appearance and vegetative characters of this species are so nearly those of *A. tridentata* that it is often so labeled in herbaria, but the presence of marginal flowers plainly different from those of the disk assign it on technical characters to another section of the genus, namely *Abrotanum*. The total number of flowers in the head is greatly reduced. The number of ray-flowers is never more than 2, usually 1, and sometimes none. This last condition, if constant, would assign the species to the section *Seriphidium*, but in no case has a plant been found in which more than a small percentage of the heads were without ray-flowers. It may therefore be accepted as a highly modified member of *Abrotanum*, although not approached by any other species of this section.

In thus temporarily assigning *bigelovi* to *Abrotanum* the possibility of its representing the starting point of the *Seriphidia* should be considered. The similarity to *A. tridentata*, of this section, seems to be more than accidental. The tridentate character of the leaves, for example, is almost identical in these two species and does not occur in any other American species. The southerly distribution of *bigelovi*, along the borders of the much more widespread *tridentata*, also suggests that it may be the precursor of this species and hence probably of all of the American *Seriphidia*. If this conclusion is correct, then this section, as generally accepted, had two origins, the other being from Old World species. This polyphyletic origin would account for the fact that the American members of *Seriphidium* have little in common with the Eurasian members, and the wide geographic gap between these two groups also would thus be explained. Since such a hypothesis necessitates parallel development on the two continents in only one character, namely, the suppression of the ray-flowers, there is no serious objection to its acceptance, but, on the other hand, there is no immediate need of breaking the section *Seriphidium* into two sections until this point can be better substantiated and characters brought forward to serve for their differentiation. This is impossible at the present time, because of the want of a thorough knowledge of many Old World species.

The variation in the number of ray-flowers and of disk-flowers is indicated in table 7. The tabulation also brings out the fact that there is but slight variation in any of the characters enumerated. This constancy and apparent absence of plasticity is noticeable also in the habit and vegetative characters, and tends to confirm the view that *bigelovi* is an ancient form which, although perhaps once serving as a starting-point for the *Seriphidium* stock, at least as to American species, is now in a quiescent condition.

TABLE 7.—Variation in involucre and floral characters of *Artemisia bigelovi*.

	Herbarium.	Height of involucre.	No. of ray-flowers.	No. of disk-flowers.	Length of disk-corolla.
		mm.			mm.
South Pueblo, Colo.....	Gr	3.0 2.5 3.0	2 0 1 1	1 2 1 2	2.2 2.5 2.1
Cañon City, Colo.....	205778 UC	2.8 2.4 2.5	0 1 0 1 1	2 2 2 2 2	2.0 2.2 2.0
Do.....	205785 UC	2.5 2.7 2.6	1 1 1	2 2 2	1.7 2.0 1.8
Western Texas (type).....	Gr	2.6	1	2	2.1
Near Farmington, N. Mex.....	205779 UC	3.0 3.2	1 1 1	2 2 2	2.5 2.4 2.5
Northwestern N. Mex.....	205783 UC	3.2 3.5 3.5	0 1 1 1 1	3 2 2 2 2	2.8 2.7 2.5
Near Farmington, N. Mex.....	11128 CI	3.0 2.8 2.9	1 1 1	2 2 2	2.6 2.6 2.4
Painted Desert, Ariz.....	11172 CI	2.8 2.9 2.8	1 1	2 2	2.0 2.1
Do.....	205782 UC	3.4 3.5 3.5	2 2 1	1 1 2	2.3 2.5 2.5
Cocconino County, Ariz.....	205784 UC	3.0 2.9 3.0	0 1 1 1 1	2 2 2 1 2 2	2.5 2.6 2.6
Chambers, Ariz.....	11150 CI	3.4 3.5 3.5	1 1 0 1 1	2 2 2 2 2	2.6 2.5 2.6
Chalcedony Park, Ariz.....	205780 UC	3.2 3.3 3.1	1 1 1	2 2 2	3.0 2.8 2.8
Near Flagstaff, Ariz.....	205781 UC	3.0 2.8 2.7	1 1 1	2 2 1	2.0 2.0 1.9
Grand Cañon, Ariz.....	11187 CI	3.0 3.3 3.3	0 2 1 1 1	2 0 1 1 1	2.5 2.4 2.5

ECOLOGY.

Artemisia bigelovi is a dwarf shrub, closely resembling low forms of *A. tridentata* produced by overgrazing and burning. In the mixed prairie of northern New Mexico and Arizona it often forms a dominant society similar to the low savannah produced by sagebrush on the northern Great Plains. Like the latter, it is really a consociety post-climax to the dominant grasses, and hence is most abundant in the subclimax stage preceding them. It is itself dominant in low areas and on rocky ridges where it is gradually replaced by the grasses as the succession advances. It is especially characteristic of cedar savannah, owing to the generally rocky soil. It is regularly associated with *Hilaria jamesi*, *Sporobolus cryptandrus*, and *Bouteloua gracilis*, but gradually disap-

pears as the grama sod becomes close. It mixes more or less with *A. tridentata*, *Chrysothamnus nauseosus junceus*, *Atriplex confertifolia*, and especially *Gutierrezia sarothrae*.

This species is an indicator of somewhat less xerophytic conditions, particularly in consequence of less competition, and is to be regarded as a relict in the drier grassland areas. It doubtless owes its form largely to grazing, and overgrazing of the grasses causes it to persist in the climax where it would otherwise disappear.

USES.

The foliage is more palatable to stock than that of the common sagebrush. The taste is less bitter, the odor less strong, and the slender, leafy twigs are less woody. It is browsed in preference to other shrubs in the regions where it grows and is reported by grazing examiners as "very good." Over much of its distributional area, however, the plants are not sufficiently abundant to add largely to the value of the range. It is of greatest importance in northern Arizona and northern New Mexico.

SECTION II. ABSINTHIUM.

PHYLOGENY OF THE SPECIES.

The species which gives its name to this section occurs in America only as an introduction and is not directly connected with the others. The remaining three are of one stock, and apparently stand in direct relation to one another. The ancestral form was quite certainly a perennial Siberian or at least Arctic herb. The development of a subshrubby habit and dissected foliage resulted in *A. frigida*, which spread out over Eurasia in a variety of forms and also invaded North America, occupying large areas on the plains and foothills as far south as Texas and Arizona. From this developed *scopulorum* and *pattersoni*, which came to occupy the higher altitudes in the mountains of western North America, where they are now widely isolated from all of their relatives except *frigida*. They retained the herbaceous habit, but the inflorescence was so narrowed as to become scarcely more than a raceme. *A. pattersoni* apparently arose directly from *scopulorum* in response to more intense alpine conditions. *A. rupestris* does not occur in America, but is inserted in the chart, since possibly it represents the ancestor of *frigida*. It is probable, however, that evolution has developed in the opposite direction, that is, *rupestris* arose through the loss of pubescence. The detailed statistics and other data from which the above conclusions have been drawn are given in the paragraphs on relationships that accompany each of the species in the following account.

16. ARTEMISIA ABSINTHIUM Linnaeus, Sp. Pl. 848, 1753. Plate 11. ABSINTHE SAGEWORT.

A perennial herb, but sometimes slightly woody at base, 4 to 10 dm. high, very fragrant; stems clustered, simple below, erect, striate, thinly cinereous or glabrate and then commonly reddish; basal leaves long-petioled, rounded-ovate in outline, 3 to 5 cm. long in addition to the petiole, 2 or 3 times pinnately parted into oblong or oblanceolate obtuse often toothed lobes, silky-canescens, sometimes less so on the upper side; upper leaves with fewer lobes and these mostly lanceolate and acute, those of the inflorescence from parted to merely cleft or entire and sessile, all silky like the lower; inflorescence a profuse leafy panicle with straight ascending branches, 15 to 40 cm. long, 5 to 20 cm. broad, occasionally much narrowed, the tips of the branches extending beyond the leaves; heads heterogamous, short-peduncled, nodding; involucre hemispheric, 2 to 3 mm. high, 3 to 4 mm. broad; bracts 12 to 18, the outer linear, the inner broadly elliptic and obtuse, all canescent, but the inner with broad scarious margins; receptacle covered with long white hairs; ray-flowers 9 to 20, fertile, corolla 1.5 mm. long, obliquely short-

toothed; disk-flowers 30 to 50, fertile, corolla campanulate, about 1.5 to 2 mm. long, 5-toothed, glabrous; style-branches spreading, those of the disk-flowers truncate and penicillate at the ends; achenes nearly cylindrical, but narrowed at base and slightly rounded to the summit, smooth, glabrous.

Native of Europe, thoroughly established as an introduced wayside plant in eastern Canada and northern New England; less common from North Carolina to Utah, eastern Washington (where spreading rapidly), central Oregon, and British Columbia. Type locality, Europe. Collections: Near Topsail, Conception Bay, Newfoundland, *Howe*

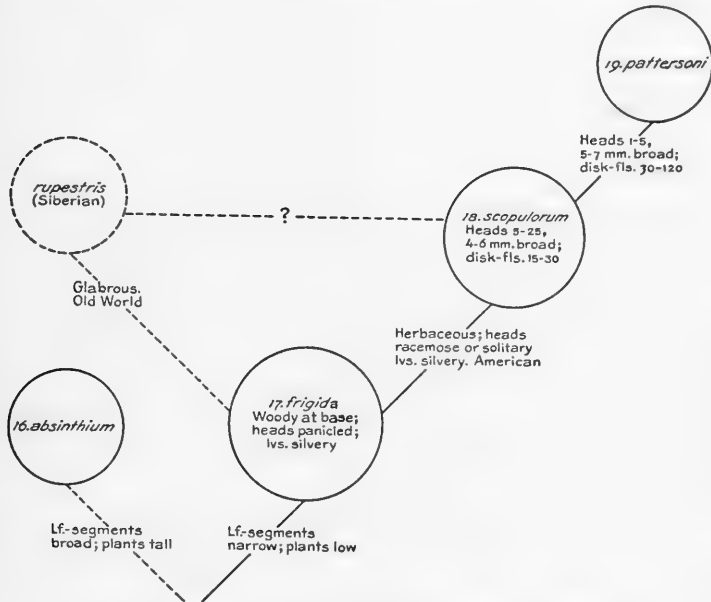


FIG. 14.—Phylogenetic chart of the species of *Artemisia* section *Absinthium*.

and *Lang 1214* (Gr, NY); Brome, Quebec, *Pease 1311* (Gr); Plevna, Ontario, August 14, 1902, *Fowler* (Gr); Veazie, Maine, July 31, 1891, *Fernald* (Gr); Milford, Connecticut, *Williams 5539* (Gr); Morristown, New York, *Phelps 1767* (Gr); Brookings, South Dakota, September, 1893, *Thorner* (UC); Yellow Bay, Montana, *Butler 470* (NY); Medicine Hat, Assiniboia, *Macoun 10980* (Gr); Salem, Oregon, *J. C. Nelson 2395* (Gr, US).

RELATIONSHIPS.

This differs from the native members of its section in the much more robust habit and ample foliage. It is never decidedly woody at the base, as is usually true of *A. frigida*, and the profuse leafy panicle at once distinguishes it from *A. scopulorum*. However, in technical characters it is very close to both of these, thus lending support to the view that the section *Absinthium* is a natural group, even though its members are few and widely separated geographically. Outside of the members of its own section, it is most nearly like the native *A. franserioides*, of the southern Rocky Mountains.

ECOLOGY AND USES.

The ecology of this species as a native plant is unknown; in this country it is a ruderal, associated for the most part with other roadside weeds.

This herb, now commonly known as wormwood, was much used by the ancients for various maladies and for counteracting witchcraft and necromancy. It is still grown in Europe and to some extent in this country as a medicinal plant. An infusion prepared from the leaves and tops is useful as a mild tonic when taken in moderate doses, but it is very powerful when administered in quantity. It was formerly used also as an anthelmintic and thus acquired its common name of wormwood. A dark-green volatile oil is obtained by distillation of the dry tops. This oil has the strong odor of the plant and is a powerful local anaesthetic, being useful when applied locally for rheumatic pains and in the form of a liquor as a narcotic stimulant in cerebral exhaustion. It has been found by Charabot and Laloule (Bull. Soc. Chim. France 4:280-290, 1907) that this oil forms most abundantly just before the flowering period and that it is more plentiful in the leaves than in the stems. These investigators suggest that it is used in completing the ripening of the seed. No oil was found in the roots until after the period of flowering, when its relative proportion was considerably increased. Salt of wormwood is the ash left after burning and consists chiefly of carbonate of potash. The well-known absinthe, used especially in France, is a beverage made by infusing the plant in alcohol. In some European countries the leaves are used in place of hops in the manufacture of beer.

17. ARTEMISIA FRIGIDA Willdenow, Sp. Pl. 3:1838, 1804. Plate 11. PRAIRIE SAGEWORT.

A perennial herb but often decidedly woody at the base or even somewhat shrubby, 1 to 4 dm. high, very fragrant; stems freely branched from the base, decumbent or spreading below, the annual branches erect, very leafy, not striate, cinereous or silky, the old bark brown; basal leaves crowded, petiolate, roundish in outline, 0.5 to 1 cm. long beyond the petiole, twice ternately or quinately dissected into linear or narrowly oblanceolate acute divisions and usually a pair of simple or 3-parted stipule-like divisions at base of petiole, silvery-canescens; upper leaves like the lower, but less dissected and becoming sessile; inflorescence a narrow short-leafy panicle with nearly erect racemiform branches, 10 to 30 cm. long, 1 to 10 cm. broad, or much reduced and raceme-like in dwarf forms of poor soil; heads heterogamous, sessile or short-peduncled, nodding; involucre hemispheric, 2 to 3 mm. high, 4 to 5 mm. broad; bracts 11 to 18, those of the outer series linear and herbaceous (scarcely shorter than the inner), the others lanceolate to ovate, all densely long-villous, the inner with broad whitish scarious margins; receptacle densely villous; ray-flowers 10 to 17, fertile, corolla contracted above, about 1 mm. long; disk-flowers 25 to 50, fertile, corolla funnelliform, 1.5 to 2 mm. long, 5-toothed, glabrous or granular-granuliferous especially on the tube; style-branches of ray-flowers obtuse, of disk-flowers truncate and fimbriate at the ends; achenes subcylindric, narrowed at base, truncate or slightly rounded at summit, scarcely ribbed, glabrous.

On high plains and in the mountains, Saskatchewan to Minnesota, Kansas, western Texas, northwestern Arizona, Utah, British Columbia, and Alaska; also native of Siberia; introduced in Nova Scotia, eastern Canada, and New Jersey. Type locality, Davuria, eastern Siberia. Collections: Vicinity of Ottawa, Ontario, *Rolland 6120* (Gr); Fairville, New Brunswick, in train yards, *Fernald 2266* (Gr); Custer, Montana, September 10, 1890, *Blankinship* (UC); Brookings County, South Dakota, August, 1892, *Thorner* (Gr, UC); near Minneapolis, Minnesota, August, 1889, *Sandberg* (UC, US); Laramie Hills, Wyoming, *Nelson 5336* (UC); Thomas County, central Nebraska, *Ryberg 1733* (Gr, US); Denver, Colorado, *Eastwood 122* (Gr, UC); east of Eagle Mountain, Texas, November 1881, *Havard* (US); near Pecos, San Miguel County, New Mexico, *Standley*

5212 (Gr, NY); Flagstaff, Arizona, September 5, 1894, *Toumey* (UC); Table Mountains, Nevada, *Purpus* 6382 (UC); eastern Washington, *Griffiths* and *Colton* 362 (NY); Thompson Falls, Idaho, *Sandberg* 981 (Gr, NY); vicinity of Banff, Alberta, *McCalla* 2019 (NY, US); Fort Chippewyan, Athabasca, *Preble* 187 (US); Kamloops, British Columbia, July 28, 1890, *Macoun* (US); Klondike Valley, near Dawson, Yukon, *Macoun* 79016 (NY).

MINOR VARIATIONS AND SYNONYMS.

1. *A. FRIGIDA* GMELINIANA Besser, Hooker, Fl. Bor. Am. 1:321, 1833.—Only a foliage form of *A. frigida*. Lower leaves long-petioled, 3-parted, the segments 5-parted, lobes linear, acute, the middle ones short, lowest lobes stipule-like; cauline leaves pinnatisected, the lower segments remote from the upper. Collected on the Saskatchewan.

2. *A. VIRGATA* Richardson, Franklin's Journey, App. 747, 1823.—According to W. J. Hooker (Fl. Bor. Am. 1:321, 1833), this is identical with No. 1 of this list.

RELATIONSHIPS.

Artemisia frigida is most nearly approached by species of northern Europe and Siberia. Since it is most plentiful and variable in northern regions, it seems quite certainly to be of boreal origin. It is in no way connected with Mexican or other southern forms. Several Old World species of its section resemble it in general appearance, but differ in such details as having pilose or even lanate corollas. This leaves but one species to which it can be directly compared, namely, *A. rupestris* Linnaeus, a rather common plant from Scandinavia to Siberia, where it overlaps the range of *frigida*. These two approach each other so closely in habit as well as in all important characters that they might almost be taken as one collective species. *A. rupestris* is apparently the derivative, since in it

TABLE 8.—Variation in *Artemisia frigida* (a stable species).

	Herbarium.	Involucre.		No. of ray-flowers.	No. of disk-flowers.	Length of ray-corolla.	Length of disk-corolla.
		Height.	No. of bracts.				
		mm.				mm.	mm.
Near Bosler, Wyo. (dwarf).....	CI	2.2	13 16	9 12	28 33	1.5	1.6
Golden, Colo.....	CI	2.0	14 15	10 10	23 26	1.3	1.6
Palmer Lake, Colo.....	CI	2.2	14 13	13 16	33 29	1.3	1.4
Do.....	UC	2.1	15 14	10 14	35 29	1.5	1.7
Salida, Colo.....	205770 UC	2.0	13 15	8 12	25 29	1.4	1.6
East Denver, Colo.....	UC	2.0 to 2.5	11-18	10-17	20-37	1.2-1.7	1.5-2.0
Table Mountains, Nev.....	91208 UC	2.0	15 14	10 11	34 29	1.3	1.7
Alaska.....	190648 UC	2.1	14	14	32	1.4	1.7
Average.....		2.1	14	11	33	1.4	1.6

the inflorescence has undergone reduction to a nearly or quite simple raceme, as in *A. scopulorum*, and the leaves have a more decidedly pinnate arrangement of the segments. The foliage is almost glabrous and therefore green instead of silvery-white as in *A. frigida*. It apparently has larger heads with more numerous flowers, about 70 in the specimens at hand, but this may not be constant. While these characters prevent the merging of *A. frigida* into this older species, the phylogenetic connection between the two is established with reasonable certainty. The nearest American representatives are *A. scopulorum* and *A. pattersoni*. It seems probable that these have descended directly from *A. frigida*, as shown under the next species.

Variation within the species has resulted in the recognition in Asiatic collections of a considerable number of forms, some of which have been treated as species. In America, however, there is a remarkable constancy in all essential characters. The only form indicated as in any way divergent is the one listed above under Minor variations.

The abundance of the species here and its practically continuous distribution over the greater part of its range accounts perhaps for its failure to develop divergent forms. Table 8 shows that the extent of variation in characters usually employed for taxonomic segregation is not great. It will be noted also that the variation is quite as extensive in plants growing close together as when they are selected from widely separated localities. This is seen in the sixth entry, where the figures represent the extremes of 8 plants, all gathered on the plains at East Denver, Colorado, from an area of only a few hectares. The variation here is about as great as between the other collections listed, showing that there is no tendency towards a segregation of forms in the territory covered by this test.

ECOLOGY.

Artemisia frigida is a perennial mat-forming herb, often with a more or less woody base. It is one of the most characteristic autumnal societies of the mixed prairie, ranking second only to *Gutierrezia sarothrae*. Its abundance in the climax is partly a consequence of grazing, and is due to the position of the leaves in a mat. As a result it is one of the chief indicators of overgrazing on the Great Plains, usually mixing with *Gutierrezia* in the central portion, exceeding it in the northern part, and falling far below it in abundance in the south. In fallow and abandoned fields it often forms a nearly pure consociety, subclimax to the grass dominants. In its behavior to disturbance it is similar to *A. campestris* and *A. dracunculus*, with which it is often associated.

USES.

The prairie sagewort is reported by stockmen and foresters as furnishing an important supply of forage in late fall, winter, and early spring. According to Macoun, it is of great economic importance as a forage plant in Canada (N. Am. Fauna 27:534, 1908), but in the Plains States, where there is a better supply of other range plants, it is regarded as a weed. It has been used medicinally to some extent in the Rocky Mountain States under the names of Sierra salvia, Rocky Mountain sage, and wild sage. A cold infusion was prepared and this administered as a diuretic and mild cathartic, but it is now largely replaced by other drugs. The constituents have been studied by Rabak (U. S. Dept. Agr. Bur. Plant Ind. Bull. 235:21, 1912). This investigator found that the herbage contained 0.41 per cent of a very fragrant essential oil at the period of flowering, and 0.26 per cent after blossoming. Rabak reports that the oil contains borneol camphor and cineol (eucalyptol), both of which have valuable antiseptic qualities; also some fenchone and both free and combined acids. He makes the suggestion that *Artemisia frigida* be planted for medicinal use and for use in the manufacture of celluloid; also as an ingredient for medicinal soaps or as a scenting substance. The pollen, which is smooth and 3-lobed, is the cause of some of the most severe cases of hay-fever in the districts where the plant is abundant. It therefore enters into pollen therapy as a preventive (see *A. vulgaris*, p. 100).

18. ARTEMISIA SCOPULORUM Gray, Proc. Acad. Phil. 1863:66, 1863. Plate 12. DWARF SAGEWORT.

A perennial herb with a slenderly branched or cespitose rootstock, 1 to 3 dm. high, mildly odorous; stems several or numerous, simple up to the inflorescence, erect, moderately leafy, faintly striate, lightly tomentulose or glabrate, sometimes becoming reddish; basal leaves crowded, petiolate, 2 to 3.5 cm. long including the petiole, ovate to obovate in outline, mostly twice pinnately parted or divided into narrowly linear or linear-oblancoleolate divisions, about 1 mm. wide, silky-canescenscent; upper leaves much reduced, less parted, those of the inflorescence often simple, silky like the lower; inflorescence (of 5 to 25 heads) raceme-like, congested towards the summit, 2 to 10 cm.

long, 0.5 to 1.5 cm. broad; heads heterogamous, subsessile or the lower long-peduncled, inclined to nod; involucre hemispheric, about 4 mm. high, 4 to 6 mm. broad; bracts 11 to 18, ovate or broadly lanceolate, somewhat acute, the inner ones narrowed at base, villous, with greenish narrow backs and broad blackish scarios margins; receptacle copiously villous; ray-flowers 6 to 13, fertile, corolla about 1.5 mm. long, funnellform, often nearly regular and 4- or 5-toothed; disk-flowers 15 to 30, fertile, corolla funnellform, 2 to 2.5 mm. long, 5-toothed, long-villous on the teeth and usually also on the throat; style-branches of ray-flowers smooth and obtuse at apex, of disk-flowers truncate and penicillate at summit; achenes nearly cylindrical but slightly narrowed at base, mostly truncate at summit, smooth or faintly nerved, not pubescent.

In the Rocky Mountains from Montana to southern Utah and New Mexico; most common in Colorado; from just below to well above timber-line. Type locality, Rocky Mountains, Colorado. Collections: Spanish Peaks, Gallatin County, Montana, July 20, 1901, *Vogel* (Gr, US); La Plata Mines, Wyoming, *E. Nelson 5273* (UC); type collection 1862, *Parry* (Gr); Pike's Peak, Colorado, at edge of timber-line, August 7, 1919, *Hall R72*, also well above timber-line *A97* (CI); mountains about headwaters of Clear Creek, Colorado, *Patterson 72* (Gr, NY, UC, US); Sierra Sangre de Cristo, Colorado, *Brandege 788* (UC); Bullion Creek near Marysvale, Utah, *Jones 5872* (NY); La Sal Mountains, Utah, at 3,000 to 3,200 m. altitude, *Rydberg* and *Garrett 8964* (NY, normal form with elongated inflorescence); La Sal Mountains, Utah, at 3,300 to 3,600 m. altitude, *Rydberg* and *Garrett 8675* (NY, UC, a dwarf form with condensed inflorescence but with the usual small heads); Pecos Baldy, New Mexico, *Standley 4313* (NY, US).

RELATIONSHIPS.

Artemisia scopulorum is regarded as a direct descendant of *A. frigida*, which has been evolved in response to alpine conditions. The style-branches and achenes are practically identical, and the bracts are the same in number and similar in shape, while the measurements of involucre and corolla overlap, as do the numbers of ray-flowers and disk-flowers. The leaves are distinctly different, and there are considerable differences in size, habit, flower-cluster, and pubescence, characters all readily modified by the environment. This is shown by the form of *A. frigida* that grows on cold montane plains at 9,000 feet altitude, which is dwarfed, herbaceous, less silky, and with a raceme-like inflorescence. It proves the readiness with which the vegetative features of this plains species may be changed by greater moisture and cold, and suggests the actual line of development to *scopulorum*. The woody base of *frigida* is clearly an adaptation to its warmer and drier habitat, and it disappears at higher elevations. Moreover, while the two species have not been found in actual contact, it is probable that they were in recent times, as *frigida* ascends to 3,000 meters and *scopulorum* descends to 3,400 meters. Hence, it appears probable that the boreal *A. frigida* migrated to the southward, becoming more woody and xeroid on the plains, but retaining its herbaceous character in the subalpine region, and developing into the dwarf alpine *A. scopulorum* on the high peaks of Wyoming, Montana, Colorado, Utah, and New Mexico.

ECOLOGY AND USES.

Artemisia scopulorum is a dwarf alpine perennial with short rootstocks, and hence with a gregarious habit. It may occur in small clans in new areas, but it is usually associated with other species, such as *Erigeron uniflorus*, *Antennaria alpina*, *Pedicularis parryi*, *Arenaria fendleri*, and *Haplopappus pygmaeus*, in a mixed society of the alpine sedgeland climax.

No uses are known for this species, and none are to be expected from its small size and alpine habitat.

19. ARTEMISIA PATTERSONI Gray, Syn. Fl. 1^o: 453, 1886. Plate 12. ALPINE
SAGEWORT.

A perennial herb with a branched or cespitose rootstock, 1 to 2 dm. high, mildly odorous; stems several, unbranched, erect, moderately leafy, not striate, tomentulose or glabrate, not turning red; basal leaves crowded, petiolate, 2 to 4 cm. long including the petiole, obovate-oblong or spatulate in outline, once pinnately parted into few lobes, 1 to 2 mm. wide or only trifid from the summit, silky-canescenscent; upper leaves much reduced, mostly entire, silky like the lower; inflorescence (of 2 to 5 racemously arranged heads or reduced to a single terminal head) 1 to 5 cm. long, about 1 to 1.5 cm. broad; heads heterogamous, subsessile or the lower long-peduncled, mostly horizontal or nodding; involucre broadly hemispheric, about 5 mm. high, 5 to 8 mm. broad (up to 12 mm. in pressed specimens); bracts 15 to 30, ovate, or broadly lanceolate, acutish, the inner ones narrowed at base, villous, with greenish backs and broad blackish scarious margins; receptacle copiously villous; ray-flowers 7 to 27, fertile, corolla about 2 mm. long, funnelliform, irregularly toothed; disk-flowers 32 to 120, fertile, corolla funnelliform, 2.5 to 3 mm. long, 5-toothed, glabrous or rarely sparsely villous; style-branches of ray-flowers lanceolate, acutish, of disk-flowers flat, penicillate at the truncate apex; achenes nearly cylindrical, slightly narrowed at base, broad at summit, smooth or faintly nerved, not pubescent.

High mountains of Colorado and New Mexico, apparently always above timber-line. Type locality, Rocky Mountains of Colorado. Collections: Type collection, 1862, Parry (Gr, type of *A. scopulorum* var. *monocephala* Gray); about the headwaters of Clear Creek, Gray's Peak, and vicinity, July 30, 1885, *Patterson* 74 (Gr, UC, US); Pike's Peak, above timber-line, *Hall 11079* (UC); summit of Mount Garfield (Baldy), Colorado, *Clements 415* (DS, Gr, NY, US); Long's Peak, Colorado, *E. L. Johnston 689* (NY); Baldy, New Mexico, August 14, 1910, *Wooton* (US).

SYNONYMS.

1. ARTEMISIA MONOCEPHALA Heller, Muhl. 1:118, 1905. *A. pattersoni*.
2. A. SCOPULORUM VAR. MONOCEPHALA Gray, Proc. Acad. Phila. for 1863:66, 1863. The original name for *A. pattersoni*, as indicated later.

RELATIONSHIPS.

Artemisia pattersoni appears to be directly derived from *A. scopulorum*, and so recently that all of the characters overlap, with the exception of the number of disk-flowers, where they meet. This is further indicated by the fact that it appears to be known from but four high peaks—Gray's Peak, Long's Peak, and Pike's Peak in Colorado, and Mount Baldy, New Mexico. While the two species are now often found together on these peaks, the smaller plants, reduced leaves, and larger heads of *pattersoni* indicate that it was developed at greater altitudes or on colder slopes, and then migrated into the area of *scopulorum*.

This species is very similar in general characters to *A. scopulorum*, so much so that it sometimes has been taken for the extreme alpine form of this more common species. Both were first described by Gray, and at the same time. Having only the one-headed form of the present species, this authority named it *A. scopulorum* var. *monocephala*. Later, however, Patterson called Gray's attention to differences previously overlooked and the latter then described it as a distinct species, *A. pattersoni* (Syn. Fl. 1^o:453, 1886), which was characterized as follows:

More dwarf and white-tomentose, but sometimes glabrate in age; leaves 3- to 5-parted or cleft, or uppermost entire; heads much larger and broader, solitary or 2 to 5, 40- to 50-flowered; corollas glabrous; receptacle extremely long-woolly. (Syn. Fl. 1^o:453, 1886.)

This is not merely a dwarf of *scopulorum*, as is evident from the occurrence of a truly dwarf form of the latter, in which the essential characters of *pattersoni*—cut of leaf, large heads with numerous flowers, long glabrous corollas, etc.—are not attained. Such

dwarfs are found in the La Sal Mountains of Utah (*Rydberg and Garrett 8075*) and on Gray's Peak, Colorado (*Shear 4997*). *A. pattersoni* is not an altitudinal variant of *scopulorum*, as is indicated also by the occurrence of both within a few feet of each other without the presence of intergrading forms. Thus on Pike's Peak, at a point about 1 km. south of Windy Point, but still well above timber-line, one may find small areas where only *scopulorum* grows, while only 4 meters removed there are areas of pure *pattersoni*, the intervening space being occupied by other plants.

The morphological differences between these two species are indicated in table 9. As there shown, they exhibit not only well-marked divergent tendencies in some characters, but in one of these there is also an absence of overlapping. Thus, the number of disk-flowers runs from 10 to 31 for *scopulorum*, with an average of 18, while *pattersoni* has 32 to 130, with an average of 85. Further examinations might exhibit an overlapping, but on the other hand, the lowest counts in both cases are probably due to the dropping out of some of the flowers before the counts were made. Attention is also called to universally pubescent corollas of *scopulorum* as contrasted with the almost constantly glabrous ones

TABLE 9.—Statistical comparison between the characters of *Artemisia scopulorum* and *A. pattersoni*.

	Herbarium.	No. of heads per plant.	No. of bracts.	No. of ray-flowers.	No. of disk-flowers.	Total flowers.	Corolla-lobes.
<i>A. scopulorum</i> :							
Pike's Peak, Colo.....	11077 CI	22	17 17	11 13	23 17	34 30	Pubescent.
Do.....	Do.....	16	14 10	10 9	13 10	23 19	Do.
Do.....	Do.....	15	14 12	8 7	21 18	29 25	Do.
Do.....	Do.....	6	14 12	11 6	18 16	29 22	Do.
Do.....	Do.....	15	16 12	6 6	19 13	25 19	Do.
Pike's Peak, Colo.....	11078 CI	18	15 14	6 7	17 17	23 24	Do.
Do.....	Do.....	13	12 12	6 7	12 10	18 17	Do.
Do.....	Do.....	25	12 12	6 6	21 17	27 23	Do.
Do.....	Do.....	22	16 13	9 7	26 20	35 27	Do.
Do.....	Do.....	15	12 14	7 7	20 19	27 28	Do.
Pike's Peak, Colo.....	11080 CI	13	14 15	7 7	18 18	25 25	Do.
Seven Lakes, Colo.....	858541 US	10 16	18	8	31	39	Do.
Gray's Peak, Colo.....	488933 US	5 10	13	7	10	17	Do.
La Plata Mountains, Colo.....	337427 US	12 18	13	6	22	28	Do.
Mineral County, Colo.....	892761 US	15	11	8	26	34	Do.
Vallecito, N. M.....	489803 US	12	13	7	19	26	Do.
Medicine Bow Mountains, Wyo.....	433965 US	9 11	15	9	25	34	Do.
Big Horn Mountains, Wyo.....	253360 US	7 9	16	7	24	31	Do.
Wind River Mountains, Wyo.....	203786 US	7 11	14	7	25	32	Do.
Spanish Peaks, Mont.....	416310 US	9 15	12	9	22	31	Do.
Average.....		14	13	7	20	26	
<i>A. pattersoni</i> :							
Pike's Peak, Colo.....	11076 CI	1	32	20	115	135	Glabrous.
Do.....	Do.....	4	12 22	8 15	40 101	48 116	Do.
Do.....	Do.....	3	15 24	11 22	38 82	49 104	Do.
Do.....	Do.....	2	15 30	11 27	43 119	54 146	Do.
Do.....	Do.....	1	29	19	130	149	Do.
Do.....	11079 CI	1	21	20	99	119	Do.
Do.....	Do.....	3	15 24	7 15	32 86	39 101	Do.
Do.....	Do.....	2	17 27	7 16	45 104	52 120	Do.
Do.....	Do.....	1	19	19	79	98	Do.
Do.....	Do.....	1	27	20	128	148	Do.
Do.....	Do.....	1	25	15	106	121	Do.
Do.....	CI	3	17	10	46	56	Do.
Do.....	A29 CI	3	16	57	73	Pubescent.
Baldy Peak, Colo.....	CI	3	29	23	65	88	Glabrous.
Gray's Peak, Colo.....	593762 US	1 4	20	11	87	98	Do.
Baldy, N. Mex.....	738710 US	1 4	18	10	67	77	Do.
Average.....		2	21	15	85	99	

of *pattersoni*. This character, however, is exceedingly variable in other species of *Artemisia*. The most important differences not brought out in the table are the large heads and simply cut foliage of *pattersoni* as contrasted with the smaller heads and mostly dissected foliage of *scopulorum*.

ECOLOGY AND USES.

Artemisia pattersoni closely resembles *A. scopulorum* in life-form and ecological relations. However, it never forms societies, but is restricted to small clans, often more or less mixed with *A. scopulorum*. No uses are known for this species.

SECTION III. DRACUNCULUS.

PHYLOGENY OF THE SPECIES.

One species of the section is so unlike the others that it is considered as representing a very early divergence. This is *A. spinescens*. Since it was once taken as the type of the proposed genus *Picrothamnus*, its relationships have been already discussed in detail (see p. 32). The remaining four species are readily divisible into two wholly natural pairs. *A. dracunculus* and *A. campestris* are presumably of Old World origin, although both are now abundantly represented in America by a number of subspecies. Their migration seems to have been by a route across or around the North Atlantic, since they are not

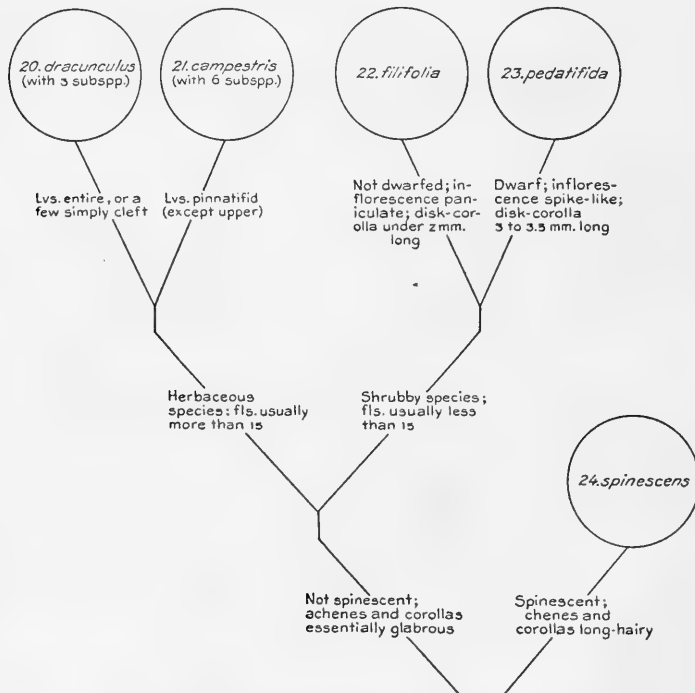


FIG. 15.—Phylogenetic chart of the species of *Artemisia* section *Dracunculus*.

represented in the Northwest nor in eastern Asia. As contrasted with these, *filifolia* and *pedatifida* are restricted to America. The latter shows the greatest amount of modification and possibly was derived directly from the former. Both exhibit specialization in their shrubby habit and in the reduction of the number of flowers. Perhaps it is because of these special adaptations that they are of comparatively limited distribution.

20. ARTEMISIA DRACUNCULUS Linnaeus, Sp. Pl. 849, 1753. Plate 13. DRAGON SAGEWORT.

A perennial herb with a thick, sometimes nearly woody rootstock, 5 to 15 dm. high, varying from strongly odorous to inodorous; stems not crowded, simple up to the inflorescence, erect, striate, either pilose and glabrate or usually glabrous, commonly tinged with red; basal and lower leaves crowded when young but not forming tufts, sessile by a narrow base, linear to oblong or somewhat lanceolate, acute, 3 to 8 cm. long, 1 to 6 or 10 mm. wide, mostly entire, occasionally some 1- to 3-cleft, or the lowest even more divided, usually glabrous but silky-canescens and glabrate in some forms; upper leaves only slightly reduced, entire, glabrous or pubescent; inflorescence a leafy-bracted panicle with ascending branches, 15 to 40 cm. long, 3 to 12 cm. broad; heads heterogamous, sessile or peduncled, nodding; involucre hemispheric, 2 to 2.5 mm. high, 2 to 4 mm. broad; bracts 8 to 15, elliptic or lanceolate, mostly obtuse, the outer from one-half to nearly as long as the inner, glabrous or sparingly pubescent, yellowish green save for the white-scarious margins; receptacle naked; ray-flowers 6 to 30, fertile, corolla 0.5 to 1 mm. long, cleft on one side, glabrous; disk-flowers 10 to 30, sterile, corolla campanulate, 1.5 to 2 mm. long, 5-toothed, glabrous; style of disk-flowers 1 to 1.8 mm. long, the branches erect or slightly spreading, penicillate at apex, or probably the branches sometimes completely united; achenes ellipsoid, not ribbed, glabrous, those of the disk-flowers abortive.

On the plains and in the mountains, often common, Manitoba to Illinois, Texas, Chihuahua, Arizona, Lower California, and British Columbia, also in central Asia and Siberia and less common in middle Europe.

SUBSPECIES.

Since this is one of the most polymorphous of the Artemisias, an extensive series of forms might be worked out. The following key provides for the only important segregates thus far described from North America. Intermediate forms are so common and the characters unite in so many combinations that it is often impossible to place specimens in any of these subspecies with certainty.

Key to the Subspecies of Artemisia dracunculus.

- Heads 3 to 4 mm. broad; branches of inflorescence not drooping at ends; leaves 2 to 10 mm. wide; herbage glabrous..... (a) *typica* (p. 115).
 Heads 2 to 3 mm. broad; branches of inflorescence inclined to droop at ends (except perhaps in *glauca*); leaves 1 to 3 mm. wide or to 6 mm. in *dracunculina*; herbage either glabrous or pubescent.
 Panicle comparatively dense, peduncles mostly 2 mm. or less long..... (b) *glauca* (p. 116).
 Panicle loose, peduncles 2 to 6 mm. long and very slender. Southwestern United States and Mexico..... (c) *dracunculina* (p. 116).

20a. ARTEMISIA DRACUNCULUS TYPICA.—Plant glabrous throughout, aromatic; leaves 4 to 8 cm. long, 2 to 10 mm. wide, rather thick and firm; branches of the panicle compact, erect or ascending to the tip, the peduncles stout and rarely 2 mm. long; involucre 3 to 4 mm. broad. (*A. dracunculus* Linnaeus, l. c.) The common form in western North America, cultivated and rarely escaped in the eastern States, common also in the Old World. Wyoming and Colorado to Lower California, Washington, Saskatchewan, and Alberta. Type locality, Siberia. Collections: Vicinity of Banff, Alberta, *McCalla 2018* (NY, US); Yellowstone Lake, Wyoming, *A. and E. Nelson 6602* (DS, Gr, NY, type

collection of *A. aromatica* Nelson, minor variation 1); Breckenridge, Colorado, *Shear 4564* (NY); near Marysville, Utah, *Jones 5942* (NY); Chama, northern New Mexico, *Baker 631* (NY); Cochise County, Arizona, *Eggleston 10815* (US); San Pedro Martir, Lower California, *Robertson 18* (UC); Ballona, coast of Los Angeles County, California, *Braunton 437* (UC); San Leandro, middle California, *Bolander 395* (NY); Peavine Mountain, western Nevada, *Heller 10676* (DS, Gr, NY, US); Wallowa County, Oregon, *Sheldon 8635* (NY, UC); Peshastin, Okanogan County, Washington, *Sandberg* and *Leiberg 829* (Gr, SF, UC); Cañon County, Idaho, *Macbride 721* (Gr, UC, US).

20b. ARTEMISIA DRACUNCULUS GLAUCA (Pallas.)—Plant silky on the young parts and glabrate or glabrous from the beginning (minor variation 4, *A. dracunculoides* Pursh), inodorous; leaves 3 to 8 cm. long, 1 to 4 mm. wide, rather thick and firm; branches of the panicle comparatively dense, inclined to droop at the ends because of the slender branches, the peduncles mostly less than 2 mm. long; involucre 2 to 3 mm. broad. Apparently there are Siberian variations with wider leaves and others with larger heads. (*A. glauca* Pallas; Willdenow, Sp. Pl. 3:1831, 1804.) Manitoba to Wisconsin, Texas, Chihuahua, New Mexico, and British Columbia; also in Siberia. Specimens from the San Bernardino Mountains and Catalina Island, California, sometimes referred here belong to subspecies *typica*. Type locality, Siberia. Collections, mostly of the glabrous form and therefore of minor variation 4: Brandon, Manitoba, *Macoun 12257* (NY); Leeds, North Dakota, September 6, 1901, *Lunnell* (Gr.); Hennepin County, Minnesota, August, 1890, *Sandberg* (UC); Des Moines, Iowa, *Pummell 1277* (Gr); Fort Collins, Colorado, October 3, 1893, *Crandall* (NY); southeastern Utah, *Rydberg* and *Garrett 9133* (NY, only a few of the branches inclined to droop); White Mountains, Lincoln County, New Mexico, *Wooton 306* (UC); Texas, *Lindheimer 869* (Gr, NY, UC); near Colonia Garcia, in the Sierra Madre, Chihuahua, *Townsend* and *Barber 295* (Gr, UC); Silver Cañon, Inyo Range, eastern California, *Hall 10636* (UC); sandy banks of the Columbia River, west Klickitat County, Washington, *Suksdorf 1609* (UC); Eagle Creek, Saskatchewan, *Macoun* and *Herriot 72828* (NY).

20c. ARTEMISIA DRACUNCULUS DRACUNCULINA (Watson). Plant softly long-villous or finely canescent on all the young parts, in age glabrous, or occasionally glabrous from the beginning, inodorous; leaves 3 to 8 cm. long, 2 to 6 mm. wide, rather thin and soft; branches of the panicle very loose and open, slender but scarcely drooping at the ends, the slender peduncles (sometimes drooping) 2 to 5 mm. long; involucre 2 to 2.5 mm. broad. (*A. dracunculina* Watson, Proc. Am. Acad. 23:279, 1888.) Kansas, Texas, and Chihuahua to New Mexico and Arizona. Type locality, at the base of cliffs in the Sierra Madre, Chihuahua. Collections: Riley County, Kansas, *Norton 298* (NY); Corundos, Texas, November, 1881, *Havard* (US); type collection, under calcareous cliffs, October 18, 1887, *Pringle 1309* (Gr, NY, UC, US); same general locality, *Pringle 1651* and *1652* (UC); Cañon de San Diego, Chihuahua, *Hartman 778* (Gr, NY, US); summit of San Jose Mountains, Sonora, *Mearns 1677* (US); among rocks, Sierra County, New Mexico, *Metcalfe 1444* (Gr, NY, SF, US, type collection of *A. gracillima* Rydberg, minor variation 12); Organ Mountains, Doña Ana County, New Mexico, September 28, 1902, *Wooton* (US, same variation); Bright Angel Trail, Grand Cañon of the Colorado River, Arizona *Eastwood 3683* (SF).

MINOR VARIATIONS AND SYNONYMS.

1. ARTEMISIA AROMATICA Nelson, Bull. Torr. Club 27:273, 1900.—*A. dracunculus typica* (see p. 117). This was included in *A. dracunculoides* by Gray, in the Synoptical Flora, but it is not the genuine *dracunculoides*. Type locality, Yellowstone Lake, Wyoming.

2. A. CERNUA Nuttall, Gen. 2:143, 1818.—A form of *A. dracunculus glauca* with slightly pubescent herbage at least when young, and with branches inclined to droop at the ends. Described by Rydberg (N. Am. Fl.

34:252, 1916) as glabrous, but the leaves are at first canescently pubescent—according to the original description. A piece of Nuttall's type at the Gray Herbarium is puberulent on the foliage and upper portion of the stem. Chiefly of the lower Mississippi Valley. Type locality, shrubby savannahs around St. Louis and on the banks of the Mississippi and Missouri Rivers.

3. *A. DRACUNCULINA* Watson, Proc. Am. Acad. 23:279, 1888.—*A. dracunculus dracunculina*.

4. *A. DRACUNCULOIDES* Pursh, Fl. Am. Sept. 742, 1814.—A form of *A. dracunculus* var. *glauca*, differing from the type only in having perfectly glabrous herbage. Much more common in the United States than the typical form. The name *dracunculoides* was extended by Gray (Syn. Fl. 1²:369, 1884) to include all of the North American variations of *A. dracunculus* except *glauca*, the one to which it is most closely related. In fact, typical *dracunculoides* seems no more than an ecologic state of this. Through Gray's treatment the commonest form of the Rocky Mountain and Pacific States, that is, subspecies *typica*, had been assumed by western botanists to be typical of the quite different *dracunculoides*, until Nelson noted the discrepancy and named it *A. aromatica*, apparently overlooking its identity with the European *A. dracunculus*. The type locality is "Upper Louisiana," now South Dakota.

5. *A. DRACUNCULOIDES BREVIFOLIA* Torrey and Gray, Fl. N. Am. 2:416, 1843.—*A. dracunculus glauca*. Somewhat cinereous or glabrate. Type locality, St. Louis to the Rocky Mountains and the Saskatchewan.

6. *A. DRACUNCULOIDES INCANA* Torrey and Gray, l. c.—Probably *A. dracunculus glauca*, but inflorescence unknown. Type locality, Jacques River [Quebec?].

7. *A. DRACUNCULOIDES TENUIFOLIA* Torrey and Gray, l. c.—*A. dracunculus glauca*. Canescent or glabrous; leaves narrow, elongated. Type locality, St. Louis to the Rocky Mountains and the Saskatchewan.

8. *A. DRACUNCULOIDES* var. *WOLFFI* Rydberg, Bull. Torr. Club 32:128, 1905.—*A. dracunculus typica*. Type locality, Twin Lakes, Colorado.

9. *A. DRACUNCULUS GLAUCA* Besser, Hooker, Fl. Bor. Am. 1:326, 1833.—*A. dracunculus* subspecies *glauca*.

10. *A. GLAUCA* Pallas, Willdenow, Sp. Pl. 3:1831, 1804.—*A. dracunculus glauca*.

11. *A. GLAUCA FASTIGIATA* Besser, Bull. Soc. Hist. Nat. Mosc. 8:59, 1835.—*A. dracunculus glauca*. Branches fastigiate, canescent when young. Type locality, plains of the Saskatchewan.

12. *A. GRACILLIMA* Rydberg, N. Am. Fl. 34:253, 1916.—*A. dracunculus dracunculina*, but with the pubescence canescent rather than villous. Type locality, 1 mile west of Hillsboro, Sierra County, New Mexico.

13. *A. NUTTALLIANA* Besser, in Hooker, Fl. Bor. Am. 1:326, 1833.—From the description this seems to be a glabrous, short-leaved form of *A. dracunculus glauca*. Type locality, Red River of the North.

RELATIONSHIPS.

There is a broad gap between *A. dracunculus* and its nearest relatives when the species is taken in the broad sense as here defined. Even in Europe, where its origin is perhaps to be sought, there seems to be no species with which it is in very close alliance. In America it is most closely approached by *A. campestris*, as will be indicated under that species.

The history of the attempts at segregation within the species, both here and in the Old World, is one of confusion. This is due in part to a lack of parallelism in the variation of the different characters, in part to indefinite characterization of the segregates, and in part to a disregard of forms already described. For about a century nearly all of the American forms have passed in most floras as *A. dracunculoides* Pursh. The type of this, the common form in the Mississippi Valley, has leaves so narrow and heads so small that there was some justification in separating it from the Old World *A. dracunculus*, but the form which is by far the most abundant in all of the western States is so much more like *dracunculus* than it is like *dracunculoides*, that is, subspecies *glauca* of the present treatment, that its inclusion in the latter by Gray (Syn. Fl. 1²:369, 1884) has resulted in much confusion. It was the recognition of the difference between the two common American forms that led Nelson to describe the broader-leaved, larger-headed one as *A. aromatica*, apparently without considering the Asiatic type, which it practically duplicates and to which it is reduced in this paper. One of the chief characters assigned to *aromatica* by Nelson was its strong odor as contrasted with *dracunculoides*. If this difference was constant, which seems very doubtful from field observations, it would throw *aromatica* back into *dracunculus*, for the only tangible character given by Gray in the Synoptical Flora for *dracunculoides* is that it is "wanting the scent and taste of *A. dracunculus*." The odor alone is quite untrustworthy as is indicated by the

experiments of Gmelin, who found that the seeds of odorous plants produced inodorous individuals when grown in the botanical garden (according to Ledebour, Fl. Rossica 2:563, 1846). In the latest account of our species (Rydberg, N. Am. Fl. 34:244 to 285, 1916), *aromatica* is retained as a species and separated from the Old World *dracunculus* on two principal characters: (1) the outermost bracts are said to be almost as long as the innermost instead of only about one-half as long; (2) the flowers are given as 30 to 100 in number as compared with 20 to 40 in *dracunculus*.

The supposed difference in the bracts is not evident. In fact, a close examination of a series of collections indicates the same relative length of outer and inner bracts in American and European material. As to the number of flowers, the figures just quoted show a sufficient overlapping to suggest the doubtful value of this criterion and when a large series is examined it is found that the distinction almost completely vanishes.

TABLE 10.—Variation in the subspecies of *Artemisia dracunculus*.

	Herbarium.	No. of involucrel bracts.	No. of ray-flowers.	No. of disk-flowers.	Total no. of flowers.	Length of corolla of disk-flowers.
<i>Subspecies typica:</i>						
Great Falls, Mont.	29745 UC	9 11	8 13	16 16	24 29	<i>mm.</i> 2.0
Laramie, Wyo.	51693 UC	8 14	12 13	14 15	26 28	1.7
Gunnison Watershed, Colo.	34508 UC	8 10	18 20	19 20	37 40	2.0
Washoe County, Nev.	175965 UC	8 10	8 13	14 15	22 28	1.8
Davis Ranch, Nev.	91256 UC	14 15	13 15	18 10	31 25	1.6
Palomar Mountains, Calif.	65449 UC	9 11	9 11	12 14	21 25	1.6
Little Green Valley, Calif.	64995 UC	12 12	9 11	27 29	36 40	1.6
Atascadero, Calif.	205777 UC	10 13	15 26	16 25	31 51	1.7
Eel River, Calif.	196572 UC	11 12	17 14	13 20	30 34	1.7
Grants Pass, Oreg.	CI	10 14	15 20	9 15	24 35	1.6
Enterprise, Oreg.	170013 UC	11 12	21 26	25 23	46 49	1.7
Waitsburg, Wash.	73885 UC	10 12	11 13	12 10	22 25	1.7
Payette, Idaho.	205776 UC	11 14	12 26	12 23	24 49	1.8
Cañon County, Idaho	160228 UC	13 15	17 16	15 16	32 32	1.6
Santa Barbara, Calif.	NY	11 13	14 17	11 14	25 31	1.7
Sarepta (Europe)	549840 US	11 10	15 13	12 14	27 27	2.2
Somme, France.	200431 US	12 11	13 11	11 14	24 25	2.0
Cultivated, Europe.	NY	12 11	13 12	13 12	24 24	2.0
Liverpool, England.	NY	10 11	9 12	12 11	21 23	2.0
Tibet.	Gr	14 15	22 18	20 17	42 35	1.9
Average		11	14	16	30	1.8
<i>Subspecies glauca:</i>						
Winona, Minn.	67845 UC	9 11	10 11	8 10	18 20	1.7
Hennepin County, Minn.	29743 UC	7	8	11	17 19	2.0
Cañon City, Colo.	172710 UC	7 10	8 9	9 10	17 19	2.0
Monticello, Utah.	176480 UC	8 10	12 14	18 20	30 34	2.1
Dofia Ana County, N. Mex.	112378 UC	6 8	8 9	10 14	18 23	1.6
Lincoln County, N. Mex.	135380 UC	10 11	12 17	12 20	24 37	1.1
Comanche Springs, Tex.	147505 UC	8 9	8 9	10 11	18 20	1.5
Chihuahua, Mex.	135379 UC	7 9	10 10	8 12	18 22	1.7
Klickitat County, Wash.	130207 UC	9 10	9 9	6 8	15 17	2.6
Brandon, Manitoba.	(12257) NY	12 12	15 12	14 21	29 33	1.9
Leeds, N. Dak.	Gr	11 10	12 12	13 16	25 28	1.8
Siberia.	Gr	11 12	12 10	13 12	25 22	1.5
Average		9	10	12	22	1.8
<i>Subspecies dracunculina:</i>						
New Mexico	NY	8 10	12 10	16 12	28 22	1.8
Grand Cañon, Ariz.	SF	7 8	9 11	9 16	18 27	1.6
Sierra Madre, Mex.	91224 UC	8 8	14 14	6 7	20 21	2.0
Chihuahua, Mex.	91225 UC	10 12	8 10	10 17	18 27	1.8
Do.	29742 UC	8 10	11 18	10 12	21 30	1.6
Cañon de San Diego, Mex.	91226 UC	9 10	12 15	11 13	23 28	1.7
Average		9	12	11	23	1.7

This is shown in table 10, where the first 14 collections under subspecies *typica* are of the American, or "*aromatica*," type and the last 6 of the Old World type. The latter group includes one collection from California, since it was considered by Rydberg as genuine *dracunculus*, introduced into America. These counts show that the number of flowers is 21 to 51 for the American form, with an average of 32, and 21 to 42 for the Old World form, with an average of 27. These results would of course be different if a larger series were studied, especially as regards the maximum in both forms, but it is extremely unlikely that the difference between the averages would be sufficient to indicate even a tendency towards a separation. The figures here given are based upon counts in normal, well-formed heads selected from about the same relative position in the inflorescence in every case. In this connection it may be suggested that the low number sometimes obtained for Old World material may be due to the fact that specimens from across the sea are usually less carefully preserved than those from this country, and as a result of this and of frequent handling some of the flowers have fallen out.

Because of the wide hiatus in geographic distribution, some have thought that characters should be found upon which to base a taxonomic separation of the New World plants from the original *A. dracunculus*, at least varietally. But every attempt thus far made has completely failed. The leaves average perhaps a little narrower, 3 and 4 mm. being common widths, but leaves up to 7 and 8 mm. wide are not rare. In many cases exact counterparts of European or Asiatic plants can be found here. The inevitable conclusion, therefore, is that the most common and widespread form in western North America is not even varietally separable from the Old World *A. dracunculus*.

Of the other subspecies, *glauca*, as now restricted, is a narrow-leaved, small-headed plant with every appearance of being an undernourished or competition form. Yet its occurrence on this continent in greatest abundance toward the east of the range of *typica* indicates that its characters may be somewhat permanently fixed. It is here made to include *A. dracunculoides* Pursh. This is in agreement with Gray's treatment (Syn. Fl. 1²:369, 1884, etc.), except that this author did not use the earlier name and extended the concept to include all of the American plants of subspecies *typica*. The only difference between *glauca* and *dracunculoides* is the loose pubescence on the young parts of the former, and this is variable in amount and in persistence. Geographic distribution offers no aid here, since both forms occur in the northern United States. Even after the most refined segregation, such as that illustrated in the North American Flora, it is necessary to admit the same form, in this case *glauca*, both in Siberia and in central North America, although no variety of *A. dracunculus* is known from Alaska or other intervening territory, a distance of over 4,000 km. The subspecies *dracunculina* is also pubescent when young, but is very different from all of the others in its thin foliage, very open inflorescence, and delicate, elongated peduncles. These characters do not vary in unison, as is evidenced by collections with the whole habit, inflorescence, etc., of this subspecies, but

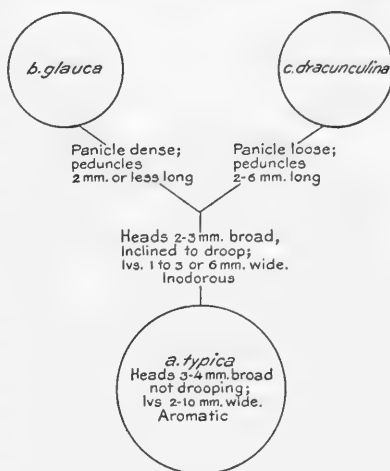


FIG. 16.—Phylogenetic chart of the subspecies of *Artemisia dracunculus*.

perfectly glabrous even on the young branches (Chihuahua, *Lumholtz 778*). The open panicle with elongated peduncles is generally found in plants from the Southwest, but villous shoots are present only in the type material. Moreover, open panicles and long peduncles (2 to 6 mm.) are found in northern material (*Pammel 1277*), while open panicles are not at all infrequent in subspecies *typica* and *glauca*. Finally, Mexican material (*Pringle 304*) may show open panicles and short peduncles. It is therefore evident that *dracunculina* can not be accorded specific rank, although it may be accepted as a southwestern subspecies based chiefly upon the form of the inflorescence, at the same time admitting that similar inflorescences sometimes occur in other forms.

ECOLOGY.

Artemisia dracunculus is a perennial herb with a stout rootstock, blooming in late summer and autumn, as do practically all the species. It is a typical society of the grassland formation during late summer and autumn, but it is much more abundant toward the north and in the foothill and montane regions. It is most characteristic of the true and mixed prairies, but is also important in the bunch-grass and subclimax ones, though rare or lacking in the desert plains. While it increases somewhat under grazing, it is eaten in sufficient quantity to prevent its becoming a particular indicator of overgrazing. It sometimes indicates disturbance of the soil, but is much less frequent in this rôle than either *A. campestris* or *A. frigida*. It is often associated with one or both of these, and also with *A. v. gnaphalodes*.

USES.

This species is extensively browsed by sheep after frost, especially in the western mountains. Although the foliage is too scant to give it a high value as compared with some of the sagebrushes, the dragon sagewort, or smooth sageweed, as it is sometimes called on the range, is one of the principal forage weeds for sheep in late autumn and winter.

The plant is cultivated to some extent in Europe under the name of tarragon, or estragon, and its leaves are there used for seasoning salads and cooked dishes. Presumably only the aromatic forms are employed for this purpose. The leaves are used in the fresh state, or they may be cut and dried in the autumn for use afterwards. It is also utilized in the manufacture of a variety of vinegar known as *estragonessig*. The plants are easily grown from divisions of the root or from cuttings and do best in warm, rather dry situations. In some parts of California, especially in the Tehachapi region, the plant is known locally as Indian hair tonic and is said to be used to stimulate the growth of the hair. The pollen, which is smooth and 3-lobed, sometimes causes severe cases of hay-fever in western North America. Its importance as a causative factor is not so great as that of certain other species, such as *vulgaris* and *tridentata*, chiefly because it seldom occurs in quantity near cities.

21. ARTEMISIA CAMPESTRIS Linnaeus, Sp. Pl. 846, 1753. Plates 14, 15. FIELD SAGEWORT.

A biennial or perennial herb, 1 to 6 dm. high, scarcely odorous; stems usually several, or solitary in the short-lived forms, erect or ascending, often from a decumbent base, striate, glabrous or slightly pubescent (rather densely villous in one variety), more or less tinged with red; basal leaves crowded, petioled, 2 to 10 cm. long including the petiole, 0.7 to 4 cm. wide, 2- to 3-pinnately or only 1- to 2-ternately divided into linear or linear-filiform (rarely linear-oblongate) divisions, these rarely more than 1 mm. wide, appressed silky or villous to glabrous; upper leaves smaller, once or twice divided into 3 to 7 lobes, the uppermost often ternate or simple, densely pubescent to nearly glabrous; inflorescence an elongated panicle with raceme-like or spike-like branches, these leafy

below, or reduced in northern and high-mountain forms to a nearly simple spike, 5 to 50 cm. long, 1 to 15 cm. broad; heads heterogamous, sessile or short-peduncled, erect or nodding; involucre hemispheric, 2 to 4 mm. high, about as broad; bracts 8 to 20, round-elliptic, obtuse or subacute, light brown or yellowish green with a brown medial line, scarious-margined, densely villous to glabrous; receptacle naked; ray-flowers 5 to 20, fertile, corolla 1 to 1.5 mm. long, narrowed above; disk-flowers 6 to 30 or perhaps 40, sterile, corolla campanulate, 1.5 to 3 mm. long, regularly 5-toothed, yellowish-white or often purplish above, glabrous or the teeth pubescent; style of disk-flowers 1.5 to 3 mm. long, either undivided and arose around the cup-shaped summit or slightly cleft into more or less spreading branches; achenes subcylindric, glabrous, those of the disk-flowers abortive.

On the plains and in the mountains almost throughout North America except in the desert districts: Greenland, Hudson Bay, and the Atlantic seaboard to Florida, Texas, New Mexico, California (along the northern coast only), Oregon, and Alaska; also in Asia, Europe, and northern Africa.

SUBSPECIES.

No less than 17 American forms of this species have been segregated by various botanists and dignified with specific rank; 13 are recognized in the North American Flora. Some of these segregates are strikingly unlike in appearance, yet all are held in one natural group by a remarkable uniformity in all essential characters. The varietal differences are chiefly those of duration (with its resulting differences in branching), number of flowers (with differences in the size and shape of the head), and nature or amount of the pubescence. For present purposes it seems necessary to recognize but 6 of the variations, and these are here given subspecific rank. Other segregates are minor variations of these.

Key to the Subspecies of Artemisia campestris.

- Involucre mostly 2 to 3 or rarely 3.5 mm. high, 2 to 3.5 mm. broad; root either biennial or perennial.
- Plant perennial; stems usually several.
 - Inflorescence open-paniculate; heads nearly ovoid; leaves moderately pubescent, glabrate. (a) *typica* (p. 121).
 - Inflorescence densely paniculate; heads nearly hemispheric at maturity; leaves densely and permanently pubescent. (b) *pacifica* (p. 122).
 - Plant biennial; stem usually single. (c) *caudata* (p. 122).
- Involucre 3 to 4 mm. high, 3.5 to 5 mm. broad; root strictly perennial.
- Pubescence when present appressed and silky.
 - Involucre glabrous or nearly so; divisions of leaves linear or very narrowly oblanceolate. (d) *borealis* (p. 122).
 - Involucre densely villous; divisions of leaves often linear-oblanceolate. (e) *spithamaea* (p. 123).
 - Pubescence loosely silky-villous, very dense and extending to all parts. Pacific coast. (f) *pycnocephala* (p. 123).

21a. *ARTEMISIA CAMPESTRIS TYPICA*.—Root perennial; stems usually several, 3 to 5 dm. high, very leafy at base, sparsely leafy above; leaves mostly twice pinnately divided into linear or linear-filiform divisions about 0.5 mm. wide, the upper less divided or entire, all pubescent at first but often glabrate; inflorescence openly paniculate, 3 to 15 cm. broad, the branches few and spreading; heads nodding, ovoid when young, expanding in age to hemispheric; involucre 2 to 3 mm. high, about 2.5 mm. broad, glabrous; disk-flowers 5 to 12, the corolla 1.8 to 2.5 mm. long. (*A. campestris* Linnaeus, Sp. Pl. 846, 1873.) Abundant on the plains of Europe and western Asia; occasionally found on the Atlantic Coast of North America, where perhaps introduced. Type locality, Europe. Collections: Marthas Vineyard, Massachusetts, August, 1888, *Burgess* (no roots but inflorescence open); Naugatuck, Waterbury, Connecticut, July 14, 1903, *Bristol* (Gr); Aiken, South Carolina, *Eggleston 5063* (NY, probably this subspecies, although without root).

21b. *ARTEMISIA CAMPESTRIS PACIFICA* (Nuttall).—Root perennial; stems several or numerous, 4 to 6 dm. high, erect from a spreading base, densely leafy below, moderately leafy up to the inflorescence; leaves twice pinnately divided into narrowly linear divisions about 1 mm. wide, canescent or silky pubescent, seldom if ever glabrate; inflorescence an elongated panicle of numerous closely ascending branches, 3 to 12 cm. broad or occasionally narrowed to 1 cm.; heads subsessile, horizontal or erect, hemispheric; involucre 2 to 3 mm. high, about 2.5 mm. broad, glabrous or sparingly short-hairy, greenish; disk-flowers 10 to 25, the corolla 1.8 to 2.5 mm. long. (*A. pacifica* Nuttall, Trans. Am. Phil. Soc. II, 7:401, 1841.) The common form in western United States: South Dakota and western Nebraska to New Mexico, Arizona, Oregon, Yukon, and Saskatchewan. Type locality, shores of the Pacific at the outlet of the Oregon (Columbia River), in sandy places. Collections: Brookings, South Dakota, September, 1894, *Thorner* (UC); Laramie, Wyoming, *Nelson 7983* (Gr, NY, UC, as *A. camporum* Rydberg, minor variation 7); Kiowa Valley, western Nebraska, *Rydberg 203* (NY, same variation); Ruxton Dell, Pikes Peak, Colorado, *Clements 156* (DS, Gr, NY, US, same variation); La Sal Mountains, Utah, *Purpus 7019* (UC); near Silver City, New Mexico, October 8, 1880, *Greene* (UC); San Francisco Mountains, Arizona, *Leiberg 5840* (US); Bingen, Klickitat County, Washington, *Suksdorf 4602* (DS, US); Vancouver Island, British Columbia, August 16, 1887, *Macoun* (NY, US); Clarks Fork Valley, northern Idaho, *Leiberg 1580* (Gr, UC, NY, US); Bozeman, Montana, *Blankinship 304* (hb. Blankinship); Whiteshore Lake, Saskatchewan, *Macoun* and *Herriot 72832* (NY, minor variation 7, *A. camporum* Rydberg).

21c. *ARTEMISIA CAMPESTRIS CAUDATA* (Michaux).—Root biennial, often very large when growing in sand-dunes, but perhaps never perennial; stem usually single unless injured, erect, 3 to 5 dm. high, leafy at base and up to the inflorescence or sparsely leafy above; leaves twice or thrice pinnately divided into elongated diverging filiform or very narrowly linear divisions 0.5 mm. or less wide, the upper ones more simply cut, glabrous or sometimes canescent when young (in *A. forwoodi* Watson, minor variation 18); inflorescence a narrowly pyramidal panicle of ascending rather close branches, 3 to 10 cm. broad; heads peduncled, nodding or erect, narrowly hemispheric; involucre 2 to 3 or rarely 3.5 mm. high, about as broad, glabrous, yellowish green; disk-flowers 5 to 15, the corolla 1.5 to 2.2 mm. long. (*A. caudata* Michaux, Fl. Bor. Amer. 2:129 1803.) Widely distributed but most common in the eastern and central States: New Brunswick and Maine to Florida, Texas, Wyoming, Washington, Saskatchewan, and Ontario. (Specimens seen from south of Connecticut and Illinois are without roots and their identification therefore not absolutely positive.) Type locality, sandy banks of the Missouri River. Collections: Pine Point, Maine, *Parlin 1097* (N. E. Bot. Club); Lynn Beach, Massachusetts, August, 1887, *Summers* (US); North Haven, Connecticut, *Bissell 878* (Gr); Hennepin County, Minnesota, August, 1890, *Sandberg* (UC); Washington Island, Wisconsin, September 12, 1889, *Shuette* (Gr, UC); sandy barrens near Oquawka, Illinois, August, 1877, *Patterson* (UC); sand dunes at Millers, Indiana, September 4, 1911, *Sherff* (US); Blue River, Nebraska, September, 1888, *Wibbe* (UC); vicinity of Pine Grove, Colorado, *Crandall 2640* (US); Deadwood, South Dakota, *Carr 29* (NY, minor variation 18, *A. forwoodi* Watson); Willow City, North Dakota, September 11, 1899, *Lunell* (NY, same variation); near Bingen, Washington, August, 1907, *Suksdorf* (NY); Brandon, Manitoba, *Macoun 12247* (NY).

21d. *ARTEMISIA CAMPESTRIS BOREALIS* (Pallas).—Root perennial; stems several, crowded on a multicapital caudex, 1 to 3 dm. high, erect from a sometimes spreading base; densely leafy only below, sometimes moderately leafy to midway of the inflorescence; leaves once or twice ternately divided into linear divisions, mostly 1 to 2 mm. wide, or

with a few extra lobes along the rachis and hence somewhat pinnately divided, the upper ones simply ternate or undivided, glabrous to somewhat silky-villous and then glabrate at least on upper surface; inflorescence raceme-like or spike-like to loosely paniculate, 1 to 5 cm. broad; lower heads peduncled, the upper sessile, mostly nodding, hemispheric; involucre 3 to nearly 4 mm. high, 3.5 to 4 mm. broad, glabrous or nearly so, yellowish green (or brownish), the bracts with brown medial line; disk-flowers apparently 15 to 30, the corolla 2.2 to 2.6 mm. long. (*A. borealis* Pallas, Reise 3:755, 1776.) Greenland and Hudson Bay to Vermont, western Ontario, Colorado (?), and Washington, thence probably far to the north and northwest, since it is reported from Kotzebue Sound (Hooker, Fl. Bor. Am. 1:327, 1833) and is not rare in Siberia. Type locality, Siberia. Collections: Grand Falls, Newfoundland, on ledges and talus, *Fernald and Wiegand 6388* (DS, Gr, UC); Gaspé County, Quebec, on serpentine detritus, *Collins and Fernald 145* (NY, UC, US); Gaspé County, Quebec, on cliffs, *Collins, Fernald, and Pease 6183* (UC); Mount Mansfield, Vermont, *Eggleston 2027a* (NY); Mount Harvard, Colorado, *Clements 31* (NY, referred here because of the glabrous involucre, but doubtless a local derivative of subspecies *spithamaea*); near Banff, Alberta, *McCalla 2016* (US, type of *A. macallae* Rydberg, minor variation 22); White Horse Rapids, Yukon River, *Macoun 79015* (NY, same variation).

21c. *ARTEMISIA CAMPESTRIS SPITHAMAEA* (Pursh).—Root perennial; stems several, crowded on the crown, 1 to 4 dm. high, erect or ascending, the base often spreading, densely leafy below, less so up into the inflorescence; leaves once or twice ternately or somewhat pinnately divided into short linear or linear-oblong divisions, the upper ones less divided or entire, all densely silky-pubescent; inflorescence spike-like, very dense towards the summit, about 0.5 to 1.5 cm. broad, or closely paniculate and up to 4 cm. broad (form = *A. bourgeauana* Rydberg, minor variation 5); heads sessile or subsessile, erect to nodding, hemispheric; involucre about 4 mm. high, 4 to 5 mm. broad, densely villous, brownish except where covered by the gray pubescence; disk-flowers 15 to 20 or more, the corollas about 3 mm. long. (*A. spithamaea* Pursh, Fl. Am. Sept. 522, 1814.) Greenland and the Arctic coast to Quebec and in the mountains to Colorado and northern Oregon, thence northwest to the Aleutian Islands and Kamchatka. Type locality, Labrador. Collections: Near Fyllas, Greenland, August 2, 1884, *Warming and Holm* (Gr); Nikok, western Greenland, August 10, 1907, *Hansen* (hb. Blankinship); island of Omenak, Greenland, *White and Schuchert 163* (US, intermediate to subspecies *borealis*, some involucre glabrous, some moderately pubescent with long loose hairs); Rama, Labrador coast, *Sornborger 62* (Gr, US, intermediate to subspecies *borealis*); Okkak, Labrador, *Moravian Fathers* (Gr); on serpentine, Mount Albert, Quebec, *Fernald and Collins 258* (NY); northwestern Wyoming, *Rose 655* (US); Cameron Pass, Colorado, July 31, 1896, *Baker* (NY, UC); high mountains about Empire, Colorado, *Patterson 215* (Gr, NY, UC); Crestone's, Sangre de Cristo, Colorado, September, 1877, *Brandege* (UC); Mount Henry, Montana, *Umbach 612* (NY, US); gravelly banks of the Columbia River, Wasco County, Oregon, April 14, 1886, *Suksdorf* (Gr); Biggs, Oregon, near the banks of the Columbia River, May 31, 1910, *Heller* (NY, UC, type collection of *A. ripicola* Rydberg, minor variation 29); summit of Olympic Mountains, Washington, August 28, 1898, *Flett* (US); Cold Bay, Alaska, *Piper 4223* (US, type of *A. manca* Rydberg, minor variation 23); Petropaulovski, Kamchatka, 1853-56, *Wright* (Gr, with intermediates to *borealis*).

21f. *ARTEMISIA CAMPESTRIS PYCNOCEPHALA* (Lessing).—Root perennial; stems several or numerous on a stout woody caudex, 2 to 6 dm. high, erect, very leafy up to the inflorescence; leaves twice or thrice pinnately divided into linear or linear-spatulate divisions 0.5 to 1 mm. wide, densely and permanently silky-villous; inflorescence a strict virgate

panicle, 2 to 10 cm. broad; heads sessile, erect, hemispheric; involucre 3.5 to 4.5 mm. high, 3.5 to 4.5 mm. broad, densely villous, disk-flowers 12 to 25, the corolla 2 to 3 mm. long. (*Oligosporus pycnocephalus* Lessing, *Linnaea* 6:524, 1831.) Sandy beaches along the Pacific Ocean from Oregon south to Point Sur, California. Type locality, California. Collections: Coos County, Oregon, *House 4991* (NY); Samoa, Humboldt County, California, *Tracy 3023* (DS, UC, US); Bodega Point, California, *Eastwood 4801* (SF); West Berkeley, San Francisco Bay, California, *Davy 858* (UC); Point Sur, Monterey County, California, July, 1888, *Brandegee* (UC).

MINOR VARIATIONS AND SYNONYMS.

Several of the variations indicated below have been assigned specific rank by other writers. This is not surprising in view of the striking superficial differences between some of them. This unlikeness is sometimes due to varying amounts of pubescence. Thus, within a single subspecies there may be found some plants that are quite green and glabrous as well as others that are hoary pubescent. Again, the degree of branching gives rise both to spicate and loosely panicle inflorescences, but with all intermediate stages represented. Such characters are so obviously ecologic, as indicated especially by field observations, that the resulting forms are not given even subspecific rank. A large number of varieties are recognized by European botanists (see especially Rouy in *Rev. Bot. Syst. Geog. Bot.* 1:295, 1903, and *Fl. France* 8:293, 1903).

1. *ARTEMISIA BOREALIS* Pallas, *Reise* 3:755, 1776.—*A. campestris borealis*.

1a. *A. BOREALIS BESSERI* Torrey and Gray, *Fl. N. Am.* 2:417, 1843.—Based upon *A. borealis purshii* Besser, which see.

2. *A. BOREALIS PURSHI* Besser, in Hooker, *Fl. Bor. Am.* 1:326, 1833.—Based upon *A. spithamaea* Pursh, which see.

3. *A. BOREALIS SPITHAMAEA* Torrey and Gray, l. c.—*A. campestris spithamaea*.

4. *A. BOREALIS WORMSKIOLDI* Besser, in Hooker, *Fl. Bor. Am.* 1:327, 1833.—The same as *A. campestris borealis*, from the description. The original specimens came from "Columbia River and Islands, Northwest America" and Kotzebue Sound.

5. *A. BOURGEOUANA* Rydberg, *Bull. Torr. Club* 37:454, 1910.—A form of *A. campestris spithamaea* characterized by a slightly taller habit and a dense, leafy panicle. The types, which came from Saskatchewan, are 3 to 4 dm. high and therefore nearly matched in height by specimens from Cameron Pass, Colorado (July 24, 1894, *Crandall*, NY), which are 3 dm. high but with all other features of *spithamaea*. The panicles in the types are 25 cm. long and 3 cm. broad. Although closely approached in some specimens of *spithamaea*, the large size of the inflorescence constitutes the best character of the form.

6. *A. CAMPESTRIS GENUINA* Herder, *Pl. Radd.* 3:57, 1864.—Probably the same as *A. campestris typica*.

7. *A. CAMPORUM* Rydberg, *N. Am. Fl.* 34:254, 1916.—The lower and less leafy form of *A. campestris pacifica*, although authentically named specimens are often up to 7 dm. high and as leafy as in this. The inner bracts are said to be rounded as compared with the acutish inner bracts of *pacifica*. In order to test the constancy of this character, 6 sheets were selected from the herbarium of the New York Botanical Garden, 3 of which had been determined for the North American Flora as *pacifica*, the other 3 as *camporum*. Heads from these specimens were given to the artist with directions to draw to scale an average inner bract from each, preserving the original shape as far as possible. The resulting drawings are shown in figure 17, and seem to indicate that the shape of the inner bracts does not here afford a safe criterion for the separation of forms. The type locality of *camporum* is Saskatchewan.

8. *A. CANADENSIS* Michaux, *Fl. Bor. Am.* 2:128, 1803.—A variation of *A. campestris borealis*. The original characterization is too brief to permit a determination of the exact form. But since the type locality is Hudson Bay, where typical *borealis* grows, there is no reason to assume that it is fundamentally different from that subspecies. In the Synoptical Flora, Gray greatly extended Michaux's species to include the common small-headed form of the western United States now referred to subspecies *pacifica* and separated this from his *A. borealis* Pallas, chiefly on the numerous heads in a compound, oblong or pyramidal, virgate panicle. But Gray himself admitted that the panicle was reduced in northern forms. It proves impossible to use the form of the inflorescence to distinguish varieties in this region. The original figure of Pallas (*Reise*, 3:129, 1776)

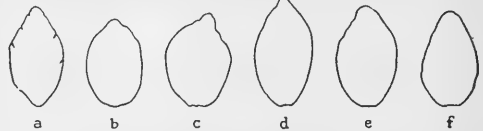


FIG. 17.—Inner bracts of *Artemisia campestris pacifica*; a, b, c, from specimens of genuine *pacifica*; d, e, f, from specimens authentically determined as *A. camporum* Rydberg (minor variation 7). Collections represented: a, *Leiberg 1580*; b, *Macoun 26344*; c, *Buller 643*; d, *Clemens 156*; e, *Oerholts*; f, *Rydberg 203*; all in the Herbarium of the New York Botanical Garden. All $\times 8$.

shows spicate clusters on the same plant with a paniculate one. A plant from the Gaspé Peninsula (Fernald and Collins 754) possesses one paniculate and two spicate stems, and Fernald states that the inflorescence varies with the situation. In moist protected soils the plants are larger and the clusters paniculate, while in drier or more exposed places they are reduced, and the inflorescence becomes spicate. In recent floras *canadensis* is characterized with green involuercs and *borealis* with brown, but these colors are not sharply defined in the plants themselves.

9. *A. CAUDATA* Michaux, Fl. Bor. Am. 2: 129, 1803.—*A. campestris caudata*.
10. *A. CAUDATA CALVENS* Lunell, Am. Midl. Nat. 2: 188, 1912.—From the description this appears to be the form of *A. campestris caudata* in which the herbage is thickly tomentulose when young. Type locality, in gravel at Willow City, Bottineau County, North Dakota.
11. *A. COMMUTATA DOUGLASIANA* Besser, Bull. Soc. Nat. Mosc. 8: 70, 1835.—Referred in N. Am. Fl. to *A. camporum* Rydberg, here considered a minor form of *A. campestris pacifica*. Type locality, Saskatchewan.
12. *A. COMMUTATA HOOKERIANA* Besser, l. c. 70, 1835.—Same as *A. desertorum hookeriana*, which see.
13. *A. COMMUTATA RICHARDSONIANA* Besser, l. c. 74, 1835.—Based on *A. desertorum richardsoniana*, which see.
14. *A. DESERTORUM DOUGLASIANA* Besser, in Hooker, Fl. Bor. Am. 1: 325, 1833.—Referred in N. Am. Fl. to *A. camporum* Rydberg, which is here considered as a minor form of *A. campestris pacifica*. Type locality not stated.
15. *A. DESERTORUM HOOKERIANA* Besser, l. c., 325, 1833.—Apparently includes two or more of the subspecies of *A. campestris*. Distribution originally given as throughout Canada and to the Arctic Circle.
16. *A. DESERTORUM RICHARDSONIANA* Besser, l. c., 325, 1833.—Referred in N. Am. Fl. to *A. maccallae*, which is here considered as a minor form of *A. campestris borealis*, but since it was first described as having ashy-sericeous involuercs it is more likely the subspecies *spithamaea*. Original distribution given as throughout Canada and thence to the Arctic Circle.
17. *A. DESERTORUM SCOULERIANA* Besser, l. c., 325, 1833.—One of the subspecies of *A. campestris*, probably *pacifica*. Type locality, Fort Vancouver and Straits of de Fuca.
18. *A. FORWOODI* Watson, Proc. Am. Acad. 25: 133, 1890.—*A. campestris caudata*, but a form with the leaves mostly canescent with a short villous pubescence. Type locality, Black Hills of South Dakota. This is chiefly a western variation, but ranges east at least to Point Edward on Lake Huron (*Macoun 26343*), while typical *caudata* occurs as far west as Wyoming (according to Rydberg, N. Am. Fl.).
19. *A. FORWOODI* var. *CALVENS* Lunell, Am. Midl. Nat. 5: 68, 1917.—*A. campestris caudata*. (See note under *A. caudata calvens*.)
20. *A. GROENLANDICA* Wormskjold, Fl. Dan. 27: 10, 1818.—*A. campestris spithamaea*. Type locality, Greenland.
21. *A. LEWISI* Torrey and Gray, Fl. N. Am. 2: 417, 1843 (excluding synonymy).—*A. campestris caudata*, but a form with heads in a large, open panicle. Type locality, Missouri.
22. *A. MACCALLAE* Rydberg, N. Am. Fl. 34: 254, 1916.—*A. campestris borealis*. Separated because of the short outer bracts, these about one-half as long as the inner. The rather numerous heads are soon ascending or erect. Type locality, gravelly slopes of Tunnel Mountain, vicinity of Banff, Alberta.
23. *A. MANCA* Rydberg, N. Am. Fl. 34: 256, 1916.—*A. campestris spithamaea*. This is a dwarf, compact form of the far north, differing only in the lower stature (5 to 7 cm.) and short leaves (1 to 2 cm.). Type locality, Cold Bay, Alaska.
24. *A. PACHYSTACHYA* De Candolle, Prodr. 6: 114, 1837.—*A. campestris pycnocephala*. Erroneously referred by De Candolle to the section *Abrotanum*, although also properly placed, but with erroneous distribution, in the section *Dracunculus* under the name *A. pycnocephala*.
25. *A. PACIFICA* Nuttall, Trans. Am. Phil. Soc. II, 7: 401, 1841.—*A. campestris pacifica*.
26. *A. PEUCEDANTIFOLIA* Jussieu; Besser, Bull. Nat. Soc. Mosc. 8: 91, 1835.—*A. campestris borealis*.
27. *A. PYCNOCEPHALA* De Candolle, Prodr. 6: 99, 1837.—*A. campestris pycnocephala*.
28. *A. PYCNOTACHYA* Nuttall, Trans. Am. Phil. Soc. II, 7: 401, 1841.—*A. campestris pycnocephala*. Obviously an error in name.
29. *A. RIPICOLA* Rydberg, N. Am. Fl. 34: 256, 1916.—*A. campestris spithamaea*. In the North American Flora this is separated from *spithamaea* in the key by the narrowly linear instead of linear-oblanceolate segments of the basal leaves, but these are slightly oblanceolate as stated in the description. Furthermore, specimens of the type collection from Biggs, Oregon, are almost exactly matched by others from the high mountains of Colorado (for example, Cameron Pass, July 31, 1896, *Baker*, and Eagle Mountain, August 12, 1913, *Allen*). It thus seems that neither constant morphologic characters nor geographic distribution gives support to this form.
30. *A. SCOULERIANA* Rydberg, Bull. Torr. Club 33: 157, 1906.—Based upon *A. desertorum scouleriana* Besser, which see.
31. *A. SPITHAMAEA* Pursh, Fl. Am. Sept. 522, 1814.—*A. campestris spithamaea*.
32. *A. VARIABILIS AMERICANA* Besser, Bull. Soc. Nat. Mosc. 8: 24, 1835.—*A. campestris caudata* but a form with large panicles.
33. *OLIGOSPORUS PYCNOCEPHALUS* Lessing, Linnaea 6: 524, 1831.—*A. campestris pycnocephalus*.

RELATIONSHIPS.

The species of *Artemisia* most closely connected phylogenetically with *A. campestris* are natives of Asia or possibly of Europe. Of these, *A. commutata* Besser is so close that it should be merged into it, as has been already done by some. As a subspecies, or series of subspecies, for it passes into numerous forms similar to those occurring in America, *commutata* stands between *typica* and the other perennials described above. Its distribution from the Caucasus to Baikal and Davuria, in Siberia, together with its trait of breaking up into forms similar in character to ours, suggests that it may represent the ancestral strain which, crossing the Bering Straits, has given rise to at least some of the American subspecies. A coordination between the Siberian and American forms is impossible at the present time from a lack of field knowledge. Another Siberian species of close relationship is *A. desertorum* Sprengel, to which several of the American forms were once assigned by Besser. This has all of the essential characters of *campestris*, but is perhaps to be retained because of its much wider leaf-segments. The only American *Artemisia* closely allied to *campestris* is *A. dracunculus*, and even here the separation probably took place in the Old World. There is no constant floral difference between the two, but the much more pronounced segmentation of the leaves and the tendency to produce most of these in a basal rosette give to *campestris* a very different aspect.

In taking up the segregates of this cosmopolitan species it is first noted that the typical form is common on the plains of Europe and western Asia. In America it is known from only a few isolated stations along the Atlantic seaboard, where it is probably adventive from Europe. It is a tall, perennial herb with numerous stems from the base, very narrow leaf-segments, and small, ovoid heads in an open, loosely branched inflorescence. On the plains and in the lower mountains of the western States grows a subspecies so similar that it is easily mistaken for *typica*. This is *pacifica* (often erroneously referred to *canadensis*). In this the heads are usually broader at the same stage of development, but they sometimes so closely match the heads of the Old World type that the two can not be distinguished by this feature alone. The pubescence in *pacifica* is more dense and persistent than the general run of *typica*, but some mature specimens of the latter are densely sericeous (Lower Austria, November 3, 1898, Klebs). *A. commutata*, which is not specifically separable from *campestris*, is said by Ledebour (Fl. Rossica 2:567, 1845) to vary from apparently glabrous to villous-sericeous. The most nearly constant character of subspecies *pacifica* is its compact inflorescence, the branches of which are strict and ascending, not outwardly curved as in the other. Since even this distinction requires a series of specimens for its practical use, and since the other characters are shown to be of but little moment, it now seems impossible to retain *pacifica* in more than subspecific rank.

The Old World type of *campestris* is more closely approached in size and shape of head and in the inflorescence by subspecies *caudata*, of the eastern and central States, but this is unique in the genus in having a biennial taproot and usually but a single stem, the latter character perhaps a result of the biennial habit. These traits are so strikingly constant that the subspecies seems possibly not to have arisen from any of the others here described, but from some Old World form with which we are not familiar. Taxonomically it is the most distinct of all of the subspecies except *pycnocephala*.

The next two subspecies, that is, *borealis* and *spithamaea*, are both of northerly distribution, scarcely reaching the United States except in the higher mountains. They extend from Greenland to the Aleutian Islands, and *borealis* has its type locality in Siberia. The influence of the boreal habitat is seen in the large size of the heads, in the reduced inflorescence, and in the strictly perennial root. This stout root supports at the surface a branching caudex from which arise several or numerous annual stems. Fundamentally this is not different from the habit of *typica* and *pacifica*, but the caudex is more branched,

sometimes cespitose, and the flowering stems are usually shorter. It may appear desirable to some to set these forms off as a species distinct from *campestris* and *pacifica* on the basis of the larger heads, but a glance at table 11 will show the impossibility of this course. In fact, the overlapping is much greater than indicated by the few specimens there reported upon. Neither Besser nor Gray was able to find specific distinctions between *canadensis* (here included with subspecies *borealis*) and *pacifica*. Moreover,

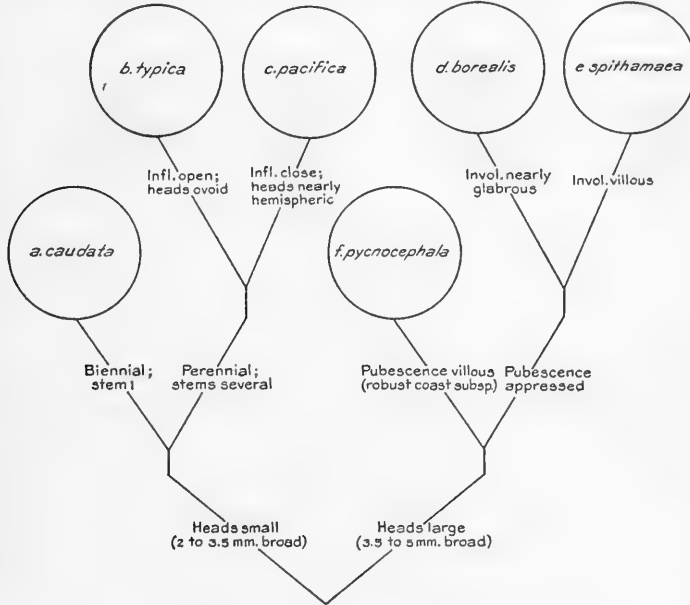


FIG. 18.—Phylogenetic chart of the subspecies of *Artemisia campestris*.

this last-named subspecies exhibits forms intergrading with *spithamaea*. For example, 3 sheets at the National Herbarium from Glacier National Park (*Standley 17307, 17331, 17716*) represent plants 3 to 5 dm. high and with the usual broad panicle, while another (*Standley 16688*) from the same park is a dwarf only 1.5 dm. high, the inflorescence less than 1 cm. broad and yet with heads much too small for subspecies *spithamaea*. The northern subspecies *borealis* and *spithamaea* differ between themselves only in very minor characters and in pubescence. It would be entirely logical to unite them, and recognize several ecologic forms, but the marked difference in the appearance of the extremes and the absence of intergrades over certain large areas render the subspecific rank of some use. Still further segregations have been made, but these are based upon habitual and other characters now known to be of little taxonomic value. They are here indicated under minor variations.

The most remarkable deviation within the species is represented by subspecies *pycnocephala*, a form restricted to the coastal sands of northern California and southern Oregon and at least 1,000 km. removed from any of the others. Its robust habit and coarse pubescence give to it an aspect so unique that it seems scarcely to belong to the present

TABLE 11.—Variation in the subspecies of *Artemisia campestris*.

	Herbarium.	Involucre.		No. of bracts.	No. of ray-flowers.	No. of disk-flowers.	Total no. of flowers.	Length of disk-corolla.
		Height.	Breadth.					
<i>Subspecies typica:</i>								
Berlin Botanical Garden.	617460 US	mm.	mm.	9 10	7 7	5 7	12 14	mm.
Stendel, Germany.	NY	2.0	1.8	8 8	7 5		11 10	1.8
Kolpenick, Germany.	6560 Baker	2.5	2.6	10 9	8 10	6 6	14 16	2.4
Carlsruhe, Germany.	545707 US	2.7	2.6	9 10	7 7	8 8	15 15	2.4
Tirol, Austria.	343717 US	2.7	2.4	11 11			10 10	2.1
Upsala, Sweden.	US	2.8	2.6	9 9	7 7	7 9	14 16	2.4
Finland.	UC	2.5	2.4	9 10	6 7	11 7	17 14	1.8
Do.	UC	2.7	2.8	12 13	17 19	11 9	28 28	2.1
Le Mans, France.	6492 Baker	2.6	2.6	9 10	9 9	9 6	18 15	2.1
Suffolk, England.	812960 US	2.5	2.5	10 10	11 13	9 9	20 22	2.3
Europe.	29728 UC	3.0	2.9	10	9	12	21	2.0
Waterbury, Conn.	Gr.	2.1	2.0	10 9	15 14	5 4	20 18	
Average.		2.6	2.4	9	9	7	17	2.3
<i>Subspecies pacifica:</i>								
Inyan Kara Divide, Wyo.	29730 UC	3.0	2.6	10 11	15 17	15 16	30 33	2.0
Laramie, Wyo.	146507 UC	2.5	2.3	10 9	12 15	17 19	29 34	1.8
New Windsor, Colo.	34331 UC	2.0	2.5	12 10	12 10	13 10	25 20	2.0
Tolland, Colo.	10491 CI	2.5	2.5	15 10	16 13	22 18	38 31	young
Austin Bluffs, Colo.	CI	2.0	2.5	13 12	12 17	12 14	24 31	Do.
Manitou, Colo.	CI	2.0	2.5	10 10	15 17	14 10	29 27	Do.
Cañon City, Colo.	172665 UC	2.8	2.2	12 13	15 14	11 13	26 27	2.1
Turquoise Lake, Colo.	11061 CI	3.0	3.0	14 11	15 11	23 13	38 24	2.1
West-central Colo.	34514 UC	2.5	2.4	12 12	11 13	22 18	33 31	2.0
Silver City, N. Mex.	29732 UC	2.8	2.3	9 11	12 10	19 14	31 24	2.0
San Francisco Mts., Ariz.	193467 UC	2.3	2.2	12 8	9 11	8 8	17 19	1.8
La Sal Mountains, Utah.	135383 UC	2.7	2.5	10 12	13 12	10 16	23 28	2.0
Clarks Fork Valley, Ida.	154393 UC	3.0	2.4	11 12	9 10	12 13	21 23	2.3
Average.		2.5	2.4	11	12	14	27	2.0
<i>Subspecies caudata:</i>								
Frenchville, Me.	(Fernald) Gr	3.5	3.6	22 20	8 9	13 13	21 22	2.2
Marthas Vineyard, Mass.	29735 UC	2.1	2.3	14 13	11 9	6 8	17 17	1.5
Washington Island, Wis.	181940 UC	2.8	2.5	8 7	8 5	9 10	17 15	1.7
Oquawka, Ill.	172666 UC	2.5	2.1	13 16	11 9	7 5	18 14	1.8
Peoria, Ill.	91216 UC	2.7	2.5	11 14	13 13	11 12	24 25	2.0
Evanston, Ill.	193517 UC	2.6	2.7	13 15	20 13	11 15	24 31	2.0
Blue River, Nebr.	193608 UC	2.5	2.3	15 14	12 11	11 11	23 22	1.4
Average.		2.6	2.6	13	10	10	20	1.8
<i>Subspecies borealis:</i>								
Table Mountain, Nfd.	Gr	3.3	3.4	15 17	13 13	12 15	25 28	2.5
Exploits River, Nfd.	201606 UC	3.1	3.6	15 18	21 19	20 25	41 44	2.3
Mount Albert, Quebec.	Gr	3.6	3.7	17 15	17 16	27 28	44 44	2.3
Do.	Gr	3.1	3.5	14 16	13 15	25 30	38 45	2.5
Do.	Gr	3.2	3.4	15 14	14 14	17 17	31 31	2.6
Gaspé County, Quebec.	147968 UC	3.5	3.5	17 13	15 13	21 20	36 33	2.5
Do.	69740 UC	3.2	3.3	12 13	18 14	17 22	35 36	2.1
Average.		3.2	3.4	15	15	21	37	2.3
<i>Subspecies spithamea:</i>								
Clear Creek, Colo.	29726 UC	4.2	4.8	15 11	10 10	19 17	29 27	3.0
Saguache, Colo.	91237 UC	4.0	4.3	11 12	10 9	15 20	25 29	2.8
Biggs, Oreg.	196037 UC	4.0	4.5	15	7	16	23	3.0
Average.		4.0	4.5	12	9	17	26	2.9
<i>Subspecies synocephala:</i>								
Lake Earl, Calif.	128619 UC	3.8	4.0	18	7	26	33	3.0
Opposite Eureka, Calif.	164826 UC	4.0	4.0	17	14	20	34	2.2
West Berkeley, Calif.	71897 UC	4.0	4.3	17	6	12	18	3.0
Del Monte, Calif.	184483 UC	4.4	4.0	9	10	20	30	2.5
Point Sur, Calif.	91213 UC	4.0	4.0	10	9	17	16	2.0
Average.		4.0	4.0	14	9	19	26	2.5

assemblage, but in all essentials it is so close to some of the other subspecies, especially the tall (*bourgeauana*) forms of *spithamaea* that a workable key can not be constructed that will satisfactorily separate it. It is undoubtedly a derivative of some boreal form which has become isolated and has responded to protection and the more genial climate through the development of an exceptionally robust habit and other characters especially suited to its southerly maritime habitat. This view finds some substantiation in the fact that while the plants of the middle California coast represent the extreme type as to robustness, enlarged inflorescence, and spreading pubescence, those from farther north have these characters much less developed. Thus, a collection from Lake Earle, Del Norte County, California (Univ. Calif. 128619), has sparsely leafy stems only 2 dm. high and leaves small in proportion, while the inflorescence is spike-like and only 1.2 cm. broad at the broadest place. These plants have the whole aspect, although not quite the pubescence, of some forms of *spithamaea*.

Another collection (*Tracy 3023*) from the next county south of Del Norte is intermediate in these characters between the Lake Earle collection and the common form of middle California. The northern ancestor of this subspecies is perhaps to be found in *spithamaea*, of which some forms are 2 to 3 dm. high and with an inflorescence 1 to 4 cm. broad, thus completely overlapping the dimensions of *pycnocephala*. In pubescence, also, they are scarcely distinct from this coastal plant, so that if it were not for the habitat they would quite certainly be called the same. Such plants come from sandy river banks at Bingen, Klickitat County, Washington (*Suksdorf 2685* and *2686*, both at the National Herbarium, where determined as *A. ripicola* Rydberg). It is also of interest to find that a variety with some of these characteristics has been recognized in plants growing on sandy shores in France. This is described as a stout plant with short and broad leaf-segments and comparatively large heads. To it has been given the name, *A. campestris* var. *maritima* Lloyd (see Coste, Fl. France 2:333, 1903).

The relationships of the subspecies of *A. campestris* are graphically represented in the accompanying diagram (p. 127).

ECOLOGY.

Artemisia campestris is typically a rosette-former, though this habit is more marked in the biennial than the perennial forms. For the most part the subspecies are seral dominants, but *pacifica* in particular is an important society of the mixed-prairie climax. *Typica*, *caudata*, and *pycnocephala* regularly form consocieties or societies on sandy shores and dunes, from which they sometimes find their way into waste places. *Pacifica* is one of the most unpalatable of Artemisias to stock and hence is excelled only by *A. frigida* as an indicator of overgrazing. The pioneering quality of the species is also shown in the frequent occurrence of *pacifica* in disturbed soils, especially sands and gravels.

USES.

The field sagewort is a common weed on many of the stock ranges of the West, especially in the northern Rocky Mountain States, but it is so unpalatable that it is grazed only when all other sources fail. It occasionally tides animals, especially sheep, over exceptionally hard seasons, but its value for this purpose is slight. In these same regions the herbage is gathered, dried, and placed upon the market as a substitute for imported sage, used in cookery and somewhat in medicine, and the name of "wild hair tonic" sometimes applied to it indicates that perhaps it is employed to stimulate the growth of the hair. The properties of the essential oil present in the herbage of subspecies *caudata* have been studied by Rabek (Pharm. Rev. 24:324, 1906). It is one of the causes of hay-fever, as shown by tests made in the Rocky Mountain region.

22. ARTEMISIA FILIFOLIA Torrey, Ann. Lyc. N. Y. 2:211, 1828. Plate 16.
SAND SAGEBRUSH.

A rounded shrub, 5 to 12 dm. high, mildly and pleasantly scented; stems freely branched throughout, the older parts with a close and smooth dark-gray or blackish bark, the numerous slender twigs striate beneath a canescent pubescence; principal leaves sessile, often with fasciated ones in their axils, filiform, 3 to 8 cm. long, less than 0.5 mm. wide at base, ternately divided into long filiform divisions or some of them entire, canescent; upper leaves but little reduced, more often entire, ascending or incurved, canescent; inflorescence a narrow, dense, leafy panicle, 10 to 30 cm. long by 1 to 5 cm. broad; heads heterogamous, crowded, nodding on recurved peduncles; involucre subglobose, 1.5 to 2 mm. high and nearly as broad; bracts 5 to 9, the outer ones short and thick, the inner ones thinner, broadly elliptic, obtuse, all densely canescent on exposed parts, none scarious; receptacle smooth and naked; ray-flowers 2 or 3, fertile, corolla tubular, about 1 mm. long; disk-flowers 1 to 6, sterile, corolla broadly funnellform, 5-toothed, 1.5 to 2 mm. long, resinous-glandular; style of disk-flowers 1 to 1.5 mm. long, either cup-shaped at the erose summit, the branches being entirely fused, or shortly bifid and the lobes with erose margins; achenes ellipsoid, narrowed to the corolla, either smooth or with 4 or 5 raised ribs, glabrous, those of the disk-flowers abortive.

Wyoming and western Nebraska to Texas, Chihuahua, Arizona, Nevada, and Utah. Type locality not given. Collections: Uva, Laramie County, Wyoming, *Nelson 8636* (Gr, NY, UC); North Denver, Colorado, *Eastwood 32* (Gr, UC, many of the heads transformed into galls); Deuel County, western Nebraska, *Rydberg 206* (NY); Tribune, Greeley County, Kansas, September 18, 1893, *Reed* (UC); near Alva, Oklahoma (common) *Stevens 2811* (Gr); Box Springs, Texas, *Tracy 8155* (NY); near Del Norte, Chihuahua, *Pringle 770* (Gr, NY, UC, US); Mesilla Valley, Doña Ana County, New Mexico, October 2, 1889, *Wooton* (UC, many of the heads transformed into galls); Willcox Flat, southeastern Arizona, *Shreve 4257* (SF, UC); above Rioville, southeastern Nevada, *Jones 5036* (UC); between Kanab and Carmel, Utah, *Jones 6047* (NY, UC).

MINOR VARIATION.

1. ARTEMISIA PLATTENSIS Nuttall, Trans. Am. Phil. Soc. II, 7:397, 1841.—*A. filifolia*. Separated from *A. filifolia* only on its inflorescence, which is described as a loose and regularly simple-branched panicle. All degrees of density of inflorescence may be observed in a field of these plants. Type locality, upper plains of the Platte River.

RELATIONSHIPS.

The only American *Artemisia* which can claim close relationship is *A. pedatifida*, as will be pointed out under that species. In the opinion of Rydberg, these two are sufficiently well set-off from the other species of his subgenus *Dracunculus* to form a separate section. This he distinguishes by the shrubby or subshrubby habit and the "usually more or less 2-cleft" style of the disk-flowers (N. Am. Fl. 34:245, 1916). This cleavage of the style is fairly well marked in the specimens examined of *pedatifida*, although even in this species there is a partial fusion in some cases, but in *filifolia* it is often obscure and sometimes it fails entirely. Since species of Rydberg's section with entire styles, particularly *campestris*, also have evident branches in somewhat over 30 per cent of the flowers examined, this feature is seen to be too variable to be of much real value as a specific or sectional criterion. It is, however, of great assistance in working out the phylogeny of the species of this group. For example, since the original condition undoubtedly was one in which the branches were distinct for some distance, entire styles are to be looked upon as the result of fusion of these branches and therefore as representing a more advanced type of plant. According to this view, *A. filifolia* is intermediate in its development, for, while its style is usually branched, in some cases the parts are completely fused and terminated by an unbroken cup-like border (e. g.,

plants from Cañon City, Colorado, August 30, 1919, *Hall*). This allies it with *A. campestris* and *A. pedatifida*, which are also in a transitory stage as regards this character, and places it below *A. dracunculus*, in which the branches are usually completely fused. This last species, however, is less highly developed in certain other particulars, such as the herbaceous habit, and is therefore provisionally retained first in the sequence of species. The results of a detailed examination of style-branches are given in the introductory remarks on criteria (p. 38).

In comparing *A. filifolia* with species outside its own section, one is impressed with the remarkable similarity to *A. californica*. This extends to the habit, foliage, inflorescence, and ecologic behavior. If such a relationship exists, *californica* is obviously the more primitive, chiefly because of its fertile disk-achenes, larger number of flowers in the head, and evidently closer connection with the genus *Crossostephium*. The derivation of *filifolia* would involve a considerable reduction in the number of flowers, an abortion of the central achenes, and the rounding of the summit of the ray-achenes, as well as the smoothing out of the angles of these latter. It is also to be noted that in *A. californica* there is no tendency toward a fusion of the style branches. Therefore, while this connection is considered as possible, it is not demonstrable with the evidence now at hand.

ECOLOGY.

Artemisia filifolia resembles both *A. tridentata* and *californica* in life-form, but is more like the latter in its rounded bushy habit. It is typically a subclimax dominant of sandy soils, and perhaps the most widespread shrub on inland dunes and sandhills from Nebraska to Arizona. In the north especially it often forms pure consocieties, but southward it is usually associated with *Yucca*, *Chrysothamnus*, *Dalea scoparia*, *Poliomintha incana*, or *Atriplex canescens*. Toward the close of the succession, the sand sagebrush persists for a long time in the mixed prairie cover, producing the appearance of a savannah. It is one of the most characteristic indicators of sand, and changes in abundance serve to denote the amount of sand in the soil. The heads are often enlarged and transformed into galls by species of *Rhopalomya*.

USES.

The value of the sand sagebrush as a browse shrub depends upon the region where it grows. In the grassland districts it is seldom much eaten, because of the abundance of other food. Thus it is reported from Texas and the Rocky Mountain States north to the Dakotas as of little value, and the normal development of the plants verifies this statement. But in the more arid southwest, particularly New Mexico and Arizona, the plant is reported to be of considerable value, and the closely cropped, irregular shrubs give evidence of close browsing. In the last-named State it is of importance only in the eastern part, since it becomes sparse toward the west and is entirely wanting as the California line is approached. Attention should be given to this species as a cause of hay-fever, since it possesses all of the necessary characteristics and is fairly common near settled districts, especially in eastern Colorado.

23. ARTEMISIA PEDATIFIDA Nuttall, Trans. Am. Phil. Soc. II, 7:399, 1841. Plate 16. BIRDFOOT SAGEBRUSH.

A low perennial subshrub with a tough woody root, 0.5 to 1.5 dm. high, the odor unknown; stems numerous, erect from the short woody base (this with fibrous exfoliating bark), obscurely striate, cinereous-pubescent; basal leaves tufted, petioled, 1 to 2 cm. long including the petiole and nearly as wide across the lobes, once or twice ternately divided into narrowly spatulate or nearly linear short divisions, gray with a fine dense pubescence; upper leaves smaller, with few divisions or entire, permanently cinereous

like the lower; inflorescence raceme-like or spike-like, sparsely leafy, 1 to 7 cm. long by about 0.5 cm. broad; heads heterogamous, short-peduncled or sessile, erect; involucre hemispheric, about 3.5 mm. high, 3 to 4 mm. broad; bracts 6 to 10, round-oval, obtuse or slightly acute, moderately unequal, scarious-margined, the outer ones densely tomentulose; receptacle naked; ray-flowers 4 to 7, fertile, corolla 1.5 to 2 mm. long, very slender, constricted at the few-toothed summit; disk-flowers 5 to 10, sterile, corolla tubular-funnelform, 3 to 3.5 mm. long, 5-toothed, rose-colored toward the summit, glabrous; style of disk-flowers 2.5 to nearly 3 mm. long, 2-cleft at summit, the branches penicillate at apex or the branches sometimes fused along one sinus, the other remaining open, probably completely fused in some cases; achenes ellipsoid, faintly ribbed, glabrous, those of the disk-flowers wanting.

Northern Rocky Mountains on dry plateaus and ridges. Wyoming, Idaho, and probably Montana. Type locality, arid plains of Lewis (Snake) River. Collections: Steamboat Mountain, Sweetwater County, Wyoming, *Nelson 7058* (Gr, NY, UC); Cooper Lake, Albany County, Wyoming, *Gooding 21* (Gr, NY, UC, US); type collection, *Nuttall* (Gr, Phila.).

RELATIONSHIPS.

The shrubby habit, reduced number of flowers, narrow disk-corollas, and the cleft styles of the disk-flowers all indicate *A. pedatifida* as an ally of *A. filifolia*, notwithstanding its very different appearance. It is the high-altitude and northerly representative of that, with the woody portion and the inflorescence much reduced. Whether either of these species has been derived from the other can not be stated definitely, for intermediate forms do not now exist. Notwithstanding the plainly sterile disk-flowers *A. pedatifida* was originally placed in the section *Abrotanum*, presumably through an oversight. It is in no way connected with any of the forms of that group. A notable peculiarity of the species is the remarkable length of the disk-corollas, these averaging about twice as long as those of other and much larger plants of the same section. Because of its low stature, the plant is sometimes confused with *A. tridentata trifida*, but—aside from technical characters such as the sterile disk-achenes and much larger and broader corollas—*pedatifida* may be distinguished by the divergent leaf-lobes, the larger heads, the lower of which are distinctly peduncled, and by the gray fibrous bark of the caudex and root.

ECOLOGY AND USES.

Artemisia pedatifida is a dwarf shrubby rosette-former, resembling *A. spinescens* and *pygmaea* in habit. It forms the characteristic consocieties of flat alkaline depressions in Wyoming, and persists for a long time in the succeeding *Agropyrum* consociation of the mixed prairie. It is an indicator of the presence of alkali in moderate amounts. In the less alkaline associations it is frequently mixed with *A. frigida*, and less so with *A. tridentata*.

The foliage of this *Artemisia* is doubtless browsed to a limited extent by cattle and sheep, but the plants are too small to be compared in value with the larger sagebrushes. Since also the species is of limited distribution, its economic importance is apparently quite negligible.

24. ARTEMISIA SPINESCENS D. C. Eaton, in Watson, Bot. King's Expl. 180, 1871. Plate 17. BUD SAGEBRUSH.

A rounded spiny shrub, 0.5 to 5 dm. high, with a strong penetrating odor and bitter taste; stems crowded, much branched from the base, thick and rigid, the older parts with a brown fibrous bark, the twigs ascending, not striate, white-tomentose or short-

villous; principal leaves petioled, flabellate in outline, 0.5 to 2 cm. long including the petiole, 0.5 to 1.5 cm. wide, pedately 3- to 5-divided, and the divisions again cleft into linear-spatulate lobes, densely villous; upper leaves similar but less divided, those of the inflorescence about equaling the heads; inflorescence consisting of numerous short racemes in the axils and at the ends of the short branches, sometimes reduced to only 1 or several heads, leafy-bracted, 1 to 5 cm. long, 0.5 to 1 cm. broad, the persistent rachis transformed into a slender rigid spine after the heads have fallen; heads heterogamous, short-peduncled or sessile, nodding; involucre broadly turbinate, 2 to 3.5 mm. high, 3 to 4.5 mm. broad; bracts 4 to 8, all much alike and scarcely unequal, obovate-cuneate or nearly orbicular with a cuneate base, rather thick and herbaceous, with narrow scarious margins, densely villous; receptacle naked; ray-flowers 2 to 6, fertile, corolla very slender, about 1 mm. long, 2- or 3-toothed, long-hairy; disk-flowers 5 to 13, sterile, corolla funnelliform with narrow tube, 5-toothed, 2 to 3 mm. long, copiously clothed with long flaccid hairs except on the limb; style of disk-flowers undivided at the expanded and radiately penicillate summit, included; achenes of ray-flowers ellipsoid, densely arachnoid-hairy, achenes of disk-flowers wanting. (*Picrothamnus desertorum* Nuttall, Trans. Am. Phil. Soc. II, 7: 417, 1841, not *A. desertorum* Sprengel, Syst. Veg. 3: 490, 1825-28.)

Common on arid plains and slopes from Montana and Colorado to New Mexico, eastern California (from the San Bernardino Mountains north), eastern Oregon, and Idaho. Type locality, Rocky Mountain plains, in arid deserts, toward the north sources of the Platte River. Collections: Beaverhead County, Montana, *Tweedy 19* (according to Rydberg, Mem. N. Y. Bot. Gard. 1: 427, 1900); Palisade, western Colorado, May 29, 1894, *Crandall* (NY); Steamboat Mountain, Sweetwater County, Wyoming, *Nelson 7047* (Gr, NY, UC); Marysvale, Utah, *Jones 5326* (NY, UC, US); Navajo Indian Reservation, Arizona, *Standley 7479* (US); Rabbit Springs, north base San Bernardino Mountains, California, April 25, 1915, *Shreve* (UC); Truckee Valley, Nevada, *Kennedy 1966* (UC); Malheur Butte, eastern Oregon, *Leiberg 2020* (UC, US); near Pocatello, Idaho, *Palmer 14* (NY, SF, US).

RELATIONSHIPS.

Although *Picrothamnus* is sometimes taken as a separate monotypic genus because of the spiny habit and notably pubescent flowers, it is in all essentials an *Artemisia* of the section *Dracunculus*. The only differentiating characters are those of habit and the pubescence of the flowers, as has been already indicated (p. 33). Its nearest relatives are doubtless species of central Eurasia that do not extend to this continent. There are, however, two cosmopolitan species, namely, *A. dracunculus* and *A. campestris*, with which it is in agreement in all important technical characters and with which it shares the almost unique feature of a tendency towards a fusion of the style-branches of the disk-flowers. Whether it really is most closely connected with these can be determined only after a detailed study of all the Old World *Dracunculi*. Whatever its origin, *A. spinescens* is now sharply set off from all other species both morphologically and geographically. No other American species approaches it in its spinescent twigs, although several, especially *pygmaea*, *pedatifida*, *rigida*, and the dwarf varieties of *tridentata*, all but one members of another section, assume a dwarfed and rigid habit as a result of similar unfavorable environments.

The degree of variation in involucre and floral characters is indicated by table 12. The most striking feature here brought out is the remarkably low variability, indicating a stable non-plastic species. Even the small differences in the number of flowers may be due to the falling-out of these in some cases where the count runs low. Perhaps it is because of its fixed characters and consequent incapacity for adaptation to new environments that the species has produced no forms that have received taxonomic recognition.

ECOLOGY AND USES.

Artemisia spinescens is a dwarf shrubby rosette-former, suggesting *A. pedatifida* and *pygmaea* in habit. It is usually found in a mixed consocieties of the sagebrush climax with other halophytes, and, like them, is an indicator of considerable alkali in the soil.

Notwithstanding its spiny habit, this is a valuable browse plant on the range, especially in Utah, Nevada, and eastern California, where it is known to stockmen as bud-sage. This is because of its leafage, which develops ahead of that of most other shrubs in the same districts. Its chief value is as an early food for sheep. Apparently authentic cases of stock-poisoning have been reported for this species, but such were probably due to excessive browsing without the addition of other foods. Feeding experiments conducted by Fleming at the Nevada Station have shown that the plant is sometimes but not always injurious to calves and that sheep are perhaps never killed by it, at least not in the presence of other browse. The pollen has been found to be active as a cause of hay-fever and is therefore used to some extent for preventing this disease in the Great Basin States.

TABLE 12.—Variation in *Artemisia spinescens*.

	Herbarium.	No. of involucre bracts.	No. of ray-flowers.	No. of disk-flowers.	Length of disk-corolla.
					mm.
Meadow Valley, Nev.....	NY	5 6	4 4	8 7	2.2
Artec, N. Mex.....	Gr	6 7	4 4	8 8	2.3
Fort Steele, Wyo.....	NY	5 5	4 4	8 8	2.3
Carbon County, Wyo.....	Gr	8	4	13	2.4
Meadow Valley, Nev.....	Gr	7 5	4 4	8 5	2.5
Steamboat Mountain, Wyo.....	146508 UC	8 7	4 4	8 7	2.2
Truckee Valley, Nev.....	190180 UC	4 4	5 4	8 12	2.4
Candelaria, Nev.....	193577 UC	6 7	5 6	8 10	2.4
Barstow, Calif.....	126503 UC	7	4	8	3.0
Average.....		6	4	8	2.4

SECTION IV. SERIPHIDIUM.

PHYLOGENY OF THE SPECIES.

All of the American members of the section *Seriphidium* are shrubs, this habit having been developed in response to arid climates. There is at present no obvious connection with any of the herbaceous species. It seems that such connection was broken very early, perhaps during the Pleistocene, and that the shrubby *Seriphidia* developed in the south at a later period. Later on, during the dry phase following the Pleistocene, they appear to have moved northward, and during this process some of the present-day species were doubtless evolved. This hypothesis very nicely accords with the fact that the most highly modified forms now occupy the most northern habitats. If the American members of the section arose independently of the Old World species, and there is now no obvious connection between the two groups, then *A. bigelovi* is to be considered as most closely representing the primitive stock. This has been universally classified in the section *Abrotanum*, because of the presence of ray-flowers, but these are so few, or even sometimes wanting, and the other features ally it so closely with *A. tridentata* that it is taken to mark the borderland between the two sections. For this reason it is shown on the phylogenetic chart as slightly overlapping the line between them. Its southern distribution is further evidence that the later evolution of *Seriphidium* has been associated with migrations towards the north. (See the account further on of the relationships of the subspecies, p. 141.)

Within the section proper, the common sagebrush (*A. tridentata*) seems to be the most primitive, largely because of its connection as just mentioned with a member of the obviously lower section *Abrotanum*. In addition to 6 subspecies and numerous minor variations, it has produced 3 distinct species along the northern edge of its distributional area. Of these, only *cana* is at all common. The other two, *rigida* and *pygmaea*, evidently are adaptations to peculiar and exacting conditions in the Great Basin and the districts immediately northward. Both exhibit unusual modifications in the habit

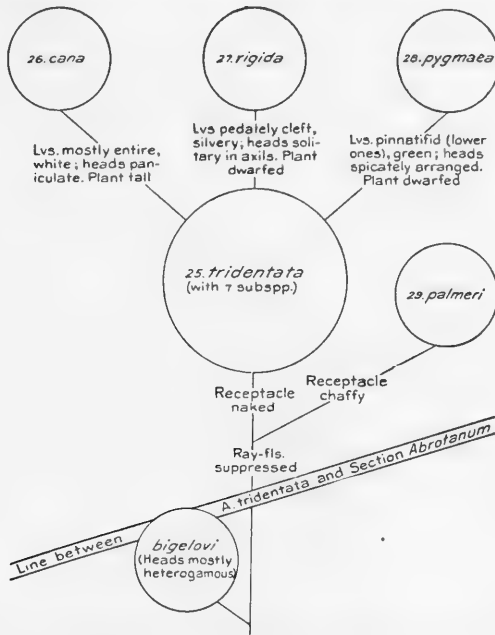


FIG. 19.—Phylogenetic chart of the species of *Artemisia* section *Seriphidium*.

and cut of leaf as well as in a considerably reduced inflorescence. *A. palmeri* is so unlike the other species that its origin is extremely doubtful. It is indicated, therefore, on the chart as arising independently near the base of the group. Further data upon which this outline is based will be given when discussing the relationships of each of the species mentioned.

25. ARTEMISIA TRIDENTATA Nuttall, Trans. Am. Phil. Soc. II, 7:398, 1841. Plates 18, 19, 20. SAGEBRUSH.

A shrub, typically 5 to 30 or 50 dm. high but with subspecies only 1 to 5 dm. high, aromatic with a pungent odor; stems erect, with usually ascending branches, the main one commonly trunk-like, or the branches spreading and depressed, the old parts with brown or nearly black shreddy fibrous bark, the twigs gray or white with a dense but thin and fine tomentum, obscurely striate; principal leaves sessile by a narrow base or apparently petioled, cuneate or flabelliform, obtuse, 1 to 4 cm. long, 2 to 5 mm.

wide, obtusely 3-toothed (rarely 4- to 7-toothed) or 3- to 5-cleft or parted at the truncate summit, canescent or silvery with a very fine and close tomentum, slightly if at all viscid; upper leaves linear or cuneate-linear, mostly entire, acute, pubescent like the lower ones; inflorescence a leafy-bracted panicle, this commonly diffusely branched and open, then 10 to 25 cm. long by 2 to 10 cm. broad, but sometimes much narrowed or even spike-like and only 0.5 to 2 cm. broad; heads homogamous, sessile, erect, or the branches of the inflorescence sometimes drooping, usually 2 in each peduncled cluster; involucre ovoid or campanulate, 3 to 4.5 or rarely 5 mm. high, 1.8 to 3.5 or rarely 4 mm. broad; bracts 8 to 18, the outer very short and orbicular-ovate or occasionally narrowed to an herbaceous tip, the inner elliptic-spatulate, obtuse, all with broad scarious margin, canescent to nearly glabrous; ray-flowers wanting; disk-flowers 3 to 12, or in subspecies *rothrocki* even to 20, fertile, corolla funnelform, 5-toothed, 2 to 3.3 mm. long, resinous-glandular especially on the tube; style-branches flat, enlarged at summit, where the margins are erose; achenes cylindric-turbinate, the summit slightly contracted or broader and with a raised border, 4- or 5-angled or ribbed, resinous-granuliferous, pubescent only in subspecies *parishi*.

The most common and widely distributed shrub of western North America, especially on arid plains of the Great Basin, but ranging to timber-line in the mountains; central Montana to North Dakota, eastern Colorado, New Mexico, Lower California, and eastern British Columbia.

SUBSPECIES.

The number of well-marked variations is not so great as might be expected in a plant of such wide distribution. This may be due to an inherent lack of plasticity or it may be because of the immense abundance and nearly continuous distribution over most of the area covered. This continuity provides for copious interbreeding and the consequent swamping of most variations almost as rapidly as they occur. The commonly recognized variations, which are more or less fixed, notwithstanding the influence just mentioned, are provided for in the following key, and their characters are also indicated in the diagram, page 141. Minor additional variations, for the most part fluctuating or plainly ecological, are of course numerous.

Key to the Subspecies of *Artemisia tridentata*.

- Achenes conspicuously arachnoid-villous. A tall, rare shrub of southern California and western Nevada (b) *parishi* (p. 137).
 Achenes glabrous or only resinous-granuliferous.
 Heads 1.5 to 2.5 mm. broad, with usually 3 to 5 or rarely 6 to 9 flowers; inflorescence spike-like to diffusely paniculate; shrubs either low or tall.
 Inflorescence 1.5 to 7 cm. broad, loosely paniculate; shrubs normally tall (a) *typica* (p. 136).
 Inflorescence only 0.5 to 2 or rarely 3 cm. broad, narrowly paniculate or spike-like; shrubs often low.
 Leaves merely 3-toothed; involucre greenish yellow (c) *nova* (p. 137).
 Leaves in part cleft into linear lobes 0.5 to 1 cm. long; involucre canescent (d) *trifida* (p. 137).
 Heads 2.5 to 4.5 mm. broad with 6 to 20 or rarely only 5 flowers; inflorescence less than 3 cm. broad, often spike-like; shrubs mostly of low stature.
 Pubescence gray or dull white, the hairs closely appressed; leaves cuneate or spatulate in outline.
 Leaves mostly 1.5 cm. or less long; flowers 5 to 8 (e) *arbuscula* (p. 138).
 Leaves 1.5 to 3 cm. long; flowers 8 to 20, rarely 6 or 7 (f) *rothrocki* (p. 138).
 Pubescence white, loose and floccose; leaves narrowly linear, only slightly dilated at summit even when cleft (g) *bolanderi* (p. 139).

25a. ARTEMISIA TRIDENTATA TYPICA.—Shrub normally 4 to 40 but even to 50 dm. high, sometimes reduced to 1 dm. under unfavorable conditions, usually with definite trunk or several ascending trunk-like branches; leaves narrowly cuneate, 1.5 to 4 cm. long, 3-toothed (rarely 4- to 7-toothed) at the apex or the uppermost linear or oblanceolate and entire; inflorescence openly paniculate, 1.5 to 10 cm. broad; heads ovoid, about 2 to 2.5 mm. broad; involucre canescent; flowers 4 to 6; corolla 2 to 2.5 mm. long; achenes

resinous-granuliferous. (*A. tridentata* Nuttall, Trans. Am. Phil. Soc. II, 7:398, 1841.) Montana, by far the most abundant form over all this region. Type locality, plains of the Columbia River. Collections: Near Glendive, Montana, *Sandberg 1010* (Gr, NY, US); Laramie Hills, Wyoming, *Nelson 5335* (UC); near Dulce, New Mexico, *Standley 8107* (US); Navajo to Hawthorn, Arizona, *Griffiths 5798* (US); east of Enseñada, Lower California, *Goldman 1117* (US); San Pedro Martir, Lower California, May 6, 1893, *Brandegee* (UC); Alamo Mountain, Ventura County, California, *Baldwin 104* (UC); Butte Valley, Siskiyou County, California, *Butler 1883* (UC, US); Steins Mountains, Nevada, *Griffiths* and *Morris 656* (NY, US); type collection, "plains of the Columbia and Lewis River," *Nuttall* (Gr), also "Rocky Mountains and Lewis River," *Nuttall* (Phila.); eastern Oregon, *Cusick 2505* (Gr, NY, UC, US); Bingen, Klickitat County, Washington, *Suksdorf 2687* (Gr, US); Kamloops, British Columbia, July 28, 1890, *Macoun* (NY, US); Big Butte Station, Idaho, *Palmer 498* (US).

25b. *ARTEMISIA TRIDENTATA PARISHI* (Gray).—Shrub normally 10 to 20 dm. high, erect, with ascending branches, the main ones trunk-like; leaves spatulate (usually very narrowly so) or linear, 2 to 3 cm. long, mostly entire but some obtusely 2- or 3-toothed at the summit; inflorescence openly paniculate, 2 to 10 cm. broad (much condensed in unfavorable seasons); heads narrowly campanulate, 2.2 to 3 mm. broad; involucre canescent; flowers 4 to 6; corolla 2 to 2.5 mm. long; achenes glandular and also short-villous with crisp hairs or these sometimes longer and arachnoid. (*A. parishii* Gray, Proc. Am. Acad. 17:220, 1882.) Southwestern part of the Mojave Desert, California, extending to the coastal slope along the Santa Clara River, also in western Nevada.¹ Type locality, Newhall, Los Angeles County, California. Collections (all in California except the last): Near Rosamond, Antelope Valley, *Davy 2933* (UC); 2 km. west of Rosamond, *Hall 10959*; type collection, 1881, *Parish 1065* (Gr, NY, UC, US); dry valley bottom at junction of Piru Creek and Santa Clara River, Ventura County, October 20, 1919, *Hall* (UC); Carson Sink Region, west central Nevada, *Kennedy 1692* (DS, NY, UC at least as to flowering specimens).

25c. *ARTEMISIA TRIDENTATA NOVA* (Nelson).—Shrub 1 to 3 dm. high, with numerous erect slender branches from a spreading base; leaves cuneate or broader, 0.5 to 1.5 cm. long, 3-toothed at the apex, or the upper ones (toward summit of inflorescence) linear and entire; inflorescence a narrow but open panicle, 0.5 to 1.5 cm. broad; heads ovoid, about 2 mm. broad; involucre greenish-yellow and nearly glabrous, except for the short outer canescent bracts; flowers 3 to 6; corolla 2 to 2.5 or 3 mm. long; achenes resinous. (*A. nova* Nelson, Bull. Torr. Club 27:274, 1900.) Idaho, Montana, and western Colorado to New Mexico, Arizona, and eastern California, especially on hillsides and ridges of plateaus and desert mountains. Type locality, Medicine Bow, Wyoming. Collections: Midway between Strevell and Albion, southern Idaho, September, 1919, *Hall* (CI); near Radersburg, Montana, August 27, 1882, *Canby* (Gr); Laramie Hills, Wyoming, *Nelson 5334* (Gr, NY, UC); Gunnison, Colorado, *Underwood* and *Selby 400* (US); Panguitch Lake, Utah, *Jones 5997* (NY, UC, US); near Dulce, New Mexico, *Standley 8099* (US); mesa west of Buckskin Mountains, Arizona, *Jones 6063F* (NY, UC); Mount Irish, Nevada, *Purpus 6333* (UC, US); Silver Cañon, Inyo Range, California, *Hall 10639* (UC).

25d. *ARTEMISIA TRIDENTATA TRIFIDA* (Nuttall).—Shrub 2 to 6 dm. high (perhaps sometimes much higher), usually with erect trunk-like main stems; leaves cuneate or flabelliform, 1.5 to 4 cm. long, deeply 3-cleft into linear or linear-oblongeolate divisions

¹ Reported in the original description as occurring also in Cajon Pass, California, but this was an error (Parish, Zee 5:120, 1901).

which are themselves 3-cleft, or the uppermost ones linear and entire; inflorescence loosely paniculate, 1 to 3 cm. broad; heads ovoid, 2.5 mm. or less broad; involucre canescent; flowers 5 to 8; corolla 2 to 2.5 mm. long; achenes resinous-granuliferous. (*A. trifida* Nuttall, Trans. Am. Phil. Soc. II, 7:398, 1841.) Northern Rocky Mountain and Great Basin States, on open plains; Montana to Colorado and west to eastern Oregon and Washington, apparently also in eastern California and reported from British Columbia. Type locality, plains of the Rocky Mountains. Collections: Type collection, Nuttall (Phila., with a piece of *A. rigida*); Alaska Basin, Montana, Nelson 6809 (Gr, NY, US); Big Butte Station, Idaho, Palmer 497 (US); Teton Forest, northwestern Wyoming, Tweedy 568 (NY); Laramie Plateau, Wyoming, September 9, 1919, Hall (UC); near Lancaster, Mojave Desert, California, Parish 1177 (identical with Nuttall's plants, according to Gray); eastern Oregon, Cusick 2501 (Gr, NY, UC, US); base of Cascade Mountains, Washington, 1882, Brandegee (UC).

25e. ARTEMISIA TRIDENTATA ARBUSCULA (Nuttall).—Shrub 1 to 4 dm. high, stiffly and irregularly much branched, the lower branches spreading and often spinescent, the twigs slender and erect; pubescence gray, appressed; leaves cuneate or flabelliform, mostly 1.5 cm. or less long, 3- to 5-lobed or cleft at apex, the lobes sometimes 10 mm. long, the uppermost entire; inflorescence spike-like, 1.5 cm. or less broad; heads campanulate, 2.5 to 3 mm. broad; involucre canescent; flowers 5 to 9; corolla 2 to nearly 3 mm. long; achenes granuliferous. (*A. arbuscula* Nuttall, Trans. Am. Phil. Soc. II, 7:398, 1841, in part, the remainder being subspecies *nova*.) Northern Rocky Mountains and Great Basin, on dry, rocky hillsides and plains, especially on the scab-lands; Idaho, Wyoming, and western Colorado to eastern California and Washington. Type locality, arid plains of the Snake River. Collections: Type collection, Nuttall (Gr, Phila.; the specimen at Philadelphia is a young plant with racemose inflorescence, the involucre very tomentose, and the whole appearance that of *arbuscula* as here described rather than of *nova*); near Evanston, Wyoming, September 12, 1919, Hall; Hayden Flats, Routt County, Colorado, Osterhout 2260 (NY); Mount Rose, western Nevada, Heller 9883 (DS, Gr); near Olancha Peak, southern Sierra Nevada, California, Purpus 1868 (UC); Mono County, California, August, 1898, Congdon (UC); ridge northwest of Donner Pass, California, Heller 12914 (Gr, SF, UC, US, see minor variation 9); divide between American and Rubicon Rivers, Eldorado County, California, Kennedy 203 (UC); near Hay Creek, eastern Oregon, Leiberg 859 (DS, Gr, UC, US); Yakima region, Washington, Brandegee 146 (UC).

25f. ARTEMISIA TRIDENTATA ROTHROCKI (Gray).—Shrub 1 to 8 dm. high, or perhaps more, branching from the base to form low rounded bushes with erect twigs, not especially rigid; pubescence gray, appressed, sometimes viscidulous; leaves elongate-cuneate, 1 to 4 cm. long, 3-toothed at apex, or 3-cleft and the lobes toothed, many of the upper or even some below the inflorescence linear and entire; inflorescence spike-like or very narrowly paniculate, 1 to 3 cm. broad; heads campanulate, 3 to 4.5 or rarely 5 mm. broad; involucre varying from greenish-yellow or straw-color and only obscurely tomentulose as in the original *rothrocki*, to closely canescent (minor variation 7, *A. spiciformis* Osterhout), somewhat viscidulous in the green form (outer bracts broadly ovate and canescent, inner ones broadly elliptic and scarious in minor variation 18, *A. vaseyana* Rydberg); flowers 6 to 15, rarely to 20; corolla 2.5 to 3.5 mm. long; achenes only granular. (*A. rothrocki* Gray, Bot. Calif. 1:618, 1876.) Widely distributed in the western United States but wanting over much of the area, confined to the higher zones in the mountains: Rocky Mountains of Wyoming, Colorado, and Utah; San Bernardino Mountains of southern California; Olancha Peak, in the southern Sierra Nevada of California, to eastern Washington, western Nevada, and Idaho. Type locality, Sierra Nevada of

Tulare County, California, Olancha Mountains and Monache Meadows. Collections (those from Utah and east chiefly of minor variation 7, that is *A. spiciformis* Osterhout): Cooper Hill, Albany County, Wyoming, *Nelson 8941a* (UC); North Park, Colorado, *Osterhout 2255* (NY, UC, topotype of *A. spiciformis* Osterhout, minor variation 7); Minturn to Leadville, Colorado, *Hall, 11064, 11055, 11057* (UC); Crested Butte, west central Colorado, *Baker 810* (Gr, NY, UC, US); Aquarius Plateau, Utah, *Ward 593* (Gr); head of Pass Cañon, Tooele, Utah, August 9, 1913, *Blankinship* (hb. Blankinship); California: east end of Bear Lake, San Bernardino Mountains, *Bailey 1244* (UC); type collection, in part, Monache Meadows, at 2,200 meters altitude, September, 1875, *Rothrock 298* (Gr, US); type collection, remainder, Olancha Peak, at 2,870 meters altitude, September, 1875, *Rothrock 343* (Gr, Phila, US); Little Cottonwood Creek, Inyo County, September 6, 1911, California Museum of Vertebrate Zoology (UC); near Soda Creek, southern Sierra Nevada, *Purpus 5165* (UC, US); Volcano Meadows, Tulare County, *Hall and Babcock 5490* (UC); Soda Springs of the Tuolumne, August 22, 1894, *Congdon* (UC); Mono Pass, August 13, 1898, *Congdon* (Gr, UC); Mount Dana, *Bolander 6018* (UC, US); Tioga Pass, *Hall 10847* (UC); Ebbets Pass, *Brewer 1996* (UC); Angora Peak, near Tahoe, *Smiley 20* (Gr); Bear Valley, on Truckee River, Placer County, September 9, 1888, *Sonne* (NY, UC, leaves from merely dentate to cleft into lobes up to 10 mm. long); Webber Lake, August, 1878, *Leemmon* (Gr); south side of Slide Mountain, Washoe County, Nevada, *Heller 10667* (NY); Hurricane Creek, Wallowa Mountains, Oregon, *Cusick 2486* (NY, UC, US); Washington, *Vasey 480* (NY, type of *A. vaseyana* Rydberg, minor variation 18); Yakima Region Washington, *Brandegee 910* (UC); Ketchum, Blaine County, Idaho, *Nelson and Macbride 1190* (UC, US).

25g. ARTEMISIA TRIDENTATA BOLANDERI (Gray).—Shrub 2 to 6 dm. high, branching to form low bushes with erect densely leafy twigs, not rigid or at all spinose; pubescence white, loose and floccose; leaves mostly narrowly linear and entire but many dilated at apex, where cleft into 3 narrow lobes (see fig. 22d, p. 145), 1 to 2 cm. long or perhaps longer; inflorescence varying from spike-like and less than 1 cm. broad to narrowly paniculate and 3 cm. broad; heads campanulate, 2.5 to 3 mm. broad; involucre loosely white-canescens; flowers 8 to 15; corolla 2 to 2.5 mm. long; achenes granulariferous. (*A. bolanderi* Gray, Proc. Am. Acad. 19:50, 1883.) Known only from Mono county, California. Type locality, Mono Pass in the Sierra Nevada. Collections: Type collection, *Bolander 6149* (Gr, UC, US); Sand Flat, south of Mono Lake, California, *Clements and Hall 11702* (UC); between Walker and Mono Lakes, California, August 6, 1898, *Congdon* (DS).

MINOR VARIATIONS AND SYNONYMS.

A tabulation of the characters of the subspecies and of most of the following forms is given in table 13. From this it is seen that the taxonomic recognition of all possible combinations of characters would result in a classification too cumbersome for general use. The more important variations not already provided for as subspecies are the following:

1. ARTEMISIA ANGUSTA Rydberg, N. Am. Fl. 34:283, 1916.—Based upon *A. tridentata angustifolia*, which see.
2. A. ARBUSCULA Nuttall, Trans. Am. Phil. Soc. II, 7:398, 1841.—*A. tridentata arbuscula* and *A. t. nova*.
3. A. BOLANDERI Gray, Proc. Am. Acad. 19:50, 1883.—*A. tridentata bolanderi*.
4. A. NOVA Nelson, Bull. Torr. Club 27:274, 1900.—*A. tridentata nova*.
5. A. PARISHI Gray, l. c. 17:220, 1882.—*A. tridentata parishi*.
6. A. ROTHROCKI Gray, Bot. Calif. 1:618, 1876.—*A. tridentata rothrocki*.
7. A. SPICIFORMIS Osterhout, Bull. Torr. Club 27:507, 1900.—*A. tridentata rothrocki*. The original specimens, from North Park, Colorado, are more densely cinereous than the originals of *rothrocki* from the southern Sierra Nevada, and the latter are somewhat viscid. Colorado plants are generally of a decided gray or whitish color, due to the dense pubescence, but in a collection from near Leadville (*Hall 11057*) the lower leaves are as

green as in specimens from the type locality of *rothrocki*, and in one from Crested Butte, Colorado (Baker 810) the involucre are essentially glabrous, except for the short outer bracts. In the former collection the (young) involucre are gray-tomentose, in the latter the foliage is densely cinereous. These perplexing combinations, together with the fact that Sierra Nevada plants are for the most part decidedly cinereous-canescens and scarcely viscidulous, render impossible the recognition of *spiciformis*. (See further under No. 18 of this list.)

8. *A. SPICIFORMIS* var. *LONGILOBA* Osterhout, Muhlenbergia 4: 69, 1908.—A low form of *A. tridentata rothrocki* with densely canescent foliage, the leaves 3-cleft for nearly one-half their length. Plants about 3 dm. high. Scarcely differs from subspecies *trifida*, except in size of head and number of flowers. Type locality, Sulphur Springs, Colorado.

9. *A. TRIDENTATA* *ANGUSTIFOLIA* Gray, Proc. Am. Acad. 19: 49, 1883.—A narrow-leaved form of *A. tridentata typica*. Lower leaves spatulate-linear and scarcely 3-toothed at the rounded apex; upper entire and linear. Original distribution given as southern Idaho and western Nevada to the Mojave Desert and the southern borders of California.

10. *A. TRIDENTATA* *ARBUSCULA*, but with the leaves deeply cleft as in No. 8 of this list and in subspecies *trifida*. Best represented by plants from Placer County, California, Heller 12914 (UC).

11. *A. TRIDENTATA* *NOVA*, but the involucre canescently tomentulose and the stem commonly reddish. It seems better to accept this as a minor variation of subspecies *nova* rather than to give it subspecific rank, partly because of the presence of intergrading forms (Mount Irish, Nevada, Purpus 6333 UC), partly because the short outer bracts are always canescent even in genuine *nova*, and partly because of the demonstrated variability of this character in related subspecies, for example *rothrocki*. This form sometimes forms pure stands in eastern California and eastern Oregon in regions where the surrounding vegetation is composed chiefly of subspecies *typica*. The line between the two is often very sharp, the low reddish-twigged *nova*-like plant occupying the less favorable locations and persisting because of repeated fires or grazing, if not actually produced by them. Typical of this form is a collection from between Bodie and Bridgeport, Mono County, California, August 18, 1898, Congdon (UC). It is common on upper slopes between Mono Lake and Bridgeport (Hall 11696, UC). Also in eastern Lassen County, California (Hall 11674, UC) and in eastern Oregon (near Antone, Loftfield 2113, UC). Almost the same thing, but the slender inflorescences more branched, comes from draws south of Laramie, Wyoming (September 9, 1919, Hall, UC).

12. *A. TRIDENTATA* *NOVA*, but with dark foliage, this appearing almost black as compared with other forms. Plants low and with narrow inflorescences. Apparently a more palatable strain kept low by grazing. Occurs in southern Idaho and elsewhere.

13. *A. TRIDENTATA* *ROTHROCKI*, but some of the leaves cleft one-third their length. Volcano Meadows, southern Sierra Nevada, Hall and Babcock 5490 (UC).

14. *A. TRIDENTATA* *TYPICA*, but with the branches of the inflorescence drooping. The best examples are large shrubs growing in moist, sandy soil. Found especially in northwestern New Mexico (Hall 11124). Well worthy of cultivation as an ornamental shrub if the character persists.

15. *A. TRIDENTATA* *TYPICA*, but much dwarfed, usually as a result of competition with grasses. Resembles subspecies *nova* in its stature, but lacks its slender habit, narrow inflorescence, and smooth involucre. Common in Wyoming, for example, west of Bosler, September 10, 1919, Clements (UC).

16. *A. TRIFIDA* Nuttall, Trans. Am. Phil. Soc. II, 7: 398, 1841.—*A. tridentata trifida*.

17. *A. TRIPARTITA* Rydberg, Mem. N. Y. Bot. Gard. 1: 432, 1900.—Based upon *A. trifida* Nuttall, here reduced to a subspecies of *A. tridentata*. The specific name was changed by Rydberg because of the earlier *A. trifida* Turczaninow, 1832, an untenable species.

18. *A. VASEYANA* Rydberg, N. Am. Fl. 34: 283, 1916.—*A. tridentata rothrocki*. Separated by Rydberg chiefly on its broadly ovate outer bracts, which are less than half as long as the innermost, *rothrocki* being described as having one of the outer bracts often a little foliaceous, the others ovate, acute, and half as long as the innermost. The slight herbaceous elongation of outermost bracts is common in all of the subspecies and is so variable as to suggest a correlation with factors affecting growth. A careful comparison has been made between the types of the two "species." If the outer bracts are broader and more obtuse in *vaseyana*, they are not convincingly so and they are no shorter in proportion to the inner ones. They are quite canescent as contrasted with the nearly glabrous bracts of the type of *rothrocki*, but the lack of constancy in this feature has been pointed out under *A. spiciformis*. Its use would necessitate the extension of the range of *vaseyana* to the type locality of *rothrocki* (Univ. Calif. Herb. 202229). The number of flowers in the head and the height of the involucre do not serve, as is shown in Table 14, where the type of *vaseyana* and other specimens from its region are entered. It would seem, therefore, that if *vaseyana* can be recognized at all, it must be on its canescent and slightly broader outer bracts, and, if further collections substantiate the measurements given in the table, on its narrower heads. Even as thus defined, the range must be extended to include most of the Sierra Nevada, and here *spiciformis* must also be admitted, because of plants with acutish but decidedly canescent bracts (for example, Bear Valley, on road to Tahoe, September 9, 1888, Sonne). It is thus seen that these forms can not be correlated with geographic distribution, except that genuine *rothrocki* is closely confined to the vicinity of its type locality. The type locality of *vaseyana* is Washington.

RELATIONSHIPS.

The considerable number of herbaceous species of *Artemisia* common to Eurasia and North America justifies the assumption that it is a boreal genus which has extended far southward. This migration brought it into regions with climates growing drier as a consequence of the action of climatic cycles, and led to the evolution of two new ecological groups of species. The one was characterized by the assumption of the shrub habit in response to arid climates, while the other was marked by halophytic adaptation to local saline areas, usually in the form of a half-shrub. It seems probable that *Artemisia tridentata* was one of the first shrubby species to be developed in response to climatic

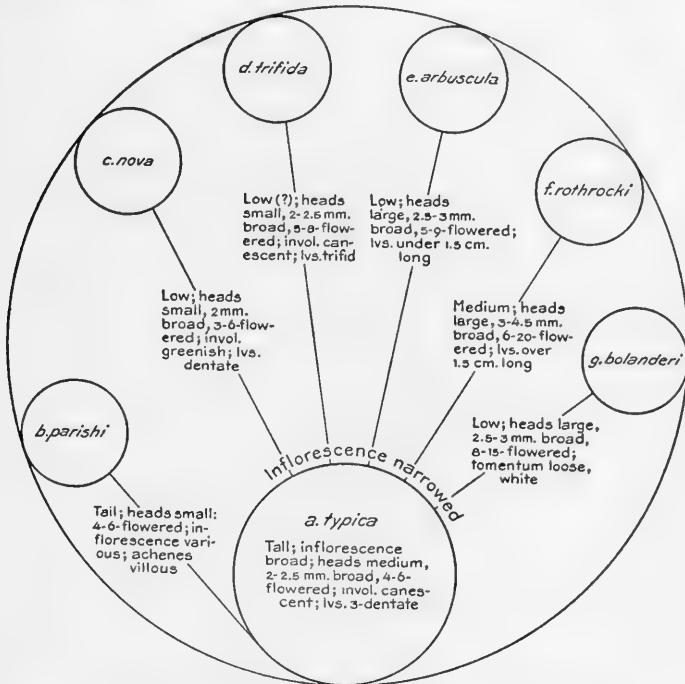


FIG. 20.—Phylogenetic chart of the subspecies of *Artemisia tridentata*.

aridity in the southwestern United States and in Mexico. During the dry phase following the Pleistocene it appears to have moved northward, occupying the southern half of the Great Basin as the great dominant and extending northward into Idaho, Wyoming, Oregon, and Washington to form a low savannah in the bunch-grass and mixed prairies. With the beginning of the historical period, grazing gradually eliminated the grasses, and the sagebrush increased correspondingly, until much of the savannah was converted into a pure sagebrush community.

The phylogenetic origin of *A. tridentata* is connected with the evolution of the section to which it belongs, namely, *Seriphidium*. It has been shown in the introduction that this is one of the most highly developed sections, that it is a derivative of the section

Abrotanum, and that the connection is represented in America by *A. bigelovi*, a rare southern species of the latter group. On the *Seriphidium* side of the line, the nearest approach to *bigelovi* is found in *A. tridentata*. Except in the character indicative of the section, the two species are so nearly alike that they are frequently mistaken for each other. Of especial significance, as indicating their phyletic connection, is the occurrence in each of the unique tridentate character of the leaves. This occurs nowhere else in the genus and certainly its appearance in these two species, so closely similar in most other characters, is more than a coincidence. The conclusion therefore is that, since the section *Seriphidium* is derived from *Abrotanum* and the connection is best represented on the side of the former by the species *tridentata*, this species inevitably must be considered as the most primitive of the group to which it belongs. Its connections with the other members of the section will be taken up as these are reached.

In considering the subspecies of *A. tridentata* an annoying nomenclatorial difficulty is encountered. It so happens that, if the rule of priority is extended to include position on the page, the name of the species must be changed to *A. trifida* Nuttall and the combination of each subspecies must be changed to correspond. This follows from the fact that *trifida* and *tridentata* were first published on the same page (Trans. Am. Phil. Soc. II, 7:398, 1841) and that the description of the former precedes that of the latter. But still another name must be chosen by those who adhere to the American Rules (and they are the only ones strictly bound to follow the rule of priority of position), for Nuttall's *A. trifida* is antedated by *A. trifida* Turczaninow (Bull. Soc. Nat. Mosc. 5:196, 1832), a species now universally considered as belonging to *Tanacetum*. The first available name under these rules would be *A. arbuscula*, since this was published by Nuttall on the same page as *trifida* and *tridentata* and placed so as to follow the former but to precede the latter. It is partly because of these several possible applications of the rules with the inevitable shifting of names that the International Code is here followed and no attention paid to priority of position. By this method a choice is allowed between *arbuscula*, *trifida*, and *tridentata* as the name for the collective species. Since the form described by Nuttall as *A. tridentata* is by far the most common and widespread and since this name is much better known than either of the others, it is here selected. In the narrow original sense *A. tridentata* Nuttall here becomes *A. tridentata typica*.

Of all the subspecies of *A. tridentata* perhaps none comes nearer to representing the ancestral type than does *typica* itself. This conclusion follows not so much because of its great abundance over large areas of territory, as because of its obvious connection with *A. bigelovi*, which in turn represents the still more primitive group from which the species probably has arisen. No other is so much like *bigelovi* in habit, foliage, and involucre. Furthermore, each of the other subspecies exhibits characters or distributional peculiarities indicative of more recently derived forms. As is so often the case when dealing with small taxonomic units, the subspecific characters are found to group themselves into a bewildering array of combinations, so that one is perplexed to know which forms to accept as of this rank. Previous treatments have merely selected the more striking variations and assigned to them either specific or varietal standing. As a method this can scarcely be improved upon, since a recognition of all of the combinations of minute characters is obviously impracticable. It should be pointed out, however, that the number of possible combinations is exceedingly great and these are becoming more and more numerous in herbaria as the result of more extended collections. This is one reason for bringing all of the 7 subspecies here described into one species, although some of them have not been heretofore considered as a part of *A. tridentata*. The various combinations that have thus far received names, as well as some that have not, are indicated in table 13, which, however, does not include all of the minor peculiarities of some of the forms. The subspecies *parishi* is omitted, since it differs from all others by a constant

character. Its inclusion would introduce a new series of combinations, with the additional characters of pubescence of achene, drooping of the inflorescence, and width of leaf.

Some of the tabulated forms exhibit additional divergent features. Since these may be expected in each of the other forms, the total number of possible combinations becomes so great that no practicable system of nomenclature can provide for them. Such features include drooping inflorescences, reduced number of flowers, dark foliage associated with low stature and narrow inflorescence, density of pubescence, color and looseness of pubescence (see subspecies *bolanderi*), and relative lengths of inner and outer bracts of the involucre.

TABLE 13.—Character combinations found in *Artemisia tridentata*.

Habit.	Leaves.	Inflorescence.	Heads.	Involucre.	Subspecies or minor variation.
Tall	3-toothed.....	Broad.....	Small.....	Gray.....	subsp. <i>typica</i> .
Low.....	Do.....	Do.....	Do.....	Do.....	m. v. 15.
Low.....	Do.....	Narrow.....	Do.....	Do.....	m. v. 11.
Low.....	Do.....	Do.....	Do.....	Greenish.....	subsp. <i>nova</i> .
Low.....	3-cleft.....	Do.....	Do.....	Gray.....	subsp. <i>trifida</i> .
Tall.....	3-toothed.....	Do.....	Large.....	Do.....	m. v. 7.
Low.....	3-cleft.....	Do.....	Do.....	Do.....	m. v. 8.
Low.....	3-lobed.....	Do.....	Do.....	Do.....	subsp. <i>arbuscula</i> .
Low.....	3-cleft.....	Do.....	Do.....	Do.....	m. v. 10.
Tall or low.....	3-toothed.....	Do.....	Do.....	Greenish.....	subsp. <i>rothrocki</i> .
Low.....	3-cleft.....	Do.....	Do.....	Do.....	m. v. 13.

The most anomalous subspecies is *parishi*, but except for a single character this form and *typica* are very much alike. The two are practically identical in habit, odor, and other general features. Subspecies *parishi* is not "mainly herbaceous" as Gray was led into supposing from the nature of the types, which were only the hurriedly gathered tops of the plants. The chief distinguishing mark is the villous or almost arachnoid pubescence of the achenes. This often is accentuated in a misleading manner through the viscid nature of the surface glands, which catch and hold the loose tomentum of the involucre during the process of dissection, so that the achenes appear more copiously pubescent than they really are. The leaves are much narrower than in typical *tridentata* and there is a much larger percentage of entire ones. In these respects *parishi* is quite similar to the extremely narrow-leaved form of *tridentata* once named by Gray as variety *angustifolia*. The panicles are often profuse, with widely spreading and recurving or even pendant branches. Some of the specimens of the type collection exhibit this tendency to a limited extent, while others have erect branches. Plants with drooping inflorescence mingle with those in which the panicles are narrow and strictly erect, the other characters remaining unchanged (for example, Piru Creek, October 20, 1919, *Hall*). This feature is not of specific value, as is indicated by the fact that a parallel variation occurs in *A. tridentata typica*. In specimens otherwise exact *typica*, the drooping of the panicle branches is sometimes very evident (Carroll Creek, Sierra Nevada Mountains, California, Museum of Vertebrate Zoology; Nighthawk, Washington, October 4, 1911, *Jones*). Along sandy banks of irrigation canals and other streams in northwestern New Mexico the plants of *typica* often display beautifully pendant sprays of flowers (*Hall 11124 UC*), and in alkaline soil of northern Nevada dwarf plants have been found to exhibit the same feature, perhaps as a result of frequent browsing (*Hall 11235, UC*). All of the specimens of *parishi* thus far collected in Antelope Valley, California, have much condensed and irregular inflorescences, this perhaps indicating a different strain

from those growing on the coastal slopes, or this may be only the result of unfavorable conditions obtaining in that bleak, wind-swept, and more elevated valley. The most congested inflorescences are on plants collected in 1919, after three years of exceptionally low rainfall (*Hall 10959*, UC). In the same year the plants on the coastal slopes had well-developed inflorescences. A parallel reduction in the inflorescences of *typica* is also common (for example, Granger, Wyoming, September 12, 1919, *Hall*, UC). From these various considerations it is seen that *parishi* bears all the evidence of being a local mutation from the common form of *A. tridentata*.

The remaining forms of *A. tridentata* are all of small size. It is apparent that grazing and burning have reacted upon the sagebrush itself to produce a series of new dwarf forms in various stages of fixation. It appears certain that these forms have arisen in more than one region, and hence constitute examples of polygenetic origin. Similar

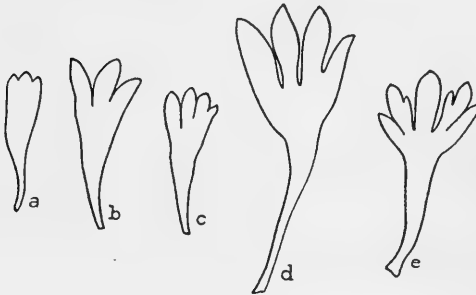


FIG. 21.
Unusual leaves of *Artemisia tridentata typica*, all from sterile shoots of a single plant otherwise typical. Leevining Grade, Mono County, California, 2,600 m. altitude, September 15, 1921, *Clements* (UC). All $\times 0.8$.

forms have been produced where the sagebrush entered rocky, sterile, or subalpine areas, as in the case of *trifida*, *arbuscula*, *nova*, and *rothrocki*. The distribution of these forms is likewise such as to furnish further evidence of the action of polygenesis. This is particularly true of *rothrocki*, which occurs only in Sierran and Rocky Mountain stations 750 miles apart.

Of all these dwarfed subspecies, *nova* is perhaps the one which most closely approaches *typica*. Its narrow inflorescence is very striking in the extreme form and is commonly associated with low stature. This combination, to which is to be added the small number of flowers developed in each head, suggests that the normal nutrition of the plant may be interfered with. This subspecies, whether fixed in its characters or not, seems to be the result of malnutrition, as is indicated by the fact that it usually and perhaps always grows where the soil is shallow, stony, or otherwise unfavorable to full development. Between Strevell and Albion, in extreme southern Idaho, the plants of *nova* are not only low and with narrow inflorescences, but they are also quite black as contrasted with *typica*. It here alternates and mixes with *typica* on apparently uniform soil and does not intergrade with it. This suggests that it may be a more palatable strain kept low by grazing. In other places the subspecies *typica* itself becomes much dwarfed, especially when competing with grasses, but without assuming the slender habit and narrow inflorescence of *nova*. At other times it takes on all of the characters of *nova*, except that the involucre remains canescent (see minor variation 11). This nicely indicates the lack of unison in the variation of the characters used to separate the two forms. The connection between *typica* and *nova* may be indicated by citing a series of specimens with the former at one end, and the latter at the other, but with each of the series differing from its neighbor by only a single trivial character. This series, easily duplicated

in any large herbarium, has been constructed from specimens in the herbarium of the University of California as follows:

- (1) *Typica*, near Empire, Colorado, *Patterson 219* (UC 29790).
- (2) Reduced size without other change, west of Bosler, Wyoming, September 10, 1919, *Clements* (UC). Minor variation 15.
- (3) Same as 2, but with reduced upper leaves, south of Laramie, Wyoming, September 9, 1919, *Hall* (UC).
- (4) Same as 2, but with narrow inflorescence, Mono County, California, August 18, 1898, *Congdon* (UC). Minor variation 11.
- (5) Same as 4, but with green involucres, Laramie, Wyoming, *Nelson 8185* (UC, 146504). Genuine *nova*.

In the subspecies *trifida* the narrow inflorescence is combined with a foliage more deeply cleft than in either *typica* or *nova*. This tendency toward cleft or parted leaves is common also in other subspecies, that is, it combines promiscuously with other characters. It is especially frequent in *arbuscula* (*Heller 12914*, from Placer County, California, etc.), highly developed in some specimens of *spiciformis* (*Nelson 8941a*, from Albany County, Wyoming, etc.), and a form of the latter has been named *A. spiciformis longiloba* (*Osterhout, Muhlenbergia 4:69, 1908*). Although the character has been

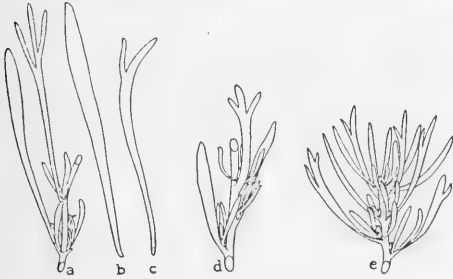


FIG. 22.

Artemisia tridentata trifida, *A. t. bolanderi*, and *A. cana*: a, b, c, all from the same plant, referred to *trifida* but perhaps a hybrid between this and *cana* (Lima, Montana, *Hall 11669*); d, from *A. t. bolanderi* (Mono County, California, *Clements* and *Hall 11702*); e, an unusual form of *cana* from Wyoming (*Hall 10992*), listed as minor variation 4. All $\times 1$.

accepted as of specific value in the case of *trifida*, it is usually passed over as a trivial variation when it occurs in these. In the present paper it is used as a character to aid in the recognition of a variety of long standing in the literature, marked also by its narrow inflorescence and an indescribable thyme-like aspect of the leafy twigs. It should be emphasized, however, that not all of the sagebrushes with trifid leaves belong to the subspecies *trifida*.

The next two subspecies, that is, *arbuscula* and *rothrocki*, differ from the four already discussed in having usually larger heads. The difference is not so great, however, as the measurements given in descriptions would seem to indicate, for specimens are frequently found which, although plainly of this group, have heads scarcely larger than in the other subspecies. The size of the involucre is associated with the number of flowers which it incloses, and this is evidently a more definite criterion for general use. From table 14 it will be seen that the number of flowers in the subspecies thus far discussed is 3 to 6, rarely 7, 8, or 9, while in these two the number runs from 6 to 13 and even to 20 in erratic plants, and is only rarely as low as 4 or 5. While there is thus a notable tendency in opposite directions, the overlapping is sufficient to indicate that the two groups of subspecies are not specifically distinct.

The subspecies *arbuscula* is apparently more primitive than *rothrocki*, or at least it presents less evidence of being a highly modified form. It is a low, straggling shrub with numerous rigid branches and is especially suited to the rigorous environment in which it grows. Its popular name of scabland sagebrush is indicative of the unfavorable soil and moisture conditions with which it must contend. It seems almost certain that it is a derivative of *typica* developed under the unfavorable conditions so common to the

northerly part of the area covered by *A. tridentata*. In his original description Nuttall included with this some specimens of what is now known as *nova*, another subspecies also adapted to a severe environment but along somewhat different lines.

The subspecies *rothrockii* is of uncertain derivation. Its sporadic occurrence at widely separated localities indicates that it is of polygenetic origin. In this case the parent quite certainly is *typica*, since none of the other forms has a range sufficiently extensive to cover all of the stations for *rothrockii*. The attempt of others to specifically recognize forms here included under this subspecies would seem to indicate that it is not homogeneous, but when identical forms are found in areas so widely separated as California and Colorado the distinctions break down entirely. The proposals referred to are *speciformis* and *vaseyana*, both of which are fully discussed under the heading of minor variations. The identical forms are perhaps best considered as parallel variations from the parent *typica* stock. The large number of flowers in the head may indicate *rothrockii*

TABLE 14.—Variation in the subspecies of *Artemisia tridentata*.

	Herbarium.	Involucre.			No. of flowers per head.	Length of corolla.
		Height.	Breadth.	No. of bracts.		
Subspecies <i>typica</i>:						
Medicine Bow, Wyo.	CI	mm. 3.0	mm. 2.5	7 10	4 4	2.0
Bosler, Wyo. ¹	CI	3.0	2.2	7 9	4 4	2.2
West of Bosler, Wyo. ¹	CI	3.2	2.2	7 8	4 4	2.7
Do. ¹	CI	3.0	2.2	12 12	4 4	2.5
Clear Creek, Colo.	29790 UC	3.1	2.4	8 10	4 5	2.0
Tintic, Utah.	172630 UC	3.2	2.7	9 11	4 4	2.4
Snowville, Utah.	CI	3.3	2.3	13 14	4 5	2.4
Albion, Idaho.	CI	3.2	2.3	10 14	4 5	2.4
Eastern Oregon.	29789 UC	3.5	2.5	8 10	3 3	2.5
Weber Cañon, Utah.	CI	9 10	4 4	2.0
Pleasant Valley, Oreg.	CI	3.1	2.2	11 12	3 4 5	2.0
Siskiyou County, Calif.	166157 UC	3.5	2.4	10 11	4 5	Young
Shasta Valley, Calif.	CI	3.4	2.1	9	3 4	2.5
Mint Cañon, Calif.	CI	3.0	2.7	16 17	4 4	2.6
Kern County, Calif.	34171 UC	3.3	2.5	8 9	3 4	2.0
Nighthawk, Wash.	175960 UC	3.5	2.1	15	4 6 5	2.0
Average.		3.2	2.3	11	4	2.2
Subspecies <i>parishi</i>:						
Rosamond, Calif.	CI	3.5	3.0	16 18	5 5	2.0
Do.	75851 UC	3.0	2.6	15 18	5 6	2.3
Do.	74055 UC	3.2	2.4	13 11	5 6	young
Newhall, Calif. ²	54010 UC	3.8	2.6	16 19	6 6	2.4
Ventura County, Calif.	205802 UC	3.0	2.3	9 11	4 4	2.6
Mojave Desert, Calif.	Gr	3.0	2.5	12 13	4 4	2.0
Carson Sink, Nev.	128181 UC	3.0	2.1	9 10	4 5	2.0
Average.		3.2	2.5	13	5	2.3
Subspecies <i>nova</i>:						
South of Laramie, Wyo.	CI	2.8	2.0	8 10	3 3	2.1
Albany County, Wyo.	69457 UC	3.4	2.2	6 7	5 6	2.6
Laramie, Wyo.	146504 UC	3.7	2.4	8 7	3 3	3.0
Laramie Hills, Wyo.	91181 UC	3.3	2.0	9 9	4 3	2.4
San Francisco Mountains, Ariz.	135368 UC	3.2	1.8	10 11	3 5	Young
Buckskin Mountains, Ariz.	159117 UC	3.4	2.2	11 12	4 4	2.5
Panguitch Lake, Utah.	159393 UC	3.3	1.9	7 8	4 4	2.5
Mount Irish, Nev.	135367 UC	2.7	1.8	7 8	3 3	Young
Strevell-Albion, Idaho.	CI	3.0	2.4	12 12	4 4	1.9
Inyo Range, Calif.	202351 UC	3.0	1.7	7 8	3 3	Young
Average.		3.1	2.0	8.9	4	2.4

TABLE 14.—Variation in the subspecies of *Artemisia tridentata*—Continued.

	Herbarium.	Involucre.			No. of flowers per head.	Length of corolla.
		Height.	Breadth.	No. of bracts.		
Subspecies <i>trifida</i>:						
South of Laramie, Wyo.	CI	mm.	mm.			mm.
Do.	CI	4.0	2.2	11 13	5 5	2.2
Do.	CI	3.0	2.5	8 12	5 5	2.3
Teton Forest, Wyo.	CI	4.0	2.3	16 14	4 5	2.0
Yellowstone, Wyo.	NY	3.2	2.1	10 9	9 8	2.3
Near Strevell, Idaho	NY	3.4	2.4	11 8	5 7	2.4
Madison, Mont.	CI	3.3	2.2	8 10	6 5	2.5
Cascade Mountains, Wash.	NY	3.3	2.7	10 10	7 7	2.3
Oroville, Wash.	172638 UC	3.3	2.0	10 10	5 7	2.0
Rattlesnake Mountains, Wash.	175975 UC	3.0	2.0	8 8	4 5	2.0
Eastern Oregon	NY	3.1	2.0	10 12	5 5	2.2
Eastern Oregon	29793 UC			10 12	5 5	Young
Average		3.3	2.3	11	6	2.2
Subspecies <i>arbuscula</i>:						
Yakima Region, Wash.	172649 UC	4.0	2.3	7 9	6 7	2.7
Crook County, Oreg.	176735 UC	4.1	2.8	10 11	5 7	2.2
Lake County, Oreg.	175219 UC	4.1	3.0	11 11	8 8	2.0
Eastern Oregon	176736 UC	4.1	2.7	12 15	7 7	2.5
Silver Lake, Oreg.	176784 UC	4.0	2.5	11 12	4 5	2.7
Placer County, Calif. ¹	202223 UC	4.0	2.4	11 12	6 6	2.8
Hayden Flats, Routt County, Colo.	NY			15	7	2.8
Eldorado County, Calif.	205842 UC	4.1	3.0	15 14	9 8	2.7
Average		4.1	2.7	11	6	2.5
Subspecies <i>rothrocki</i>:						
Mount Olancho, Calif.	47383 US	5.0	4.0	12	13	2.6
Tioga Pass, Calif.	203183 UC	4.5	4.2	11 13	8 10	2.8
San Bernardino Mountains, Calif.	101098 UC	4.4	3.5	12 14	10 10	Young
Inyo County, Calif.	202294 UC	4.7	4.2	14 14	18 20	2.4
Mount Dana, Calif.	29666 UC	4.8	4.1	10 12	12 13	3.0
Do.	29806 UC	5.0	5.0	11 14	13 13	3.3
California	34702 UC	4.4	4.0	12 12	9 10	3.4
Middle California	91185 UC	4.6	5.0	12 13	9 10	3.5
Mariposa County, Calif.	29710 UC	4.5	4.6	13	10 11	2.9
Camas Prairie, Idaho	231676 US	5.0	4.5	11 13	11 11	3.4
Red Cliff, Colo. ⁴	NY	5.0	3.2	12	11	3.3
North Park, Colo. ⁴	NY	5.0	3.5	12	14	3.3
Slide Mountain, Nev.	NY	3.3	2.7	9 10	8	2.4
Washington ⁵	NY	4.7	3.0	11 8	10 9	2.7
Union County, Oreg.	NY	4.0	2.8	7 10	7 8	3.0
Type specimen	Phila.	5.0	4.0	13 12	13 11	2.9
Cooper Hill, Wyo.	146493 UC	4.2	3.3	13 14	10 11	2.9
Crested Butte, Colo. ⁴	34512 UC	4.6	3.7	13 16	12 17	2.8
Yakima Region, Wash.	173161 UC	4.1	3.0	9 10	6 9	2.5
Wallowa Mountains, Oreg.	29788 UC	4.2	3.0	7 8	6 7	2.8
Placer County, Calif.	193453 UC	4.4	3.2	2 13	8 8	2.8
Truckee, Calif.	193454 UC	3.8	2.7	8 11	6 7	2.8
Average		4.4	3.6	12	10	2.8

¹ Dwarf forms.² Type collection of *A. parishii* Gray.³ Minor variation 10.⁴ Minor variation 7, *A. spiciiformis* Osterhout.⁵ Type of *A. vaseyana* Rydberg, minor variation 18.

as the most primitive of all the subspecies, but it is not the beginning of *A. tridentata*, as seems evident from its lack of connection, either morphologically or geographically, with *A. bigelovi*, which, as previously shown (pp. 104, 142), seems to represent the ancestral type from which this collective species has sprung. Whatever its previous history, *rothrocki* is now a readily distinguished type, restricted in distribution to a few widely separated localities, all within the general area of *typica*, but near its uppermost limits

in the mountains. While apparently always at high altitudes, it commonly occupies the belt between the grassland and the higher, better drained, but less fertile slopes where *typica* abounds.

The least known of all the subspecies is *bolanderi*. This was based upon specimens said to be gathered at Mono Pass, California, but perhaps they came from well down the eastern side of the Sierra Nevada. It is most like *trifida* in shape and lobing of the leaves, but has larger heads with more flowers and the white tomentum is loose, not closely appressed as in that. The type collection consists only of flowering twigs and the leaves are nearly all entire. The only other collection is one from 2,400 meters altitude at Sand Flat, south of Mono Lake, California (*Clements and Hall 11702*). In this the leaves are largely trifid, and it therefore seems likely that the lower ones of the type were also more generally cleft than in the portions preserved. The Sand Flat plants were growing in the main belt of typical *tridentata*, but on an exceptionally cold and bleak plain where they were competing with a low, turf-forming *Sporobolus*. It is conceivable that these conditions are responsible for the modification of *tridentata* into this form and that *trifida* was similarly produced along the northern limits of the range of the species. A nearly identical form has been noted as minor variation 4 of *A. cana*. Except for the preponderance of entire leaves, which are also somewhat longer, this duplicates *bolanderi* and indicates the possibility of the origin of morphologically equivalent plants from quite different, although related, stocks. Figure 22 shows the manner in which leaves of *trifida* and *bolanderi* sometimes come to look much alike (except in the loose, white pubescence of the latter) and also the similarity of both to occasional leaves of the variation from *A. cana* just mentioned.

A recent suggestion by Smiley (Univ. Calif. Publ. Bot. 9:396, 1921) that *bolanderi* may be a hybrid between typical *tridentata* and *rothrocki* will be further investigated in the field. It is not believed, however, that the latter grows in the neighborhood of the Sand Flat station cited above.

A study has been made of variation in the shape of the inner bracts of the involucre in subspecies *bolanderi*, since in the original description Gray described these as "narrowly oblong" as contrasted with the "broad" bracts of *A. cana*, and this difference has been used by later writers as a specific criterion. However, when dissected out and carefully compared, it is found that the inner bracts of heads from the type collection, although smaller, are not essentially different in shape from those commonly found in *A. cana* (see fig. 23).

ECOLOGY.

Artemisia tridentata is typically a low shrub, but it ranges from a dwarf form less than a foot high to a small tree 20 feet high. It is the characteristic dominant of the sagebrush climax of the Great Basin, where it often forms a pure consociation over large areas. It ranges far beyond the climax area into the mixed prairie and bunch-grass prairie, especially where overgrazing has given it the advantage in competition with the grasses. This is especially true of the bunch-grass association in eastern Oregon, north-eastern California, and southern Idaho, which has been almost completely replaced by sagebrush. The latter seems to have all the marks of a climax community, but the abundance of the bunch-grass dominants in protected places makes it clear that the sagebrush has become controlling only in the historical period as a result of overgrazing. On the east the sagebrush makes a broad mixture with the mixed prairie in Wyoming, in which it is favored by the overgrazing of the more palatable grasses. In the western edge of the Dakotas and Nebraska it becomes a subclimax community of the more stable valleys of the Bad Lands. The sagebrush scarcely reaches the plains of Colorado, owing to the mountain barriers, but it is more or less abundant in the mixed

prairie of several of the great parks. The mictium of sagebrush and mixed prairie is a characteristic feature of northwestern New Mexico and northeastern Arizona.

While the greatest contact of sagebrush is with the bunch-grass and mixed prairies, it touches the desert scrub in Nevada and in a few places in desert California. It makes occasional contacts with the coastal sagebrush in southern California and northern Mexico, but usually as more or less isolated communities. It frequently constitutes parks with the piñon-cedar woodland from Nevada to New Mexico, and these are usually connected by a kind of sagebrush-cedar savannah. It sometimes bears a similar relation to the lower portion of the yellow-pine woodland, and on the west slope of the Rocky Mountains is often mixed with Petran chaparral.

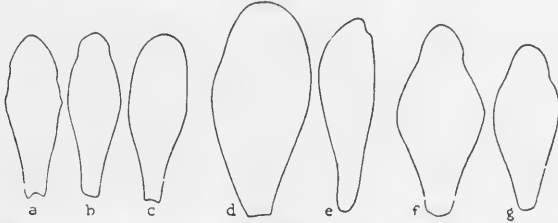


FIG. 23.—Inner bracts of the involucre of *Artemisia tridentata bolanderi* and *A. cana*: a, b, c, from the type collection of *bolanderi* (29305 UC); d, e, from typical *cana* (70513 UC); f, g, also from typical *cana* (51632 UC). All $\times 8$.

The most frequent associates of *A. tridentata* are the other shrub dominants of the sagebrush association. Chief among these is *Atriplex confertifolia*, followed closely by *Chrysothamnus nauseosus* and *viscidiflorus*. Other important associates are *Atriplex canescens*, *Grayia spinosa*, *Tetradymia spinosa*, and *Eurotia lanata*. Among the dwarf shrubs the most important are *Gutierrezia sarothrae* and *Kochia vestita*, the former indicating disturbance in some degree and the latter the presence of alkali. The sagebrush proper is also frequently associated with one or more of its variads, such as *A. t. arbuscula*, *nova*, and *trifida*, as well as with other species of *Artemisia*, such as *cana*, *rigida*, and *spinescens*. In practically all these cases, the different forms alternate rather than mix intimately, corresponding to some factor difference, usually of water. For example, *A. cana* is usually found below *tridentata* in valley or depressions, while the latter occupies small valleys and ravines below *trifida*.

The typical form of the sagebrush is an indicator of deep soils of somewhat greater water-content and largely free from alkali. While it occurs frequently with such halophytes as *Kochia* and *Sarcobatus*, it either alternates with them or its working roots probably occupy a less saline layer of the soil. It is found also on rocky slopes and ridges, but usually in the deeper pockets of soil, and as a result of the higher water-content due to the lack of competition. In the mixed prairie and especially in the Bad Lands, it is an indicator of greater water-content. While the sagebrush does form root-sprouts to some extent, this is not sufficient to make it an indicator of fire as a rule, except when a dwarf form is produced.

Of the subspecies of *tridentata*, one, *parishi*, resembles it in practically all ecological respects, while the others, *arbuscula*, *bolanderi*, *nova*, *rothrocki*, and *trifida*, are characteristically dwarfed, as is true also of the typical form in less favorable conditions. They occupy the thinner or drier soils, with the exception of *rothrocki*, which prefers meadows and depressions in the subalpine region, while *typica* occupies the drier slopes. Two dwarf forms of the latter, one of recent and the other of more remote origin, are typical indicators of fire and overgrazing, to which they doubtless owe their origin.

USES.

The common sagebrush or "black sage," as it is often erroneously called, is by far the most important species of *Artemisia* in western North America as regards its value as a browse shrub. This is largely because of its abundance over large areas and its ability to withstand close cropping, even by sheep. It is of special value in the autumn and winter when grass and other pasturage is dried up or covered with snow. At other seasons it is much less browsed by free-ranging animals. The testimony of range experts varies as to its exact value for different kinds of stock. This is because of the greater need in some places of browse shrubs, even less palatable ones like this, and also because certain breeds of animals are more fastidious than others of the same species. Hence, reports range from "eaten by sheep but not by starving cattle" to "good browse for cattle and sheep" and "excellent." Direct observation by the authors shows that sagebrush is not much eaten by horses, but that it enables stockmen to carry enormous numbers of cattle through the winter months, and that it is the principal dependence of sheep in many districts during periods of drought and in the winter. A chemical analysis of the plant is given by Dinsmore and Kennedy (Nevada Exp. Sta. Bull. 62:38, 1906). The close cropping by animals markedly affects the branching, size, and general appearance of the shrubs. Sometimes this results in all of the plants being much dwarfed and it is now infrequent to find the large, normally formed, tree-like growths that must have been the usual type before stock was introduced.

The Indians, and also many of the white settlers, find much use for sagebrush in the construction of shelters and for fuel. The stems are usually too irregular and brittle to serve well for construction, although sometimes so used, but the branches are employed as thatch in the building of temporary houses and sheds. The wood makes a quick, hot fire, partly because of the oil and partly because of the dry shredded bark.

This shrub has been cultivated as an ornamental since 1881, but apparently it has not found much favor. It is especially suited to dry or stony situations, and its value lies chiefly in the clean gray foliage. The larger forms, with expanded drooping inflorescences, such as mentioned under minor variation 14, would be the most desirable for this purpose.

Attempts have been made in the West to utilize sagebrush for its rather high content of potash, but the cost of preparation was found to be prohibitive. It has also been used to a limited extent for a flotation oil in mining and smelting operations, but again its cost was found to be greater than that of other oils equally useful. Less complex substances are now more in demand for this purpose. The report that sagebrush contains rubber is entirely erroneous.

A common malady in the West, known as mountain fever, but in reality only a form of hay-fever, has been demonstrated to be due in many cases to the pollen of *Artemisia tridentata*. This pollen is produced in great abundance and is so light that it is easily carried in enormous quantities by the wind. Its saline extract is now used as a preventive for hay-fever after the manner described under *A. vulgaris* (p. 100).

26. ARTEMISIA CAÑA Pursh, Fl. Am. Sept. 521, 1814. Plate 21. HOARY SAGEBRUSH.

A low shrub, commonly 4 to 9 but sometimes 15 dm. high, with pungent turpentine-like odor; stems freely branched throughout, forming rounded bushes, the older parts with a dark-brown fibrous bark, the branches densely clothed with a gray or yellowish-green tomentum which masks the striae; principal leaves sessile, linear, acute, 2 to 4 or 5 cm. long, 1 to 4 mm. wide, entire or occasionally with 1 or 2 irregular teeth or lobes, silky-canescens or floccose or sometimes glabrate and slightly viscid in age; upper leaves scarcely different and only slightly reduced even to midway of the inflorescence, silky-pubescent; inflorescence a narrow leafy panicle, 15 to 30 cm. long, 2 to 6 cm. broad;

heads homogamous, mostly sessile in small glomerules, erect; involucre campanulate, 4 to 5 mm. high, 3 to 4 mm. broad, or considerably smaller in minor variation 4 in which the heads are crowded and small; bracts 8 to 15, the outer orbicular or abruptly narrowed above, the inner elliptic-spatulate, very obtuse, broadly scarious-margined, canescent or tomentose; ray-flowers wanting; disk-flowers 6 to 15 or rarely 20, fertile, corolla tubular-funneliform, sharply 5-toothed, 2 to 3 mm. long, resinous-glandular; style-branches disk-like at summit, the margins lacerate; achenes cylindrical-turbinate, truncate and with a slightly raised rim at summit, angled or with 4 or 5 evident ribs, granuliferous.

On the plains and lower mountains, Saskatchewan to western Nebraska, New Mexico, Utah, northeastern California, British Columbia, and Alberta. Type locality, on the Missouri River. Collections: Saskatchewan Plains, *Macoun 1011* (Gr); Indian Head, Assiniboia, September 3, 1891, *Spreadbough* (US); Bozeman, Montana, September 3, 1902, *W. W. Jones* (DS, Gr, UC, US); Fort Bedford, North Dakota, *Waldron 418* (NY); Centennial, southeastern Wyoming, *Goodding 2118* (Gr, NY, UC, US); Sioux County, Nebraska, June 17, 1897, *Bates* (Gr); Steamboat Springs, Routt County, Colorado, *Osterhout 2012* (Osterhout, NY, UC, type collection of *A. cana viscidula* Osterhout, minor variation 1); Marshall Pass, Colorado, *Baker 880* (Gr, NY, UC, US); Fish Lake, Utah, *Jones 5824* (NY, UC); Dulce, Rio Arriba County, New Mexico, *Bailey 908* (US); 30 km. north of Bridgeport, Mono County, California, *Hall 11690* (UC); Little Truckee River, California, September 1887, *Sonne* (UC); near Reno, Nevada, *Kennedy 374* (UC); Lake County, Oregon, *Cusick 2737* in part (Gr, NY, UC, US); Caribou Forest, Idaho, *Eggleston 9975* (US).

MINOR VARIATIONS AND SYNONYMS.

1. *ARTEMISIA CANA VISCIDULA* Osterhout, Bull. Torr. Club 27:507, 1900.—A state or condition of *A. cana* in which the tomentum is light and obscured by a glutinous exudate, the herbage therefore greenish. Type locality, Steamboat Springs, Routt County, Colorado.

2. *A. COLUMBIENSIS* Nuttall, Genera 2:142, 1818.—*A. cana*. In connection with the original description Nuttall states that this "appears to be *A. cana* of Pursh," but later on he says that it is "certainly distinct from the *A. cana* of Pursh" (Trans. Am. Phil. Soc., II, 7:399, 1841). No differentiating characters are given other than that the leaves are all entire. A specimen in the herbarium of the Philadelphia Academy of Sciences labeled as from the banks of the Missouri and Columbia Rivers and indicated by Nuttall as one of the types is plainly *A. cana*.

3. *A. VISCIDULA* Rydberg, Bull. Torr. Club 33:157, 1906.—Based upon *A. cana viscidula* Osterhout, which see. Later reduced by Rydberg to *A. cana* (N. Am. Fl. 34:282, 1916), a disposal with which the present authors agree.

4. An unnamed form with linear mostly entire leaves only about 1 mm. wide, on short, crowded twigs is occasionally found in Wyoming: Evanston, *Hall 10992*; 40 km. west of Rawlins, *Hall 10991*; west of Laramie, September 10, 1919, *Clements*. As far as observed these always grow in the proximity of plants of typical *cana* and all show evident injury to the main stems, perhaps by browsing. This latter is believed to be responsible for some of the changed characters. Except for the entire leaves, these plants are like *A. tridentata bolanderi*, and even this distinction does not constantly hold, since occasional leaves are cleft, as shown in figure 22. The twig illustrated is exceptional, since most of the leaves on this plant are entire. In one collection (10991) the involucre bracts are almost exactly like those shown of *bolanderi* (fig. 23, a, b, c); in another (10992) the bracts are like the last two drawings of genuine *cana* (fig. 23, f, g), but of smaller size, corresponding to the reduced size of the heads.

RELATIONSHIPS.

In technical characters as well as in habit this species finds its nearest ally in *A. tridentata*. Its whiter silvery pubescence and longer upper leaves serve to distinguish it in the field. These leaves are typically entire and acuminate as contrasted with the uniquely 3-toothed leaves on all but the upper twigs of *tridentata*. Moreover, each of the subspecies of the latter has some individual peculiarity which serves to distinguish it. In the case of *tridentata typica*, the one most likely to be confused with *cana*, this consists in a reduced number of flowers, only 4 to 6 as contrasted with 6 to 20 in *cana*. The close-

ness of relationship is indicated by an occasional lobe on some of the leaves, and usually when this is present it has very much the shape and direction of the lobes in certain subspecies of *tridentata* with cleft foliage. It is also significant that the inflorescence, heads, and flowers of *A. tridentata rothrocki* so nearly duplicate those of certain forms of *A. cana* that specimens can be identified with certainty only when lower leaves are present. The geographic ranges of the two overlap along a large extent of territory, from Utah and northern California nearly to the Canadian boundary, and they sometimes bring the two species into the same ecologic habitat. To the south of this belt inhabited by the two in common, only *tridentata* is found, this occurring in abundance even to beyond the Mexican border, while to the north *cana* makes its way well up into Canada. Since *tridentata* is of southerly origin, as has been already demonstrated, the natural conclusion from a consideration of these facts of distribution is that *cana* is a derivative of this abundant and widespread species.

The relationships of the forms here included under *A. cana* have been sufficiently discussed in dealing with the minor variations. Table 15 supplies the evidence upon which some of the conclusions were based.

TABLE 15.—Variation in *Artemisia cana*.

	Herbarium.	Involucre.			No. of flowers per head.	Length of disk-corolla.
		Height.	Breadth.	No. of bracts.		
Genuine <i>cana</i> :						
		mm.				mm.
Gallatin County, Mont.	166429 UC	4.8 4.5	3.5 3.0	11	10	2.9
Montana (part)	29729 UC	5.0 4.8	3.8 3.4	12 9	6 7	2.5
Do.	29729 UC	4.7 4.8	3.5 3.6	11	9	2.5
Centennial, Wyo.	70518 UC	4.5 4.8	3.0 3.0	10	6	2.5
West of Laramie, Wyo.	CI	4.0 4.2	3.0 3.1	8 10	7 8	2.7
Seven Mile Lake, Wyo.	51692 UC	4.5 5.0	2.5 2.8	10 11	6 8	2.7
Howell Lake, Wyo.	51638 UC	5.0 5.1	2.7 2.6	8 10	9	2.3
Fish Lake, Utah.	160265 UC	5.0 4.5	3.5 3.6	10 12	8 9	2.6
Little Truckee River, Calif.	193576 UC	4.0 4.5	3.0 3.1	12	12	2.1
Lake County, Oreg.	34375 UC	5.2 5.0	4.2 4.5	13	19	2.3
Near Prineville, Oreg.	176719 UC	4.5 4.4	3.5 3.0	10 12	8 10	2.6
Steamboat Springs, Wyo. ¹	2012 Osterh.	4.6 4.2	2.6 2.7	9 10	8 9	2.3
Average.		4.6	3.1	10	9	2.5
Minor variations:						
West of Laramie, Wyo. ¹	CI	3.3 3.4	2.3 2.5	11 9	7 4	2.6
Evanston, Wyo. ²	205534 UC	3.6 3.8	2.5 2.7	9 11	10 12	2.5
West of Rawlins, Wyo. ²	205535 UC	3.3 3.4	2.2 2.4	9 10	7 7	2.1
Teton Forest, Wyo.	177138 UC	3.2 3.1	2.7 2.5	13 13	17 17	2.4
Average.		3.4	2.5	11	10	2.4

¹ Type of variety *viscidula* Osterhout. See minor variation 1.² Minor variation 4; heads crowded and small.

ECOLOGY.

Artemisia cana closely resembles *A. tridentata* in habit, as well as in the tendency to form pure communities. It requires more water and hence often constitutes a subclimax consociety in valleys of the northern half of the sagebrush formation. In Montana especially it replaces the sagebrush, forming valley communities subclimax to the mixed prairie, and making a low savannah with the grasses as it disappears before the climax. In the Bad Lands of Montana and North Dakota it often plays an important rôle in the succession, preceding the final grasses. It is regularly an indicator of greater water-content, though in bad-land areas this is the result of a lack of competition.

USES.

The principal use of this sagebrush is as a browse shrub, especially for sheep. According to experts in grazing it is very important throughout most of its range and is eaten quite extensively when other feed is scarce. In eastern California, where commonly known as "white sagebrush," it is reported as a good browse shrub, even for horses and cattle.

Together with *A. tridentata*, it furnishes settlers and campers with fuel and shelter and is much used for these purposes by the Indians, especially in regions where trees are scarce. In England, it is cultivated to a limited extent as an ornamental, because of its silvery leaves and stems. Finally, its importance both as a cause and a remedy for hay-fever is perhaps no less than that of *A. tridentata* in proportion to its relative abundance.

27. ARTEMISIA RIGIDA (Nuttall) Gray, Proc. Am. Acad. 19:49, 1883. Plate 22.
STIFF SAGEBRUSH.

A low shrub, 4 dm. or less high, with pungent odor; stems thick and rigid, much branched from near the base, the branches spreading or erect, forming rounded clumps, clothed with a dark fibrous bark, the very short twigs not striate but canescent or glabrate and then yellowish; principal leaves sessile, spatulate in outline but with narrowly linear base, 1.5 to 4 cm. long, 1 mm. wide below the lobes, parted or cleft from the summit into 3 to 5 narrowly linear lobes, silvery-canescenscent on both sides; upper leaves similar and only slightly reduced, sometimes entire, all longer than the heads; inflorescence a leafy spike, 2 to 15 cm. long, less than 1 cm. broad exclusive of leaves; heads homogamous, sessile and solitary in the axils or the upper ones somewhat glomerate, erect; involucre campanulate, 4 to 5 mm. high, 2.5 to 3.5 mm. broad; bracts 12 to 26, the short outer ones orbicular to elliptic and acute, the inner elliptic or spatulate and very obtuse, with a white-scarious margin, all canescently tomentulose; ray-flowers wanting; disk-flowers 5 to 15, fertile, corolla funnellform, deeply and acutely 5-toothed, 2 to 2.8 mm. long, glabular at least on the tube, often reddish; style-branches oblong, truncate, erose across summit; achenes somewhat prismatic, 4- or 5-angled or with 4 or 5 ribs, glabrous. (*A. trifida* β *rigida* Nuttall, Trans. Am. Phil. Soc. II, 7:398, 1841.)

On rocky ridges and plains, western Montana to eastern Washington and Oregon. Type locality, plains of Lewis (Snake) River. Collections: Wild Horse Island, Flathead Lake, Montana, Jones (according to Jones, Bull. Univ. Mont. 61:48, 1910); type collection, Nuttall (Gr); Seven Devils Mountains, Washington County, Idaho, September 9, 1899, Jones (US); Yakima region, Washington, 1882, Brandegee; bluffs of Snake River, above Wawawai, Washington, Piper 3814 (Gr, NY); eastern Oregon, Cusick 2504 (Gr, UC, NY, US); east of The Dalles, Oregon, September 25, 1919, Hall (CI); south rim of the Grande Ronde Valley, Union County, Oregon, Eggleston 13664 (US).

RELATIONSHIPS.

This is apparently an offshoot from the *tridentata* group of species, but because of the absence of connecting forms its exact phylogeny is difficult to determine. In many respects it suggests *A. tridentata trifida*, especially in its reduced stature, silvery pubescence, and cut of leaf. The achenes are essentially prismatic and 4-angled as in other members of this group. The reduction in size and inflorescence that is so evident in *trifida* is here carried to its extreme, the plants being very low and the inflorescence narrowed to a leafy spike. These traits suggest a direct derivation from *trifida*, and this is not at all improbable. In addition to the reductions mentioned, *rigida* differs in its elongated upper leaves, each with a head in its axil, in the more silvery pubescence, in details of habit, and in its adaptation to less favorable soil and climatic conditions. It is not a successful competitor with other shrubby Artemisias, as is indicated by its

restriction to poor, stony soils over a limited area from western Montana to eastern Washington, where there is a deficiency of rainfall in summer and the winters are comparatively cold and bleak.

The original reference of this species to a variety of *A. trifida* by Nuttall was due to the incomplete nature of the type specimens. These were in leaf only and were thus wanting in the only characters whereby *rigida* may be readily distinguished.

ECOLOGY AND USES.

Artemisia rigida is a low shrub with deciduous leaves. Its stature and leaf habit correspond with its position on thin or stony soil under a low rainfall. It frequently alternates with *tridentata* where deeper soils permit the growth of the latter. It tends to form pure communities with few or no secondary species.

The scant foliage is browsed somewhat by sheep, but it is so well protected by the stiff branches and the species is of such limited distribution that *A. rigida* is of almost negligible importance as a browse shrub. It is probably a cause of hay-fever, especially in Oregon.

28. ARTEMISIA PYGMAEA Gray, Proc. Am. Acad. 21:413, 1886. Plate 22. PIGMY SAGEBRUSH.

A depressed shrub less than 2 dm. high, the odor unknown; stems flexuous at base, with numerous short, erect branches, the old bark dark brown and fibrous, the twigs pale or nearly white, not striate, puberulent; principal leaves sessile, oblong to obovate in outline, with linear base, 0.2 to 0.5 cm. long, pinnately 3- to 7-parted or with as many divergent teeth, the linear segments obtuse but mucronate, rigid, green, nearly glabrous, more or less viscid; upper leaves smaller, 3-parted or 3-toothed, those of the inflorescence mostly entire and all shorter than the heads; inflorescence spike-like, 1 to 4 cm. (or more?) long, about 0.5 cm. broad; heads homogamous, sessile, erect; involucre at first nearly cylindric, later spreading and campanulate, 4 to 5 mm. high, about 3.5 to 4 mm. broad; bracts about 15 to 20, all similar but the outer ones regularly shorter, linear or linear-spatulate and obtuse, or the outer ones lanceolate and somewhat acute, yellowish-green, with narrow and very thin white-scarious margins, sparsely villous or nearly glabrous; ray-flowers wanting; disk-flowers 3 to 5 (or more?), fertile, corolla turbinate, 4- or 5-toothed, 2.5 to 3 mm. long, glandular at least on the tube; style-branches flat, truncate, fimbriate at summit; achenes ellipsoid, truncate at summit, obscurely angled, glabrous.

Known only from eastern Nevada and western Utah. Type locality, Desert region of Nevada, at Fisk [Fish] Creek near Eureka. Collections: Type collection, August, 1885, *Brandegee* (Gr, UC); Pioche, Lincoln County, southeastern Nevada, August 31, 1912, *Jones* (UC); Ortons Ranch, Utah, *Jones 5984* (NY).

RELATIONSHIPS.

This species differs from all others of its group in having the lower leaves pinnately parted into lateral lobes instead of toothed or lobed from the summit. Some of the upper leaves, however, are 3-lobed, very much after the manner of the other species. The ribs of the leaf are quite prominent in the type collection, but in others they are no more conspicuous than they are in some forms of *A. tridentata* (for example, in subspecies *trifida* as represented by M. E. Jones's Oroville, Washington, collection, Herb. Univ. Calif. 175975). The aspect of the plant is unique in *Artemisia*. The low tufted stems, the minute rigid foliage, and the greenish imbricated involucre suggest the appearance of an *Haplopappus* of the *Ericameria* section. The technical characters relate it to *A. tridentata* and *A. rigida*, but beyond this its phylogenetic origin can not now be determined.

ECOLOGY AND USES.

Artemisia pygmaea is a dwarf shrub with greatly reduced leaves, corresponding with its climatic position and its habitat in alkaline areas, where it is associated with the halophytic *Chrysothamnus nauseosus consimilis*. Its small size and rare occurrence preclude any uses.

29. ARTEMISIA PALMERI Gray, Proc. Am. Acad. 11:79, 1876. Plate 23.
TALL SAGEBRUSH.

A shrub 12 to 30 dm. high, with straight, wand-like herbaceous stems that commonly make clusters about 10 dm. across, the habit then similar to that of *A. abrotanum*, or sometimes in younger plants the stems few or solitary, nearly simple, and more herbaceous, the odor strong, but not unpleasant; flowering stems erect, conspicuously striate, glabrous or minutely puberulent, reddish; principal leaves petioled or sessile by a narrow base, 5 to 15 cm. long, pinnately parted into 3 to 5 long linear lobes with closely revolute margins or entire and linear, green and glabrous or minutely puberulent above, densely white-tomentose beneath; upper leaves similar but more of them entire, nearly wanting in the inflorescence; inflorescence an open terminal pyramidal panicle, 15 to 40 cm. long, 3 to 10 cm. broad; heads homogamous, on peduncles 1 to 5 mm. long or sometimes sessile, mostly nodding at maturity; involucre hemispheric, 3 to 4 mm. high, 2 to 3.5 mm. broad; bracts 7 to 12 (and in addition 10 to 20 elliptic obtuse bracts scattered among the flowers), ovate, acutish, the outer ones but little shorter than the inner, sparingly pubescent or glabrous, scarious-margined; ray-flowers wanting; disk-flowers 12 to 25 or rarely up to 35, fertile, corolla narrowly funnelform or nearly tubular, 5-toothed, 1.5 to 2.2 mm. long, glandular-granuliferous especially on the tube; style-branches flat, truncate and arose at summit (sometimes described as included but long-exserted and coiled at maturity in most specimens); achenes nearly prismatic but slightly narrowed below, 4-angled, the summit truncate, granuliferous.

Southwestern San Diego County, California and northern Lower California. Type locality, San Diego County, California, in Jamul Valley, 20 miles east of San Diego. Collections: Type collection, 1875, *Palmer* (Gr, NY as No. 193); near San Diego, 1899, *Purpus* (UC, Phila); same locality, September 9, 1899, *Brandege* (Pomona College Hb.); near National City, *Brandege* (UC, US); Oneonta, San Diego County, July, 1900, *Brandege* (Phila); Alpine, San Diego County, August 6, 1894, *Mearns 3942* (US); bluffs near the sea, La Jolla, *Abrams 4013* (DS, Gr, NY); All Saints Bay, Lower California, July, 1882, *Fish* (Gr).

SYNONYM.

1. ARTEMISIASTRUM PALMERI Rydberg, N. Am. Fl. 34:285, 1916.—*A. palmeri*.

RELATIONSHIPS.

The relationships of this species are exceptionally obscure. The presence of chaff on the receptacle is not known elsewhere in *Artemisia* and it was principally because of this that Rydberg recently set the species aside as a new genus, namely, *Artemisiastrum* (N. Am. Fl. 34:285, 1916). The objections to this treatment have been stated earlier in this paper (p. 33). Aside from this character, *A. palmeri* plainly goes into the section *Seriphidium*, although it differs from all of the other members of this section in several details. No other American species has such elongated herbaceous branches, although true herbs are common among Old World species; the cut of the leaf and the peduncled heads are more suggestive of *A. dracunculus* or of certain forms of *A. vulgaris* than of any member of the section *Seriphidium*; and the involucre bracts are more nearly equal in size than in other species, while at the same time their number is greatly reduced. It is possible that some of the bracts on the outer part of the disk are in reality bracts of the involucre which have taken up a more central position, but the number is sometimes too great to

be accounted for in this way. As far as examined, each bract subtends one of the disk-flowers. When the latter are numerous, some of them are devoid of bracts. It therefore seems more reasonable to look upon the presence of receptacular bracts as a case of reversion. This is not due to the persistence of an ancestral trait, as is evident from the high position of *Seriphidium* within the genus and from the absence of these structures in immediately related genera many of which are more primitive than *Artemisia*.

Since no one of the American *Seriphidia* approaches *A. palmeri*, its relationships are perhaps to be sought in the Old World, and this must be left for later studies. A possible alternative is its evolution from some group of the section *Abrotanum*. The habit, cut of leaf, and other features are very suggestive of *A. vulgaris mexicana*, but a derivation from this group would involve at once the loss of ray-flowers, the development of receptacular bracts, and a change in the shape of the achenes in addition to minor changes. This connection is therefore scarcely more than a remote possibility.

As compared with most *Artemisias*, the achene more closely approaches a truly prismatic shape. It is even more decidedly quadrangular and evenly truncate at summit than in other species of the section *Seriphidium*, where subprismatic achenes are the rule. Although sharply 4-angled, the achene is not otherwise ribbed or crowned, as sometimes described. The characters of the corolla, even down to the peculiar glandular-granuliferous tube and the style-branches, are as in other members of its section. Other characters are indicated in the subjoined table.

ECOLOGY AND USES.

Artemisia palmeri is a tall shrub with more or less herbaceous branches. It forms a sparse consociety in ravines and along moist banks, and also pushes a short distance up slopes, where it meets *A. californica* and its associates.

It is rare and local, and hence has not been used, though its odor suggests that it may possess the value of certain European species for flavoring.

TABLE 16.—Variation in *Artemisia palmeri*.

Herbarium.	Involucre.			No. of bracts of receptacle.	No. of flowers.	Length of disk-corolla.
	Height.	Breadth.	No. of bracts.			
		<i>mm.</i>	<i>mm.</i>			<i>mm.</i>
San Diego County, Calif. (type).....	Gr	2.8 3.0	2.0 2.5	9	14	15
Near San Diego, Calif.....	29705 UC	3.5 4.0	3.5	10 10	10 10	35 20
National City, Calif.....	91220 UC	3.5 4.0	2.5 3.0	10 9	10 8	22 20
La Jolla, Calif.....	Gr	3.3 3.0	2.0	11	13	12 13
Alpine, Calif.....	239844 US	3.0 3.3	2.1 2.5	11	11	15 15
All Saints Bay, Lower Calif.....	Gr	3.1 3.7	2.0 3.0	7	18	16 26
Average.....		3.3	2.5	9.6	11	19

EXPLANATIONS OF PLATES 1 TO 23, GENUS ARTEMISIA.

PLATE 1.

Artemisia abrotanum. (Drawn from material collected in Virginia from an introduced plant, 29718 UC; supplemented by foliage from a plant in the Botanical Garden of the University of California.)

- (1) Erect shoot showing the narrow leaf-lobes and the broad inflorescence, $\times 1$.
- (2) Young head, $\times 8$.
- (3) Outer bract of the involucre, $\times 16$.
- (4) Middle bract, $\times 16$.
- (5) Inner bract, $\times 16$.
- (6) Ray-flower, showing a few glands on the corolla, $\times 16$.
- (7) Style-branches of a ray-flower, $\times 24$.
- (8) Disk-flower with a few resin-glands on the achene and corolla, $\times 16$.
- (9) Style of the disk-flower showing the truncate tips, $\times 24$.

Artemisia pontica. (Drawn from material collected in Europe, 161793 UC.)

- (10) Erect stem showing the finely pinnatifid foliage and the elongated inflorescence, $\times 1$.
- (11) Mature head, $\times 8$.
- (12) Outer bract of the involucre, $\times 16$.
- (13) Inner bract, $\times 16$.
- (14) Ray-flower showing the irregularly angled achene, $\times 16$.
- (15) Style of the ray-flower, $\times 24$.
- (16) Disk-flower showing the broad-topped, angular achene, $\times 16$.
- (17) Style of the disk-flower showing the truncate and penicillate branches, $\times 24$.

PLATE 2.

Artemisia californica. (Drawn from fresh material, Oakland Hills, California, except the leaves of fig. 12.)

- (1) Inflorescence, $\times 1$.
- (2) Habit of plant as normally developed on gentle slopes, $\times 0.07$.
- (3) Ray-flower, $\times 16$.
- (4) Style of ray-flower, $\times 24$.
- (5) Disk-flower, $\times 16$.
- (6) Style of disk-flower, $\times 24$.
- (7) Head, $\times 8$.
- (8) Outer bract of the involucre, $\times 16$.
- (9) Middle bract, $\times 16$.
- (10) Inner bract, $\times 16$.
- (11) Leaves showing variation in lobing, all from a single plant; most of the leaves are entire or only once pinnatifid; $\times 1$.
- (12) Leaves of an insular form described under minor variation 7, $\times 1$. (Material from San Clemente Island, California, UC.)

PLATE 3.

Artemisia norvegica heterophylla. (Material from Mount Rainier, Washington, 9776 UC.)

- (1) Stem with leaves and inflorescence, $\times 1$.
- (2) Disk-flower, $\times 16$.

Artemisia norvegica globularia. (Material from St. Paul Island, Alaska, 73910 UC.)

- (3) Stem with leaves and inflorescence, $\times 1$.
- (4) Disk-flower, $\times 16$.

Artemisia norvegica glomerata. (Material from Arakamtchetchene Island, Bering Sea, Gr.)

- (5) Stem with leaves and inflorescence, $\times 1$.
- (6) Disk-flower, $\times 16$.

Artemisia norvegica saxatilis. (Material from Pyramid Peak, California, 54076 UC.)

- (7) Stem with basal leaves and a portion of the inflorescence, $\times 1$.

PLATE 3—continued.

- (8) Ray-flower, $\times 16$.
- (9) Outer bract of the involucre, $\times 16$.
- (10) Inner bract, $\times 16$.
- (11) Head, $\times 8$.
- (12) Disk-flower, $\times 16$.
- (13) Style of disk-flower, $\times 24$.

PLATE 4.

Artemisia parryi. (Drawn from type specimen, Gr.)

- (1) Stem showing leaves and inflorescence, $\times 1$.
- (2) Outer bract of the involucre, $\times 16$.
- (3) Middle bract, $\times 16$.
- (4) Ray-flower, $\times 16$.
- (5) Disk-flower, $\times 16$.
- (6) Style of a disk-flower, $\times 24$.
- (7) Head, $\times 8$.

Artemisia senjavinensis. (Material from Arakamtchetchene Island, Bering Sea, Gr. US.)

- (8) Portion of a mat, showing stem, leaves, and inflorescence, $\times 1$.
- (9) Leaf, showing lobes, $\times 2$.
- (10) Head, $\times 8$.
- (11) Ray-flower, $\times 16$.
- (12) Disk-flower, $\times 16$.
- (13) Style of a disk-flower, $\times 24$.

Artemisia macrobotrys. (Material from above Fort Selkirk, Yukon, Tarleton, NY.)

- (14) Leaf showing the divergent lobes, $\times 1$.
- (15) Ray-flower, $\times 16$.
- (16) Disk-flower, $\times 16$.
- (17) Style of a disk-flower, $\times 24$.
- (18) Head, $\times 8$.

PLATE 5.

Artemisia stelleriana. (Material from Ocean Beach, Massachusetts, 193468 UC.)

- (1) Shoot and inflorescence, $\times 1$.
- (2) Style of ray-flower, $\times 24$.
- (3) Ray-flower, $\times 16$.
- (4) Disk-flower, $\times 16$.
- (5) Style of disk-flower, $\times 24$.
- (6) Outer bract of the involucre, $\times 16$.
- (7) Middle bract, $\times 16$.

Artemisia alaskana. (Drawn from a portion of the type specimen, NY.)

- (8) Section of the inflorescence, showing the long peduncles, $\times 1$.
- (9) Various types of leaves from same plant, $\times 1$.
- (10) Ray-flower, $\times 16$.
- (11) Style of ray-flower, $\times 24$.
- (12) Disk-flower, $\times 16$.
- (13) Style of disk-flower, $\times 24$.

PLATE 6.

Artemisia franserioides. (Drawn from fresh material and photo. from San Juan Mountains, Colo.)

- (1) Inflorescence showing the second arrangement of the heads, $\times 1$.
- (2) A pair of lower leaves, $\times 1$.
- (3) Habit sketch of an entire plant, $\times 0.1$.
- (4) Inner bract of the involucre, $\times 16$.
- (5) Outer bract, $\times 16$.
- (6) Head, $\times 8$.
- (7) Ray-flower, $\times 16$.
- (8) Style of ray-flower, $\times 24$.
- (9) Disk-flower, $\times 16$.
- (10) Style of disk-flower, $\times 24$.
- (11) Principal leaf from near base of stem, showing the obtuse lobes, $\times 1$.

Artemisia vulgaris serrata. (Material from northern Illinois, 193540 UC.)

- (12) Portion of inflorescence and a leaf from lower down on the stem, $\times 1$.

EXPLANATIONS OF PLATES 1 TO 23, GENUS ARTEMISIA.

PLATE 7.

Artemisia vulgaris tilesi (the tall form, = *A. elatior*).
(Material from the Klondyke River at Dawson, Canada, SF.)

- (1) Inflorescence; this much more elongated and with smaller heads than in typical *tilesi*, $\times 1$.
- (2) Leaf from middle portion of the stem, $\times 1$.

Artemisia vulgaris typica. (Material from along St. John River, Maine, 29797 UC, the detached leaves from near Andover, New Jersey, 29801 UC.)

- (3) Inflorescence, $\times 1$.
- (4) Lower leaf, $\times 1$.
- (5) Middle cauline leaf, $\times 1$.
- (6) Upper cauline leaf, $\times 1$.
- (7) Cluster of leaves from the same stem as 3, $\times 1$.
- (8) Disk-flower, $\times 16$.
- (9) Style of disk-flower, $\times 24$.
- (10) Head, $\times 8$.
- (11) Style of ray-flower, $\times 24$.
- (12) Ray-flower, $\times 16$.
- (13) Outer bract of the involucre, $\times 16$.
- (14) Inner bract, $\times 16$.

PLATE 8.

Artemisia vulgaris heterophylla. (Drawn from a living plant, Berkeley, California.)

- (1) Upper portion of the inflorescence, $\times 1$.
- (2) Habit sketch of a portion of a plant; the low shoots are from rootstocks connected below the surface with the larger stems; $\times 0.03$.
- (3) Series of leaves so arranged as to preserve the original sequence up the stem, $\times 1$.
- (4) Lower leaf from the same plant but gathered earlier in the season, $\times 1$.
- (5) Disk-flower, $\times 16$.
- (6) Style of disk-flower, $\times 24$.
- (7) Ray-flower, $\times 16$.
- (8) Style of ray-flower, $\times 24$.
- (9) Head, $\times 8$.
- (10) Middle bract of the involucre, $\times 16$.
- (11) Inner bract, $\times 16$.

PLATE 9.

Artemisia vulgaris gnaphalodes. (Drawn from fresh material from Reno, Nevada.)

- (1) Inflorescence and a portion of the leafy stem, showing lobed leaves in the middle, with entire ones both below and above, $\times 1$.

Artemisia vulgaris wrightii. (Drawn from fresh material from Colorado Springs, Colorado.)

- (2) Top of plant with inflorescence, $\times 1$.
- (3) Head, $\times 8$.
- (4) Outer bract of the involucre, $\times 16$.
- (5) Inner bract, $\times 16$.
- (6) Ray-flower, $\times 16$.
- (7) Style of ray-flower, $\times 24$.
- (8) Disk-flower, $\times 16$.
- (9) Style of disk-flower, $\times 24$.

Artemisia bigelovi. (Drawn from fresh material from Cañon City, Colorado.)

- (10) Main portion of stem with inflorescences, $\times 1$.
- (11) Outer bract of the involucre, $\times 16$.
- (12) Inner bract, $\times 16$.
- (13) Head, $\times 8$.
- (14) Ray-flower, $\times 16$.
- (15) Style of ray-flower, $\times 24$.
- (16) Disk-flower, $\times 16$.
- (17) Style of disk-flower, $\times 24$.

PLATE 10.

Artemisia annua. (Material from St. Louis, Missouri, 193447 UC.)

- (1) Inflorescence, $\times 1$.
- (2) Leaves from middle portion of the stem, $\times 1$.
- (3) Ray-flower, $\times 16$.
- (4) Style of ray-flower, $\times 24$.
- (5) Disk-flower, $\times 16$.
- (6) Style of disk-flower, $\times 24$.
- (7) Head, $\times 8$.
- (8) Outer bract of the involucre, $\times 16$.
- (9) Inner bract, $\times 16$.

Artemisia klotzschiana. (Material from Pachuca, Hidalgo, 135382 UC.)

- (10) Upper portion of inflorescence, $\times 1$.
- (11) Middle portion of stem, with leaves, $\times 1$.
- (12) Head, $\times 8$.
- (13) Outer bract of the involucre, $\times 16$.
- (14) Inner bract, $\times 16$.
- (15) Ray-flower, $\times 16$.
- (16) Style of ray-flower, $\times 24$.
- (17) Disk-flower, $\times 16$.
- (18) Style of disk-flower, $\times 24$.

Artemisia biennis. (Drawn from living plants, Berkeley, California.)

- (19) Principal leaves from middle part of stem, $\times 1$.
- (20) Upper portion of inflorescence, $\times 1$.
- (21) Head, $\times 8$.
- (22) Outer bract of the involucre, $\times 16$.
- (23) Inner bract, $\times 16$.
- (24) Ray-flower, $\times 16$.
- (25) Style of ray-flower, $\times 24$.
- (26) Disk-flower, $\times 16$.
- (27) Style of disk-flower, $\times 24$.
- (28) Habit sketch, $\times 0.025$.

PLATE 11.

Artemisia absinthium. (Drawn from living material from the Botanical Garden, University of California.)

- (1) Portion of shoot and inflorescence, $\times 1$.
- (2) Disk-flower, $\times 16$.
- (3) Style of disk-flower, $\times 24$.
- (4) Head, $\times 8$.
- (5) Narrow outer bract of the involucre, $\times 16$.
- (6) One of the principal bracts, $\times 16$.
- (7) Style of ray-flower, $\times 24$.
- (8) Ray-flower, $\times 16$.

Artemisia frigida. (Drawn from living material growing near Manitou, Colorado; the details from material collected on the Laramie Plains, Wyoming.)

- (9) Inflorescence, $\times 1$.
- (10) Leaf from midway up the stem, $\times 1$.
- (11) Head, $\times 8$.
- (12) Outer bract of the involucre, $\times 16$.
- (13) Inner bract, $\times 16$.
- (14) Ray-flower, $\times 16$.
- (15) Style of ray-flower, $\times 24$.
- (16) Disk-flower, $\times 16$.
- (17) Style of disk-flower, $\times 24$.
- (18) Habit sketch of an entire plant, $\times 0.125$.

PLATE 12.

Artemisia pattersoni. (Drawn from fresh material from Pike's Peak, Colorado.)

- (1) Entire plant, $\times 1$. The details of heads and flowers are similar to those of *A. scopulorum*, except that the parts are larger and the corollas glabrous.

EXPLANATIONS OF PLATES 1 TO 23, GENUS ARTEMISIA.

PLATE 12—continued.

Artemisia scopulorum. (Drawn from fresh material from Pike's Peak, Colorado, except fig. 2.)

- (2) Entire plant of a much reduced alpine form from La Sal Mountains, Utah (175205 UC); $\times 1$.
- (3) Average plant, $\times 1$.
- (4) Ray-flower, $\times 16$.
- (5) Style of ray-flower, $\times 24$.
- (6) Disk-flower, $\times 16$.
- (7) Style of disk-flower, $\times 24$.
- (8) Head, $\times 8$.
- (9) Outer bract of the involucre, $\times 16$.
- (10) Inner bract, $\times 16$.

PLATE 13.

Artemisia dracunculus typica. (Drawn from living plants in eastern Colorado.)

- (1) Upper portion of inflorescence, $\times 1$.
- (2) Lower portion of stem, with foliage, $\times 1$.
- (3) Habit sketch of a portion of a plant, $\times 0.1$.
- (4) Outer bract of the involucre, $\times 16$.
- (5) Inner bract, $\times 16$.
- (6) Ray-flower, $\times 16$.
- (7) Style of ray-flower, $\times 24$.
- (8) Disk-flower, $\times 16$.
- (9) Style of disk-flower, showing 2 very short lobes; $\times 24$.
- (10) Style of disk-flower, showing deeper cleavage; $\times 24$.
- (11) Head, $\times 8$.

PLATE 14.

Artemisia campestris typica. (Material from Brandenburg, 6488 Baker Herb.)

- (1) Inflorescence, $\times 1$. The details of the heads and flowers are identical with those of subspecies *pacifica*.

Artemisia campestris pacifica. (Drawn from fresh material from Manitou, Colorado.)

- (2) Inflorescence, $\times 1$. The two portions were continuous; other inflorescences on the same plant were more widely branched, but the branches were all close and more nearly erect than in fig. 1.
- (3) Habit sketch, $\times 0.1$.
- (4) Basal leaf, $\times 1$.
- (5) Head, $\times 8$.
- (6) Outer bract of the involucre, $\times 16$.
- (7) Inner bract, $\times 16$.
- (8) Ray-flower, $\times 16$.
- (9) Style of ray-flower, $\times 16$.
- (10) Disk-flower, $\times 16$.
- (11) Style of disk-flower, $\times 24$.

PLATE 15.

Artemisia campestris borealis.

- (1) A plant with a narrow inflorescence, $\times 1$. (Material from Mount Albert, eastern Quebec, 147968 UC.)
- (2) A more spreading inflorescence, see minor variation 8, $\times 1$. (Material from Mount Ste. Abbe, Gaspé County, Quebec, 69740 UC.)
- (3) Basal leaves from the same plant as fig. 2, $\times 1$.
- (4) Habit sketch of the plant represented in figs. 2 and 3, $\times 0.14$.

Artemisia campestris spithamea. (Material from Saguache Mountains, Utah, 91237 UC.)

- (5) Style of disk-flower, showing cleavage on one side, $\times 24$. The style-branches are completely fused in most of the flowers.

PLATE 15—continued.

Artemisia campestris pycnocephala. (Drawn from fresh material from Carmel, California.)

- (6) Upper portion of the inflorescence, $\times 1$.
- (7) Head, $\times 8$.
- (8) Ray-flower, $\times 16$.
- (9) Style-branch of ray-flower, $\times 24$.
- (10) Disk-flower, $\times 16$.
- (11) Style-branch of disk-flower, $\times 24$.
- (12) Leaf, $\times 1$.

PLATE 16.

Artemisia pedatifida. (Material from western Wyoming; partly fresh, partly herbarium specimens.)

- (1) Portion of a plant, showing habit and inflorescence, $\times 1$.
- (2) Leaf, $\times 3$.
- (3) Outer bract of the involucre, $\times 16$.
- (4) Inner bract, $\times 16$.
- (5) Head, $\times 8$.
- (6) Style-branch of ray-flower, $\times 24$.
- (7) Ray-flower, $\times 16$.
- (8) Disk-flower, $\times 16$.
- (9) Style of disk-flower, showing the distinct branches, $\times 24$.
- (10) Style of disk flower, showing the branches fused along one side; $\times 24$.

Artemisia filifolia. (Drawn from fresh material from Cañon City, Colorado, the details from Willcox Flat, Arizona, 195188 UC.)

- (11) Upper portion of stem and inflorescence, $\times 1$.
- (12) Style of disk-flower, $\times 24$.
- (13) Disk-flower, $\times 16$.
- (14) Head, $\times 8$.
- (15) Style of ray-flower, $\times 24$.
- (16) Ray-flower, $\times 16$.
- (17) Outer bract of the involucre, $\times 16$.
- (18) Inner bract, $\times 16$.

PLATE 17.

Artemisia spinescens. (Material from sandy benches near Barstow, California, 126503 UC, except fig. 2.)

- (1) Branch showing spiny habit and the arrangement of the heads, $\times 1$.
- (2) Habit sketch, $\times 0.125$.
- (3) Leaves showing different degrees of lobing, $\times 3$.
- (4) Ray-flower, showing the loose pubescence of the achene and corolla; $\times 16$.
- (5) Style of ray-flower, $\times 24$.
- (6) Head, $\times 8$.
- (7) Inner bract of the involucre, $\times 16$.
- (8) Outer bract of the involucre, $\times 16$.
- (9) Disk-flower, showing the loose pubescence of the corolla; $\times 16$.
- (10) Style of disk-flower, $\times 24$.

PLATE 18.

Artemisia tridentata typica. (Drawn from fresh material from northwestern New Mexico.)

- (1) Typical inflorescence, $\times 1$.
- (2) Leafy shoot, showing tridentate leaves, $\times 1$.
- (3) Head, $\times 8$.
- (4) Outer bract of the involucre, $\times 16$.
- (5) Inner bract, $\times 16$.
- (6) Flower with scattered resin-granules, $\times 16$.
- (7) Style, $\times 24$.
- (8) Habit sketch of a common form, from a photograph of a plant at Wells, Nevada; $\times 0.04$.

EXPLANATIONS OF PLATES 1 TO 23, GENUS ARTEMISIA.

PLATE 18—continued.

- Artemisia tridentata parishi.* (Drawn from fresh material from the type locality, except the flower, which is from type collection, 54010 UC.)
- (9) Leafy shoot with entire, bidentate, and tridentate leaves, $\times 1$.
 - (10) Portion of a young inflorescence with drooping heads, $\times 1$. The heads on neighboring plants are erect, as in the usual form of *typica* (see p. 143).
 - (11) Flower showing the pubescent achene and scattered resin-granules, $\times 16$.

PLATE 19.

- Artemisia tridentata trifida.* (Drawn from fresh material from southern Wyoming.)
- (1) Branch showing the mostly trifid leaves and narrow inflorescences, $\times 1$.
 - (2) Habit sketch, $\times 0.08$.
- Artemisia tridentata nova.* (Material from Laramie Hills, Wyoming, 51760 UC.)
- (3) Branch showing the tridentate leaves and moderately narrow inflorescences, $\times 1$.
 - (4) Shoot with some leaves tridentate, others trifid, $\times 1$.
 - (5) A very narrow inflorescence, $\times 1$.
 - (6) Head, $\times 8$.
 - (7) Outer bract of the involucre, $\times 16$.
 - (8) Inner bract, $\times 16$.
 - (9) Flower with scattered resin-granules, $\times 16$.
 - (10) Style, $\times 24$.

PLATE 20.

- Artemisia tridentata arbuscula.*
- (1) Leafy shoot with 2 inflorescences, $\times 1$. (Material from eastern Oregon, 175216 UC.)
 - (2) Leafy shoot showing the more deeply lobed leaves of minor variation 10 (p. 140), $\times 1$. (Material from near Donner Pass, Placer County, California, 202223 UC.)
- Artemisia tridentata rothrockii.*
- (3) Stem with narrow inflorescence, $\times 1$. (Material from Tioga Pass, California.)
 - (4) Leafy shoot, $\times 1$. (Material from Little Cottonwood Creek, California.)
 - (5) Stem with typical branching inflorescence, $\times 1$. (From the same plant as fig. 4.)

PLATE 21.

- Artemisia cana.* (Drawn from fresh material from Bosler, Wyoming.)
- (1) Branch with leafy shoots, $\times 1$.
 - (2) Inflorescence, $\times 1$.

PLATE 21—continued.

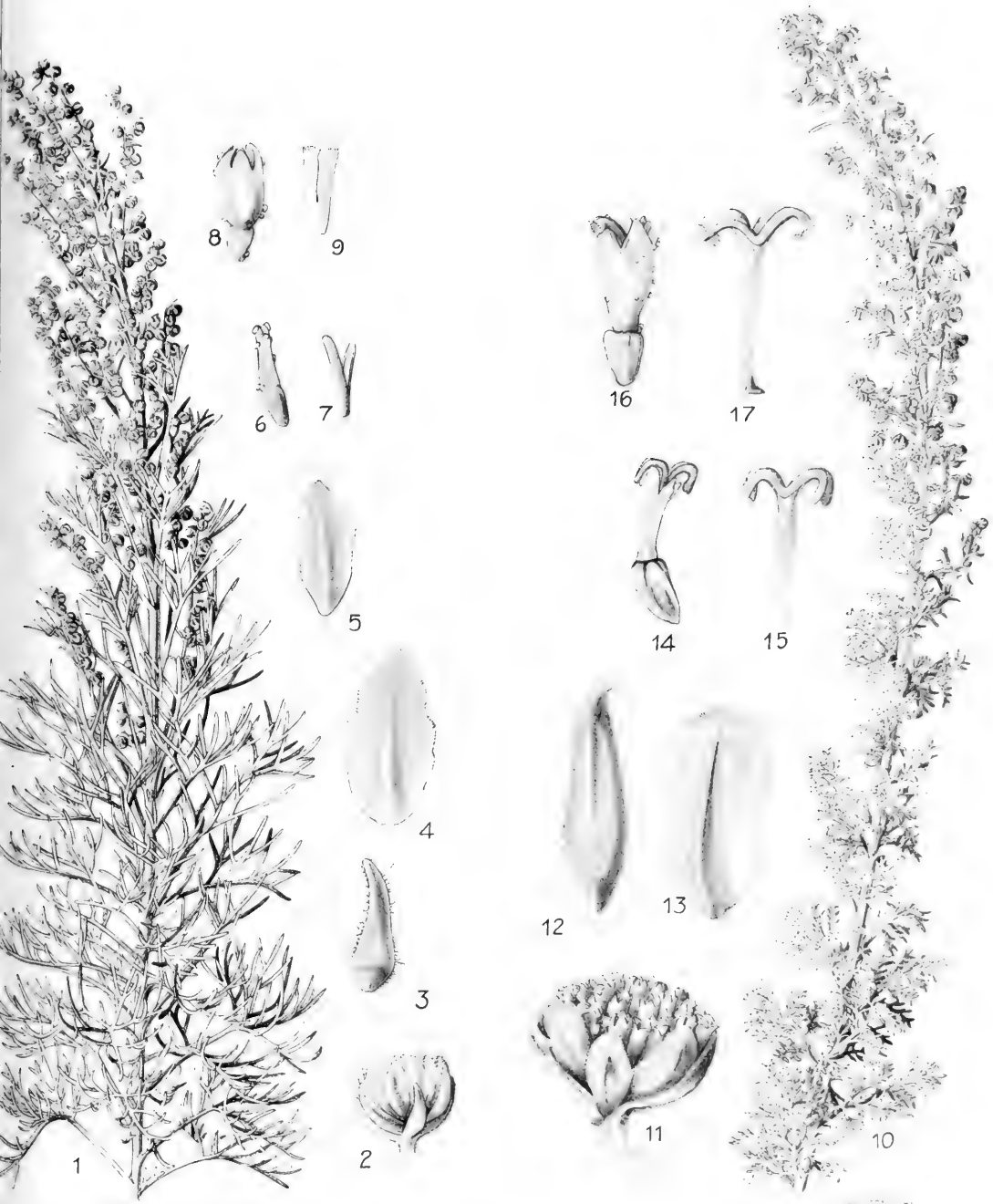
- (3) Inflorescence showing more elongated branches, $\times 1$.
- (4) Shoot with leaves of maximum width, $\times 1$.
- (5) Head, $\times 8$.
- (6) Middle bract of the involucre, $\times 16$.
- (7) Inner bract, $\times 16$.
- (8) Flower, $\times 16$.
- (9) Style, $\times 24$.
- (10) Habit sketch, $\times 0.03$.

PLATE 22.

- Artemisia rigida.* (Drawn from fresh material and photographs from northeastern Oregon.)
- (1) Portion of plant with inflorescences, $\times 1$.
 - (2) Head, $\times 8$.
 - (3) Bract from the base of the involucre, $\times 16$.
 - (4) Inner bract, $\times 16$.
 - (5) Flower, $\times 16$.
 - (6) Style, $\times 24$.
 - (7) Three leaves, showing variation in lobing; $\times 3$.
 - (8) Leaf of the inflorescence, $\times 3$.
 - (9) Habit sketch of entire plant, $\times 0.125$.
- Artemisia pygmaea.* (Material from Pioche, Nevada, 179478 UC.)
- (10) Twigs, showing the inflorescence; $\times 1$.
 - (11) Leaves, $\times 3$.
 - (12) Habit sketch, apparently of a plant growing on a slope, since the roots are horizontal; $\times 0.17$.
 - (13) Inner bract of the involucre, $\times 16$.
 - (14) Bract from outer portion of the involucre, $\times 16$.
 - (15) Flower, $\times 16$.
 - (16) Style, $\times 24$.
 - (17) Head, $\times 8$.

PLATE 23.

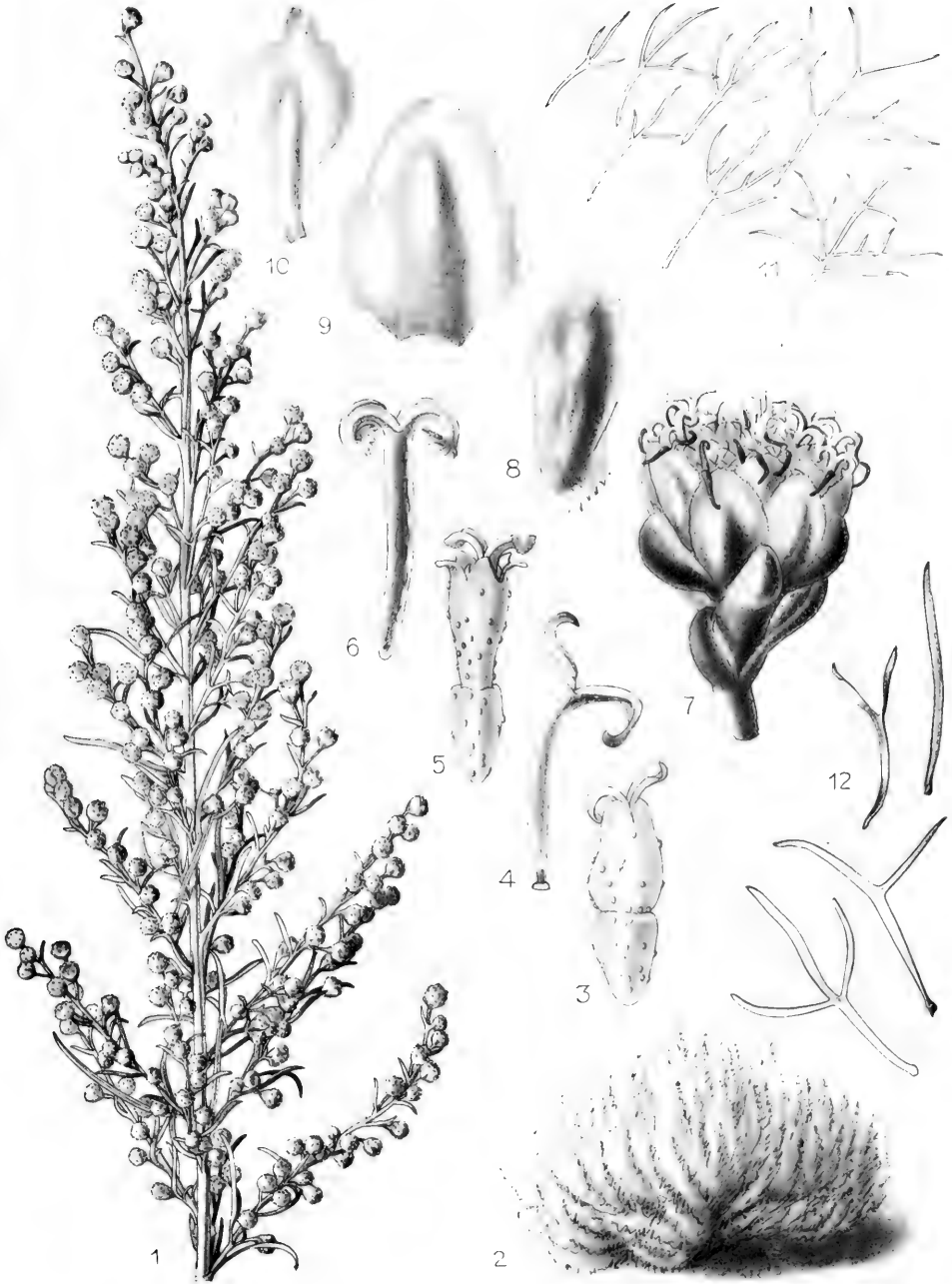
- Artemisia palmeri.* (Drawn from fresh material from La Jolla, California.)
- (1) Portion of the inflorescence showing also a few of the entire upper leaves, $\times 1$.
 - (2) A common type of leaf with five lobes, $\times 1$.
 - (3) An upper leaf with three lobes, $\times 1$.
 - (4) An upper leaf with a single lateral lobe, transitional to the simple leaves of the inflorescence; $\times 1$.
 - (5) Head with subtending bracts, $\times 8$.
 - (6) Outer bract of the involucre, $\times 16$.
 - (7) Inner bract, $\times 16$.
 - (8) Disk-flower showing scattered resin-glands on the achene and corolla, $\times 16$. The ray-flowers are wanting in this species.
 - (9) Style, $\times 24$.



Powell del.

Artemisia abrotanum, figs. 1 to 9.

Artemisia pontica, figs. 10 to 17.



Ruth J. Powell del.

Artemisia californica.



Artemisia norvegica heterophylla, figs. 1 and 2.
Artemisia norvegica globularia, figs. 3 and 4.

Artemisia norvegica glomerata, figs. 5 and 6.
Artemisia norvegica saxatilis, figs. 7 to 13.



Ruth J. Powell del.

Artemisia parryi, figs. 1 to 7.

Artemisia senjavinensis, figs. 8 to 13.

Artemisia macrobotrys, figs. 14 to 18.



Ruth J. Pocrell del.

Artemisia stelleriana, figs. 1 to 7.

Artemisia alaskana, figs. 8 to 13.



Artemisia franserioides, figs. 1 to 11.

Artemisia vulgaris serrata, fig. 12.

H. J. Powell del.



J. Powell del.

Artemisia vulgaris tilesi, figs. 1 and 2.

Artemisia vulgaris typica, figs. 3 to 14.



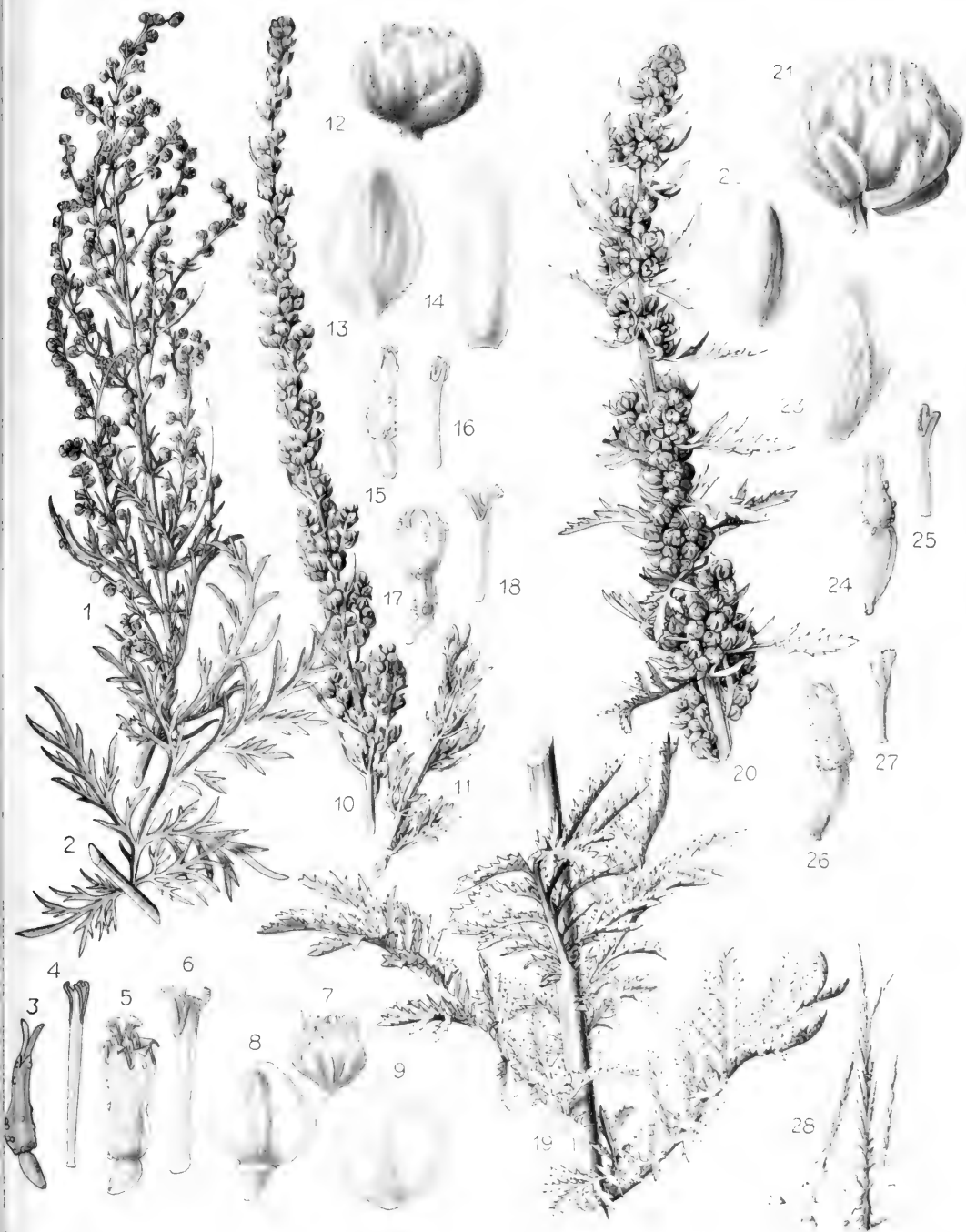
Ruth J. Powell del.

Artemisia vulgaris heterophylla.



By J. Powell del.

Artemisia vulgaris gnaphalodes, fig. 1. *Artemisia vulgaris wrightii*, figs. 2 to 9. *Artemisia bigelovi*, figs. 10 to 17.



Ruth J. Powell del.

Artemisia annua, figs. 1 to 9.

Artemisia klotzschiana, figs. 10 to 18.

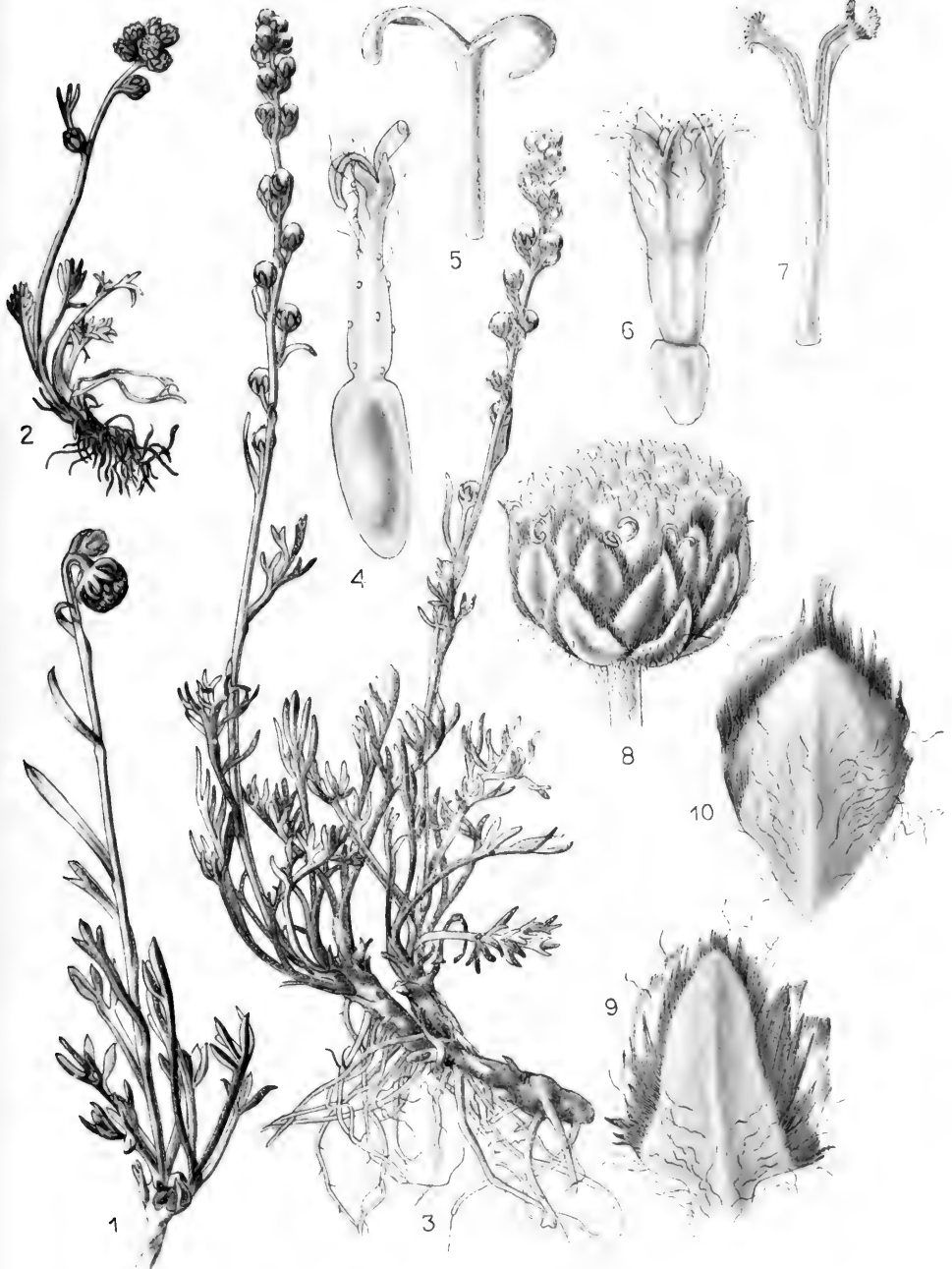
Artemisia biennis, figs. 19 to 28.



Artemisia absinthium, figs. 1 to 8.

Artemisia frigida, figs. 9 to 18.

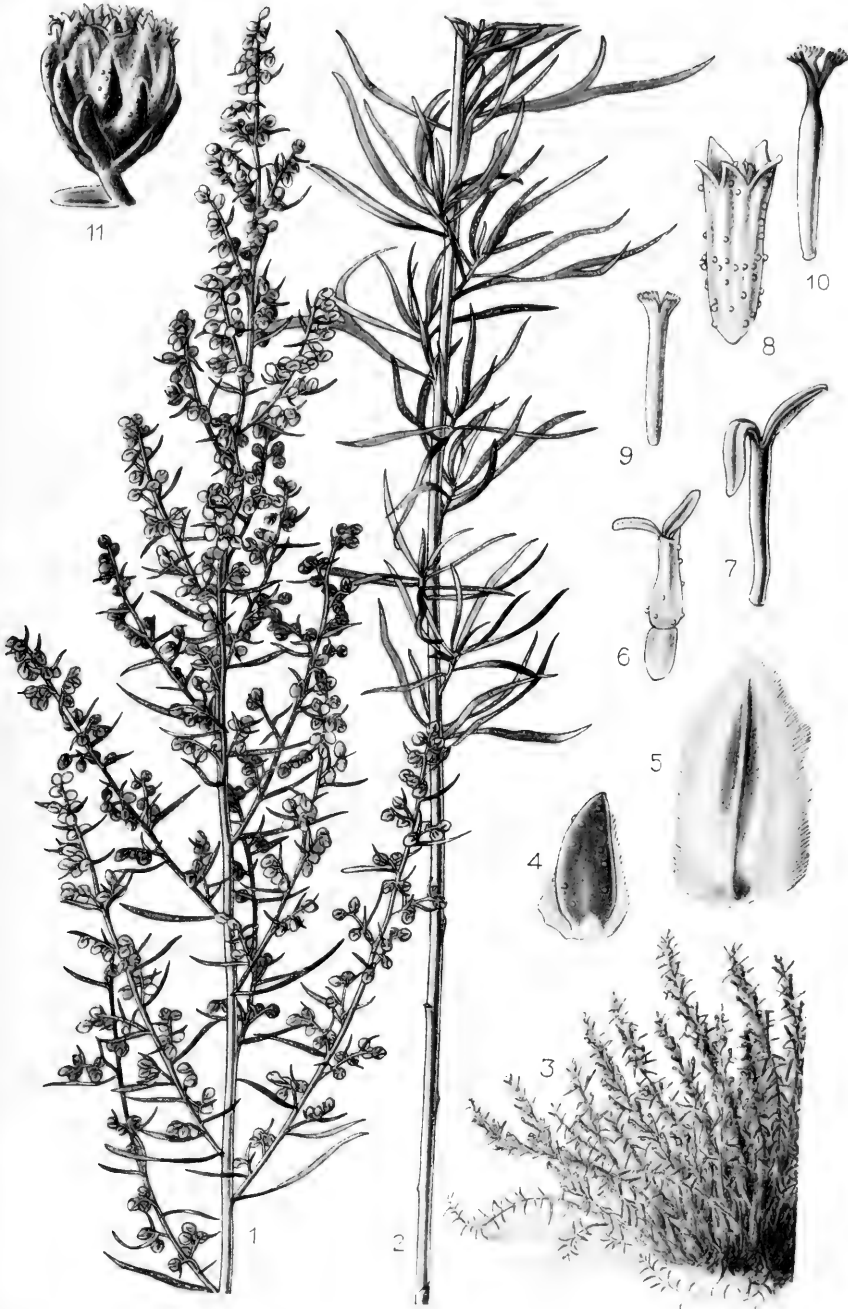
Parell del.



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Artemisia pattersoni, fig. 1.

Artemisia scopulorum, figs. 2 to 10.



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Artemisia dracunculus typica.



Artemisia campestris typicala, fig. 1.

Artemisia campestris pacifica, figs. 2 to 11.

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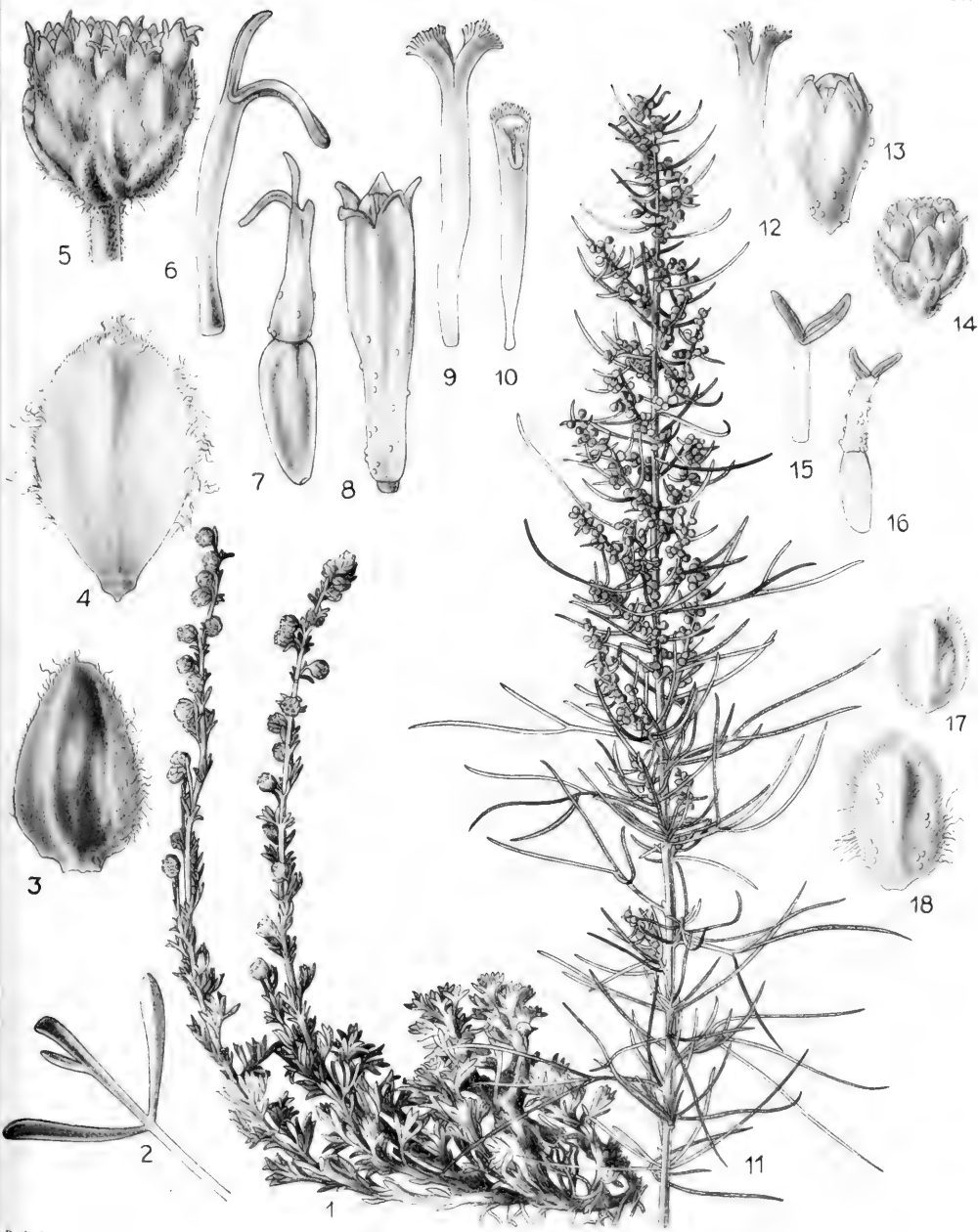


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Artemisia campestris borealis, figs. 1 to 4.

Artemisia campestris spithamea, fig. 5.

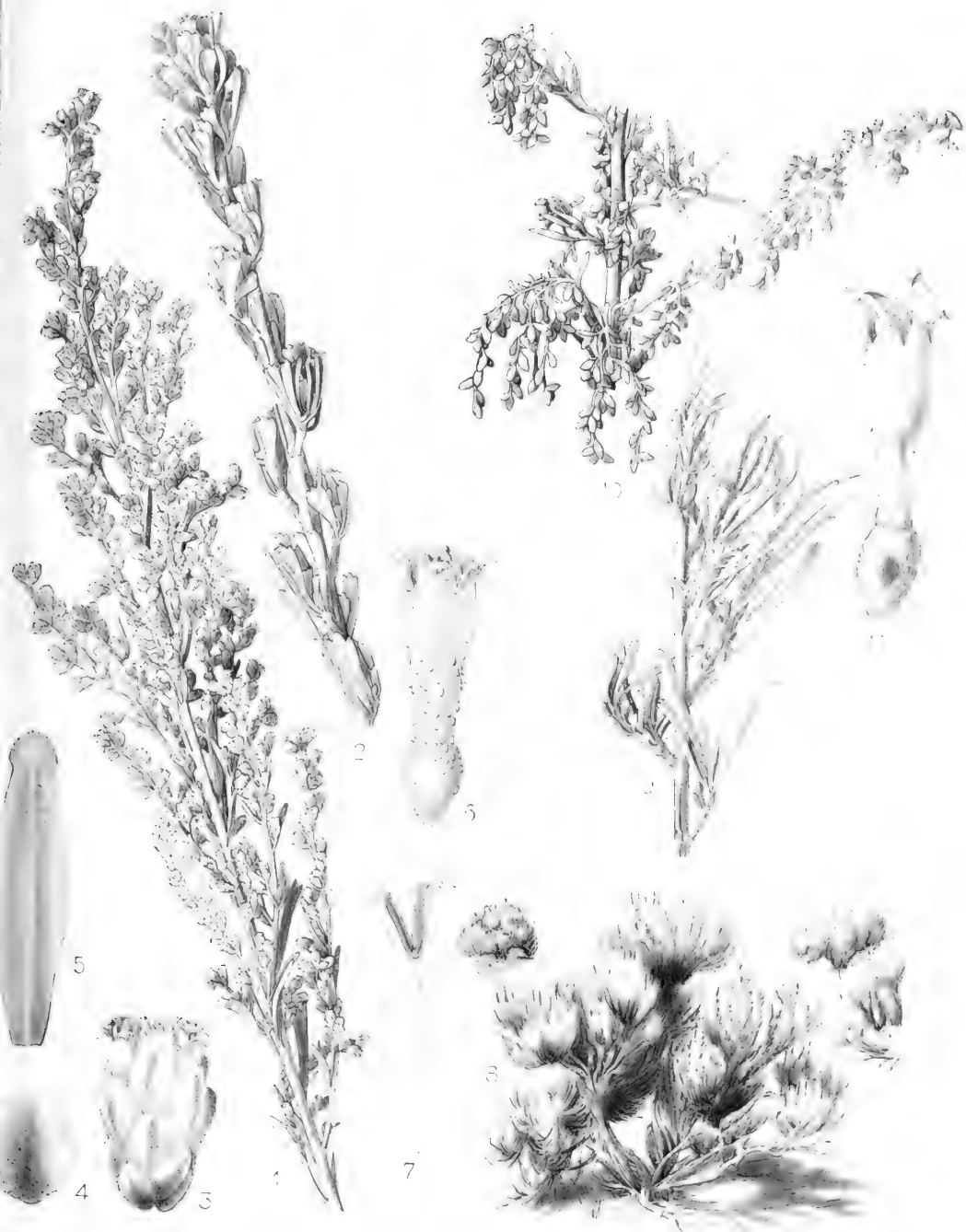
Artemisia campestris pycnocephala, figs. 6 to 12.



Artemisia pedatifida, figs. 1 to 10.

Artemisia filifolia, figs. 11 to 18.

Ruth J. Powell del.



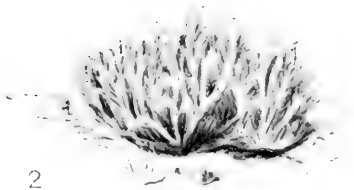
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Artemisia tridentata typicala, figs. 1 to 8.

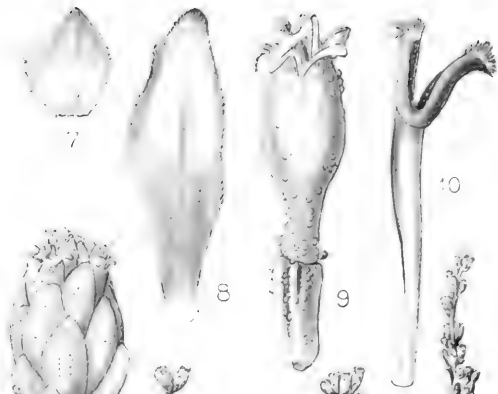
Artemisia tridentata parishi, figs. 9 to 11.



1



2



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8

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3

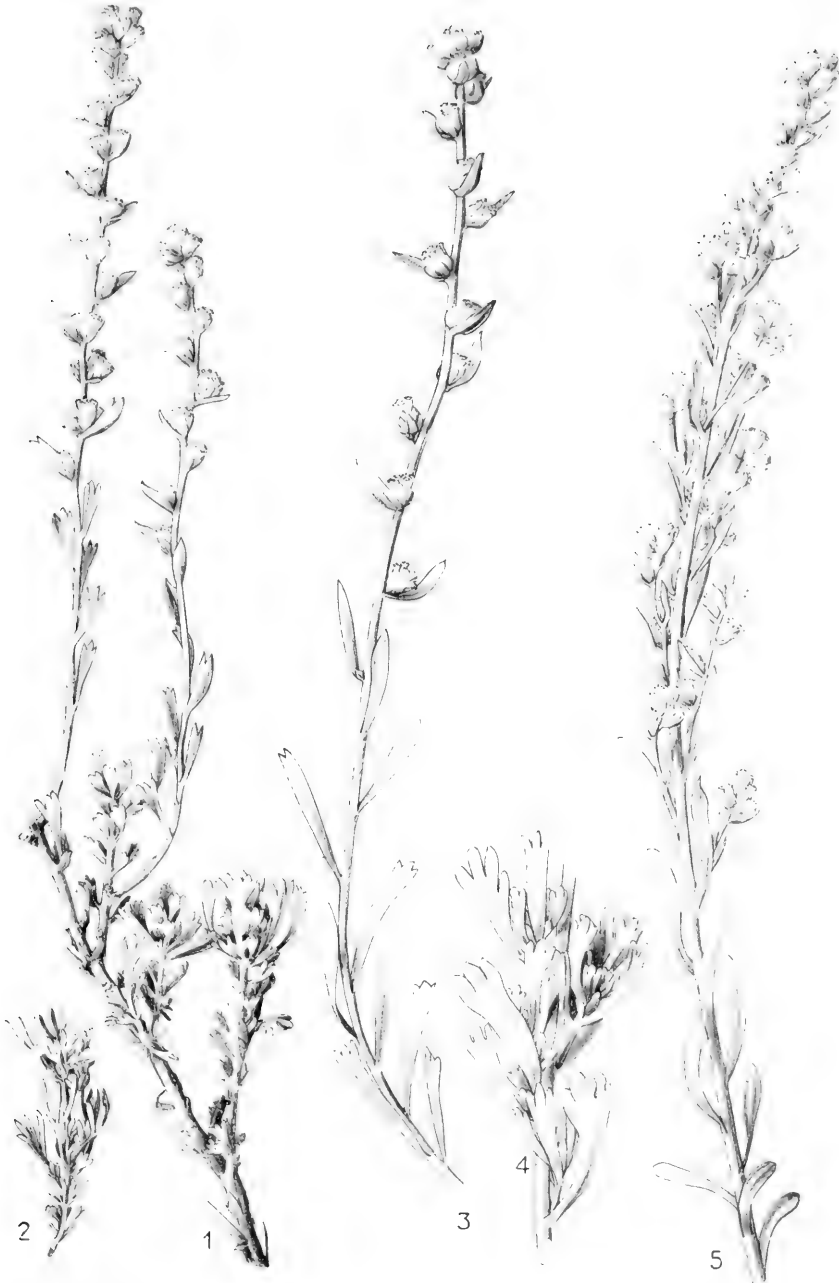
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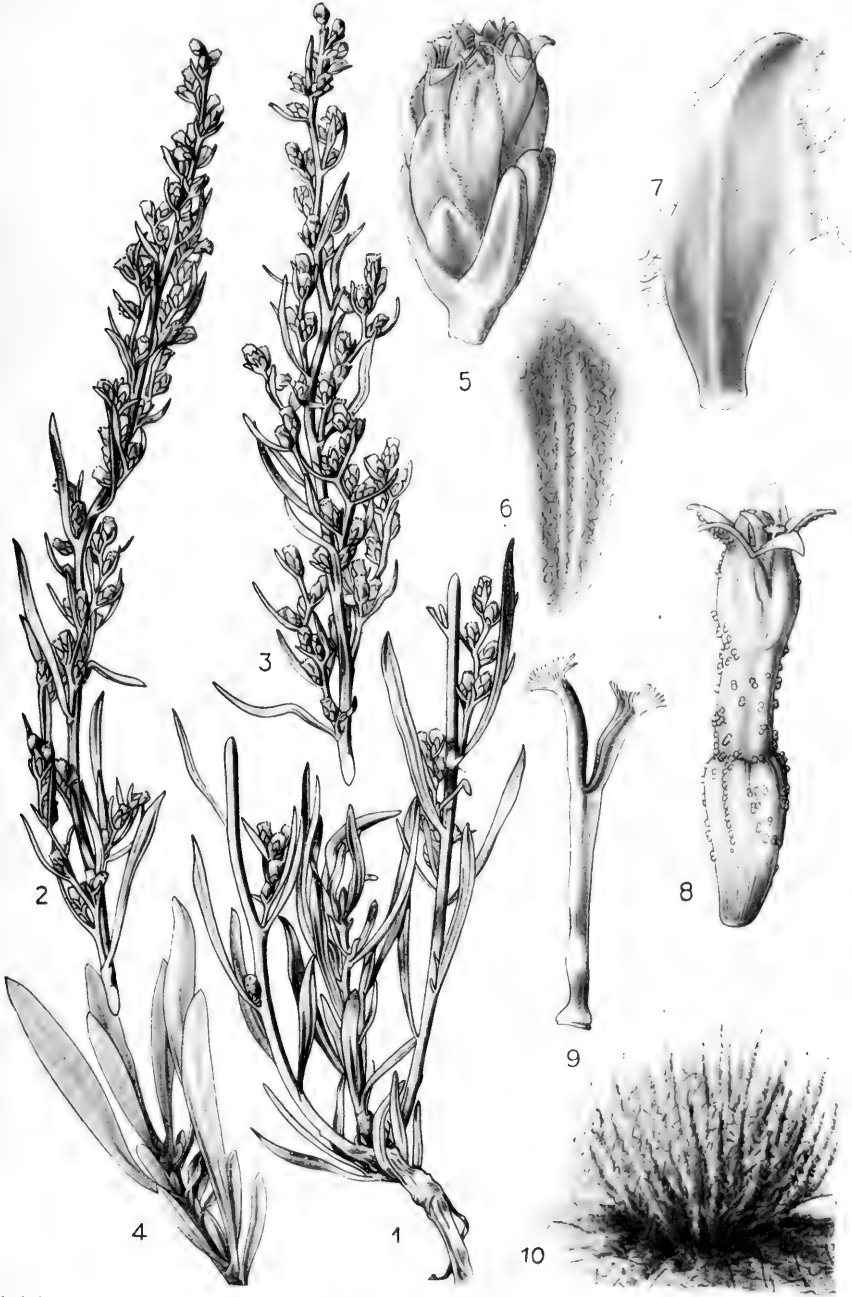
Artemisia tridentata trifida, figs. 1 and 2.

Artemisia tridentata nova, figs. 3 to 10.



Ruth J. Powell del.
Artemisia tridentata arbuscula, figs. 1 and 2.

Artemisia tridentata rothrockii, figs. 3 to 5.



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Artemisia cana.



Artemisia rigida, figs. 1 to 9.

Artemisia pygmaea, figs. 10 to 17.



with J. Powell det.

Artemisia palmeri.

GENUS CHRYSOTHAMNUS.

HISTORY, LIMITS, AND RELATIONSHIPS.

The genus *Chrysothamnus* is a member of the *Astereae* or aster tribe of the *Compositae* and is closely related to *Haplopappus*. Within the limits of the genus as here set, there have been described a total of 88 forms, nearly all of which have been given the rank of species at one time or another. These are now organized into 4 sections, 12 species, and 40 subspecies. Since it is well known that generic lines are difficult to draw in this group of the *Compositae*, it is not surprising that the species have been assigned at various times to no fewer than 6 different genera. Although *Chrysothamnus* was proposed by Nuttall in 1840, it was not until within the last 25 years that there has been an approximate agreement among systematists as to its proper limits. Even at the present day there is a strong tendency to unite the section *Punctati* of this treatise with *Ericameria*, a section or subgenus of *Haplopappus*. On the other hand, however, in only three instances have species of other genera been referred to this one, and there is little doubt that the group as now accepted is a natural one.

The first species of *Chrysothamnus* to receive recognition were described by Pursh as members of the South African *Chrysocoma* (Pursh, Fl. Am. Sept. 2:517, 1814), a genus well separated from the one now under consideration by its nearly globose, solitary heads, the bracts of which are foliaceous and not at all vertically ranked, and by its compressed achenes. This usage was followed by Nuttall four years later in his *Genera of North American Plants*, where two species are described. In 1834 Hooker (Fl. Bor. Am. 2:24) described a species under the name *Crinitaria viscidiflora*, but the true *Crinitarias* are species of *Aster* and were so accepted by Bentham and Hooker in their *Genera Plantarum* (2:274, 1873), in which work *viscidiflora* is referred to *Chrysothamnus* (p. 256).

It was in 1836 that DeCandolle established for these plants a name under which they were destined to be known more or less continuously for over half a century. This was *Bigelovia* (DeCandolle, Prodr. 5:329, 1836), a name which, as Greene has pointed out, had at least five chances to revert because of its having been previously used for other genera, and what is still worse, a name that was made to include species so widely separated phylogenetically that it can not possibly be retained for all of them. Fortunately for *Chrysothamnus*, DeCandolle took as the type of his *Bigelovia* not one of the West American shrubs now under consideration, but the decidedly herbaceous southeastern *B. nudata*, or *Chondrophora nudata* as it is sometimes known. The true *Bigelovias* as represented by *nudata*, differ from all species of *Chrysothamnus* not only in their very different habit, but also in a number of other characters, which may be contrasted as follows:

Bigelovia (Chondrophora).
Perennial herbs.
Leaves chiefly basal, the few upper ones different in shape from the lower.
Involucral bracts spirally imbricated, with no tendency to form vertical rows.
Flowers 3 or 4.
Receptacle with central cusp.
Corolla-lobes very long, strongly recurved.
Achenes short, turbinate.
Style-branch abruptly narrowed to the appendage.

Chrysothamnus.
Shrubs.
Leaves equitably distributed, all alike.
Involucral bracts imbricated in vertical rows, or at least with an obvious tendency towards a vertical alignment.
Flowers 5 to 20 (occasionally only 4).
Receptacle without cusp.
Corolla-lobes shorter, seldom much recurved.
Achenes longer, narrower.
Style branch tapering to the appendage.

Every attempt should be made to conserve genera and generic limits after they have been in use for long periods of time. It would therefore seem desirable to use *Bigelovia* in a sense so inclusive as to embrace both of the above groups. This, however, would

convey an erroneous idea as to their relationships, for it is quite certain that the true *Bigelovias* and the *Chrysothamni* are not descendants of the same immediate stock and that in each case there are more closely related genera to be considered. Some of these, such as *Petradoria*, for example, may indeed come squarely between the two. The only possible connection between *Bigelovia* and *Chrysothamnus* seems to lie in the only half-shrubby *C. gramineus*. In addition to differing from *Bigelovia* in nearly all of the characters just enumerated, this species has exceptionally long achenes even for a *Chrysothamnus*. If connected with the former genus at all, the relation would need to be sought through *Petradoria*. Although *Bigelovia* was in use for more than 50 years, and even to the present is occasionally so used as to include *Chrysothamnus*, the limits set for the genus have been constantly moved about. Thus Gray, in 1873, enlarged it to include the section *Haplodiscus* (Proc. Am. Acad. 8:638), a section now belonging to *Haplopappus* section *Isocoma*, and in 1884 the same authority still further extended the boundaries to include a portion of what now passes as *Haplopappus* section *Ericameria* (Gray, Syn. Fl. 1:141, 1884). This final extension left, as the only mark of distinction between *Haplopappus* and *Bigelovia*, the presence of ray-flowers in the former and their absence in the latter. This was obviously an artificial separation, as is evidenced by certain species, such as *H. monactis*, *H. arborescens*, etc., in which the ray-flowers are either present or absent even on the same plant. What now seems to be a more logical arrangement is given farther on, the only object in mentioning these matters here being to call attention to the diverse conception of the limits set at various times for *Bigelovia*.

Chrysothamnus was established as a genus by Nuttall in 1840 (Trans. Am. Phil. Soc. II, 7:323) with *C. pumilus* as the type species. Chronologically it therefore follows De Candolle's *Bigelovia* by four years. This in turn was succeeded two years later by Torrey and Gray's *Flora*, in which *Bigelovia* was restricted to the genuine herbaceous species, while the species of *Chrysothamnus* were referred to *Linosyris*, a genus previously considered as belonging only to the Old World. This usage was continued by Gray in the *Botany of the Mexican Boundary Survey*, by D. C. Eaton in the *Botany of the King Expedition*, and in a few other papers, until it was pointed out by Bentham and Hooker (*Genera Plantarum* 2:255, 274, 1873) that *Chrysothamnus* was not of close affinity with true *Linosyris*, the latter being better considered as a part of *Aster*. The former was thus reestablished as a genus and extended to include the earlier *Bigelovia* of De Candolle. Gray readily accepted this arrangement (Proc. Am. Acad. 8:637, 1873), except that he asserted the priority of the name *Bigelovia*, under which he renamed all of the species. *Bigelovia* then came into general use. It was adopted by Bentham and Hooker (*Genera Plantarum* 2:536, 1876) and was used by Gray in the *Synoptical Flora* and elsewhere.

It thus transpired that between the spurious claims of *Linosyris* on the one hand and of *Bigelovia* on the other, the generic name *Chrysothamnus* received but scant attention until it was revived by Greene in 1895 (*Erythea* 3:92). Not only did Greene point out the dubious status of the name *Bigelovia*, but he stoutly defended Nuttall's segregation of *Chrysothamnus* from the herbaceous species which De Candolle took as the type of that genus, without, however, hitting upon some of the more important distinctions as above set forth. Greene's conception of the genus was adopted by Nelson in his paper, "Some Rocky Mountain *Chrysothamni*" (*Bot. Gaz.* 28:369 to 377, 1899), and, with some slight modifications, by nearly all of the writers of recent manuals in which, however, the number of recognized species has been steadily increasing. It is also the concept adopted in the present paper, except that *C. bloomeri* (Gray) Greene is now referred to *Haplopappus* and that two species here included were assigned to *Ericameria* by Greene. It was characteristic of this author that, although he possessed a keen sense of natural grouping, he seldom defined groups with any degree of precision. In the present instance no generic diagnosis was given and, aside from the comparison with *Chondro-*

phora and a few incidental remarks, no discussion of relationships was entered into and no differences were pointed out between *Chrysothamnus* and the several species of *Haplopappus*, with which it seems to come into very close phylogenetic connection.

While the relation of *Chrysothamnus* to *Bigelovia* has received much attention, its possible connection with *Haplopappus* has been scarcely more than suggested, and this mostly through the transfer of species from one to the other genus without critical comment. This is unfortunate, for the origin of the one has presumably been through the other, that is, *Haplopappus* probably includes the nearest representatives of the ancestral type of *Chrysothamnus*. Indeed, the two are so close at some points that, if it were not for the almost universal recognition of the latter during the last twenty-five years under one name or another, their complete union into one genus might be seriously considered. It seems unwise, however, to disturb generic lines as long as the present arrangement does no violence to the facts. Any other course would open the way for innumerable generic combinations and segregations, each based upon individual judgment.

Although the two genera now under consideration closely approach each other in some respects, there is nevertheless a good basis, in addition to usage, for recognizing them as distinct. *Chrysothamnus* differs from all species of *Haplopappus* in its consistently narrower heads and, what is of greater importance, a decided tendency of the bracts of the involucre to fall into vertical rows. The difference between this arrangement of the bracts and the regularly imbricate arrangement encountered in the latter genus is perhaps comparable to the difference between opposite and alternate leaves, but the bracts are the modified leaves of a highly specialized structure, the involucre, and hence any variation in their relative positions is of profound significance. In some species, such as *C. pulchellus*, the vertical rows are very distinct, in others, especially among the *Parryani*, the alignment is sometimes quite obscure. It is believed, however, that this is of significance as indicating an ancestral trait, even when there is scarcely more than the tendency left. In fact, it would be quite remarkable if the sharp vertical arrangement should be strictly adhered to in any group of forms as large as this, when the various influences that affect growth and development are taken into account. Another distinguishing character, doubtless associated with the vertical arrangement of the bracts, is the usually well-developed keel of these structures. In the more typical species the bracts are rather sharply folded longitudinally along the midrib, which is thus emphasized to form a distinctly sharp edge or keel. This is most noticeable in those species in which the vertical rows are also plainly marked, while it may be quite obscure when the rows themselves are not easily made out.

Chrysothamnus is thus seen to differ from *Haplopappus*, its nearest relative, in the narrow, cylindraceous heads, in the vertical arrangement of the involucre bracts, and in the more strongly developed midrib of these bracts. However, in all of these characters there is a shading-off in certain species, so that the two genera are not sharply defined from each other. The contact between them is perhaps closest through the section *Ericameria* of *Haplopappus*, of which certain members, such as *H. brachylepis* and *Ericameria diffusa*, approach species of *Chrysothamnus* section *Punctati* very closely. These two groups meet in their geographic distribution, possess a similar habit, and in both cases the foliage is marked with impressed resin-dots. This easily determined presence of resin-dots has, in fact, led to the union of the *Punctati* with *Ericameria* (that is, with *Haplopappus* section *Ericameria*) in most accounts, but this strictly vegetative character, which has probably been independently developed in the two groups and is associated with their xerophytic habitat, can not be considered as of importance when compared with the shape of the heads and the shape and arrangement of the involucre bracts, by which characters the *Punctati* are plainly to be associated with *Chrysothamnus*. This section is closely related also through *C. albidus*, which, although of

another section and universally admitted as a *Chrysothamnus*, has resin-dots almost as prominent as those of the *Punctati* (compare enlarged leaves of plates 24 and 28, and fig. 24).

A different point of contact between the two genera under consideration was suggested by Gray (Proc. Am. Acad. 8:641, 1873) and the suggestion was followed up by Greene (Erythea 3:114, 1895). According to these authorities, there is scarcely any difference between *Chrysothamnus bolanderi* and *Haplopappus discoideus*. It must be admitted that the superficial similarity is very marked and that the peculiar dense tomentum of the twigs is suggestive of a genetic affinity. But the heads of the former are much narrower than those of the latter, the involucre is decidedly narrowed at the base, and the bracts are carinate and positively arranged in vertical rows, although these rows are somewhat obscure. In the *Haplopappus* the bracts are much more foliaceous, flatter, wider, more loosely arranged, not carinate, and with not even a suggestion

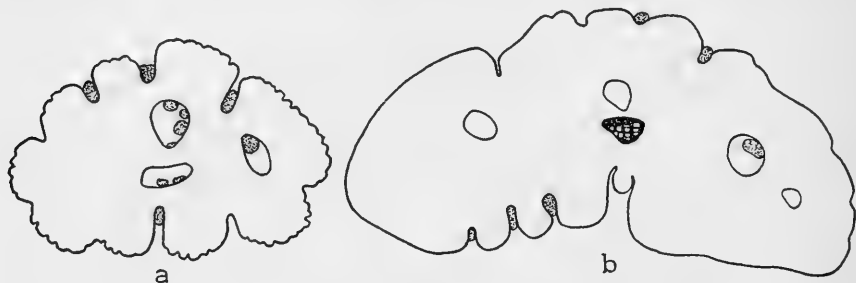


FIG. 24.—Leaves of *Chrysothamnus teretifolius* and *C. albidus*, to illustrate resin pits: a, *C. teretifolius*; b, *C. albidus*. Both $\times 50$.

of a vertical arrangement. It seems that here again we have, not a case of close phylogenetic relationship, but rather one of superficial resemblance between plastic groups that have come under the same environmental influence. It seems quite likely that the two botanists whose opinion has just been stated, were misled through errors in identification. At the National Herbarium, where Greene did his work, there are only three sheets labeled *C. bolanderi* and two of these are plainly *Haplopappus discoideus*. The same error occurs in the Greene Herbarium and certain early determinations at the Gray Herbarium were similarly erroneous.

Chrysothamnus is thus seen to be a fairly homogeneous assemblage of species; to be most closely related to *Haplopappus* section *Ericameria* (or possibly section *Macronema*); and to bear a less direct relation to *Chondrophora*, this latter consisting of the typical species of De Candolle's *Bigelovia*.

DIVISION INTO SECTIONS.

The first attempt at an arrangement of the species into natural sections was by Gray in 1873 (Proc. Am. Acad. 8:638). This was under the generic name of *Bigelovia*, which was then so extended as to include many species since referred elsewhere. Those belonging to what now constitutes the genus *Chrysothamnus* were embraced in two sections, namely, *Chrysothamnopsis*, including three species, all of which now form part of *C. parryi*, and *Chrysothamnus*, composed of 8 species belonging to the sections *Punctati*, *Typici*, *Pulchelli*, and *Nauseosi* of the present treatise. The primary division under this second section was based chiefly upon the pubescence of the achenes, a character

so untrustworthy as to render the arrangement decidedly artificial. With the constant increase in the number of species and of our knowledge concerning them, Gray's two sections have become less and less satisfactory. Since the proposed sectional names are not applicable under *Chrysothamnus*, an entirely new classification was advanced by Hall in 1919 (Univ. Calif. Publ. Bot. 7:160). According to this latest arrangement, the numerous forms are assembled into five natural groups, each of which is given a formal section name. Four of these sections are adopted in the present paper, the fifth, or *Parryi*, being now united with the *Nauseosi*, and the sequence is modified to bring the more primitive sections at the beginning of the list. They are defined as follows:

SECTION 1. *Punctati*. Herbage resinous-punctate, the dots plainly showing as definite depressions; twigs brittle, glabrous, the bark at first green but soon changing to brown; leaves terete; heads in open panicles; bracts of the involucre in vertical rows which are fairly well defined, moderately keeled, obtuse and pointless, chartaceous, either with or without an obscurely thickened greenish subapical spot; flowers 5 to 7; style-appendage either shorter or longer than the stigmatic portion; achenes slightly angled; densely pubescent. Species: *teretifolius*, *paniculatus*.

SECTION 2. *Typici*. Herbage not resinous-punctate (somewhat punctate in one species); twigs brittle, glabrous or only puberulent, the bark usually white; leaves oblanceolate to narrowly linear but not terete; heads in rounded or flat-topped cymes, or solitary and subracemose only in *C. gramineus*; bracts of the involucre in poorly defined vertical rows, not strongly keeled, obtuse to acuminate but none continued into slender herbaceous tips, more or less chartaceous, not rarely some of the outer with firmer and indistinctly greenish apex; flowers 5 to 7; style-appendage either shorter than or much exceeding the stigmatic portion; achenes slightly angled, pubescent or in two species glabrous and 10-striate. Species: *albidus*, *greenei*, *gramineus*, *vaseyi*, *viscidiflorus*.

SECTION 3. *Pulchelli*. Herbage not resinous-punctate; twigs brittle, glabrous or puberulent, the bark greenish-white; leaves oblanceolate to revolute filiform; heads in rounded cymes; bracts of the involucre in very sharply defined vertical ranks, strongly keeled, attenuate but never to an herbaceous tip, firmly chartaceous throughout; flowers about 5; style-appendage shorter than or only slightly exceeding the stigmatic portion; achenes nearly prismatic, not striate, glabrous or nearly so. Species: *pulchellus*, *depressus*.

SECTION 4. *Nauseosi*. Herbage not resinous-punctate; twigs flexible, densely covered with a pannose tomentum, this more or less infiltrated with a resinous substance; leaves lanceolate or oblanceolate to linear-filiform but never truly terete, sometimes reduced to scales; heads in small panicles, racemes, or spikes or reduced to flat-topped, rounded, or more elongated cymes or thyrses; bracts of the involucre in fairly well defined vertical ranks, or these obscure, moderately to strongly keeled, obtuse to acute, never with greenish apex but prolonged in one species into a slender tip, thin-chartaceous throughout; flowers usually 5 to 15 but sometimes as many as 20; style-appendage very slender and long exerted, nearly equaling or exceeding the stigmatic portion; achenes slightly angled, pubescent or glabrous, not striate. Species: *pyramidalis*, *parryi*, *nauseosus*.

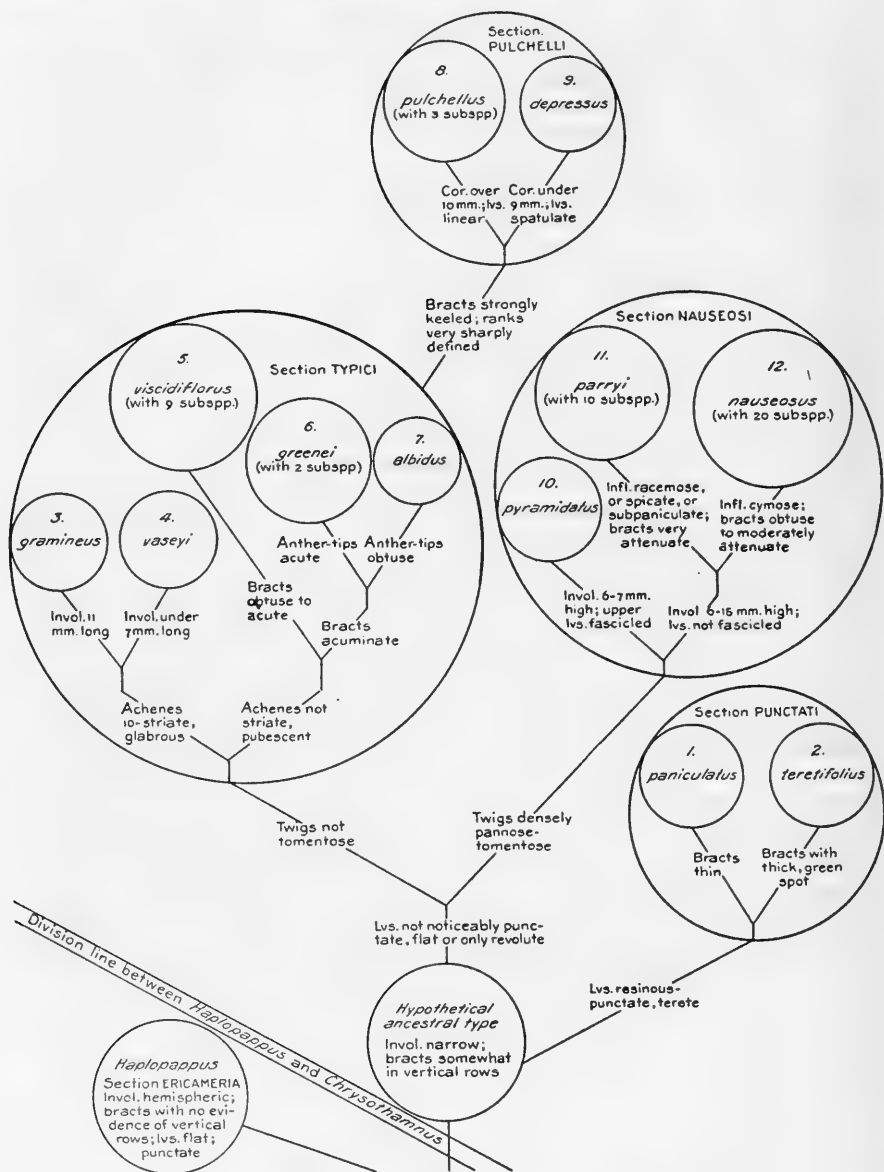


FIG. 25.—Phylogenetic chart of the sections and species of *Chrysothamnus*.

ORIGIN AND DEVELOPMENT OF THE SECTIONS.

The relationships between the various species will be taken up in detail in connection with the descriptive accounts of each, as will also the relationships between the subspecies. However, it seems desirable here to sketch the lines of evolutionary development, at least as far as this concerns the principal species and the sections, and to present the results in diagrammatic form. Although the general laws of phylogeny, as far as they are understood, form the basis of this discussion, it does not follow that the results represent more than the probable relationships. It is believed, however, that this attempt to throw the species into natural evolutionary groups will be of service, especially if the doubtful cases are not definitely placed until more is known concerning them.

It has been shown that the contact of *Chrysothamnus* with its most closely related genus, that is, *Haplopappus*, is apparently best represented by the *Punctati*. This does not necessitate the assumption that the other sections have arisen through this one. Such a hypothesis would lead to the conclusion that the character of impressed-punctate foliage was once developed and then lost. While this is possible, it seems improbable. More logical is the assumption that the *Chrysothamnus* stock was developed from an ancestral group close to *Haplopappus* section *Ericameria* but without the resin-dots of that group. The development first concerned itself with modifications of the involucre until this structure, or rather this assemblage of structures, was different from anything in *Ericameria*, especially in its subcylindric shape and in the arrangement of the bracts. It was perhaps from such a group that the *Punctati* were derived, their vegetative changes, especially the formation of resin-dots, paralleling to some extent those going on in *Ericameria*. In some such manner were these two sections evolved, sections so alike in superficial appearance as often to be confused with each other, yet so unlike in origin, indicated by difference in fundamental characters, as now to be assigned to different genera. This is apparently a case of parallel variation in two groups not widely separated phylogenetically. The connection with *Ericameria* is best seen by comparing *Chrysothamnus paniculatus* with *Ericameria diffusa*. The *Punctati* are only two in number, both shrubs of the Southwest and very closely related to each other.

Without running counter to the laws of phylogeny, it may next be assumed that the hypothetical group already mentioned gave rise somewhat farther up to the *Typici*. It seems reasonable that this section is more primitive than any of the three remaining ones, in view of the fact that each of these exhibits some striking peculiarity not possessed by the *Typici* and indicative in each case of a higher order of development. Taking then the *Typici* as the central section, we find its most characteristic representative to be *C. viscidiflorus*. This is a very widely distributed species, which has itself undergone modifications in several directions, as is indicated by the nine subspecies and numerous forms discussed in detail farther on. But aside from its success as a biologic type, it possesses no characters indicative of an extreme evolutionary development. The involucre gives positive evidence of vertical rows in the arrangement of its bracts, but these rows are not very sharply defined; the twigs are devoid of any highly specialized pubescence; and neither bracts nor style-appendages are unusually elongated. It has a very intimate relative in *C. greenii*, but the other three members of the section, *gramineus*, *vaseyi*, and *albidus*, are less closely connected.

The *Pulchelli* are so much like the *Typici* that there can be no doubt as to their close phylogenetic origin. The habit, the nature of the wood and bark, the type of inflorescence, and the relative length of appendage and stigmatic portion of the style-branch are almost identical. But in the *Pulchelli* the carination of the bracts and their vertical arrangement is carried to an extreme not otherwise known in the genus, and the long, glabrous but not striate achenes are very different from those of the *Typici*. The two species comprising this section are very closely related to each other.

In order to reach the *Nauseosi* it is now necessary to leave the line which culminates in the highly modified *Pulchelli* and pick up the evolutionary thread somewhere below the *Typici*. This is necessitated by the appearance in the *Nauseosi* of a seemingly superficial but really very important character, namely, the remarkably pannose tomentum of the twigs. To one familiar with this matted, felt-like covering so closely applied to the bark, it represents a character of greater importance than is usually found in the pubescence. Since this indicates an evolutionary stage not reached by the *Pulchelli*, and since these on the other hand present highly specialized characters not found in the *Nauseosi*, the conclusion follows that neither has been derived from the other. The latter is therefore indicated as branching off from near the *Typici*. It includes *C. pyramidatus*, a little-known Mexican species which separated from the original stock in early times, and two others which are much better known. These are *C. parryi*, a polymorphous species with its center of distribution in the Great Basin, and *C. nauseosus*, an abundant and widely distributed species of western North America. Ten subspecies of the former and 20 of the latter are recognized in the present treatment.

CRITERIA FOR RECOGNITION OF SPECIES AND SUBSPECIES.

Achene.—Two very unlike types of achene are encountered in the genus, but it is easy to see how one of these may have been derived from the other. In the common form it is either obscurely 5-angled or terete and 5-nerved, always tapering slightly from summit to base but not sufficiently so to be described as turbinate, and usually covered with a dense pubescence. In the other form, which occurs only in *C. vaseyi* and *C. gramineus*, the essentially glabrous achene is nearly terete or slightly flattened, tapers but slightly toward the base, and is distinctly 10-striate. This type is so different from the extreme of the other that the character might be considered as generic were it not for other features, especially of *vaseyi*, which definitely relate these species to the other *Chrysothamni*. The two are not so far apart as would at first seem, as is indicated by such achenes as those of *C. nauseosus leiospermus*, which are glabrous, terete, and with 5 principal striae, but often with an additional fainter nerve between each pair of the more prominent ones, thus approaching the terete, 10-nerved type of *C. gramineus*. The pubescence, or its absence, has been used as a specific character, even in cases where the achenes are otherwise identical with those of other species. But it has been shown in a recent paper (Hall in Univ. Calif. Publ. Bot. 7:173, 1919) that this character is a variable one and that three species based largely upon it, *bigelovi*, *glareosus*, and *leiospermus*, are all subspecies of *C. nauseosus*. In *C. pulchellus* the achenes are usually glabrous, but sometimes sparingly pubescent. Although this variation has been noted in descriptions (for example, Rydberg, Fl. Rocky Mts. 855, 1917), there has been no attempt to use it as a basis for a new species. A tendency toward the loss of the character in a species in which the achenes are almost always densely villous or strigose is seen in *C. viscidiflorus*, where a form described as *C. marianus* Rydberg has achenes only sparsely strigose or at times apparently almost glabrous. The length is a valuable feature, but one to be used with caution, since in most herbarium specimens the achenes are not fully developed.

Pappus.—The pappus is so nearly uniform in *Chrysothamnus* that it has not proved very helpful in supplying distinctions between species or subspecies. It is more rigid in some than in others. Sometimes it changes more rapidly and decidedly with age to a tawny hue or becomes ferruginous, but while such characters are of assistance, even when variable, they are impossible of expression in quantitative terms and therefore difficult of application. The length of the pappus is of more definite value, especially when taken in comparison with the length of the corolla.

Style-branches.—In *Chrysothamnus* and related genera much significance has been attached to the shape and length of the style-branch and its appendage. While these

structures undoubtedly furnish characters of much taxonomic value, it is unfortunate that their descriptions have been based upon superficial examinations, usually with the aid only of a hand-lens and not upon exact measurements. This applies particularly to statements of relative length of appendage and stigmatic portion. The tabulation of a large series of measurements now indicates that the ratio between appendage and stigmatic portion is far from constant for any one species or perhaps even for any one subspecies. It also indicates, however, that the ratio is much higher for some species than for others. Pairs of species can be selected in which no overlapping of ratios occurs, so that the character can there be used to advantage. But any attempt to apply the ratio throughout the genus as a never-failing specific character would result in a cleavage running counter to all other features and it would therefore lead to an unnatural arrangement of the forms.

The extent of variation within a single large species is indicated in table 23 (p. 230). The ratio is of further significance when used to indicate tendencies in the various sections. In the *Punctati* the stigmatic portion and the appendage are approximately equal in length, sometimes one being the longer and sometimes the other. Among the *Typici* the otherwise anomalous *C. albidus* has unusually long appendages, while in the other three the appendage is uniformly shorter than the stigmatic portion or only slightly exceeds it in occasional specimens of *vaseyi*. A similar condition holds in the *Pulchelli*, indicating as do other features that these two sections are very close phylogenetically. In the *Nauseosi*, the appendage is always well developed and usually but not always longer than the stigmatic portion. In two subspecies of *nauseosus* it is regularly shorter and in a third it is sometimes so. The shape is often given in descriptions, but, aside from the difficulty of expressing this accurately, it possesses little value. Long appendages are naturally more slender than short ones and they are usually more attenuate. The so-called "broad appendages" of certain species are perhaps not broader by measurement than others, but are only seemingly so because of their shortness.

Stamens.—The stamens have thus far furnished characters of diagnostic value in only one instance. The tips are acute in all species except *C. albidus*, but in this they are obtuse and also decidedly shorter than in the others (except the small-flowered *pyramidatus*). It is possible that detailed studies might reveal further stamen differences of value, but a preliminary survey indicates that the prospects are not promising.

Corolla.—The shape of the corolla is always tubular-funnelform, although there is some variation between the species. In some the throat enlarges more abruptly than in others, but the line of demarkation between tube and throat is so indefinite that the differences can not be expressed in quantitative terms. Since also the shape depends upon the age and condition of the specimen, whether fresh, dry, or boiled, such expressions as "abruptly expanding" or "slenderly tapering" are only relative and of slight value. The total length of the corolla is a character of greater significance. While this fluctuates to disappointing extremes in some of the polymorphous species, in certain other cases it is sufficiently constant to be of use and should always be included in descriptions of new forms. Thus, in the *Punctati* the corolla always measures between 6 and 6.5 mm. long, whereas in *C. nauseosus* it measures 6.2 to 12 mm. and in *C. parryi* 8 to 12 mm. The character is especially useful in distinguishing the two species of the *Pulchelli*, the corolla in one measuring 7 to 9.0 mm., in the other 10 to 14 mm. However, when the whole series of species in the genus is considered, it is found that the overlapping between them is so frequent and the range of variation is so great in certain cases (more than 50 per cent of the length in *C. viscidiflorus*) that the utilization of this criterion in keys is very limited. Even in applying it as a measure of the extent of differentiation where only two species are concerned, it must be used only after a considerable number of flowers from different plants have been measured. The total

lengths as well as the extent of variation for each of the major species is given in table 17, while tables 22 and 23 (p. 207 and p. 230) give similar data for the more common forms of two of the larger species.

The depth to which the corolla-limb is cleft, that is, the length of the corolla-lobe, has been used as a diagnostic character for many proposed species. The actual length, however, has never been given (except in a recent paper by one of the present authors) and the relative length, if mentioned at all, is stated in terms so general as to indicate that measurements have not been made. When a large series of specimens are measured, it is found that the absolute length of the lobe as well as the ratio between lobe-length and corolla-length usually exhibits considerable variation within a single species. The exceptions are *C. paniculatus* and *C. teretifolius*, both non-plastic species in which the lobes are constantly near 1 mm. in length, and *C. albidus*, in which they have the remarkable length of 2 to 2.5 mm. Even within the "small species" of some botanists, that is, the subspecies of the present treatment, the range of variation in the length of the lobe is too great to permit of rigid application. It is very useful, however, as indicating certain tendencies and can sometimes be correlated with other characters and with geographic distribution. This is especially noticeable in the case of three close

TABLE 17.—Length of corolla and of corolla-lobes in the species of *Chrysothamnus*.

	No. of collections measured.	Length of corolla, including lobes.	Length of corolla-lobes.	Ratio of lobe-length to total length.	Average ratio. ¹
Punctati:		mm.	mm.	per cent.	per cent.
<i>C. paniculatus</i>	8	6.0 to 6.2	0.8 to 1.2	13 to 18	15.4
<i>C. teretifolius</i>	11	6.0 6.5	1.0 1.2	15 18	16.7
Typici:					
<i>C. gramineus</i>	1	12.0	1.0 1.7	8 14	11.2
<i>C. vaseyi</i>	10	5.5 6.5	1.5 2.0	27 33	29.1
<i>C. viscidiflorus</i>	10	4.5 7.0	1.0 2.0	20 40	24.9
<i>C. greenei</i>	13	4.0 4.5	0.8 1.3	21 29	25.3
<i>C. albidus</i>	34	7.0 8.0	2.0 2.5	30 31	30.5
Pulchelli:					
<i>C. pulchellus</i>	28	10.0 14.0	1.5 2.0	9.6 17.9	13.8
<i>C. depressus</i>	12	7.0 9.0	1.2 2.3	18 21	19.7
Nauseosi:					
<i>C. pyramidatus</i>	1	4.2 5.0	1.0	21	21.8
<i>C. parryi</i>	77	8.0 11.0	0.5 2.5	7 25	19.2
<i>C. nauseosus</i>	168	6.2 12.0	0.4 2.5	6.5 32	17.3

¹ Computed by taking the average of all of the individual ratios.

subspecies of *C. nauseosus* included in table 23 (p. 232). These are *pinifolius*, of Colorado and adjacent States, with lobes which average only 0.9 mm. long (0.7 to 1.3 mm.); *consimilis*, which has its center of distribution in Nevada and in which the lobes average 1.3 mm. long (1 to 1.6 mm.); and *viridulus*, of eastern California, in which the lobes average 2.0 mm. long (1.7 to 2.5 mm.). These three subspecies, all inhabitants of alkaline soils, differ only in the lobe-lengths and in a few minor tendencies, robustness, inflorescence, etc., which can be correlated only partially with this. The overlapping in the lobe-length occurs most frequently in specimens from localities where the ranges meet, so that some individuals can not be definitely placed. This variation with geographic distribution is paralleled in certain other characters and is representative of a tendency of frequent occurrence, namely, that within a given series of forms the greatest floral development is among those of westerly or southwesterly distribution. Thus, in *C. nauseosus* the maximum and also the highest average length of both involucre and corolla are reached in the subspecies *mohavensis* and *bernardinus* of the Southwest (see table 23). Similarly within the subspecies *speciosus* it is found that specimens from

western Nevada and northwestern California have generally longer involucre and corollas than those from farther east.

The position taken by the corolla-lobe is of some interest. Long lobes are inclined to spread or even to recurve; short lobes are usually erect and in some cases are connivent around the stamen-tube. Such extremes are sometimes found within a single species, as in *C. nauseosus viridulus* and *C. n. gnaphalodes*.

The pubescence of the corolla exhibits some striking variations, without offering anything of more than subspecific value. The tube is either glabrous or minutely puberulent, even in plants belonging to the same variety. Quite different is the additional long arachnoid pubescence that appears on the tube of some subspecies of *nauseosus*. This consists of loose, crooked hairs often 1.5 mm. long. Such pubescence would be of much diagnostic value were it constant and if it did not occur in varying amounts. Among specimens referred to a broad-leaved form of subspecies *speciosus* of this species, some have abundantly arachnoid-pubescent corolla-tubes (*Hall 10853*, *Heller 7192*), while others are almost identical with these in all respects, except that the tube has only the usual crisp pubescence common throughout the genus (*Univ. Calif. Herb.*, 87243, 31163). Similarly among fairly uniform collections of subspecies *typicus*, the tube is found to be either essentially glabrous (*Howell Lakes, Wyoming, Nelson 5315*), or short-hirsute (*Laramie, Wyoming, July 29, 1889 Greene*), or more rarely arachnoid-pubescent (*Laramie, Wyoming, Nelson 2787*). In subspecies *hololeucus* the long hairs are usually very conspicuous. However, among apparently identical plants growing within a few meters of one another, some will be found to have a copious pubescence, others a scant amount, others none at all (*Benton, California, Hall 10654*). In other collections of *hololeucus* the long hairs will be only 2 or 3 in number (*Hall 10610*) or entirely wanting on plants a few kilometers removed. The tips of the corolla-lobes are sometimes conspicuously long-hairy. This character is constant for *C. parryi latior* as far as indicated by the few collections at hand. In *C. nauseosus* it constantly occurs only in subspecies *turbinatus* and *junceus*. In the latter it is of but little value, for the hairs are few in number and deciduous. The lobes of *C. nauseosus bigelovi* are usually glabrous, but in one collection they vary from sparsely to copiously villous (*Hall 11140 UC*). In the Mexican *C. pyramidatus* the lobes are puberulent at the tip. It seems, therefore, that the pubescence of the corolla-parts furnishes criteria of doubtful specific value, but of some use in the segregation of minor forms and as a clue in tracing the lines of evolution.

Number of flowers in the head.—Aside from *C. parryi* and *C. pyramidatus* the number of flowers is almost constantly 5. As one would expect, this number occasionally drops to 4, or more often it increases to 6 or 7. In *C. parryi*, however, the heads have more numerous flowers, and here the character is of some importance for recognition of subspecies. In fact, it has been heretofore considered specific as between *parryi* and *howardi*, but the series of counts enumerated in table 22 indicates very clearly that it can not be used for this purpose, especially when the other subspecies are taken into account.

Involucre.—In common with most other *Compositae*, the involucre of *Chrysothamnus* offers characters of considerable importance. The bracts are arranged in 5 more or less evident vertical rows. When these ranks are well defined the involucre is sharply 5-angled; when they are obscure it is more rounded and without definite angles. The number of bracts in each row varies from 3 to 5, there being a tendency in each species toward either the smallest or the highest number but with no absolute fixity. Such characters as these are of much service in arriving at conclusions as to specific or sectional limits when a large series of specimens are at hand for comparison, but being relative they are difficult of application when one is making determinations from keys and descriptions. The shape of the scales themselves is also of value. It is more or less cor-

related with their arrangement in vertical rows. When the rows are obscure the bracts are likely to be flattish, without a distinct keel, and usually obtuse unless appendaged; when the rows are well-defined the bracts are folded or at least incurved from the midrib, which thus forms a sort of keel, and the bract is more or less boat-shaped and usually acute. The former is characteristic of most of the *Typici*, while the latter is best seen in *C. nauseosus* and especially in the *Pulchelli*.

The texture of the bract escapes every attempt at its characterization, except when herbaceous tips or thickenings appear. A definite herbaceous tip, or appendage, is present only in *C. parryi*, where it is common for some of the outer bracts to be drawn out at the apex into a slender greenish appendage. While this is useful as a specific character when considered as a tendency, it can not be applied as a constant one. Certain specimens referable here by all other characters have the tip poorly developed or entirely wanting in some heads. The herbaceous thickening referred to is even less reliable than the prolonged apex. It is usually found as a minute rounded mark and is subapical. In using this character it must be borne in mind that except in one species the spot is distinctly green only in fresh material. In dried specimens it fades to a dull brown. It has been used as a specific trait in the segregation of at least four proposed species. In *C. teretifolius* and *C. vaseyi* it is connected with other and more important characteristics which it supplements very well. In *teretifolius* especially, the decidedly thickened spot is noticeably green, even in herbarium specimens. Quite different is the case of *elegans*. This is so close to certain other forms that the presence of the subapical spot, which is here never sharply defined and often very obscure or even wanting, can not save it from reduction to subordinate rank under *C. viscidiflorus*. Likewise in the fourth case, namely *linifolius*, a reduction to a subspecies of *viscidiflorus* is necessitated by the discovery of intermediate forms.

The size of the involucre and the number of its bracts have been investigated as to their value as differentiating criteria. The breadth of the head is a poor character, since it depends largely upon the state of maturity and the manner of taking the measurement. Furthermore, it varies somewhat with the number of flowers. The height is more definite and can sometimes be used to advantage, but only in dealing with very unlike species or when only subspecific distinctions are looked for. When a large series of measurements is taken, these are found to present an annoying range of variation, sometimes even within a single taxonomic subspecies. This is indicated for the subspecies of *C. parryi* in table 22 (p. 207). A similar tabulation but with less difference between the extremes could be presented for the subspecies of *C. viscidiflorus*. The most that can be said of the results of such studies of these two species is that there is a tendency toward either short or long involucre in certain subspecies, but that the overlapping is too pronounced to warrant the use of this criterion for specific segregation. Somewhat different is the case of *C. nauseosus*, as will be seen by reference to table 23 (p. 230). In this species the involucre has the remarkable range in length of from 6 to 12 mm. Furthermore, pairs of subspecies can be selected in which there is no overlapping, for example, *gnaphalodes* with an involucre length of 6 to 8.2 mm. and *bernardinus* with one of 10 to 12 mm. While this would furnish a specific character as between these two forms, its use for that purpose must be abandoned because of other subspecies which form intergrading series between them; for example, those in which the length runs 6.5 to 8 mm., 6 to 9 mm., 7.5 to 10 mm., and 10 to 12 mm., respectively. Furthermore, the remarkable variation exhibited within certain subspecies, as brought out in the table, is a warning to proceed cautiously in the use of this character. When the bracts are in sharply defined vertical rows the total number usually varies by fives. This necessarily follows from the fact that there are five rows and that in any particular head the number of bracts in any one row is the same as in any other. But since the number of bracts per row varies within

every species, there is an overlapping in the totals, so that this character again possesses no specific value. It is useful, however, in distinguishing divisions of those species in which the alinement of the rows has been lost and where in consequence the total varies by units rather than by fives. This is brought out in table 22 (p. 207), where, for example, it will be noted that the number for the *asper-vulcanicus-monocephalus* group of subspecies of *C. parryi* runs from 8 to 13, with an average of 10.4, whereas in the *howardi-attenuatus-nevadensis* group it runs from 11 to 21, with an average of about 13.

Inflorescence.—The heads are borne in cymes, racemes, spikes, or panicles. The cyme is by far the most common type and occurs with some modifications almost throughout the *Typici* and *Pulchelli* and in *C. nauseosus*. In the anomalous *C. gramineus* the inflorescence is apparently a much reduced raceme, while the racemose type is characteristic for *C. parryi*. In this last, however, the peduncles are sometimes so branched that small panicles are the result. This condition gives an inflorescence simulating the compound cymes sometimes seen in *C. nauseosus*. In the *Punctati* the inflorescence is essentially spicate in one species, truly paniculate in the other. Observations in the field have demonstrated that the size and density of the inflorescence are too variable to be of much taxonomic significance. Although conspicuous in their extremes, the forms resulting from such considerations can not be satisfactorily treated even as subspecies.

Leaves.—The leaves are always alternate (partly fasciated in one species) and entire. The remaining characters, such as size, shape, and texture, are seldom of diagnostic value as far as species are concerned. Terete leaves occur only in the *Punctati*; in one species (*gramineus*) they are exceptionally wide and without intraspecific gradations; and in one other case the shape is useful as a specific distinction (between *pulchellus* and *depressus*), but these leaf-characters are always used in connection with others and aside from the instances here mentioned, the foliage furnishes criteria useful only when dealing with subspecies. A consistent attempt has been made to utilize the number of nerves and their prominence, but without much success. It is only in comparing species which are rather clearly separated on other characters that such features can be called into use and then only as additional evidence. Much has been made heretofore of the number of veins as a specific character in segregations from *C. viscidiflorus*, but here the number depends largely upon the width of the leaf. There is one plain midvein and usually two others that start from the base but are soon lost or become invisible. Very often a plant will seem to have only 1-veined leaves, but on close examination a few leaves with 2 or 3 veins will be found (for example, *C. parryi monocephalus*, Univ. Calif. Herb. 76001; *C. parryi nevadensis*, Univ. Calif. Herb. 31167; *C. viscidiflorus typicus*, Univ. Calif. Herb. 51644, 203178).

Stem and bark.—To one accustomed to handling the plants in the field, there is a decided difference in the stems of certain species, although the characters are not easily described. Thus, in the *Typici*, *Pulchelli*, and *Punctati* the twigs are very brittle, whereas in the *Nauseosi* they are much more flexible. The bark of the year-old twigs is usually white in the *Pulchelli* and *Typici*, green or brownish, although sometimes covered with a white pubescence, in the *Nauseosi*. The striation of the younger stems is often of diagnostic value. In the last-mentioned section, however, this is likely to depend upon the nature of the hairy covering, which may be either loose, thus masking the striae, or closely compacted and thus exposing them. The older bark of the main trunks affords specific characters, but not of such a nature as to be usable in keys. The color of the plant as a whole, whether due to bark, foliage, or only pubescence, has been made use of in specific descriptions, but this is too variable and elusive to be of value in dealing with any category above that of subspecies.

Roots.—It is quite probable that specific distinctions could be derived from the system of root-branching if this were well understood. The only root studies made were in the

two species that are the most polymorphous in other regards, namely, *viscidiflorus* and *nauseosus*. A considerable number of each of these, several hundred in all, were examined in the field. The difference between the species was very marked. In all of the five subspecies examined of the former, the main root divides near the surface of the soil, the branches spreading out at a moderate depth and influenced in their direction by the nature of the stony soil in which the plants grow. In the ten subspecies examined of *nauseosus*, the root usually continues downward to a considerable depth as a well-defined tap-root, emitting only secondary lateral rootlets. This species grows in better and deeper soil than *viscidiflorus*. Along the edges of its habitat, where the soil is often shallower or quite stony, the root habit may simulate that of *viscidiflorus*, but it is believed that the two types are different in their origin. A striking peculiarity of the root is common in *C. nauseosus hololeucus*. In this form, which inhabits dry sandy stream-ways and fans, the large root is often twisted upon itself and easily breaks up into strands like those of a rope. The cause of this is not known, but it is suggested that such roots are really composite and have been formed by the intertwining of the single roots of several plants. At any rate, such a possibility must be taken into account when making studies in individual variation.

Pubescence.—Two very distinct types of pubescence are encountered. Although characters of the pubescence are generally untrustworthy and are easily modified by changes in the environment, in this genus the two types are so unlike, the absence of intergrading stages is so marked, and their appearance runs so nearly parallel with other characters, that pubescence furnishes a safe guide even for sectional distinctions. This applies, however, only to the presence or absence of a peculiar pannose tomentum. The number and the distribution of ordinary hairs furnish criteria as unreliable here as elsewhere.

The pannose tomentum referred to occurs in all of the *Nauseosi* but nowhere else in the genus. It consists of a dense coating of long, weak hairs, which have become more or less infiltrated with a resinous exudation from the twigs. The inner portion of this mass closely invests the twigs like a tight-fitting coat. The outer ends of the trichomes may be either loose, thus presenting a light, fluffy appearance, or they may be closely impressed with the inner layers. In the latter case, the surface is often so smooth that the woolly layer is mistaken for the bark itself, until it is scraped up by a knife-edge or scalpel. This has led even careful botanists wrongly to describe certain forms as glabrous or nearly so and thus to mask their true relationships. For example, Gray described the branchlets of *Linosyris bigelovi* as with scarcely a perceptible pubescence; the same author gives "greenish and minutely canescent" for the branches of *Bigelovia juncea*, earlier described by Greene as cinereous; Greene has described the twigs of *C. pinifolius*, *C. virens*, *C. laetevirens*, and others as glabrous or nearly so; Nuttall, in characterizing *C. speciosus*, made no mention of the pubescence of the stem, but at the same place he proposed a variety *albicaulis* based only upon the dense and white tomentum of the stems and suggested that it might be a distinct species. The types of all of these have been examined and found to have twigs clothed with a dense felt-like tomentum. For this and for other reasons they are now classified as subspecies of *C. nauseosus*.

Aside from its presence or absence, the tomentum does not afford specific characters. Its duration, amount, color, and extent are all too variable to indicate more than varietal or subspecific rank. It is certain, however, that some of these qualities are heritable, at least for a few generations. Certain subspecies of *C. nauseosus*, differing among themselves in the color and extent of the tomentum, come "true to seed" in these respects when grown under uniform conditions in the Botanical Garden of the University of California. The same holds for transplants made by transferring the roots of these subspecies. While only extremes were used in these experiments, all intermediate forms are found in the field (although not always in the same locality), so that such characters are difficult to apply in the identification of described groups.

Pubescence in *Chrysothamnus*, aside from the special type of tomentum just described, is scarcely noticeable, the twigs and foliage being never more than puberulent. In the *Punctati* and in certain species of other sections, it is entirely wanting. Sometimes, as among the subspecies of *viscidiflorus*, it will occur as a fairly dense though minute puberulence in certain plants, while others almost exactly duplicating these in every other respect will be perfectly glabrous. This is so frequent that glabrous and puberulent forms may be expected of any variety in that species. Their possible origin through mutation is suggested in discussing the relationships of *C. viscidiflorus*. When such forms are quite marked and of frequent occurrence, and especially if they have been given specific rank elsewhere, they are treated in this paper as subspecies; when they appear only occasionally, they are mentioned only in the list of minor variations. To assign specific or even subspecific rank in all such cases would so enlarge and complicate taxonomic monographs that their usefulness would be seriously impaired. It is very evident, however, that a complete systematic treatment will need to take account of all such variations.

Resins, oils, and other physiological products.—Throughout the genus there is a notable tendency to the formation of resins and oils. This is associated with the xerophytic habitat of the plants. The resins are not exuded through the trichomes, but directly through the surface of the epidermis proper. The herbage is therefore often glutinous or viscid. This character is more marked in some species than in others without, however, furnishing a useful criterion for distinguishing them. The reason is that the difference is entirely relative and dependent quite as much upon local conditions or even time of day as upon an inherent quality. Much more important is the presence of definite pits, or wells, into which the resin exudes, forming the resin-dots of the *Punctati*. These are structural and therefore of greater significance than resinous or viscid coatings. Since they are easily recognized their presence furnishes an ideal specific character.

The odor of the herbage is an aid to one familiar with the plants. Its diagnostic value is not great because of the absence of standards for comparison. The *Punctati* possess a peculiar and very pleasing odor whereby one may recognize a plant as belonging to this section, even though the flowers are wanting. In *C. nauseosus* the odors, probably due to the presence of essential oils, vary somewhat in unison with other characters, so that they are useful in a few cases for the recognition of subspecies. Thus the subspecies *viridulus* emits a very strong, disagreeable odor when the twigs are broken or when burned. A very similar though less pronounced odor is noticeable in the closely related subspecies *consimilis*, *pivifolius*, and *graveolens*. On the other hand, the herbage of subspecies *gnaphalodes*, and especially of subspecies *hololeucus*, usually has an exceedingly pleasant fragrance, "suggesting a combination of tropical fruits and berries." Under favorable conditions these forms may be recognized by the odor alone.

Habit.—All of the species of *Chrysothamnus* are shrubs. In one case, namely *C. gramineus*, the shrubby nature is not pronounced, although the base of the stem is perennial and decidedly woody. In other species the plants are sometimes quite short, but they are always woody and partake of the habit of shrubs; plainly they are reduced or dwarf forms closely related to the more shrubby types. The transition between these dwarf shrubs, some of which are only 1 dm. high, to the arborescent forms, which sometimes attain a height of 24 dm., is so gradual as to preclude the use of this character for distinguishing categories above the rank of subspecies.

FIXITY OF SPECIES AND SUBSPECIES AND OF THEIR CHARACTERS.

The best evidence regarding the fixity of forms and of their characters is obtained by experimental methods. In the case of perennials like *Chrysothamnus*, such experiments must necessarily extend over a long period of years, in order to permit of the growth of several generations from seed of known origin. Such work has been undertaken in the present case, but results are now available from only the first generation. Transplants of rooted specimens of a few of the forms have also been made and the resulting changes studied. The data from these experiments were used in arriving at the opinions here expressed, but much more extensive observations were made upon the wild plants, especially as to the extent of variation under different ecologic conditions and in various geographic areas. Finally, a close statistical and analytical study has been made of series of specimens brought in from the field for this purpose. As a result of the evidence assembled from these various sources, it is found that the genus includes a few species in which the characters are remarkably constant, species which are hence known to be non-plastic and which do not break up into minor segregates. But it is also found that certain other species are in a highly plastic condition, such species comprising a large number of closely related subspecies, many of which are in turn breaking up through mutation and gradual variation into innumerable races and ecads. The variability of the characters themselves has been already indicated to some extent in the preceding chapter on discussion of criteria.

The most nearly constant of the species are those which are assumed, for other reasons, to be the most primitive; namely, *C. paniculatus* and *C. teretifolius*. These two are sharply set off from the other members of the genus and do not intergrade into each other. As evidence of the constancy of their characters may be cited an examination of 11 specimens of *teretifolius*, all from different localities, in which the length of the corolla did not vary by more than 0.5 mm., the length of the lobes by only 0.2 mm., and the ratio of lobe-length to corolla-length by 3 per cent. As contrasted with this, the corolla of *C. nauseosus* varies by as much as 6 mm. in length, the lobes by 2 mm., and the ratio by over 27 per cent. This suggests that *nauseosus* is a composite species, while *teretifolius* is not. But even within a well-defined subspecies of the former, for example *graveolens*, the corolla varies to the extent of 2 mm., the lobes by 0.7 mm., and the ratio between the two by 7.5 per cent. Similar figures have been obtained for length of involucre, relative lengths of style-appendage and stigma, and other characters. The conclusion is therefore inevitable that *teretifolius* is in a set condition as contrasted with the highly variable and composite *nauseosus*.

With *C. teretifolius* (or the less well-known *paniculatus*) as the species with characters the most definitely fixed, and with *C. nauseosus* as the one which is the most plastic, the others exhibit varying degrees of mobility. Three of them are so local in their distribution, at least as far as present collections indicate, that they can not be definitely assigned as to variability, but all of them will doubtless be found to be fairly constant in their characters. These are *gramineus*, *albidus*, and *pyramidatus*. *C. vaseyi* is also well fixed in its characters, there being no varieties, while even its ecologic forms are few and not well marked. *C. viscidiflorus* presents a very different case. It undoubtedly represents the extreme of plasticity among the *Typici*. The ten subspecies here described represent only a small proportion of the forms known in the field. It seems that the species is capable of occupying areas of considerable diversity, and this probably accounts for its wide distribution. The large number of habitats occupied is equaled by the large number of forms. While most of these have arisen through ecologic factors and are fluctuating in their nature, others are quite certainly more deep-seated in their origin. This is indicated by the absence of intergrading forms. The more striking of these are given subspecific rank in the present paper. It is believed that none of them, with the possible exception of *linifolius*, is as well established and

as sharply defined from its neighbors as are most of the subspecies of *C. nauseosus* or of *C. parryi*. *Chrysothamnus greenei* and *C. pulchellus* both are somewhat variable, as is indicated by their subspecies. However, their variations are chiefly those of habit, foliage, and size of head and flowers, and therefore perhaps not of the importance that their taxonomic status would seem to indicate.

Chrysothamnus parryi, as here extended, comprises an extensive series of variations. In addition to the ten accepted subspecies there are a number of other forms, some representing combinations of minor characters while others are intermediate or outlying forms obviously brought about by unusual environmental conditions. A few of these are described under the heading of Minor variations. The conclusion is that *C. parryi* is in a highly unstable state.

TABLE 18.—Variation in plants of *Chrysothamnus nauseosus* growing under apparently uniform conditions.

	Corolla.			Style.		
	Length, including lobes.	Length of lobes.	Ratio of lobe-length to total length.	Length of stigmatic portion.	Length of appendage.	Ratio of appendage-length to total length of branch.
Subspecies <i>gracilens</i> :						
North of Fort Collins, Colo.:						
Plant 1.....	8.0	1.3	16.2	0.9	1.5	62.5
2.....	8.0	1.1	13.7	1.0	2.0	66.7
3.....	8.5	1.1	12.9	1.0	2.1	67.9
4.....	9.5	1.4	14.7	1.3	2.1	61.8
5.....	7.5	1.0	13.3	1.0	1.8	64.3
Golden, Colo.:						
Plant 1.....	9.6	1.6	16.7	1.5	2.0	57.1
2.....	9.7	1.5	15.5	1.5	2.0	57.1
3.....	8.7	1.1	12.6	1.2	1.4	53.8
4.....	9.0	1.5	16.7	1.3	2.0	60.6
5.....	7.9	1.1	13.9	1.1	1.3	54.2
6.....	9.0	1.3	14.4	1.5	2.0	57.1
Subspecies <i>sticticus</i> :						
Near Strevell, Idaho:						
Plant 1.....	9.8	0.8	8.1	0.9	1.5	62.5
2.....	10.0	0.5	5.0	1.0	2.0	66.7
3.....	10.0	0.7	7.0	1.2	1.8	60.0
4.....	9.0	0.7	7.8	1.0	1.8	64.3
5.....	9.0	0.8	8.9	1.0	1.5	60.0

But, as already indicated, the species now undergoing the greatest amount of change, and the one which exhibits the greatest variety of forms, is *C. nauseosus*. All of the 20 subspecies described in this paper are presumably more than ecologic forms and it is almost certain that at least most of them include still other units the characters of which are inherited. Even such characters as the amount and color of the tomentum are heritable, as indicated by plants now growing in the Botanical Garden of the University of California. In these plantings, for example, the very white herbage of subspecies *hololeucus* stands out in strong contrast to the gray of subspecies *gnaphalodes* and to the yellowish-green of subspecies *viridulus* and *leiospermus* in neighboring rows. On the other hand, the distinctive fragrance of certain forms seems to be lost when these are grown in the coastal districts. Other evidence as to the importance of minor characters is obtained by a comparison with geographic distribution. While a few subspecies extend over wide areas, most of them have a definite geographical range from which the most closely related subspecies are excluded. However, such pairs often meet at the borders of their ranges, and here they seem to grade insensibly into each other. Whether this is actually the case or the intermediate forms are the result of hybridization is a question that will require a genetic analysis for its answer. The most remarkable mixing of two subspecies in this manner which has been thus far noted, takes place at

Soda Springs, Esmeralda County, Nevada, where the ranges of *consimilis* and *viridulus* meet. Entirely different from the characters just considered are those which are plainly modified by changes in the environment. These have to do with habit, size, and direction of leaf, relative amount (but not nature) of pubescence, leafiness, size of inflorescence, etc. Such characters often can be readily accounted for when the habitat is examined. The ecologic origin of the forms is further suggested by their occurrence at numerous localities and without regard to geographic isolation, but mutations may also occur in this manner.

The extent of variation in one floral character in plants of a single subspecies and apparently of uniform germinal constitution is indicated in table 18.

The figures used in table 18 are in each case the average of several measurements. Similar studies of specimens at other localities and for other subspecies indicate an equally great variability. The conclusion is that all of the more common subspecies of *C. nauseosus* are in a highly plastic condition and that there exists even within a single colony a large number of minor forms. Whether this is due to the presence of numerous genetic strains or biotypes, or whether it is the result of fluctuating variability is not within the province of this paper to decide. In either case, it indicates that "improvement" in any desired direction may be brought about by selection, or by hybridization, or by both of these methods. In this connection it may be pointed out that the percentage content of rubber in subspecies of *C. nauseosus* varies for different plants in a single locality in much the same manner as the index characters used in the above table. This is shown in a table of 180 chemical analyses recently reported upon by Hall and Goodspeed (Univ. Calif. Publ. Botany 7:227 to 233, 1919).

GENERIC DIAGNOSIS.

CHRYSOTHAMNUS Nuttall, Trans. Am. Phil. Soc. II, 7:323, 1840.

Branching shrubs and half shrubs. Roots fibrous, either with or without a taproot. Stems erect or ascending, never twining. Herbage glabrous to tomentose, commonly resinous and aromatic, impressed-punctate in two species. Leaves alternate, without distinction between blade and petiole, entire or only scabro-serrulate. Heads in cymes, thyrses, spikes, racemes, or panicles. Involucre cylindraceous; bracts mostly carinate or with a strong midrib, well imbricated in more or less distinct vertical ranks, chartaceous or coriaceous, only the tips sometimes herbaceous. Ray-flowers entirely wanting. Disk-flowers 4 to 20. Corolla tubular-funnelform, the tube passing gradually into the throat, 5-toothed or 5-cleft. Style-appendages exerted from the corolla-tube, lanceolate-attenuate to filiform or subulate, either longer or moderately shorter than the stigmatic portion. Achenes slender, terete or slightly angled or flattened, rarely striate, glabrous to densely pubescent. Pappus copious, soft, dull white to reddish. (*Bigelovia*, section *Spuriae* De Candolle, Prodr. 5:329, 1836. *Bigelovia*, sections *Chrysothamnopsis* and *Chrysothamnus* Gray, Proc. Am. Acad. 8:641, 642, 1873, and Syn. Fl. 1:136, 137, 1884.)

According to Nuttall, the genus was named *Chrysothamnus* from its affinity to *Chrysocoma* and from its brilliant golden-yellow flowers. A literal translation is "golden wood," or "golden bush." The latter is used to some extent in the Rocky Mountain States as a common name for *C. nauseosus*. This species as well as a number of others is more commonly called rabbit-brush, which was given because of the utilization of the thickets by rabbits as places of refuge. They sometimes eat the young shoots, but this is not a universal habit. (For a discussion of common and Indian names see Univ. Calif. Publ. Bot. 7:190, 1919.)

Key to the Sections and Species of *Chrysothamnus*.

- Herbage resinous-punctate; leaves terete (PUNCTATI).
 Bracts all pale, without greenish spot..... 1. *C. paniculatus* (p. 175).
 Outer bracts with a distinct greenish subapical spot..... 2. *C. teretifolius* (p. 176).
 Herbage not resinous-punctate; leaves oblanceolate to narrowly linear or nearly terete.
 Twigs glabrous or puberulent, not closely tomentose.
 Bracts moderately keeled, the vertical rows not sharply defined; achenes either
 decidedly pubescent or glabrous and 10-striate (TYPICI).
 Achenes glabrous or nearly so and 10-striate.
 Leaves lanceolate, 5 to 10 mm. wide, strongly 3- or 5-nerved; corolla 12 mm.
 long; ¹ style-appendages twice as long as the stigmatic portion... 3. *C. gramineus* (p. 178).
 Leaves linear or very narrowly oblanceolate, 1 to 2 mm. wide, 1-nerved;
 corolla 7 mm. or less long; style-appendages scarcely exceeding
 or shorter than the stigmatic portion..... 4. *C. vaseyi* (p. 179).
 Achenes densely pubescent or rarely sparsely so, but never striate.
 Involucral bracts obtuse to acute, but never slenderly acuminate..... 5. *C. viscidiflorus* (p. 180).
 Involucral bracts (some or most of them) slenderly acuminate or with an
 abrupt mucro.
 Corolla about 5 mm. long, yellow; anther-tips lanceolate, very acute, about
 0.5 mm. long..... 6. *C. greenei* (p. 190).
 Corolla 7 to 8 mm. long, whitish; anther-tips ovate, obtuse, about 0.2 mm.
 long..... 7. *C. albidus* (p. 192).
 Bracts strongly keeled, the vertical rows very distinct; achenes glabrous or only
 minutely pubescent, not striate (PULCHELLI).
 Leaves filiform to linear; corolla 10 to 14 mm. long..... 8. *C. pulchellus* (p. 193).
 Leaves spatulate or oblanceolate; corolla 7 to 9 mm. long..... 9. *C. depressus* (p. 195).
 Twigs covered with a pannose or felt-like tomentum, this sometimes so close as to
 escape observation (NAUSEOSI).
 Heads in leafy spike-like or raceme-like clusters, these sometimes branching to form
 panicles; outer bracts of involucre commonly prolonged into
 a slender herbaceous tip or appendage (except in *C. pyramidatus*).
 Involucre about 6 mm. high; upper leaves fasciated..... 10. *C. pyramidatus* (p. 197).
 Involucre 10 to 15 mm. high; leaves not fasciated..... 11. *C. parryi* (p. 198).
 Heads cymose at the ends of the branches, the inflorescence sometimes compound
 and elongated, bracts of the involucre obtuse to acute, the outer
 ones regularly shortened and devoid of herbaceous tip..... 12. *C. nauseosus* (p. 209).

SECTION I. PUNCTATI.

1. *CHRYSOTHAMNUS PANICULATUS* (Gray) Hall, Univ. Calif. Publ. Bot. 3:58, 1907.
Plate 24.

Shrub 6 to 20 dm. high, with several or numerous main stems from the base, forming a¹ broad, rounded plant; bark of the older portions dark gray, rough; twigs brittle, spreading, leafy, glabrous but resinous and viscid, at first green (or with a gray waxy bloom) and impressed-punctate, later turning brown and striate; leaves terete, shortly mucronate, 1 to 3 cm. long (much shorter in the inflorescence), glabrous but very resinous and marked by numerous impressed resin-dots, sometimes with a gray waxy bloom; heads in profuse terminal panicles or the inflorescence occasionally reduced and subracemose but never spicate; involucre 5 to 6 mm. high; bracts 13 to 17, in 5 obvious but not sharply defined vertical ranks, oblong, obtuse, not carinate, rather thin, glabrous, stramineous, without apical spot; flowers 5 to 8; corolla tubular-funneliform, the tube passing gradually into a much wider throat, about 6 mm. long, glabrous; lobes lance-ovate, about 1 mm. long, nearly erect, glabrous; anther-tips linear, acute, 0.5 mm. long; style-branches long-exserted, the appendage varying from only slightly to twice longer than the stigmatic portion; achenes tapering from summit to base, 5-angled, about 4 mm. long when mature, appressed-villous; pappus scarcely equaling the corolla, white. (*Bigelovia paniculata* Gray, Proc. Am. Acad. 8:644, 1873.)

Arid and stony slopes, especially in dry streamways, from southwestern Utah across northern Arizona to the Colorado and Mojave deserts in California as far west as Tehachapi Pass; not common. Type locality, California. Collections: Arizona, 1902,

¹ Throughout the paper the length of the corolla is taken to include the lobes. All measurements are for fresh material or for flowers restored by boiling.

Stephens; California: Chuckawalla Bench, Colorado Desert, *Schellenger 19* (UC); between Cabezon and Whitewater, *Parish 651* (Gr, UC, US); near Bagdad, southern Mojave Desert, May 20, 1902, *Brandege* (UC); eastern slopes of Tehachapi Pass, *Hall 10961* (UC); Resting Springs Valley, Inyo County, *Coville* and *Funston 280* (US).

SYNONYMS.

1. *BIGELOVIA PANICULATA* Gray, Proc. Am. Acad. 8:644, 1873. The first publication with a description of *C. paniculatus*.
2. *ERICAMERIA PANICULATA* Rydberg, Fl. Rocky Mts. 853, 1917. Based upon *Bigelovia paniculata*.
3. *LINOSTRIS (CHRYSOTHAMNUS) VISCIDIFLORA* var. *PANICULATA* Gray, Bot. Mex. Bound. 80, 1859. This was the first publication of the name, but it was not accompanied by a description.

RELATIONSHIPS.

Because of its similarity to species of *Haplopappus* section *Ericameria*, especially in the resinous-punctate herbage, this is taken as one of the most primitive of the *Chrysothamni*, and hence it stands first in the taxonomic sequence. It differs from all species of *Haplopappus* in the vertical arrangement of the involucre bracts and in the narrow heads, while from the species which are most like it in other respects it differs also in the absence of ray-flowers. Its habitat in the southwestern deserts, where it borders upon the areas inhabited by species of *Ericameria*, also argues for its former connection with that group. The characters of *C. paniculatus* are remarkably constant, at least as far as indicated by the specimens at hand. The length of corolla varies by only 0.2 mm., or less than 5 per cent, as contrasted with variations of 3 to 6 mm., or about 100 per cent in some of the more plastic species (table 17). In relative length of style-appendage and stigmatic portion, however, the variation is nearly as great as in the most variable species, namely, *C. nauseosus*. In most other floral characters and in vegetative features the plants show but little fluctuation. In Brandege's specimens from Bagdad, cited above, the inflorescence is very narrow, almost racemose in fact, but aside from this collection there are no variations of consequence and there have been no attempts to segregate the species into varieties or other divisions. This remarkable uniformity is no doubt due in part to the restricted distribution of *C. paniculatus* and suggests that this species is much more primitive than the more plastic, variable and aggressive ones at the opposite end of the genus.

ECOLOGY AND USES.

Chrysothamnus paniculatus is a rare species of little ecological significance. In life-form it is a bush, flowering from May to October. It is sublimax in position, occurring in rocky streamways with *Lepidospartum squamatum*, *Hymenoclea salsola*, and *Encelia frutescens*, or with one or more of them, usually in the *Larrea-Yucca* ecotone.

It seems unlikely that commercial products will ever be obtained from this plant. The scarcity of the supply would alone prevent the utilization of the wild shrubs. It is possible, however, that through selection, and especially through cross-breeding with *C. teretifolius*, a rubber plant might be discovered with sufficient promise to warrant cultivation on a commercial scale. The rubber-content of wild plants has been found to average only about 2.5 per cent, but there is reason to believe that strains or at least individuals can be found that will run much higher than this. The large size of the shrubs, their resistance to low temperatures, and their ability to grow in the poorest of soil where the water content is exceedingly low, are all characteristics highly desirable in rubber plants. The nature of the product will be taken up under the next species.

2. *CHRYSOTHAMNUS TERETIFOLIUS* (Durand and Hilgard) Hall, Univ. Calif. Publ. Bot. 3:57, 1907. Plate 24.

Shrub 3 to 9 dm. or rarely even 20 dm. high, irregularly much branched and spreading to form a flattish or rounded bushy plant; bark of main stems dark gray, more or less

grooved; twigs brittle, erect, very leafy, glabrous but resinous, at first green (or with a gray bloom) and impressed-punctate, later turning to a rich reddish-brown and becoming striate; leaves terete, obtuse, not mucronate, 1 to 2 cm. long (only moderately shorter in the inflorescence), glabrous but resinous and marked by numerous impressed resin-dots, rarely with a gray waxy bloom; heads in short terminal spikes, these apparently cymose when very short, or thyrsoïd when slightly compound; involucre 6 to 8 mm. high; bracts 16 to 20, in 5 sharply defined vertical ranks, oblong, obtuse or the inner ones shortly acute, obscurely carinate, thinnish, glabrous, straw-colored, with a conspicuous green or brownish thickened spot near apex, often terminated by a thick resin-gland; flowers 5 or 6; corolla tubular-funnelform, the tube passing gradually to the moderately dilated throat, 6 to 6.5 mm. long, glabrous; lobes lanceolate, about 1 mm. long, erect or the tips slightly recurved, glabrous; anther-tips linear, acute, 0.6 mm. long; style-branches long-exserted, the appendage shorter than or only moderately exceeding the stigmatic portion; achenes slender, slightly tapering from summit to base, 5-angled, about 5 mm. long when mature, densely villous; pappus equaling the corolla or slightly shorter, white. (*Linosyris teretifolia* Durand and Hilgard, Jour. Acad. Nat. Sci. Phila. II, 3:41, 1855.)

On gravelly or stony hillsides, often in rocky cañon bottoms from central Nevada west and south to the easterly basal slopes of the Sierra Nevada and Tehachapi Mountains, and San Geronio Pass, in California; perhaps also in northern Arizona; most abundant in the White and Inyo Ranges of eastern California. Type locality, all over the mountains around Tejon Valley, California. Collections: Pancake Range, Nevada, *Purpus 6395* (UC, US); Lida, western Nevada, *Hall 10817* (SF, UC); Soda Springs Cañon, western Nevada, *Shockley 556* (Gr); California: easterly slope of the White Mountains, *Hall 10821* (UC); Surprise Cañon, Panamint Mountains, *Coville* and *Funston 596* (US); Rosamond Hills, Antelope Valley, *Hall 10572* (UC); type collection, September, 1853, *Heermann* (Gr); San Geronio Pass, *Parish 655* (Gr).

SYNONYMS.

1. *BIGELOVIA TERETIFOLIA* Gray, Proc. Am. Acad. 8:644, 1873.—*C. teretifolius*.

2. *LINOSYRIS TERETIFOLIA* Durand and Hilgard, Jour. Acad. Nat. Sci. Phila. II, 3:41, 1855.—*C. teretifolius*. This was the first publication of the species. It was soon repeated in connection with an excellent plate published by the same authors (Pacif. R. R. Rep. 5*:9, pl. 7, 1856), but no additional information was there given.

RELATIONSHIPS.

There can be no doubt that this species is mostly closely related to *C. paniculatus*, and it is almost equally certain that it represents a more highly developed type than that. While both are low shrubs of the desert borders, this is much the more abundant and widely distributed, and is thus seen to be a more successful type. The inflorescence is considered as a reduction from the more branching form found in *paniculatus*, the heads are narrower, with the bracts in more sharply defined vertical ranks, and these bracts show further specialization in the strongly marked apical or subapical green spot with its resinous exudate. All of these characters are taken as indicating an advance over the other species. As in that, the essential features are remarkably constant. The corollas are only slightly more variable than in *teretifolius* (table 17) and the style-branches much less so. The plants vary much in size and habit, but this is correlated with environmental influences. No species or varieties have ever been proposed as segregates. Such considerations indicate that this species is one of the most stable of the genus and that it is not producing mutations or other variations that might serve as the starting point of new evolutionary lines. Its position among the more primitive species is attested by the absence of plasticity, the consequent absence of variations, and the restricted distribution, as well as by the paucity of specialized features.

ECOLOGY AND USES.

Chrysothamnus teretifolius is essentially like its relative, *C. paniculatus*, in its ecological behavior. It is more abundant and more widely distributed, and consequently comes in contact with the sagebrush association as well as with the *Larrea* scrub. It is likewise sublimax in nature, but is found more frequently on gravelly or rocky slopes than in streamways, usually with *Hymenoclea salsola*.

The strongly resinous nature of its herbage precludes the use of this species as a browse shrub. Its only other possible value lies in the fact that the shrubs contain a small amount of rubber. While this averages only about 2.5 per cent in wild plants, certain individuals have been analyzed that ran as high as 5 per cent (Hall and Goodspeed, Univ. Calif. Publ. Bot. 7:267, 1919; allowance made for moisture determination), and there is no reason to suppose that the strains richest in rubber have as yet been located. The total yield would be considerably increased by any method of mechanical extraction, since much of the resin would come out with the rubber. Such a product would be of low grade, but useful as a rubber substitute if it could be placed on the market in large quantities. The supply of native shrub is not sufficient to be of consequence except in an emergency, such as during war-time, when importations might be excluded, but the improvement of the plants through selection, breeding, and various treatments under field conditions might result in a product and yield so favorable that their cultivation as a rubber crop could be successfully undertaken even in times of peace. For this purpose, however, some of the forms of *C. nauseosus* are more promising.

SECTION II. TYPICI.

3. CHRYSOTHAMNUS GRAMINEUS Hall, Muhlenbergia, 2:342, 1916. Plate 25.

Plant about 3 dm. high, woody at base but scarcely shrubby; twigs probably brittle, stiffly erect or ascending, greenish-white, striate; leaves lanceolate, acuminate, flat, 4 to 6.5 cm. long, 5 to 10 mm. wide, 3- to 5-nerved, some with faint anastomosing veinlets, rigid, the margins scabrous, otherwise glabrous or only minutely granular; heads solitary, or few in a very open raceme; involucre about 11 mm. high; bracts about 15, the vertical ranks not obvious, oblong, erose at the obtuse summit except the outer slenderly mucronate ones, chartaceous and glabrous except the outer which are greenish towards the summit and ciliate; flowers 4 to 5; corolla narrowly funnelform, 12 mm. long, glabrous; lobes 1 to 1.7 mm. long, erect, glabrous; anther-tips attenuate, about 0.6 mm. long; style-branches long-exserted, the appendage over twice as long as the stigmatic portion; achenes nearly terete, 6 mm. or more long, 10-striate, glabrous; pappus nearly equaling the corolla, brownish.

Known only from the type. Type locality, head of Lee Cañon, Charleston Mountains, Clark County, Nevada, altitude 2,450 meters. Collection, type, August 4, 1913, A. A. Heller 11075 (UC).

RELATIONSHIPS.

The position of this exceptionally rare species in the phylogenetic sequence is very uncertain. Its remarkably striate achenes are almost exactly like those of *C. vaseyi*, but in almost every other detail it is at variance with that species. Except for the number of striae, the achenes closely resemble those of the otherwise very different *C. nauseosus leiospermus*. The long stylar appendages and the subracemose inflorescence suggest an alliance with *C. parryi*, but the habit, the glabrous twigs, and especially the glabrous striate achenes, are unlike any member of that group. If it were not for the *Pulchelli* and *C. vaseyi*, which seem to relate it to *Chrysothamnus* because of the striate achenes in all, it might almost as well go into the genus *Petradoria* (that is, *Solidago pumila*), which it much resembles in habit, but even there it would be at variance with

the single known species of the genus, which has flattish 5-nerved achenes, punctate leaves, and other characters not found in *gramineus*. The latter is almost exactly matched in foliage characters by a plant collected in southern Utah by Jones and named by him as *Bigelovia menziesii* var. *scopulorum* (Proc. Calif. Acad. II, 692, 1895). While great importance can not be attached to leaf characters, the similarity in this instance may be of more than ordinary significance, for the type of leaf is entirely different from that of any other *Chrysothamnus*, or indeed from that of any member of any closely related genus. Professor Jones's variety was later taken by Greene as the type of his new genus *Hesperodoria* (Greene, *Leaflets* 1:173, 1906). Still later it was referred to *Isocoma* as *I. scopulorum* (Rydberg, Fl. Rocky Mts. 859, 1917). Thus, it has always been considered a member of the *Haplopappus* group of genera or subgenera rather than of *Chrysothamnus*. The present emphasis upon the similarity between its foliage and that of *C. gramineus* should not be taken as more than suggestive, unless additional evidence is found as to their consanguinity. The heads in *scopulorum* are turbinate, rather than subcylindric, as in *gramineus*, the flowers are nearly twice as long and more than twice as numerous, and the achenes are 4- or 5-angled and densely hispid, as contrasted with the glabrous, 10-striate achenes of *gramineus*.

The conclusion, therefore, is that, although *C. gramineus* is anomalous in *Chrysothamnus*, chiefly because of the peculiar foliage and the lack of a vertical arrangement of its bracts, it would be still more anomalous in any other genus, and, furthermore, the cylindrical involucre and the presence of similar achenes in other undoubted members of the genus leave no alternative to its acceptance as a member of *Chrysothamnus*.

ECOLOGY AND USES.

Chrysothamnus gramineus is an exceedingly rare undershrub, flowering from August to October. It grows in yellow-pine savannah as a secondary species, but is altogether too sparse to be of importance in the community. It has no known uses.

4. CHRYSOTHAMNUS VASEYI (Gray) Greene, *Erythea*, 3:96, 1895. Plate 25.

Shrub 1 to 3 dm. high, single-stemmed at base, but soon branching to form a low, rounded bush; bark of old stems brown, fibrous; twigs brittle, erect or ascending with a pale green or whitish glabrous bark; leaves linear or very narrowly oblanceolate, flat but sometimes twisted, obtuse, 1 to 2.5 cm. long, 1 to 2.5 mm. wide, 1-nerved, firm, glabrous but resinous-glandular; heads in small, compact cymes; involucre 5.5 to 7 mm. high; bracts about 15, the vertical ranks vaguely defined, oblong, obtuse, obscurely keeled, glabrous but viscid-glandular and with the thin white margins erose or ciliolate, the outer ones with a thickened greenish spot near the apex; flowers 5 to 7; corolla tubular-funnelform, passing gradually from a narrow tube to a much wider throat, 5.5 to 6.5 mm. long, glabrous or only minutely granular; lobes linear-lanceolate, 1.5 to 2 mm. long, more or less spreading, glabrous; anther-tips lanceolate, acute, 0.5 to 0.8 mm. long; style-branches slightly exserted, the thick appendage usually shorter than or only slightly exceeding the stigmatic portion; achenes terete-turbinate, about 5 mm. long, longitudinally striate with about 10 nerves, glabrous or rarely with a very sparse pubescence near summit, smooth and shining or only minutely granular; pappus scant, soft, shorter than the mature corolla, dull white. (*Bigelovia vaseyi* Gray, Proc. Am. Acad. 12:58, 1876.)

In mountain valleys and on hillsides from southern Wyoming and New Mexico to Utah. Type locality, Colorado, in Middle Park. Collections: Laramie Hills, Wyoming, *Nelson 5331* (Gr, NY, US); type collection, 1868, *Vasey* (Gr, US); *Ridgway*, Ouray County, Colorado, *Payson 2315* (SF); Gunnison, Colorado, *Baker 673* (DS, Gr, NY, UC, US); Montezuma Cañon, southeastern Utah, *Rydberg* and *Garrett 9679* (NY, UC, US); Panguitch Lake, Utah, *Jones 5998* (NY, UC, US); slope of Aquarius

Plateau, Utah, *Ward 620* (US); Chama, northern New Mexico, September 5, 1899, *Baker 652* (NY, US, type collection of *C. bakeri* Greene, minor variation 2); near Dulce, Rio Arriba County, New Mexico, *Standley 8134* (US).

MINOR VARIATIONS AND SYNONYMS.

1. *BIGELOVIA VASEYI* Gray, Proc. Am. Acad. 12:58, 1876.—*C. vaseyi*.
2. *CHRYSOTHAMNUS BAKERI* Greene, Pittonia 4:152, 1900.—Described from plants collected by Baker near Chama, New Mexico, and compared with *C. greenei*, from which, however, it differs in the obtuse bracts, glabrous achenes, and other characters. On the other hand, specimens of the type collection are exactly like the usual form of *C. vaseyi*, which was probably overlooked when *bakeri* was diagnosed.

RELATIONSHIPS.

This species is well separated phylogenetically from all of the others, as is especially indicated by the character of its achenes and of its style-branches. Greene has already pointed out (*Erythea* 3:96, 1895) that the former are longitudinally 10-striate. They are therefore unlike any others in the genus except in the *Pulchelli* and in the recently described *C. gramineus*. The style-branches are of a peculiar shape. Although plainly flattened, the short, thick, somewhat rounded appendage gives them the appearance of being almost club-shaped. This appendage is shorter in proportion to the stigmatic part than in any other *Chrysothamnus*, except in occasional specimens of *C. greenei*. It is to this species that *vaseyi* is probably most closely related, as is indicated by the appearance and by the general assemblage of characters as well as by the style-branches. However, even this alliance can not be very close, because of the very short, angular achenes and abruptly acute bracts of *greenei*. There is a close similarity in appearance between this species and certain subspecies of *C. viscidiflorus*, such as *pumilus*, but this is only superficial, as is indicated by the important differences in the achenes and style-branches already referred to. A comparison with *Petradoria pumila* has been suggested, and it is possible that there is some connection between these two species and also between them and the true Bigelovias, that is, *Chondrophora* of some botanists. *Petradoria*, however, is an herb with radiate heads, subulate style-appendages, and flattish 5-nerved achenes, while the true Bigelovias, also herbs, differ from *C. vaseyi* in a number of characters, as pointed out in the introduction (see p. 157). *Chrysothamnus vaseyi* is fairly consistent and non-variable, as is indicated by the fact that no segregate species or varieties have been described, with the single exception of *C. bakeri* Greene, and that apparently through an oversight, as already mentioned.

ECOLOGY AND USES.

Chrysothamnus vaseyi occurs in grassy mountain parks at altitudes of 6,000 to 8,500 feet, for the most part forming societies in the mixed prairie. In southwestern Colorado and adjacent Utah, it is associated with the sagebrush. It is a low undershrub, blooming during August and September.

It is unlikely that any considerable use can be made of *C. vaseyi*. The plants are doubtless browsed by sheep, but they are quite small and apparently nowhere abundant.

5. CHRYSOTHAMNUS VISCIDIFLORUS (Hooker) Nuttall, Trans. Am. Phil. Soc. II, 7:324, 1840. Plates 26 and 27.

Shrub of exceedingly diverse habit, 1 to 12 or even to 24 dm. high, commonly much branched from the simple base and forming a round-topped bushy plant; bark of the main stems brown, fibrous; twigs brittle, erect, leafy, glabrous or minutely puberulent, with a pale green or white bark, striate; leaves narrowly linear to oblong or lanceolate, often considerably twisted, acute or obtuse, 1 to 6 cm. long, 1 to 10 mm. wide, 1- to 5-nerved, rather rigid, glabrous or puberulent, viscidulous, the margins commonly scabrous; heads in terminal rounded or flat-topped cymes; involucre 5 to 8 mm. high; bracts

about 15, in poorly defined vertical ranks, broadly to linear oblong or lanceolate, acute or obtuse, firmly chartaceous, glabrous or minutely puberulent, the outer ones sometimes with a greenish thickened spot near the apex; flowers about 5; corolla tubular-funnelform, passing gradually from tube to throat, 4.5 to 7 mm. long, glabrous or only viscidulous; lobes 1 to 2 mm. long, erect to recurved-spreading, glabrous; anther-tips lanceolate, acute, about 0.5 mm. long; style-branches short-exserted, the lanceolate acutish appendage one-half to three-fourths as long as the stigmatic portion; achenes narrowed toward the base, 5-angled, 3 to 4 mm. long at maturity, densely to sparsely villous or silky; pappus slightly exceeding the corolla, of comparatively rigid sordid bristles. (*Crinilaria viscidiflora* Hooker, Fl. Bor. Am. 2:24, 1834.)

Plains and mountains of western North America, on poor soil, North Dakota to New Mexico, eastern California, British Columbia, and Montana.

SUBSPECIES.

The specific limits of *C. viscidiflorus* as here adopted are the same as those set by Gray in 1873 (Proc. Am. Acad. 8:645, as *Bigelovia douglasi*). From this assemblage of forms there have been published from time to time a total of 20 segregates, 16 of which have been accorded specific rank by those who use a narrow species concept. Even after these 17 proposals have been reduced to 10 subspecies, it is found that they pass so insensibly from one to another that they can not be satisfactorily defined. It is believed, however, that the following artificial key and the descriptions will enable one to place a majority of the specimens as they come to hand.

Key to Subspecies of *Chrysothamnus viscidiflorus*.

- Herbage densely puberulent, especially in the inflorescence, and the leaves 2.5 to 6 mm. wide. (Shrub either low or tall.)..... (a) *lanceolatus* (p. 181).
- Herbage glabrous or if pubescent the leaves then 2 mm. or less wide.
 Shrubs low, mostly 1 to 4 dm. high; leaves only 1 to 2 mm. wide.
 Bracts without distinctly thickened tips.
 Leaves linear, 1 to 2 mm. wide and the herbage glabrous..... (b) *pumilus* (p. 182).
 Leaves linear-filiform and only 1 mm. or less wide or if wider the herbage puberulent.
 Twigs and leaves densely puberulent.
 Leaves linear-filiform, 1 mm. wide..... (c) *puberulus* (p. 182).
 Leaves linear or linear-oblancoolate, 1 to 2 mm. wide..... (d) *humilis* (p. 182).
 Twigs and leaves glabrous..... (e) *stenophyllus* (p. 183).
 Bracts with a thickened green spot at tip..... (f) *elegans* (p. 183).
- Shrubs taller, mostly 4 to 24 dm. high; leaves 2 to 10 mm. wide (rarely narrower in *typicus*). Herbage glabrous.
 Bracts thin, without a distinct greenish subapical spot; plants of non-alkaline soils.
 Leaves 1 to 4 mm. wide, 1- to 3-nerved..... (g) *typicus* (p. 183).
 Leaves 4 to 10 mm. wide, 3- or 5-nerved..... (h) *latifolius* (p. 184).
 Bracts thicker (at least the outer ones) with a conspicuous greenish or brownish spot near the obtuse summit; plants of alkaline soils..... (i) *linifolius* (p. 184).

5a. *CHRYSOTHAMNUS VISCIDIFLORUS LANCEOLATUS* (Nuttall). Low or medium-sized shrub, 2 to 5 dm. high or rarely more; leaves broadly linear or linear-lanceolate, abruptly acute, 1.5 to 4 cm. long, 2.5 to 6 mm. wide, 3-nerved or 5-nerved, usually not twisted, bright green, at least the upper ones densely rough-puberulent; cyme small, compact, its branches densely puberulent; involucre 5 to 6.5 mm. high; bracts oblong, scarcely keeled, rather obtuse, without subapical spot; achenes densely strigose. (*C. lanceolatus* Nuttall, Trans. Am. Phil. Soc. II, 7:324, 1840.) Montana to Colorado, Nevada, Washington, and Idaho. Type locality, in the Rocky Mountains, toward the sources of the Platte. Collections: Helena, Montana, September 16, 1891, *Kelsey* (UC); Nowood Creek, Big Horn County, Wyoming, *Gooding 509* (Gr, NY, UC, US); Hayden, Routt County, Colorado, *Gooding 1791* (DS, Gr, NY, UC, US); Mackay, Custer County, Idaho, *Nelson and Macbride 1525* (Gr, NY, UC); Castle Gate, Utah, *Jones 5486i* (US); banks of the Columbia River at Grants, Oregon, September 15, 1887, *Howell* (UC, tall form); Coulee City, Washington, *Lake and Hull 732* (Gr, tall form).

5b. *CHRYSOTHAMNUS VISCIDIFLORUS PUMILUS* (Nuttall).—Shrub 1 to 5 dm. high; leaves linear, pungently acute, 2 to 4 cm. long, 1 to 2 mm. wide, 1-nerved or often 3-nerved, plane or tortuous, bright green, viscidulous or slightly glandular and the margins sometimes scabrid, otherwise glabrous; cyme small but sometimes lax, its branches glabrous; involucre 5 to 6 mm. high; bracts oblong, not keeled, the outer ones acute, the inner obtuse or submucronate, all devoid of subapical spot; achenes moderately or densely strigose. (*C. pumilus* Nuttall, Trans. Am. Phil. Soc. II, 7:323, 1840, in part, namely, as to the smooth plants.) Plains and foothills, Montana to Colorado, Utah, eastern California, and Washington. Type locality, on the borders of Lewis River and the Rocky Mountain Plains. Collections: Type collection, Rocky Mountains, Nuttall (Phila.); Sedan, Gallatin County, Montana, August 10, 1902, *W. W. Jones* (Gr); Wamsutter, southwestern Wyoming, August 18, 1894, *Wootton* (US); Laramie, southeastern Wyoming, *Nelson 6861* (NY); head of Poison Creek, Utah, *Rydberg and Carlton 7435* (NY); Bear Valley, San Bernardino Mountains, California, *Abrams 2889* (UC); Sonora Trail, easterly slope of the Sierra Nevada, California, *State Survey 1859* (UC, an unusual variation with broad involucre only 4.5 mm. high, the bracts very obtuse); near Hay Fork Post Office, Crook County, Oregon, *Leiberg 862* (US, intermediate to *stenophyllus*; leaves 1 to 1.5 mm. wide); Spokane, Washington, *Kreager 618* (NY); Pocatello, Idaho, July 30, 1889, *Greene* (UC).

5c. *CHRYSOTHAMNUS VISCIDIFLORUS PUBERULUS* (D. C. Eaton).—Low shrub, 2 to 5 dm. high; leaves narrowly linear, acute, 1.5 to 4 cm. long, rarely over 1 mm. wide, 1-nerved, often twisted or revolute, pale grayish-green, densely puberulent; cyme small, compact (occasionally looser and up to 7 cm. broad), its branches densely puberulent; involucre about 6 mm. high; bracts oblong, not keeled, obtuse or the outer barely acute, devoid of subapical spot; achenes densely strigose or silky. (*Linosyris viscidiflora* var. *puberula* Eaton, Bot. King's Expl. 158, 1871.) Montana to Colorado, eastern California, and British Columbia; abundant on dry hills and in dry streamways of Nevada. Type locality, near the Truckee and on the Hot Springs Mountains in western Nevada. Collections: Type collections, Truckee Valley, northwestern Nevada, July, 1867, *W. W. Bailey 569* (Gr, US), and West Humboldt Mountains, northwestern Nevada, 1,900 m. altitude, September, 1867, *Watson 569* (Gr); Crook Creek, Fremont County, Wyoming, *Goodding 524* (UC, nearly glabrous, distributed as *C. pumilus*); Sevier River, below Marysvale, Utah, *Rydberg and Carlton 6993* (NY, type of *C. marianus* Rydberg, minor variation 22); Caliente, Nevada, August 27, 1912, *Jones* (DS, UC); Lander County, Nevada, *Kennedy 4533* (DS, UC); Mesa west of Goldfield, Nevada, *Heller 10973* (DS, Gr, NY, UC, US); Reno, on dry banks near Truckee River, Nevada, *Hall 10547* (UC); Benton, Mono County, California, *Hall 10677* (UC); near Redmond, Oregon, September 29, 1918, *Whited* (UC); Crook County, Oregon, *Caville and Leiberg 664, 732, and 773* (US); Shoshone, Idaho, *Palmer 511* (NY).

5d. *CHRYSOTHAMNUS VISCIDIFLORUS HUMILIS* (Greene).—Low shrub, commonly only 1 to 2 but sometimes 3 dm. high; leaves linear or slightly oblanceolate, 1 to 2 cm. long, 1 to 2 mm. wide, 1-nerved or an occasional leaf with 3 nerves, usually plane, very pale or grayish-green, densely puberulent; cyme usually small and compact, sometimes rather loose and spreading, its branches densely puberulent; involucre 6 to 7 mm. high; bracts oblong, not keeled, obtuse, devoid of subapical spot; achenes densely strigose. (*C. humilis* Greene, Pittonia 3:24, 1896.) Arid plains of northeastern California and eastern Oregon, extending into western Nevada. Type locality, plains of the Truckee River, Nevada County, California. Collections: Type collection, sagebrush plains in Martis Valley, near Truckee, August, 1895, *Sonne* (Herb. Greene, NY, UC); Christmas Lake, Lake County, Oregon, *Leiberg 772* (DS, Gr, UC, US, leaves up to 3 cm. long);

Silvies Valley, eastern Oregon, *Cusick 2052* (UC, distributed as *Bigelovia douglasi* var. *pumila*); Carters, western middle Nevada, August 17, 1906, *Eastwood* (SF).

5e. *CHRYSOTHAMNUS VISCIDIFLORUS STENOPHYLLUS* (Gray).—Shrub 1 to 3 dm. high; leaves very narrowly linear or linear-filiform, rigidly acute, 1 to 3 cm. long, 1 mm. or less wide, 1-nerved, often tortuous, pale green, viscidulous or glandular, the margins usually scabrid and revolute, the faces glabrous; cyme small, compact, its branches glabrous; involucre 4 to 6 mm. high; bracts lance-oblong, strongly 1-nerved, not keeled, abruptly acute or mucronate, devoid of subapical spot; achenes densely strigose. (*Bigelovia douglasi* var. *stenophylla* Gray, Proc. Am. Acad. 8:646, 1873.) Dry ridges and stony slopes: Montana and Wyoming to New Mexico, southern California, eastern Oregon, and Idaho. Type locality, northwestern Nevada. Collections: Livingston, Montana, September, 1901, *Scheuber* (US); Centennial Valley, Wyoming, *Nelson 1847* (R, type of *C. pumilus varus* Nelson, minor variation 27); Point of Rocks, Wyoming, *Nelson 8142* (Gr, NY, US); type collection, Huntington Valley, at 1,830 m. altitude, northwestern Nevada, August, 1868, *Watson 566* (Gr, NY, US); San Antonio Desert, Nevada, *Purpus 6415*, in part (UC); Candelaria, western Nevada, *Shockley 310* (UC, US); vicinity of Cedar Hill, San Juan County, New Mexico, *Standley 7977* (US); Billings, Montana, *Jones 4512* (NY, US); Bear Valley, San Bernardino Mountains, California, *Grinnell 73* (UC, leaves 3-nerved and plants otherwise approaching subspecies *pumilus*); near Christmas Lake, southeastern Oregon, *Leiberg 779* (Gr, US); Big Butte Station, Idaho, *Palmer 488* (NY, US).

5f. *CHRYSOTHAMNUS VISCIDIFLORUS ELEGANS* (Greene).—Low shrub, 1 to 4 dm. high; leaves linear, pungently acute, 1.5 to 3 cm. long, 1 to 2 mm. wide, mostly 3-nerved, usually much twisted, green, scabrid-ciliolate, the upper also puberulent on the faces; cyme small, compact, its branches densely puberulent; involucre about 5 mm. high; bracts lanceolate, keeled, acute or the inner ones obtuse, with an obscurely thickened greenish or brownish subapical spot; achenes strigose. (*C. elegans* Greene, Erythra 3:94, 1895.) Plains and dry valleys, western Wyoming to Colorado, Arizona and Nevada; probably also in New Mexico, but all specimens seen from there and labeled *elegans* are glabrous and belong to subspecies *typicus*. Type locality, Gunnison Valley, Colorado. Collections: West of Evanston, Wyoming, September 13, 1919, *Hall* (CI); near Florissant, Colorado, September 2, 1919, *Clements* (CI); type collection, 1890, *Greene* (Herb. Greene, UC); Doyles, west central Colorado, *Baker 643* (DS, Gr, NY, UC, US, some leaves glabrous); between Gunnison and Parlin, Colorado, September 1, 1918, *Hall* (UC); Grand Cañon of the Colorado, Arizona, August, 1887, *Allen* (NY); Ely, Nevada, *A. E. Hitchcock 1219*, in part (US).

5g. *CHRYSOTHAMNUS VISCIDIFLORUS TYPICUS*.—Shrub usually 5 to 12 dm. high; leaves narrowly lanceolate or broadly linear, acute, 2 to 5 cm. long, 2 to 5 mm. wide (rarely only 1 mm.), 1-nerved in the original form, but often 3-nerved, either plane or twisted, bright green or bluish-green, the margins entire or scabrous-ciliolate, glabrous, viscid; cyme broad, open, its branches glabrous but glutinous; involucre 5 to 7 mm. high; bracts boat-shaped, not keeled, obtuse but commonly mucronate (acute in minor variation 29, *C. stenolepis* Rydberg), without subapical spot; achenes densely villous. (*Crintaria viscidiflora* Hooker, Fl. Bor. Am. 2:24, 1834.) Dry plains and hillsides, often among rocks, from Montana to Wyoming, Colorado, Arizona, eastern California, and Washington. Type locality, on the barren plains of the Columbia, from the Great Falls to the mountains, and along the Salmon River, Northwest America. Collections (with leaves mostly 3-nerved): Fridley, Montana, *Rydberg* and *Bessey 5044a* (Gr); Chimney Rock, Medicine Bow Mountains, Wyoming, *Nelson 2054* (R, type of *C. glaucus* Nelson, minor variation 16); Laramie Hills, Wyoming, *Nelson 5308* (Gr, NY,

UC, US, similar variation but with bracts of minor variation 29); Georgetown, southwestern Colorado, *Jones 744* (NY, US, same variation); near Grand Junction, Colorado, August 27, 1896, *Greene* (Herb. Greene, type of *C. leucocladus* Greene, minor variation 20); Salt Lake Valley, Utah, (NY, type collection of *Linosyris serrulata* Torrey, minor variation 42); Oquirrh Mountains, Tooele County, Utah, *W. W. Jones 479* (Gr); west of Buckskin Mountains, Arizona, *Jones 6063g* (US); Lee Cañon, Charleston Mountains, southwestern Nevada, *Heller 11087* (Gr, NY, US); San Jacinto Mountain, southern California, *Nevin* (DS); Truckee, California, *Heller 7189* (DS, NY, US); Bear Buttes Pass, Oregon, *Leiberg, 795* (Gr, UC); Fish Hook Ferry, Oregon, *Leiberg 926* (UC); Redmond, Oregon, September 29, 1918, *Whited* (UC, minor variation 38); Spokane County, Washington, *Suksdorf 25* (Gr); Mackay, Custer County, Idaho, *Nelson and Macbride 1559* (DS, Gr, UC); Flint Creek, Owyhee County, Idaho, *Macbride 490* (DS, R).

5h. CHRYSOTHAMNUS VISCIDIFLORUS LATIFOLIUS (Eaton).—Shrub 3 to 10 dm. high; leaves broadly elliptic or broadly lanceolate, obtuse but mucronate, 2 to 4 cm. long, 6 to 12 mm. wide, 3- or 5-nerved, plane, bright green, entire, glabrous or the margins merely scabrous; cyme either broad and lax or small and dense, its branches glabrous; involucre 6 to 7 mm. high; bracts not keeled, obtuse or acute, without subapical spot; achenes densely villous. (*Linosyris viscidiflora* var. *latifolia*, Eaton, Bot. King's Expl. 157, 1871.) Southern Idaho and western Utah across Nevada to eastern California and Oregon. Type locality, mountains at the head of Humboldt River, Nevada, at an altitude of 2,000 to 2,200 meters. Collections: Type collection, September, 1868, *Watson 568* (Gr, NY, US); West Humboldt Mountains, Nevada, *Heller 10626* (DS, Gr, UC, US); Gold Creek, Elko County, Nevada, *Kennedy 4398* (UC); Modoc County, California, *Gilman 520* (UC).

5i. CHRYSOTHAMNUS VISCIDIFLORUS LINIFOLIUS (Greene).—Shrub 8 to 24 dm. high; leaves lanceolate to oblong-lanceolate, gradually acute, 2 to 5 cm. long, 4 to 8 mm. wide, mostly 3-nerved, plane, bright green, glabrous, entire or only obscurely scabrous on the margins; cyme broad, lax, its branches glabrous; involucre 5 to 6 mm. high; bracts oblong, not keeled, obtuse, at least the outer with a thickened subapical spot, this green but drying to brown; achenes densely villous. (*C. linifolius* Greene, Pittonia 3:24, 1896.) On low, alkaline lands, Wyoming, western Colorado, Utah, and New Mexico. Type locality, in moist, alkaline soil, plentiful along a streamlet near Rock Springs, Wyoming. Collections: Type collection, August 9, 1895, *Greene* (Herb. Greene); Bitter Creek, Wyoming, *Nelson 4143* (UC); Grand Junction, Colorado, *Baker 924* (Gr, NY, UC, US); southeastern Utah, *Rydberg and Garrett 9437* (UC); Rabbit Valley, Utah, *Ward 573* (Gr); Cainville, Utah, *Jones 5698* (NY); near Farmington, San Juan County, New Mexico, *Standley 6903* (US).

MINOR VARIATIONS AND SYNONYMS.

1. BIGELOVIA DOUGLASI Gray, Proc. Am. Acad. 8:645, 1873.—*C. viscidiflorus typicus*.
2. B. DOUGLASI VAR. LANCEOLATA Gray, Syn. Fl. 1:140, 1884.—*C. viscidiflorus lanceolatus*.
3. B. DOUGLASI VAR. LATIFOLIA Gray, Proc. Am. Acad. 8:646, 1873.—*C. viscidiflorus latifolius*.
4. B. DOUGLASI VAR. PUBERULA Gray, l. c.—*C. viscidiflorus puberulus*.
5. B. DOUGLASI VAR. PUMILA Gray, Syn. Fl. 1:140, 1884.—*C. viscidiflorus pumilus*.
6. B. DOUGLASI VAR. SERRULATA Gray, Proc. Am. Acad. 8:646, 1873.—Same as *Linosyris viscidiflora serrulata*, q. v.
7. B. DOUGLASI VAR. SPATHULATA Jones, Proc. Calif. Acad. II, 5:690, 1895.—Authentic material not seen, but apparently a form of *C. viscidiflorus lanceolatus* with short lower leaves.
8. B. DOUGLASI VAR. STENOPHYLLA Gray, l. c.—*C. viscidiflorus stenophyllus*.
9. B. DOUGLASI VAR. TORTIFOLIA Gray, l. c.—*C. viscidiflorus* and its subspecies. First applied to plants similar to subspecies *typicus*, but with the leaves twisted upon themselves, later extended by various writers to other subspecies in which this trait was noticed and even used by some as of specific value. The tendency toward torsion is sometimes indicated only by an undulation of the margins and all grades are encountered from

this to extreme cases in which a blade will make two complete revolutions on its axis. Since this character is thus variously developed and fails to run parallel with any other tendency, and since it is encountered in all of the subspecies (with the possible exception of the firm-leaved *linifolius*), it is not here considered as of diagnostic value. Especially misleading is the common custom of identifying any specimen with tortuous leaves as "*tor-tifolius*," quite regardless of its other features.

10. B. GLAUCA Schumann, Just's Bot. Jahresb. 26:375, 1900.—Based upon *C. glaucus*, and therefore a form of *C. viscidiflorus typicus*. (See No. 16 of this list.)

11. B. LANCEOLATA Gray, l. c., 639, 1873.—*C. viscidiflorus lanceolatus*.

12. B. LINIFOLIA Nelson, First Rept. Fl. Wyo. 123, 1896.—*C. viscidiflorus linifolius*.

13. B. VISCIDIFLORA De Candolle, Prodr. 7:279, 1838.—Based upon *Crinaria viscidiflora* Hooker, No. 39 of this list.

14. CHRYSOTHAMNUS DOUGLASSI Clements and Clements, Rocky Mt. Fls. 266, 1914.—*C. viscidiflorus*, including several of the subspecies.

15. C. ELEGANS Greene, Erythra 3:94, 1895.—*C. viscidiflorus elegans*.

16. C. GLAUCUS Nelson, Bull. Torr. Club 25:377, 1898.—A glaucous-leaved form or state of *Linosyris viscidiflora serrulata* Torrey, which in turn is here considered as not separable from *C. viscidiflorus typicus* (see No. 42 of this list). The peduncles are sometimes obscurely puberulent. Old specimens are less glaucous, according to Nelson (Bot. Gaz. 28:376, 1899). The heads in the type material are 4-flowered, as originally described, but they are often 5-flowered, as in Nelson's 5308 from Laramie, Wyoming, and in Palmer's 257 from Wadsworth, Nevada, both of which are referable here. The type is Nelson 2054 from Chimney Rock, Medicine Bow Mountains, Wyoming.

17. C. HUMILIS Greene, Pittonia 3:24, 1896.—*C. viscidiflorus humilis*.

18. C. LANCEOLATUS Nuttall, Trans. Am. Phil. Soc. II, 7:324, 1840.—*C. viscidiflorus lanceolatus*.

19. C. LATIFOLIUS Rydberg, Bull. Torr. Club 33:152, 1906.—*C. viscidiflorus latifolius*.

20. C. LEUCOCLADUS Greene, Pittonia 5:59, 1902.—A form of *C. viscidiflorus typicus* with exceptionally large heads and rather narrow leaves. Said by Greene to be near *elegans*, but the type in his herbarium does not have the green thickenings on the bracts characteristic of that subspecies. The involucre in the type specimen are 7 to 8 mm. long, which is exceptionally large, even for *typicus*; leaves 2 mm. wide; stems of unknown height, the portion preserved being 3 dm. long, but consisting only of leafy flowering branches. Type locality, near Grand Junction, Colorado.

21. C. LINIFOLIUS Greene, Pittonia 3:24, 1896.—*C. viscidiflorus linifolius*.

22. C. LIRIANUS Rydberg, Bull. Torr. Club 37:131, 1910.—The type specimens at the herbarium of the New York Botanical Garden appear to be identical with *C. viscidiflorus puberulus*, except that the achenes are only sparsely pubescent or nearly glabrous. The original description of the leaves and bracts applies exactly to the common form of *puberulus*. The type locality is along the Sevier River, below Marysvale, Utah. Most of the material under this name at the United States National Herbarium has strongly pubescent achenes and belongs in part to *C. viscidiflorus stenophyllus*, the remainder being chiefly *C. v. elegans*.

23. C. PUBERULUS Greene, Erythra 3:93, 1895.—*C. viscidiflorus puberulus*.

24. C. PUMILUS Nuttall, Trans. Am. Phil. Soc. II, 7:323, 1840.—*C. viscidiflorus pumilus*.

25. C. PUMILUS β EUTHAMOIDES Nuttall, l. c.—A form of *C. viscidiflorus pumilus* described as with "involucre ovate, the scales ovate and short." The type locality was not indicated as different from that of *pumilus* and the type specimens have not been found. Perhaps similar to this, if not identical, is a plant from the Sonora Trail, east side of the Sierra Nevada, California (State Survey 1859, UC), in which the thick involucre is scarcely 5 mm. high and the scales very wide, the inner ones exceptionally obtuse. This may represent a subspecies distinct from *pumilus*.

26. C. PUMILUS var. LATUS Nelson, Bot. Gaz. 54:413, 1912.—An exceptionally broad leaved form of *C. viscidiflorus lanceolatus*, the leaves 4 to 8 mm. wide in the types. Very distinct from *pumilus*, not only in the much wider leaves, but also in the fine but dense pubescence of the twigs, peduncles, and foliage. The type is from Ketchum, Blaine County, Idaho, Nelson and Macbride 1236 (R).

27. C. PUMILUS var. VARUS Nelson, Bot. Gaz. 28:375, 1899.—*C. viscidiflorus stenophyllus*. The types of these have been closely compared and no difference found except that the type of *varus* is a fresher and greener specimen. In the New Rocky Mountain Manual, by Coulter and Nelson, the description of *varus* is extended to include *C. elegans* Greene, but this subspecies differs markedly in its densely puberulent inflorescence, green-tipped bracts, and wider leaves. The type of *varus* is Nelson 1847 (R) from Centennial Valley, Wyoming.

28. C. SERRULATUS Rydberg, Bull. Torr. Club 33:152, 1906.—The same as No. 42 of this list.

29. C. STENOLEPIS Rydberg, l. c., 37:131, 1910.—A perplexing variation apparently referable to *C. viscidiflorus typicus*, but differing in the narrower and very acute involucre bracts. The type specimen (Pass Creek, Bridger Mountain, Montana, Engelmann, NY) has leaves only 2 to 4 mm. wide and is described as a low shrub, 2 to 3 dm. high. The whole aspect of the plant, with its narrow, twisted, incurved leaves suggests that it may be the response to a cold, dry environment. There should be considered in this connection also Nelson 5308 (as to the glabrous plants, the pubescent ones being subspecies *lanceolatus*) from the Laramie Hills, Wyoming, and

distributed as *C. glaucus* Nelson. These specimens have the very acute bracts of *stenolepis*, but the leaves are mostly flat, 3 mm. wide, and the shrubs were not reduced in size. Their combination of characters indicates an intermediate stage. *C. stenolepis* is worthy of detailed studies in the field, where it may be found that, at least as far as the type form is concerned, it is a wide-leaved and narrow-bracted variation from subspecies *pumilus*.

30. *C. STENOPHYLLUS* Greene, *Erythea* 3:94, 1895.—*C. viscidiflorus stenophyllus*.
31. *C. TORTIFOLIUS* Greene, *Fl. Fran.* 368, 1897.—*C. viscidiflorus* and its subspecies, as noted under No. 9.
32. *C. VISCIDIFLORUS* Nuttall, *Trans. Am. Phil. Soc.* II, 7:324, 1840.—*C. viscidiflorus typicus*.
33. *C. VISCIDIFLORUS* var. *LANCÉOLATUS* Greene, *Erythea* 3:95, 1895.—*C. viscidiflorus* subspecies *lanceolatus*.
34. *C. VISCIDIFLORUS* var. *LATIFOLIUS* Greene, l. c. 96.—*C. viscidiflorus* subspecies *latifolius*.
35. *C. VISCIDIFLORUS* var. *SERRULATUS* Greene, l. c.—The same as No. 42 of this list.
36. *C. VISCIDIFLORUS* var. *TORTIFOLIUS* Greene, l. c.—Various subspecies of *C. viscidiflorus* are included under this name. (See No. 9.)

37. *C. VISCIDIFLORUS* *TYPICUS*, but with comparatively short and very green leaves. This form grows on sandy flats near Chambers Station, northeastern Arizona (*Hall 11151, 11152*, UC). The plants are 4 to 7 dm. high, woody to the top, the twigs erect and fastigiately crowded; leaves 1 to 2 mm. wide, 1 to 2 cm. long, glabrous and green; involucre 6 mm. high; bracts in distinct vertical rows, acute, greenish but without definite spot. Apparently distinct from typical *viscidiflorus*, but the differences are superficial. The plants show evidence of top-browsing, which may account for their fastigiate habit, and the reduction in leaf may be the result of unfavorable soil conditions.

38. *C. VISCIDIFLORUS* *TYPICUS*, but with leaves only 0.5 to 1 mm. wide. This variation is of rare occurrence and may be more than a response to ecologic conditions. The extreme form is represented by a collection from the Snake River sands north of Hagerman, Idaho, September 18, 1919, *Hall* (UC). A complete series of intergrading forms is not at hand but as intermediates may be cited: 8 km. southwest of Redmond, Oregon, September 29, 1918, *Whited* (UC), and Grizzly Butte Spur, eastern Oregon, *Leiberg 855* (UC).

39. *CRINITARIA VISCIDIFLORA* Hooker, *Fl. Bor. Am.* 2:24, 1834.—The type of the species, therefore *C. viscidiflorus typicaria*.

40. *LINOSYRIS LANCEOLATA* Torrey and Gray, *Fl. N. Am.* 2: 233, 1842.—*C. viscidiflorus lanceolatus*.

41. *L. PUMILA* Gray, *Pl. Wright.* 2:80, 1853.—*C. viscidiflorus pumilus*.

42. *L. SERRULATA* Torrey, *Stansbury Rep.* ed. 1:389, 1851.—The form of this as originally described from specimens from the Valley of Salt Lake differs from *C. viscidiflorus typicus* only in the scabrid or stiffly short-ciliate leaf-margins. There are numerous intermediate forms in which the margins vary from smooth to strongly scabrid, so that it becomes impossible to draw a line between *typica* and *serrulata*. Moreover, every glabrous subspecies includes forms with scabrid-margined leaves, as well as others in which the margins are smooth. Thus, the recognition of this as a subspecific character would necessitate the erection of at least 5 new subspecies. A good example of *serrulata* is *Leiberg 894*, from eastern Oregon. One of the intermediate forms is *Butler 1731*, from Siskiyou County, California, in which collection the leaves are mostly scabrid on the margins, but only minutely so and for only a portion of the distance.

43. *L. VISCIDIFLORA* Torrey and Gray, *Fl. N. Am.* 2: 234, 1842.—*C. viscidiflorus*.

44. *L. VISCIDIFLORA* var. *LATIFOLIA* Eaton, *Bot. King's Expl.* 157, 1871.—*C. viscidiflorus latifolius*.

45. *L. VISCIDIFLORA* var. *PUBERULA* Eaton, l. c., 158, 1871.—*C. viscidiflorus puberulus*.

46. *L. VISCIDIFLORA* var. *SERRULATA* Torrey in *Stansbury Rep.*, ed. 2:389, 1853.—A reduction of *Linosyris serrulata*, which see in this list. The dates here given for the two editions of *Stansbury's Report* are as indicated by Coville (*Bull. Torr. Club* 23:137, 1896).

RELATIONSHIPS.

The only species to which *C. viscidiflorus* is closely related is *C. greenei*, but there can be no doubt as to the close affinity between these two. The reasons for considering them as distinct are stated under the latter species. *C. vaseyi* has been frequently compared with varieties of *viscidiflorus*, but its achenial characters indicate that the connection is not very close, as has been already pointed out (p. 180). There is no evidence which permits a linking of *viscidiflorus* with any species of the other sections of *Chrysothamnus*.

Evolutionary forces have been operating upon *C. viscidiflorus* for a long period of time, as indicated by the large number of variations that have been produced. However, judging from the numerous intergrades that are constantly being found, it seems just as evident that the resulting variations have been held together in one rather close major species, perhaps through interbreeding where their ranges meet or overlap. Absolute intergrading is, of course, almost impossible to demonstrate without a close genetic

analysis, but the nature of the distinguishing characters is such that it is believed to exist. At any rate, the constant characters, if they occur at all, are so minute and unite in so perplexing an array of combinations that the use of more than the most obvious of them in taxonomic studies would lead only to hopeless confusion. One notable exception to this is the presence or absence of a minute but dense puberulence on the upper portions of the plants, particularly on the faces of the upper leaves and on the branches of the inflorescence. When this is present at all it is usually very evident and in two cases it occurs in subspecies each of which is matched almost exactly, except for this character, by another of a similar geographic distribution. These two pairs of subspecies are: *steno-phyllus* (glabrous) corresponding to *puberulus* (puberulent), and *pumilus* (glabrous) corresponding to *lanceolatus* (puberulent). This condition is very suggestive of an origin of the glabrous varieties through mutation from their respective pubescent counterparts, although an origin through gradual variation followed by isolation and a subsequent reunion geographically after the characters had become fixed is not an excluded explanation. A third pair of forms differing only by this same character is indicated by a collection of *typicus* made by Grinnell 6 km. east of Jackass Spring, in the Panamint Mountains of eastern California (Univ. Calif. Herb. 201227). In this collection one detached branch is perfectly glabrous, while the other two, which match the first in every other respect, are densely puberulent on the leaves and peduncles. A recurrence of this variation is found in a collection of *typicus* from Mono Lake, California (*Bolander 6142*, in part; Univ. Calif. Herb. 31174 and 31175). The puberulence here referred to is not to be confused with a scabrid or subciliate pubescence which often occurs on the margins of the leaves and is quite erratic in its behavior. Since the criteria can be most conveniently discussed under the subspecies in which they occur, these are here taken up seriatim. The accompanying diagram (fig. 26) has been prepared as an aid in elucidating the probable relationships between the various subspecies, which discussion can best be given along with that of the criteria.

The subspecies *lanceolatus* comes the nearest of all to representing the ancestral type of the species. This conclusion is based upon the assumption that the green-leaved forms preceded the pale-leaved ones, that both extremely wide and extremely narrow leaves have followed as modifications from medium-sized leaves, and that both lack of pubescence and thickening of the bracts are derived characters. If these assumptions are correct, then *lanceolatus* is the biologic type instead of *typicus*, which, however, must still be retained as the nomenclatorial type. The connection between the two is indicated by occasional specimens having all the characters of the former, except that they are robust and tall as in *typicus* (Black Cañon, Colorado, *Baker 685*). In order to provide for these more robust plants it is necessary to expand somewhat the usual conception of *lanceolatus* by admitting a considerable degree of variation in this regard. The type specimens give no clue as to the size and Nuttall's original characterization of "a moderate-sized shrub" is no more helpful. In the above citation of specimens under *lanceolatus* all are of rather low stature, mostly under 4 dm., except those otherwise indicated. If the tall plants really are distinct, they form another group close to *typicus*, but differing in the close although minute puberulence. Experimental evidence is here much needed. The origin of the other subspecies from *lanceolatus* has not proceeded from a single point. On the contrary, it seems that the primitive form has produced others through variations in several directions. One of these, which represents the end-point of one series of variations and is still in close contact with *lanceolatus* is *pumilus*. The origin of this from *lanceolatus*, or vice versa, by mutation has been already suggested (p. 187). It is apparently much less common than this and occurs farther from the center of distribution of the species. Both of these facts, as well as its glabrous nature, would seem to indicate that *pumilus* is the derivative, in case either one has arisen by mutation from the other.

Taxonomically, this is the type species of the genus, since it was the first one published by Nuttall under his new genus, *Chrysothamnus*, in 1841. It was antedated, however, by Hooker's *Crinitaria viscidiflora*, so that this specific name takes precedence when the two are united into one major species.

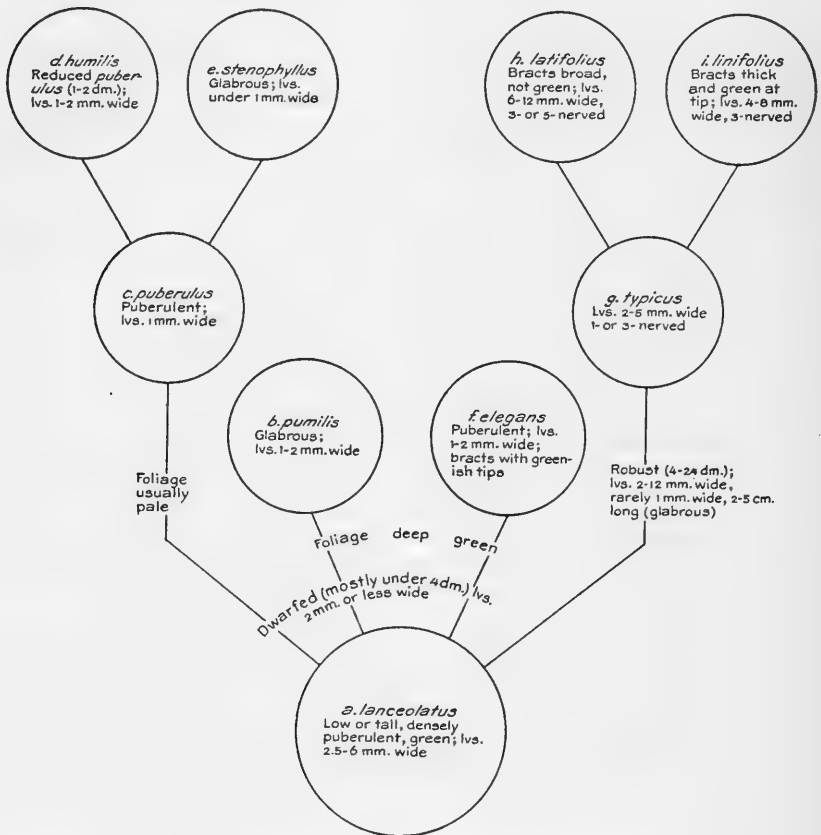


FIG. 26.—Phylogenetic chart of the subspecies of *Chrysothamnus viscidiflorus*.

The next group centers around subspecies *puberulus*, through which they are connected with *lanceolatus*. All are characterized by a peculiarly pale, usually grayish or yellowish-green herbage, although this feature is not sufficiently constant to be dependable in taxonomic work. They are most plentiful in the Great Basin area. *Puberulus* has given rise, perhaps by mutation as already noted, to the glabrous *stenophyllus* and by gradual variation to *humilis*. This latter is a reduced far-western type of high altitudes. While its distinguishing characters do not seem to possess much taxonomic value, yet the appearance of the plants is so unlike that it seems best to retain the form, at least provisionally, as a distinct subspecies.

The subspecies *elegans* has every appearance of an ecologic derivative of *lanceolatus*, from which it is best distinguished by its narrower leaves. The presence of the thickened spot on the bracts is not always easily made out, since it varies much in the degree of development. It recurs elsewhere in the species only in *linifolius*, but it does not indicate a close genetic connection between these two subspecies, as is shown by their divergence in other characters. On the contrary, *elegans* represents a closed circle in that it has given rise to no other variations of importance. The specimens indicated as the types at the Greene Herbarium are mounted on two sheets. Unfortunately, one of these (26610) bears also a piece of *C. vaseyi*, positively identified by its essentially glabrous, elongated, 10-ribbed achenes and also by the non-tortuous leaves. This specimen is the lower middle one of the three on the sheet. The other two have achenes and foliage as described for *elegans* and, together with the other sheet, all of the specimens of which are genuine, may be taken as the types.

As is so often the case, the first form described under the species is not the most primitive. Therefore, subspecies *typicus* is represented on one of the diverging lines of the diagram. The type specimen is not now accessible to us, but it is fairly well defined in the original description, which in full is as follows:

C. viscidiflora; glaberrima, foliis lineari-lanceolatis rigidis integerrimis acutissimis uninerviis basi angustatis, floribus fastigiato-corymbosis, pedunculis foliolosis, involucri glutinosi cylindrici 5-flori foliolis imbricatis oblongis exterioribus minoribus (Hooker, Fl. Bor. Am. 2:24, 1834.).

Hooker then refers to the plant as a common shrub, 6 to 12 dm. high, and in comparing it with *Chrysocoma graveolens*, he states that it differs in the leaves being only single-nerved and the branches quite glabrous, not in the least pulverulently tomentose. This identifies the type very satisfactorily with a common form of the Northwest, except that in plants which correspond in every other way the leaves are usually but not always 3-nerved. This is not taken as a matter of importance, for the character is extremely variable and the two additional nerves are often so faint as to be easily overlooked. In order to avoid the setting up of a new subspecies, it is necessary also to include in *typicus* a rare form with narrowly linear instead of linear-lanceolate leaves, as indicated by minor variation 38.

Close to the type form, but differing in its wider leaves with a larger number of veins, is subspecies *latifolius*. The center of its distribution is northeastern Nevada, whence comes the extreme form with very wide elliptic leaves. The smooth green foliage and general appearance suggest *linifolius*, but the bracts are much thinner and the plants probably are not alkali-tolerant. It is more likely a direct offshoot from *typicus*.

The robust habit, large, thick leaves, and thickened spot on the bracts render *linifolius* the most striking of all the subspecies when it occurs in its extreme development. But in all of these characters, which are doubtless the result of its strongly alkaline habitat, it intergrades into *typicus* and *latifolius*. This may be noted in the vicinity of Point of Rocks, Wyoming. Here the plants growing on alkaline soil have all of the characters of *linifolius*, while by selecting areas where the alkali is less abundant, such as those lying to the west, all gradations in the characters may be noted until the plants are in no way distinguishable from *typicus*.

ECOLOGY.

The low forms of *Chrysothamnus viscidiflorus* constitute typical societies in the southwestern portions of the mixed prairie and throughout the sagebrush association of the Great Basin, while the taller ones, such as *typicus*, are rather to be regarded as consociations of the sagebrush. The former are also abundant in cedar savannah. *Pumilus*, *lanceolatus*, and *serrulatus* are the common subspecies of the mixed prairie, and often become controlling as a result of overgrazing. In this respect they closely resemble

Gutierrezia, with which they are often associated. *Pumilus* is also very common in sagebrush areas, and is often dominant in cleared areas. *Puberulus* and *stenophyllus* are chiefly found in the sagebrush association, especially on the poorer soils and in disturbed areas.

Linifolius is the only subspecies to grow regularly in strongly alkaline soil, even being associated on alkali flats and creek bottoms with *Sarcobatus*. However, *pumilus* is frequently found with such halophytes as *Atriplex confertifolia* and *A. nuttalli*, and *stenophyllus* may occur with *A. confertifolia*, *Sporobolus airoides*, and others.

USES.

All of the variations of *C. viscidiflorus* are browsed to a limited extent by sheep and perhaps also by cattle. Some stockmen report the plants as of no value, but this applies only to districts where other feed is fairly plentiful. Throughout the Great Basin, and especially from Inyo County, California, to eastern Washington, the shrubs furnish good sheep-feed, the animals relishing especially the flowering shoots. Three of the subspecies have been examined for rubber with negative results. In *linifolius*, however, rubber was found to be present to the extent of 1 per cent of the dry weight. This is not sufficient to be of more than passing interest. It is perhaps correlated with the alkaline habitat, since in *C. nauseosus* it is found that the highest rubber-content occurs in those forms which inhabit alkaline soils. If this is a law of general application in the genus, then the other subspecies of *C. viscidiflorus* could not be expected to yield rubber, since none of them grows in alkaline situations.

6. CHRYSOTHAMNUS GREENEI (Gray) Greene, Erythea 3:94, 1895. Plate 28.

Shrub 1 to 3 dm. high, bushy, much branched from the base; bark of basal portion brown, fibrous, peeling off in sheets; twigs very brittle, erect and congested, glabrous, at first green but soon white and shining; leaves narrowly linear or nearly filiform, pungently acute, 1 to 3.5 cm. long, 0.3 to 1.2 mm. wide, 1-nerved, rigid, either nearly glabrous or only sparsely and minutely scabrous-ciliate, more or less viscidulous; heads in terminal rounded or flat-topped cymes; involucre 5 to 7 mm. high; bracts 15 to 20, in 5 poorly defined vertical ranks, oblong, abruptly narrowed to a subulate tip or the outer ones more gradually attenuate, glabrous but viscidulous; flowers 5; corolla (whitish or yellow) tubular-funnelform, the throat abruptly dilated, 4 to 4.5 mm. long, glabrous; lobes lanceolate, 0.8 to 1.3 mm. long, spreading, glabrous; anther-tips lanceolate, acute, about 0.5 mm. long; style-branches exserted, the appendage much shorter than the stigmatic portion; achenes nearly prismatic, about 3 mm. long when mature, densely appressed-villous; pappus rather scant and rigid, scarcely equaling the corolla, dull white. (*Bigelovia greenei* Gray, Proc. Am. Acad. 11:75, 1876.)

Plains and low hills from southern Colorado to New Mexico, Arizona, Nevada, and Utah.

SUBSPECIES.

C. greenei exhibits a tendency to break up into two divergent groups of forms, as follows:

Key to the Subspecies of *Chrysothamnus greenei*.

- Leaves mostly 2.5 to 3.5 cm. long, 1 mm. or more wide. (a) *typicus* (p. 190).
 Leaves mostly less than 2 cm. long, less than 1 mm. wide. (b) *filifolius* (p. 191).

6a. CHRYSOTHAMNUS GREENEI TYPICUS.—Plant low and stout; leaves narrowly linear, usually 2 to 3.5 cm. long and about 1 mm. wide, usually dark green; heads in loose cymes, mostly on distinct peduncles; involucre 5.2 to 7.0 mm. high, 2 to 3 mm. broad. (*C. greenei* Gray, Proc. Am. Acad. 11:75, 1876.) Southern Colorado, Utah, and eastern Nevada. Type locality, Huerfano Plains, southern part of Colorado. Collections (these are cited in table 19).

6b. *CHRYSOTHAMNUS GREENEI FILIFOLIUS* (Rydberg).—Plant often taller and more slender, bushy; leaves linear-filiform, usually 1 to 2 cm. long and less than 1 mm. wide, often pale green; heads in compact cymes, sessile or subsessile; involucre 5 to 6 mm. high, 2 mm. broad. (*C. filifolius* Rydberg, Bull. Torr. Club 28:503, 1901.) Range of the species. Type locality, Granite, Colorado. Collections: Black Rock, New Mexico, July 23, 1906, Wooton (US); Navajo Indian Reservation, Arizona, Standley 7365 (US). (Additional collections are indicated in table 19.)

MINOR VARIATIONS AND SYNONYMS.

1. *BIGELOVIA GREENEI* Gray, Proc. Am. Acad. 11:75, 1876.—*C. greenei typicus*.
2. *CHRYSOTHAMNUS FILIFOLIUS* Rydberg, Bull. Torr. Club 28:503, 1901.—*C. greenei filifolius*.
3. *C. LARICINUS* Greene, Pittonia 5:110, 1903.—This appears to be *C. greenei* and probably subspecies *filifolius*. The type specimen can not be found at present.
4. *C. PUMILUS* var. *ACUMINATUS* Nelson, Bot. Gaz. 28:376, 1899.—*C. greenei typicus*. Type locality, La Veta, Colorado.
5. *C. SCOPARIUS* Rydberg, l.c., 504.—*C. greenei typicus*. Reduced by Rydberg (Fl. Rocky Mts. 856, 1917). Type locality, mesas, La Veta, Colorado.

RELATIONSHIPS.

In Gray's synopsis this species was placed next to *ceruminosus* on the strength of the similarly tipped involucre bracts. This single similarity can not outweigh all of the other evidence, such as the strongly pannose flexuous twigs and strongly keeled bracts of *ceruminosus*, which plainly assign this latter to subspecies rank under *C. nauseosus*. *C. greenei*, on the other hand, is of close affinity with *C. viscidiflorus*, and the specimens in herbaria are often ticketed as one of the varieties of that polymorphous species, usually as variety *stenophyllus*. In common with these it has the low bushy habit, stiff very brittle white-barked stems, similar involucre, and comparatively short style-appendages. It is probable that its similarity to *stenophyllus* is more than superficial and indicates a close genetic relationship. However, it is well separated on the strength of its attenuate or abruptly tipped involucre bracts and of the comparatively sharp distinction between the tube and throat of the corolla. Furthermore, the style-appendages in *greenei* are shorter in proportion to the length of the stigmatic portion than in all but an occasional example of any subspecies of *viscidiflorus*. In this respect it resembles *C. vaseyi*, as will be further discussed under that species.

The division of *greenei* into two subspecies is here given with some question as to its value, but it follows the tendency of recent writers to give *filifolius* specific rank. The first of these was Rydberg, who distinguished the segregates only on size of leaf and heads and on the color of the former. This was done in distinguishing his new *filifolius* from *scoparius* (Bull. Torr. Club 28:503, 1901), the latter since reduced by Rydberg to *greenei* (Fl. Rocky Mts. 856, 1917). The gradation in these characters is indicated in table 19, in which the length of the longest leaves, average width of mature middle leaves, and the average height of fully developed involucre is given.

From table 19, which includes all of the available material, it is seen that the specimens may be divided into two groups based upon size of leaf and that the group with the smaller leaves inhabits chiefly Utah and Nevada, a more arid region than Colorado, whence come most of the collections of the larger-leaved group. The size of the involucre is seen to vary irrespective of the leaves, although there is a tendency toward reduced involucre in *filifolius*. Rydberg described *typicus* (under the synonym *scoparius*) as of lighter color than the other, but the tendency is the other way, that is, the paler plants usually belong to the more westerly *filifolius*. This is in keeping with the usual reduction in chlorophyll as a species passes into the more arid Great Basin area.

Additional characters have been introduced by Wooton and Standley (Contr. U. S. Nat. Herb. 19:661, 1915). They assign short-pedunculate or sessile heads subtended by

long bracts to *filifolius*. This is useful in that it calls attention to the fact that this narrow-leaved, small-headed form has a more compact inflorescence than *typicus*. However, the individual heads in the latter are also sometimes sessile (for example, *Purpus*, 6264), while the variation in the length of the subtending bracts does not vary in unison with other characters. Since the two forms occupy the same general territory, careful field observations should be made to see if they are not entirely ecologic in their origin.

TABLE 19.—Variation in the subspecies of *Chrysothamnus Greenei*.

	Herbarium.	Ratio of length of style-appendage to total branch.	Leaves.		Height of involucre.
			Length.	Width.	
<i>Subspecies typicus:</i>					
Huerfano Plains, Colo., 1873, <i>Greene</i> ¹	Gr.	per cent.	mm.	mm.	mm.
Twin Lakes, Colo., 1878, <i>Jones</i>	Gr.	3.5	1.0	5.8
San Luis Valley, Colo., <i>Hall 11096</i>	CI	40.0	3.2	1.0	6.0
La Veta, Colo., <i>Vreeland 698</i> ²	NY	40.0	2.5	1.1	5.2
La Veta, Colo., Aug. 21, 1897, <i>Crandall</i> ³	R	30.0	3.3	1.2	6.5
West Paradox, Colo., <i>Payson 2322</i>	UC	33.0	3.0	1.0	5.5
Southwestern Utah, <i>Rydberg and Garrett 9677</i>	NY	3.5	1.1	5.2
Panaca, Nev., Sept. 15, 1912, <i>Jones</i>	UC	2.5	1.0	7.0
<i>Subspecies filifolius:</i>					
Granite, Colo., <i>Clements 390</i> ⁴	NY	33.3	2.8	0.9	6.0
Thurber, Utah, <i>Jones 5706</i>	UC	31.6	2.3	0.3	5.7
Lund, Utah, <i>Hall 10785</i>	UC	30.0	2.0	1.0	5.5
Pancake Range, Nev., <i>Purpus 6397</i>	UC	36.1	1.8	0.5	4.8
Fish Creek, Nev., <i>Sargent</i>	Gr.	1.8	0.6	6.0
			1.2	0.4	5.0

¹ Type of *Chrysothamnus Greenei* Gray.² Type of *C. scoparius* Rydberg, minor variation 5.³ Type of *C. pumilus acuminatus* Nelson, minor variation 4.⁴ Type of *C. filifolius* Rydberg = *C. Greenei filifolius*.

ECOLOGY AND USES.

Chrysothamnus Greenei is a low shrub, blooming during August and September. It forms a climax society in mixed prairie in the San Luis Valley, Colorado, while in Utah it sometimes forms a subclimax consociety on sandy alkaline plains. It is greatly increased by overgrazing, and hence is frequently associated with *Bouteloua gracilis* in short-grass areas.

There is no specific information at hand regarding the value of this plant. As a browse shrub it is probably of about the same value as the smaller subspecies of *C. viscidiflorus*.

7. CHRYSOTHAMNUS ALBIDUS (Jones) Greene, *Erythea* 3:107, 1895. Plate 28.

Shrub 3 to 10 dm. high, fastigiate branched; twigs brittle, erect, congested, very leafy, glabrous but very resinous-viscid, imparting a resinous stain to paper, at first green and striate, later with a white smoother bark; leaves flat and 1 to 2 mm. wide but drying to filiform through revolution of the margins, pungently acute, 2 to 4 cm. long, 1-nerved, moderately rigid, glabrous but with a copious resinous exudate, the surface with small pits; heads in small congested cymes which are either simple or themselves loosely cymose; involucre 7 to 9 mm. high; bracts about 15, in very obscure ranks, lance-oblong, all but the innermost abruptly narrowed to a long setiform usually curved tip, glabrous, glutinous, the thin margins somewhat erose, the tip sometimes herbaceous; flowers 5 to 6 (whitish or at least pale yellow); corolla with slender tube and abruptly dilated short throat, 7 to 8 mm. long, glabrous; lobes linear, acute, 2 to 2.5 mm. long, erect; anther-tips triangular, obtusish, 0.2 mm. or less long; style-branches exerted, the slender appendage (about 2 mm. long) much exceeding the short stigmatic portion (0.5 to 1.0 mm. long); achenes tapering to the base, about 4 mm. long,

when fully mature, densely villous; pappus copious, exceeding the corolla, white. (*Bigelovia albida* Jones in Gray, Proc. Am. Acad. 17:209, 1882.)

A plant of the Great Basin; common only along the westerly side of the Salt Lake Desert; Utah (Wendover to Fish Springs and west, according to Jones), Nevada, and eastern middle California. Type locality, in alkaline soil, Wells, Nevada. Collections: Willow Springs, Utah, May 28 and July 29, 1891, *A. J. Jones* (Mo. Bot. Gard.); Kelton, north end of Great Salt Lake, Utah, *Wetmore 466* (US); Twin Springs, Nevada, *Purpus 6338* (NY, UC, US); type collection, August 9, 1881, *M. E. Jones* (Herb. Jones, DS, Gr, NY, UC, US); same locality, *Hall 11234* (UC); saline plains of Humboldt County, Nevada, 1865, *Torrey 218* (NY); Candelaria, western Nevada, *Shockley* (DS, NY); Soda Springs and Fish Lake Valley, Esmeralda County, western Nevada, *Shockley 554* (Gr, NY, US); Owens Valley, eastern California, 1875, *Kellogg* (Gr).

RELATIONSHIPS.

This species is remarkably distinct from all others. The setaceous tips to the involucre bracts early suggested an affinity with *C. parryi* and the resin-dots are very much like those of the *Punctati*, but the decidedly cymose inflorescence, the absence of tomentum, and several minor characters indicate that the connection with these is not very close. It seems to stand phylogenetically between *parryi* and the *Typici*, approaching the latter perhaps through *C. greenii*, with which it has much in common. It need not be confused with this latter species, however, for it is a more robust plant with glutinous foliage and larger heads of a distinct aspect. The tips to the bracts are longer and much more curved than in *greenii*, the flowers are nearly white instead of yellow, and the corolla is fully 2 mm. longer. *C. albidus* differs from all other species of *Chrysothamnus* in the remarkably short anther-tips, and in no other is the stigmatic portion of the style-branch so short in proportion to the appendage. It is this last character especially that renders the species anomalous among the *Typici* and suggests that it should perhaps be set off in a section by itself. The impressed resin-dots are suggestive of those so highly developed in the section *Punctati*, but there is no evidence of a direct phylogenetic connection with this group.

Judging only from the rather scant material thus far collected, *C. albidus* is not given to much variation. No segregate species or varieties have been proposed.

ECOLOGY AND USES.

Chrysothamnus albidus is a pronounced halophyte, as indicated by its thickish narrow leaves with revolute margins and resin-dots. In strongly alkaline flats it mixes with *C. n. consimilis*, *Elymus condensatus*, and *Sarcobatus*, but it also invades even more alkaline areas as a pioneer family. Its scarcity precludes commercial use.

SECTION III. PULCHELLI.

8. CHRYSOTHAMNUS PULCHELLUS (Gray) Greene, Erythraea 3:107, 1895. Plate 29.

Shrub 3 to 10 dm. high, densely branched at the base; bark of old stems gray or brown; twigs very brittle, short and divergent, leafy, glabrous, striate, the bark at first greenish but soon becoming gray or white; leaves revolute-filiform to linear-oblong, mucronate, 1 to 4 cm. long, 0.5 to 2 mm. wide, 1-nerved, green, glabrous or the margins and midrib ciliolate-scabrous (whole surface finely puberulous in one variety); heads several to numerous in each terminal usually lax cyme; involucre 10 to 13 mm. high; bracts 20, 25, or 30, in 5 sharply defined vertical ranks, boat-shaped, strongly keeled, attenuate, rigid-chartaceous, more or less greenish toward the apex, glabrous; flowers usually 5; corolla tubular-funnelform, the very slender tube passing gradually into the throat, about 10 to 14 mm. long, glabrous or only granular on the surface; lobes 1.5 to 2 mm.

long, lanceolate, nearly erect, glabrous; anther-tips lanceolate, acute, about 0.6 mm. long; style-branches long-exserted, the slender appendage about the length of the stigmatic portion, achenes nearly prismatic, 4-angled, and with strong vertical ribs between the angles, 6 to 7 mm. long, smooth and glabrous to minutely but densely puberulent (various degrees on the same plant); pappus exceeding the corolla, fine and soft, tawny. (*Linosityris pulchella* Gray, Pl. Wright. 1:96, 1852; Torrey, Sitgreaves Rep., plate 4, 1853.)

Southern Rocky Mountains and western Kansas south into Mexico; southern Colorado, Kansas, New Mexico, western Texas, northern Chihuahua, Utah.

SUBSPECIES.

Chiefly because of the small amount of field work that has been given to this species, its forms and their relationships to one another are not well understood. Three species have been described and are here taken as subspecies, as follows:

Key to the *Subspecies of Chrysothamnus pulchellus*.

Leaves glabrous on the faces; shrub low.	
Margins of the leaves glabrous.....	(a) <i>typicus</i> (p. 194).
Margins of the leaves scabrous-ciliate.....	(b) <i>baileyi</i> (p. 194).
Leaves finely and densely puberulous on both faces; shrub tall.....	(c) <i>elatior</i> (p. 194).

8a. **CHRYSOTHAMNUS PULCHELLUS TYPICUS.**—Shrub low, probably under 5 dm. high, openly branched; leaves filiform to narrowly linear, perfectly glabrous; peduncles glabrous; involucre 10 to 13 mm. or less high; bracts gradually acuminate. (*Linosityris pulchellus* Gray, l. c.). Throughout the range of the species, except easterly. Type locality, prairies below El Paso (western Texas), according to Gray (Pl. Wright. 2:80, 1853). Collections: Type collection, October, 1849, *Wright 287* (Gr, US); White Sands, Otero County, New Mexico, *Wooton 2501* (US); north of Deming, New Mexico, *Goldman 1505* (US); Colonia Diaz, Chihuahua, *Nelson 6454* (Gr).

8b. **CHRYSOTHAMNUS PULCHELLUS BAILEYI** (Wooton and Standley).—Shrub low, probably under 5 dm. high, densely branched; leaves linear or linear-oblong, minutely ciliate with short stout hairs, otherwise glabrous; peduncles glabrous; involucre 10 to 12 mm. high; bracts abruptly acuminate, mostly bristle-pointed. (*C. baileyi* Wooton and Standley, Contr. U. S. Nat. Herb. 16:181, 1913.) Kansas to New Mexico and Texas. Type locality, north end of the Guadalupe Mountains, New Mexico. Collections: Kearney County, Kansas, 1897, *Hitchcock* (Gr, NY, US); dunes south of Mustang Spring, Texas, September, 1881, *Havard* (NY, US); type collection, September 4, 1902, *Vernon Bailey 490* (US); bad lands at Ojo Alamo, northwestern New Mexico, *Hall 11133* (UC); White Mountains, Lincoln County, New Mexico, *Wooton 508* (NY, US).

8c. **CHRYSOTHAMNUS PULCHELLUS ELATIOR** (Standley).—Shrub tall, about 7.5 to 10 dm. high, slender; leaves linear, finely and densely puberulous on both faces; peduncles puberulous; involucre 9 to 12 mm. high; bracts abruptly acuminate. (*C. elatior* Standley, Proc. Biol. Soc. Wash. 26:118, 1913.) Southern New Mexico. Type locality, sandhills north of Goldenbergs, San Andreas Mountains, Doña Ana County, New Mexico. Collection: Type collection, October 12, 1912, *E. O. Wooton* (US).

SYNONYMS.

The synonymy of this species is so limited that it is all included in the above text, with the single exception of *Bigelovia pulchella* Gray (Proc. Am. Acad. 8:643, 1873), which is *C. pulchellus typicus*.

RELATIONSHIPS.

There can be no question that this species is more closely related to *C. depressus* than to any other. The connection between them and their relation to other forms will be taken up under that species. *C. bigelovi* also has been associated with this species,

first by Gray (Pacif. R. R. Rep. 4:98, 1857) and later in all manuals in which it was treated. It is very clear, however, that the two are not closely related and that *bigelovi* is a subspecies of *C. nauseosus*. The evidence has been stated in a previous paper (Hall, Univ. Calif. Publ. Bot. 7:172, 1919).

The three subspecies are much closer in their affinities to one another than any one of them is to *depressus*. Their differences are only such as habit, width of leaf, and amount of pubescence. Subspecies *baileyi* is very close to *typicus*, the only dependable difference being the scabrid-ciliate leaf margins. A majority of the specimens in herbaria under *pulchellus* have this character, but it is often so poorly developed as to be overlooked, as, for example, in Havard's Texan collection cited above. According to Standley (Proc. Biol. Soc. Wash. 26:119, 1913), *elatio*r differs decidedly in habit as well as in pubescence, and further field studies may warrant its recognition as a species.

ECOLOGY AND USES.

Chrysothamnus pulchellus is an undershrub, which occurs sparsely in subclimax areas with *C. n. bigelovi*, *Muhlenbergia pungens*, etc., and persists for a time after *Bouteloua gracilis* becomes dominant. No uses are known.

TABLE 20.—Variation in *Chrysothamnus pulchellus*.

	Herbarium.	Involucre-length.	Corolla.			Style.		
			Length, including lobes.	Lobe-length.	Ratio of lobe-length to total length.	Stigmatic portion, length.	Appendage, length.	Ratio of appendage-length to total length of branch.
Subspecies <i>typicus</i> :								
Las Palomas, N. Mex.	NY	mm.	mm.	mm.	p. ct.	mm.	mm.	p. ct.
Deming, N. Mex.	499434 US	12.6	10.0	1.7	17.0	2.3	2.0	46.5
Fort Smith to Rio Grande.	US	12.0	12.4	1.7	13.8	young	young
Diaz, Chihuahua.	360170 US	13.5	1.4	10.4	3.0	2.7	47.4
Canto Recia, Chihuahua.	Gr	13.1	14.1	1.8	12.8	3.1	3.0	49.2
Paso del Norte, Chihuahua.	87217 UC	10.2	13.6	2.1	15.4	3.8	2.8	42.4
		11.0	13.3	1.9	14.3	3.1	2.7	46.5
Average.		11.8	12.8	1.8	13.9	3.1	2.6	46.4
Subspecies <i>baileyi</i> :								
Nara Visa, N. Mex.	564968 US	11.0	13.5	1.3	9.6	4.0	3.2	44.4
Ojo Alamo, N. Mex.	205843 UC	12.0	9.5	1.7	17.9	2.2	2.7	55.1
Average.		11.5	11.5	1.5	13.7	3.1	2.9	49.7

9. CHRYSOTHAMNUS DEPRESSUS Nuttall, Jour. Phila. Acad. II, 1:171, 1847. Plate 29.

Shrub or undershrub, 1 to 3 dm. high, forming dense clumps, irregularly much branched, the lower branches decumbent; bark of old stems gray or brown; twigs brittle, numerous, short, densely cinerous with a minute scabrous pubescence, striate; leaves oblanceolate or spatulate, acute, erect, 0.8 to 2 cm. long, 1 to 4 mm. wide, 1-nerved, rigid, finely puberulent like the twigs; heads in small compact terminal cymes; involucre 9 to 12 mm. high; bracts 20 or 25, in 5 sharply defined vertical ranks, boat-shaped, keeled, attenuate to a short mucro or soft awn, commonly brown on the back, minutely rough-puberulent on the exposed parts; flowers 5; corolla tubular-funnelform, the tube passing gradually into the slightly broader throat, 7 to 9 mm. long, glabrous; lobes lanceolate, 1 to 2.3 mm. long, nearly erect, glabrous; anther-tips lanceolate, very acute, about 0.5 mm. long; style-branches exerted, the comparatively thick appendage only slightly exceeding or usually shorter than the stigmatic portion; achenes nearly pris-

matic, 4-angled to rather equally 8-ribbed, tapering slightly to the base, 5 to 5.5 mm. long, smooth or obscurely pubescent towards the summit; pappus slightly longer than the corolla, fine and soft, brownish tinged.

Plains and lower mountains of the Southwest: southern Colorado and New Mexico to northern Arizona, Nevada, and Utah. Type locality, "in the Sierra of Upper California," as stated by Nuttall, but the type specimen is labeled Rocky Mountains, and the species is not known from California. Collections: Type collection, *Nuttall* (Gr); Naturita, southwestern Colorado, August 25, 1920, *Payson* (UC); Sangre de Cristo, Colorado, *Parry 104* (Gr); Cimarron, Colorado, September, 1890, *Jones* (Gr, UC, US); near Dulce, Rio Arriba County, New Mexico, *Standley 8087* (US); San Francisco Mountains, Arizona, October, 1884, *Lemmon* (UC); Bright Angel Trail, Grand Cañon, Arizona, October 22, 1905, *Eastwood* (US); Pioche, southeastern Nevada, September 4, 1912, *Jones* (UC); Montezuma Cañon, southeastern Utah, *Rydberg* and *Garrett 9676* (NY, UC); Marysvale, Utah, *Jones 5847* (NY, UC, US).

SYNONYMS.

1. BIGELOVIA DEPRESSA Gray, Proc. Am. Acad. 8:643, 1873. *C. depressus*.

2. LINOSTRIS DEPRESSA Torrey in Sitgreaves Rep. 161, 1854. *C. depressus*.

RELATIONSHIPS.

There is every evidence of close consanguinity between *C. depressus* and *C. pulchellus*. The two are connected not only by the general habit, the nature of the woody twigs, etc., but by the similarly shaped corollas, the short style-appendages as compared with the stigmatic portion, and especially by the numerous strongly keeled bracts which are arranged in 5 very sharply defined rows. While there is a general tendency to vertical rows in the involucre of all of the species, it is nowhere so pronounced as here. The contact between these two species is suggested by *C. pulchellus elatior*, in which the pubescence is very similar to that of *depressus*. On the other hand, the characters separating *depressus* and *pulchellus*, although not marked, are sufficient for actual species. The leaf of the former is of the oblanceolate type, that is, widest above the middle, while in the latter the leaves are always linear; the corolla in *depressus* is only about 8 mm. long, in *pulchellus* it is 10 to 14 mm. long. This elongation of the flowers in *pulchellus*, accompanied as it is by a longer pappus, gives to the heads a very charac-

TABLE 21.—Variation in *Chrysothamnus depressus*.

	Herbarium.	Involucre-length.	Corolla.			Style.		
			Length, including lobes.	Lobe-length.	Ratio of lobe-length to total length.	Stigmatic portion length.	Appendage length.	Ratio of appendage-length to total length of branch.
		mm.	mm.	mm.	p. ct.	mm.	mm.	p. ct.
Cimarron, Colo.....	177034 UC	10.2	8.0	1.3	16.2	2.3	2.2	48.9
Gunnison, Colo.....	US	9.1	1.9	20.9	2.2	1.7	43.6
Marysvale, Utah.....	159551 UC	12.2	8.0	2.0	25.0	2.0	2.2	52.4
Iron County, Utah.....	US	9.2	1.5	16.3	2.0	2.1	51.2
Sandia Mountains, N. Mex.....	US	8.8	1.7	19.3	3.0	2.5	45.4
New Mexico (<i>Standley 8087</i>).....	US	9.2	2.3	25.0	2.2	2.0	47.6
Coconino, Ariz.....	563115 US	9.1	1.7	18.7	2.5	2.5	50.0
San Francisco Mountains, Ariz.....	193513 UC	10.2	8.0	1.7	21.2	2.5	1.7	40.5
Do.....	205824 UC	10.0	8.1	1.0	12.3	2.2	1.8	45.0
Grand Cañon, Ariz.....	205818 UC	9.0	9.2	2.2	23.9	2.6	2.6	50.0
Near Williams, Ariz.....	205819 UC	9.0	8.0	1.5	18.7	1.8	2.0	52.6
Pioche, Nev.....	179479 UC	9.0	7.2	1.4	19.4	1.7	1.8	51.4
Average.....	9.9	8.5	1.7	19.7	2.2	2.1	48.2

teristic appearance, for the flowers project beyond the involucre a distance equal to one-half their own length, the pappus thus appearing like an elongated brush.

In describing *depressus*, Nuttall stated that it was close to *pumilus*, that is to *C. viscidiflorus pumilus* of this monograph. While it is probably closer to *viscidiflorus* than to any other species outside of its own section, its connection is more likely to be through some subspecies of the pubescent-stemmed series and probably through one discovered since Nuttall's time. It is almost matched in habit by subspecies *humilis*, but the geographic isolation of this form is against it as a close relative of *depressus*. About all that can be said, therefore, is that *pulchellus* and *depressus* are intimately associated phylogenetically and that this branch is probably a derivative of, or has given rise to the *viscidiflorus* group of subspecies, presumably through some form close to *humilis*.

ECOLOGY AND USES.

Chrysothamnus depressus grows sparsely as a subclimax undershrub on rocky slopes, or in pockets of soil on cliffs. It also persists into the climax stage, where it occurs with *Bouteloua gracilis*.

This species is usually found to be closely cropped, apparently by sheep, but it is not sufficiently abundant to be of much importance as browse.

SECTION IV. NAUSEOSI.

10. CHRYSOTHAMNUS PYRAMIDATUS (Robinson and Greenman). Plate 30.

Shrub 6 to 9 dm. high, the branches probably ascending; ultimate twigs widely spreading, sparsely leafy, covered with a close white tomentum, this deciduous in the second year, the bark then brown; leaves more or less fascicled, narrowly linear, with closely revolute margins, cuspidate, 0.5 to 3 cm. long, about 0.5 mm. wide, 1- or 2-nerved, green and viscidulous above; obscurely tomentulose to white-woolly beneath; heads numerous, in dense leafy-bracted lateral spikes which are assembled into terminal pyramidal panicles; involucre 6 to 7 mm. high; bracts about 15, the ranks obscure, 1-nerved, lanceolate, the margins hyaline, loosely puberulent, none with herbaceous tips; flowers 5 to 10; corolla tubular-funnelform, 4 to 5 mm. long, the tube glabrous; lobes about 1 mm. long, lanceolate, recurved, puberulent at tip; anther-tips lanceolate, acute, about 0.3 mm. long; style-branches long-exserted, thick, barely acute, the appendage about as long as the stigmatic portion (but material young and not satisfactory); achenes appressed-villous; pappus about equaling the corolla, soft, sordid or tawny. (*Bigelovia pyramidata* Robinson and Greenman, Proc. Am. Acad. 32:43, 1896.)

Mexico; known only from four collections, all in the States of Oaxaca and Coahuila. Type locality, on the hills above Oaxaca, altitude 1,700 m. Collections: Type collection, November 16, 1894, *Pringle 6048* (Gr, UC, US); Cañada Sta. Maria, Oaxaca, *Seler 1477* (Gr); Monte Alban, near Oaxaca City, Oaxaca, between 1,700 and 1,850 m. altitude, *Smith 371* (US); Sierras de Parras, Coahuila, in rocky soil, *Purpus 1326* (UC, involucre bracts scarcely acute).

RELATIONSHIPS.

The exact position of *C. pyramidatus* in the genus is not certain, but it is placed in the *Nauseosi* because of the pannose tomentum of the twigs. The decidedly spicate or subracemose inflorescence is suggestive of a remote relationship with *C. parryi*. However, there is no tendency toward an attenuation of the tips of the involucre bracts and the style-tips are much less acute than in *parryi*. The villous-puberulent corolla-lobes occur elsewhere in *Chrysothamnus* only in *C. parryi latior* and in a few of the less specialized subspecies of *C. nauseosus*. The present species possibly represents a primitive type or offshoot from the main line, as its Mexican habitat also suggests.

ECOLOGY AND USES.

Chrysothamnus pyramidatus has not been seen in the field, and nothing is known of its ecology and uses.

11. CHRYSOTHAMNUS PARRYI (Gray) Greene, *Erythraea* 3:113, 1895. Plates 30 to 32.

Shrub 6 dm. or less high, the numerous branches erect or ascending, or widely spreading in dwarf forms; bark of main stems fibrous, brown; twigs flexible, ascending, moderately leafy, closely covered with a white or rarely greenish pannose tomentum, this deciduous only near the base, the bark then brown; leaves narrowly to broadly linear or linear-spatulate, acute or at least mucronate, 1 to 8 cm. long, 0.5 to 8 mm. wide, 1-nerved, sometimes with 2 additional nerves, green and viscid-glandular or gray and tomentulose; heads in leafy terminal racemes, these sometimes branching and sub-paniculate; involucre 10 to 14 mm. high; bracts 10 to 20, in more or less obvious vertical ranks, 1-nerved, lanceolate, acuminate, chartaceous, the outer ones often with a slender herbaceous tip, loosely puberulent at least on the margins; flowers 4 to 20; corolla tubular-funneliform, 8 to 11 mm. long, either pubescent or glabrous; lobes 0.5 to 2.5 mm. long, erect, glabrous or sparsely long-hairy; anther-tips linear-lanceolate and acute or linear and somewhat obtuse (at least in subspecies *nevadensis*), 0.5 to 0.8 mm. long; style-branches long-exserted, the subulate appendage much exceeding the stigmatic portion; achenes tapering slightly to the base, 4-angled, 5 to 6 mm. long when mature, densely appressed-villous; pappus equaling or slightly exceeding the corolla, very soft, dull white changing to tawny. (*Linosyris parryi* Gray, Proc. Acad. Phila. for 1863:66, 1863.)

Mountains and foothills of western North America: Wyoming to western Nebraska, New Mexico, California, and Utah.

SUBSPECIES.

Key to the Subspecies of Chrysothamnus parryi.

- Flowers 8 to 20 in each head, or only 5 to 7 in *latior* but the leaves then 4 mm. or more wide; leaves lanceolate or oblanceolate to broadly linear.
- Leaves 2.5 to 8 cm. long; plant 3 dm. or more high, the branches mostly erect.
- Flowers mostly 10 to 20 in the head; leaves mostly 1.5 to 3 mm. wide. Rocky Mountains. (a) *typicus* (p. 198).
- Flowers mostly 5 to 11 in the head; leaves mostly 4 to 8 mm. wide, California.
- Involucre 9 to 10 mm. high; leaves thick and rigid; inflorescence congested. (b) *bolanderi* (p. 199).
- Involucre 12 to 14 mm. high; leaves thinner, soft; inflorescence elongated. (c) *latior* (p. 199).
- Leaves 1.0 to 1.5 cm. long; plant about 1 dm. high, the branches spreading at base. Southern California. (d) *imulus* (p. 200).
- Flowers 5 to 7 in the head, or up to 10 in *asper* (the leaves then resinous-scabrid); leaves narrowly linear except in some forms of *asper*.
- Bracts of the involucre 8 to 12, not strongly keeled and the vertical rows rather obscure.
- Racemes several- to many-headed; foliage green, viscidulous, not tomentose or only sparsely so.
- Resin-glands of the leaves short-stalked, prominent. (e) *asper* (p. 200).
- Resin-glands of the leaves sessile, obscure. (f) *vulcanicus* (p. 200).
- Racemes reduced to 1 or 2 heads each; foliage gray, tomentulose. (g) *monocephalus* (p. 200).
- Bracts of the involucre 13 to 20, rarely only 11 or 12 (or even fewer in *howardi*, which may be recognized by the elongated upper leaves), more strongly keeled, the vertical rows fairly obvious.
- Uppermost leaves elongated, some of them overtopping the inflorescence; foliage gray-tomentulose; flowers pale yellow. Rocky Mountains. (h) *howardi* (p. 201).
- Uppermost leaves seldom overtopping the inflorescence; foliage variously pubescent; flowers clear yellow.
- Bracts of the involucre with very slender straight tips. Rocky Mountains. (i) *attenuatus* (p. 201).
- Bracts of the involucre with slender tips at least some of which are spreading or recurved. Nevada and California. (j) *nevadensis* (p. 201).

11a. CHRYSOTHAMNUS PARRYI TYPICUS.—Plant 3 dm. or more high; stems mostly erect; leaves broadly linear, 3 to 8 cm. long, 1.5 to 3 mm. wide, 3-nerved, but only one nerve prominent, green, glabrous or microscopically puberulent and often obscurely resinous-glandular, the uppermost usually exceeding the inflorescence; heads numerous, in dense elongated racemes; involucre 9 to 12 mm. high; bracts 10 to 15, obscurely ranked,

not strongly keeled, thin, with straight attenuate tips; flowers 10 to 20. (*Linossyris parryi* Gray, l. c.) On dry open hillsides and plains, Wyoming, Colorado, Utah, and northeastern Nevada. Type locality, Rocky Mountains, latitude 39° to 41°, according to label on type specimen. Collections: Centennial-Rambler Road, Albany County, Wyoming, *Goodding 2067* (Gr, R, NY, UC, US); type collection, 1862, *Hall and Harbour 293* (Gr); Colorado: Middle Park, 1862, *Parry* (Gr, US); North Fork, Larimer County, *Goodding 1921* (DS, Gr, NY, UC, US); mountains about headwaters of Clear Creek, *Patterson 222* (Gr, NY, UC); Marshall Pass, 3,000 m. altitude, *Baker 878* (NY, UC, US); head of Sevier River, Utah, *Jones 6028* (NY, UC, US); Big Creek and Kingston Cañon, Toiyabe Forest, Nevada, *A. E. Hitchcock 830* (US).

11b. *CHRYSOTHAMNUS PARRYI BOLANDERI* (Gray).—Plant a “low shrub”; stems erect, probably from a much-branched bushy base; leaves 3 to 4 cm. long, 4 to 5 mm. wide, many 3-nerved, green, somewhat viscidulous, the uppermost little reduced but not exceeding the inflorescence; heads crowded in short racemes which are sometimes branched, the inflorescence then appearing cymose; involucre 9 to 10 mm. high; bracts about 11 to 15, obscurely ranked, not strongly keeled, thin, with straight attenuate tips; flowers 8 to 11 (or as low as 7 according to Gray). (*Linossyris bolanderi* Gray, Proc. Am. Acad. 7:354, 1868.) Known only from the type locality. Type locality, Mono Pass, California, at 2,750 to 3,050 m. altitude. Collections: Type collection, 1866, *Bolander 6137* (Gr, UC); same locality, 1867, *Rattan* (DS, in part).

11c. *CHRYSOTHAMNUS PARRYI LATIOR*, subsp. nov.—Plant about 4 dm. high; stems erect or ascending; leaves elliptic or oblanceolate, acute, mucronate, tapering to a narrow petiole-like base, 2.5 to 4 cm. long, 4 to 8 mm. wide, rigid, 1-nerved, the nerve impressed above but prominent beneath, sometimes an additional pair of nerves from base of leaf, but these soon disappearing, surface dull green, sprinkled with microscopic glandular dots, also obscurely puberulent, the uppermost much shorter than the inflorescence; heads in narrow terminal raceme-like panicles, interspersed with a few reduced leaves (panicle 5 to 15 cm. long); involucre cylindric-turbinate, 12 to 14 mm. high; bracts 11 to 15, in 5 indistinct vertical ranks, 1-nerved, lanceolate, attenuate to rigid pungent straight or only recurved-spreading tips, the short outer ones keeled, all chartaceous and nearly glabrous; flowers 5 to 7, corolla tubular-funnelform, 11 mm. long, sparsely puberulent on the tube; lobes about 2.5 mm. long, lanceolate, erect or only slightly divergent, sparsely villous at apex in the bud; anther-tips lanceolate, acute, nearly 1 mm. long; style-branches about 5.5 mm. long, the subulate appendage moderately exceeding the stigmatic portion; achenes tapering to the base, 4-angled, densely appressed-villous; pappus slightly exceeding the corolla, rather soft, tawny to ferruginous. Known only from the mountains of northern California. Collections: Wagon Creek, at the foot of Mount Eddy, Siskiyou County, California, at an altitude of about 1,140 m., August 26, 1915, *A. A. Heller 12250* (SF, type, duplicates at DS, Gr, UC); same locality, August 30, 1912, *Eastwood 2079* (SF, UC); Little Hot Springs Valley, Modoc County, August 18, 1899, *Baker* (UC); in dry brush at Sisson, south base of Mount Shasta, at between 900 and 1,250 m. altitude, September, 1902, *Grant 5152* (UC); Mount Shasta, *Canby 111* (Gr, US).

The above description of *latior* was drawn from the type specimen. The Eastwood specimen is in close agreement and may indeed have been taken from the same or a neighboring plant. Its flowers are older and the villous pubescence of the corolla-lobes is therefore less noticeable. The corollas in the Baker specimen from Modoc County are not fully opened. The corolla and its parts are smaller than given in the description, but the lobes are very noticeably villous. Grant's collection from Sisson has some heads with well-matured achenes and some with flowers only in bud. These latter are scarcely if at all villous on the lobes. The corollas are 10 mm. long and the lobes about 2 mm.

long. This collection differs from all of the others in its somewhat thinner and less rigid leaves and nearly glabrous involucre. It is probably a form of partially shaded places. According to the original label, the plants were 3 to 4.5 dm. high. The range of *C. latior* should perhaps be extended to Mount Hamilton, on the basis of a specimen collected in June, 1890, by Price (Univ. Calif. Herb. 87224), but this is very incomplete and there is some doubt as to the accuracy of the data.

11d. *CHRYSOTHAMNUS PARRYI IMULUS*, subsp. nov.—Plant about 1 dm. high; stems spreading at base, the branches erect; leaves spatulate or linear-spatulate, obtuse, mucronate, 1 to 1.5 cm. long, 2 to 3 mm. wide, 1-nerved, gray with a dense very tardily deciduous tomentum, none overtopping the inflorescence; heads few, peduncled in a reduced raceme; involucre 11 to 12 mm. high; bracts about 16, obscurely ranked, not keeled, thin, oblong, pungently and rather abruptly acute, the outer sometimes with herbaceous reddish tips, white-tomentose; flowers 11 to 15; corolla tubular-funnelform, 9 to 10 mm. long, yellow or reddish, the tube glabrous or obscurely puberulent; lobes 1 to 1.5 mm. long, nearly erect, either glabrous or sparsely villous; achenes silky-villous; pappus slightly exceeding the corolla. Known only from the San Bernardino Mountains of southern California. Collections: Bear Valley, San Bernardino Mountains, California, at 2,000 m. altitude, July 19, 1900, *M. E. Jones* (type, in Herb. Jones); same locality, 1896, *Davidson* (UC).

11e. *CHRYSOTHAMNUS PARRYI ASPER* (Greene).—Plant 1.5 dm. or more high; stems erect or slightly spreading; leaves 2 to 4 or 5 cm. long, 1 to 3 mm. wide, 1-nerved, firm, green, slightly rough with numerous short-stalked resin-glands, the uppermost leaves scarcely equaling the inflorescence; heads few in the short racemes, or more numerous and the racemes longer (12 cm. in the type); involucre 11 to 12 mm. high; bracts 9 to 13, somewhat ranked, thin, with straight tips; flowers 5 to 10. (*C. asper* Greene, Leaflets 1:80, 1904.) On mountains bordering the desert, western Nevada and eastern California. Type locality, Hockett Trail, in the valley of Little Cottonwood Creek, eastern slope of the Sierra Nevada of Inyo County, California (see Coville, Contr. U. S. Nat. Herb. 4:271, 1893, under No. 1690). Collections: Bloody Cañon, Mono County, California, August 13, 1898, *Congdon* (UC); type collection, *Coville 1690* (US); Alamo Mountain, Ventura County, California, *Hall 6701*; Lee Cañon, Charleston Mountains, Nevada, *Heller 11036* (DS, Gr, NY, UC, minor variation 17).

11f. *CHRYSOTHAMNUS PARRYI VULCANICUS* (Greene).—Plant 1.5 dm. or more high; stems erect or ascending; leaves 2 to 5 cm. long, 0.5 to 2 mm. wide, 1-nerved or obscurely 3-nerved, green and minutely resinous-glandular, or at least viscidulous, the uppermost scarcely equaling the inflorescence; heads numerous, in elongated often lax racemes or narrow panicles; involucre 11 to 13 mm. high; bracts 9 to 12, somewhat ranked, thin, with straight attenuate tips; flowers 5 to 7. (*C. vulcanicus* Greene, l. c.) In the southern Sierra Nevada Mountains of California. Type locality, on Volcano Creek, above Volcano Falls, at about 2,500 m. altitude. Collections: Type collection, August 9, 1904, *Culbertson 4361* (Gr, SF); Golden Trout Creek and Ramshaw Meadows, *Hall 8413* (UC, US); Little Kern River, at 2,400 m. altitude, *Hall 8457* (UC); Mono Mills, in sandy soil beneath *Pinus ponderosa*, *Hall 10844* (SF, UC).

11g. *CHRYSOTHAMNUS PARRYI MONOCEPHALUS* (Nelson and Kennedy).—Plant 0.5 to 3 dm. high; stems rigidly branched, spreading; leaves 1 to 3 cm. long, 1.5 mm. or less wide, 1-nerved, rarely 2-nerved, gray, sparsely to copiously tomentulose, also viscidulous, the uppermost usually exceeding the inflorescence; heads solitary or two together, terminal on the short leafy twigs; involucre 10 to 11 mm. high; bracts about 8 to 12, the ranks very obscure, thin, tapering to a straight attenuate apex; flowers 5 or 6. (*C. monocephalus*

Nelson and Kennedy, Proc. Biol. Soc. Wash. 19:39, 1906.) High mountains of western Nevada and eastern California. Type locality, summit of Mount Rose, Washoe County, Nevada. Collections: Type collection, from 3,320 m. altitude, *Kennedy 1171* (UC); Mount Rose, Nevada, at 3,170 m. altitude, *Heller 9976* (Gr, NY, UC, US); mountains above Lundy, Mono County, California, *Minthorn 224* (UC); outlet of Jessie Lake, east side of Mount Dana, California, August 12, 1898, *Congdon* (UC); Mono Pass, California, *Bolander 6135* (Gr, with notation, "very low shrub").

11h. *CHRYSOTHAMNUS PARRYI HOWARDI* (Parry).—Plant normally 3 to 6 dm. high; stems spreading at base, but the branches mostly erect; leaves narrowly linear, 2 to 4 cm. long, about 1 mm. wide, commonly with straight slender tips, 1-nerved, gray-tomentulose, the uppermost usually overtopping the inflorescence; heads either numerous in open racemes or few and terminally glomerate in reduced forms (minor variation 18); involucre 10 to 12 or 13 mm. high; bracts 12 to 20, in rather well defined ranks, keeled by the strong midrib, with usually spreading tips; flowers 5 to 6, rarely 7. (*Linosyris howardi* Parry in Gray, Proc. Am. Acad. 6:541, 1865.) On upland slopes and tablelands, Wyoming, western Nebraska, and Colorado; perhaps also in Utah. Type locality, Colorado, on gravelly hills near "Hot Springs" of Middle Park. Collections: Encampment, Carbon County, Wyoming, *Goodding 2016* (Gr, Ny, UC, minor variation 18); Centennial-Rambler Road, Albany County, Wyoming, *Goodding 2072* (DS, Gr, NY, UC, similar variation); cañons south of Scotts Bluff, Nebraska, July 24, 1891, *Rydberg* (NY, US); rolling hills north of Walsenberg, Colorado, *Hall 10779*; Buena Vista, Colorado, *Hall 11073* (UC); Villa Grove, San Luis Valley, Colorado, *Hall 10785* (UC).

11i. *CHRYSOTHAMNUS PARRYI ATTENUATUS* (Jones).—Plant 2 to 6 dm. high; stems mostly erect; leaves narrowly linear, 2 to 4 cm. long, about 1 mm. wide, 1-nerved, not tomentulose but green and somewhat viscid, the upper ones not projecting beyond the inflorescence (in the type specimens); heads in well-developed racemes; involucre 10 to 11.5 mm. high; bracts 13 to 15, 5-ranked, keeled, with very slender usually erect tips; flowers 5 to 7. (*Bigelovia howardi* var. *attenuata* Jones, Proc. Calif. Acad. II, 5:691, 1895.) Utah, southern Colorado, northern New Mexico, Arizona, eastern Nevada, and southern Idaho. Type locality, Marysvale, Utah, at 2,150 meters altitude, in clay. Collections: Type collection, August 27, 1894, *Jones 5912* (NY, UC, US); same locality, *Jones 5847a* (NY, UC, US); Thurber, Utah, *Jones 5704*, and near Panguitch Lake, Utah, *Jones 5994* (both UC, US, and both with the less attenuate bracts of subspecies *howardi*, and a portion of 5704 with white tomentum of minor variation 15, *C. newberryi* Rydberg); Wet Mountain Valley, Fremont County, Colorado, *Brandegee 748, 749* in part (UC, a form with the bracts less attenuate); Rio Mancos, Colorado, *Brandegee 1231* (UC); Cañon Largo, New Mexico, September 15, 1859, *Newberry* (NY, type of *C. newberryi* Rydberg, minor variation 15); Buckskin Mountains, northern Arizona, *Jones 6052k* (US, same variation); Star Peak, Nevada, July 30, 1904, *Jones* (DS, UC, same variation); Challis, Custer County, Idaho, *Macbride* and *Payson 3351* (R).

11j. *CHRYSOTHAMNUS PARRYI NEVADENSIS* (Gray).—Plant 2 to 6 dm. high except in high-mountain forms; stems erect or ascending; leaves 1.5 to 4 cm. long, 0.5 to 3 mm. wide, 1-nerved, either green and resinous-glandular or more commonly gray and copiously tomentulose (the two forms sometimes growing together; see minor variation 20), the uppermost seldom exceeding the inflorescence; heads few to numerous, in racemes or narrow panicles; involucre 12 to 15 mm. high; bracts 13 to 18, in definite ranks, strongly keeled, with slender tips which tend to recurve; flowers 4 to 6. (*Linosyris howardi* var. *nevadensis* Gray, Proc. Am. Acad. 6:541, 1865.) Uplands and mountains nearly to timber line, eastern Nevada to eastern California and south to northern

Arizona. Type locality, Mount Davidson, Nevada, above Virginia City. Collections: Type collection, *Bloomer* (Gr); northwestern Nevada, *Watson 570* (Gr); Nevada: Comet Peak, Pioche, August 30, 1912, *Jones* (UC); near Verdi, July, 1888, *Sonne* (UC); Franktown, *Kennedy 1934* (DS, Gr, UC); Kings Cañon, Ormsby County, *Baker 1503* (Gr, SF, NY, UC, US); Spanish Springs Valley, Washoe County, *Kennedy 1950* (DS, Gr, NY, UC, US, minor variation 19); Ebbett's Pass, California, *Brewer 1935* (Gr, UC, subalpine form); Keddie and Portola, Plumas County, California, September, 1919, *Johnston* (UC, green and gray forms growing together, see minor variation 20); branch of Coconino Wash, Arizona, *Hall 11196* (UC); Grand Cañon, Arizona, *Eastwood 3636* (SF).

MINOR VARIATIONS AND SYNONYMS.

1. *BIGELOVIA BOLANDERI* Gray, Proc. Am. Acad. 8:641, 1873.—*C. parryi bolanderi*.
2. *B. HOWARDI* Parry, in Gray, l. c.—*C. parryi howardi*.
3. *B. HOWARDI* var. *ATTENUATA* Jones, Proc. Calif. Acad. II, 5:691, 1895.—*C. parryi attenuatus*.
4. *B. HOWARDI NEVADENSIS* Gray, l. c.—*C. parryi nevadensis*.
5. *B. NEVADENSIS* Gray, Syn. Fl. 1st:136, 1834.—*C. parryi nevadensis*.
6. *B. PARRYI* Gray, Proc. Am. Acad. 8:642, 1873.—*C. parryi typicus*.
7. *CHRYSOTHAMNUS AFFINIS* Nelson, Bot. Gaz. 28:374, 1899.—A variation close to *C. parryi attenuatus*, which was made a variety of this by Nelson (see next entry). The attenuation of the bracts is intermediate between this and subsp. *howardi*, while the low number of bracts (12 to 15) and the yellowish-green foliage suggest subspecies *typicus*. The upper leaves are reduced as in *attenuatus* and the flowers are 5 to 6 in each head. These figures are derived from the type specimen which is from Jefferson, South Park, Colorado (August 29, 1896, *Coven*, Rocky Mt. Herb.).
8. *C. AFFINIS ATTENUATUS* Nelson, l. c.—*C. parryi attenuatus*.
9. *C. ASPER* Greene, Leaflets 1:80, 1904.—*C. parryi asper*.
10. *C. ATTENUATUS* Rydberg, Bull. Torr. Club 37:130, 1910.—*C. parryi attenuatus*.
11. *C. BOLANDERI* Greene, Erythea 3:114, 1895.—*C. parryi bolanderi*.
12. *C. HOWARDI* Greene, l. c., 113, 1895.—*C. parryi howardi*.
13. *C. MONOCEPHALUS* Nelson and Kennedy, Proc. Biol. Soc. Wash. 19:39, 1906.—*C. parryi monocephalus*.
14. *C. NEVADENSIS* Greene, l. c., 114, 1895.—*C. parryi nevadensis*.
- 14a. *C. NEVADENSIS* forma *MONOCEPHALUS* Smiley, Univ. Calif. Publ. Bot. 9:357, 1921.—*C. parryi monocephalus*.
- 14b. *C. NEVADENSIS* var. *VULCANICUS* Smiley, l. c.—*C. parryi vulcanicus*.
15. *C. NEWBERRYI* Rydberg, Bull. Torr. Club 31:652, 1904.—A variation of *C. parryi attenuatus* in which the tomentum of the twigs is white instead of yellowish-green. When portions of the types of these two are directly compared, no other difference is found. Similar color variations are known in subspecies *howardi*, and in *C. nauseosus* two subspecies (*gnaphalodes* and *hololeucus*) are distinguished by this character, but here the difference extends to the foliage also, other features furnish supporting characters, and the two commonly grow side by side but with no evidence of intergradation. The type of *newberryi* is from Cañon Largo, New Mexico. An additional citation by Rydberg is Mesa Verde, southwestern Colorado, September, 1892, *Eastwood*. At the University of California this latter collection includes both the *newberryi* form and a twig, probably from another plant, of typical *attenuatus* with the usual greenish tomentum.
16. *C. PARRYI* Greene, Erythea 3:113, 1895.—*C. parryi typicus*.
17. *C. PARRYI ASPER*, but with shorter and wider leaves, the average about 2 cm. long by 2 mm. wide, and the stipitate glands so prominent as to make the foliage harsh to the touch. Lee Cañon, Charleston Mountains, Nevada, at 8,000 feet elevation, *Heller 11036* (UC). This specimen is only 1.5 dm. high, twice as broad, and with inflorescences reduced to 1 to 4 heads each. Somewhat intermediate to true *asper*, especially in the longer leaves, is a collection from Alamo Mountain, Ventura County, California, at 2,135 km. (*Hall 6701* UC).
18. *C. PARRYI HOWARDI*, but much reduced in stature and inflorescence and the tomentum of the stems white. This variation is confined to the northern part of the range of *howardi* and has the appearance of a plant contending with a more rigorous habitat and reduced water-content. It is represented by collections from Carbon County, Wyoming (*Goodding 537, 2016*), and from Albany County, Wyoming (*Goodding 2072, Nelson 8824*).
19. *C. PARRYI NEVADENSIS*, but with linear-spatulate, usually greenish leaves only 1.5 cm. long, the inflorescence reduced to 2- or 3-headed clusters at the end of each twig, and the corollas pink. The best example is a plant from Spanish Springs Valley, 1,480 km. elevation, Washoe County, Nevada, *Kennedy 1950* (UC). The same form, but with the leaves gray tomentose as in the next, comes also from hills around Reno, Nevada, September 20, 1910, *Heller* (DS, UC). These and other Nevadan collections suggest that it is a starved form, perhaps of alkaline or otherwise unfavorable habitats.

20. *C. PARRYI NEVADENSIS*, but the whole herbage white, or at least gray, with a loose tomentum. West end of Peavine Mountain, Nevada, 1,600 m. elevation, Heller 10675 (UC). The same form grows also at Portola, Plumas County, California, Johnston 2180 (UC). According to Johnston, the green and the white forms grow intermingled both at Portola and at Keddie. Although no intermediates appear as to color, no other distinguishing characters could be found. This appears to be a case of difference in a single character and perhaps the result of mutation. The color is probably influenced by the amount of resinous matter secreted by the stems and leaves.

21. *C. VULCANICUS* Greene, Leaflets 1:80, 1904.—*C. parryi vulcanicus*.

22. *C. WYOMINGENSIS* Nelson, Bot. Gaz. 28:372, 1899.—Not finally placed. The type specimens, from Buffalo, Wyoming (Nelson 2495), appear to be a variation from *C. parryi typicus*, the stems being leafy to the top, the inflorescence elongated, and the bracts decidedly acuminate. But the leaves are narrow, the inflorescence reduced in size, and the flowers only 5 in the small head. The plants grew in strongly alkaline soil, which may account for these modifications, or it is possible that detailed field studies will demonstrate *wyomingensis* as a modification of some subspecies of *C. nauseosus*. Later collections from Buffalo (Nelson 8672), identified as this, seem to be a form of *C. nauseosus typicus*, at least in part, the inflorescence being cymose and the bracts only acute.

23. *LINOSYRIS BOLANDERI* Gray, Proc. Am. Acad. 7:354, 1868.—*C. parryi bolanderi*.

24. *L. HOWARDI* Parry, in Gray, l. c., 6:541, 1865.—*C. parryi howardi*.

25. *L. HOWARDI* var. *NEVADENSIS* Gray, l. c.—*C. parryi nevadensis*.

26. *L. PARRYI* Gray, Proc. Acad. Phila. 1863:66, 1863.—*C. parryi typicus*.

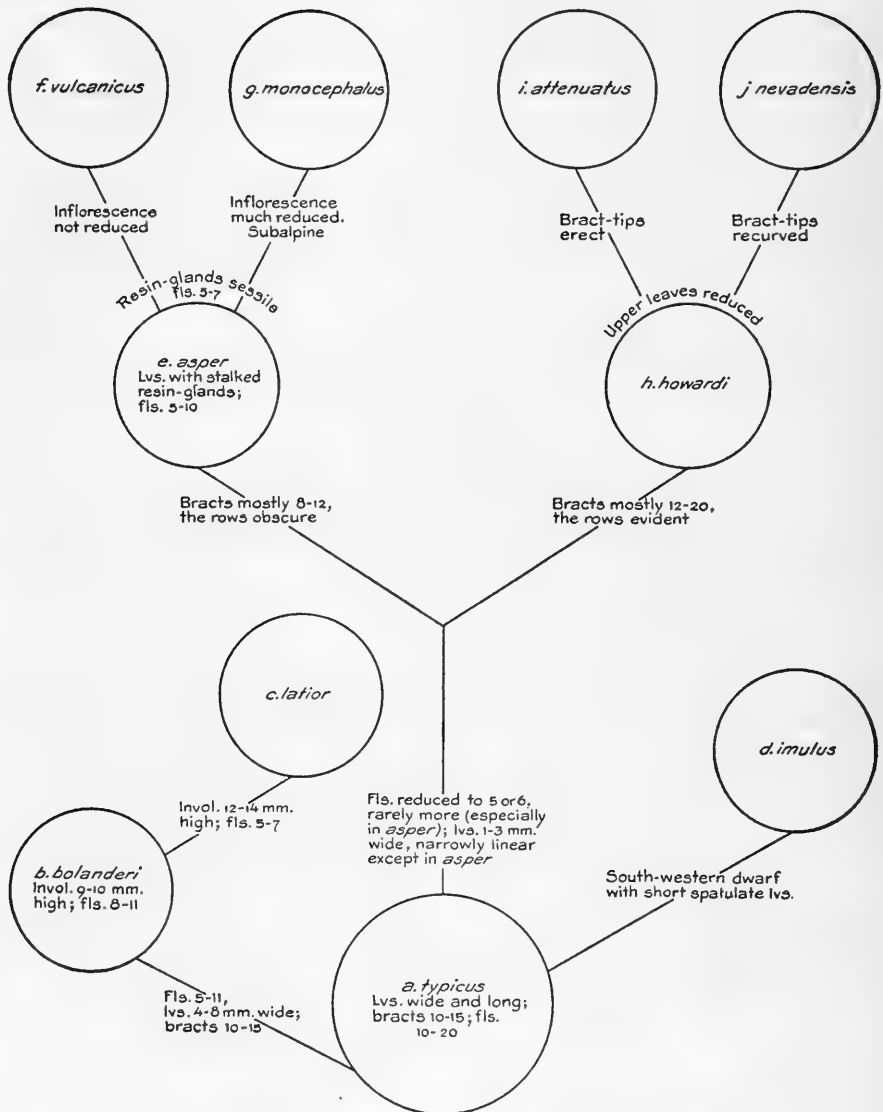
27. *MACRONEMA BOLANDERI* Greene, Leaflets 1:81, 1904.—*C. parryi bolanderi*, as to synonymy. The probable reason for this transfer has been already discussed (p. 160).

RELATIONSHIPS.

The nearest relatives of *Chrysothamnus parryi* are undoubtedly to be sought among certain forms of *C. nauseosus*, with which it has in common the notably pannose tomentum of the twigs and similarly shaped corollas and style-branches. While the inflorescence is of the racemose rather than cymose type, individual heads are sometimes scarcely distinguishable from those of *nauseosus*, except by the loosely arranged bracts. These are always more attenuate in *parryi* and less distinctly ranked. While such characters of the inflorescence and involucre serve well for specific distinctions, there can be no doubt as to the common origin of the two stocks.

Among the assemblage of forms here considered as constituting *C. parryi*, there is one with an appearance so strikingly different from the others that it has not been heretofore considered as conspecific with them. This is the original *C. parryi*, here made the basis of subspecies *typicus*. It belongs to a portion of the Rocky Mountains where the only other subspecies are *howardi* and its derivative *attenuatus*, both very different in appearance. If it were not for the occurrence of intermediate forms in the mountains farther west, *parryi* and *howardi* might both be maintained as major species. Their marked difference, however, is based upon only vegetative characters, since all others, such as the number and character of involucre bracts and flowers, exhibit complete series of intergradations, as indicated in table 22, page 207. As compared with *howardi*, typical *parryi* is a more robust plant, with wider and longer almost strap-shaped leaves and usually larger heads. No intermediates in the leaf characters are found and the two are apparently distinct where their ranges overlap. Farther west, however, we find such subspecies as *vulcanicus*, with leaves as long as in *typicus* but narrow as in *howardi*; also *asper*, with leaves as broad as in *typicus* but even shorter than in *howardi*; while in *nevadensis* both length and width of leaf are sufficiently variable to satisfy a description of either. Since none of these can be separated on other non-variable characters, they seem to indicate that the whole gamut of forms is of a common and modern stock, which is best accepted as a single major species.

As in the case of typical *parryi*, every attempt has been made to find stable characters for the specific separation of each of the described subspecies, but without success. None of the characters heretofore used for the separation of species is of more importance than those used in the key to the subspecies. Gray (Syn. Fl. 2^d 136, 1884) describes the leaves

FIG. 27.—Phylogenetic chart of the subspecies of *Chrysothamnus parryi*.

of *parryi* as glabrous, of *bolanderi* as viscidulous. In all specimens of *parryi* examined the leaves are minutely glandular and often also puberulent. The "glandular-scabrous" character assigned by Greene to *asper* is exactly the same as in *bolanderi*, except that the glands are slightly stalked and thus more prominent. Finally, the reduced number of heads in *monocephalus* is a reaction to the subalpine environment as indicated by intermediate forms at lower elevations (Heller 9976). A similar reduction, although not carried to such an extreme, is common in subspecies *asper* and occasionally in *howardi*.

In attempting to trace the lines of evolution within the species it is necessary to keep in mind the facts of geographic distribution as well as the morphology of the various subspecies and minor variations. Thus, the close phylogenetic connection between *typicus*, of the Rocky Mountains, and several of the Sierra Nevada subspecies indicates that the distributional areas of these were in contact during some past period. This may have occurred in or near the area now known as the Great Basin, where the earlier climate was much less arid than that of the present time and therefore better suited to the growth of these mesophytic types. It seems that over this central area there may have grown a primitive form, one with large heads of numerous flowers and bracts, with a well-developed foliage, and with no special structures such as now mark some of the more highly specialized subspecies. Then, as greater aridity set in, this primitive stock broke up, forming two branches. One of these migrated easterly into the Rocky Mountains, and became the present subspecies *typicus*, which comes so close to fulfilling the requirements of the original stock just assumed that it is placed at the very bottom in the chart of relationships. The other branch moved to the westward, finally coming to rest in the Sierra Nevada. In the meantime, this western migrant underwent modifications, involving especially a reduction in the number of flowers in each head and also a reduction in the inflorescence itself. These changes resulted in subspecies *bolanderi*, a wide-leaved shrub now appearing only as a relict in the middle Sierra. It may be assumed that as *bolanderi* migrated into the western plateaus and mountains its distribution became discontinuous and that distinct forms were evolved in the different areas. At any rate, there now occurs in the Siskiyou Mountains of northern California a subspecies *laticus* which has all the indications of being a lineal descendant of *bolanderi*, especially in the still further reduction of the number of flowers. The somewhat better development of the foliage and the more elongated inflorescence may be either persistent traits of a common ancestor or a more recent adaptation to the more humid habitat. A much more striking modification is subspecies *imulus*, now stranded in the high mountains of southern California. This is a dwarf with very short, spatulate leaves, commonly colored involucre, and with the whole herbage woolly. The appearance is so unique that one is tempted to give the form specific standing, but it shows no variation from *bolanderi* in the number or size of flowers and bracts or in any other feature commonly accepted as of specific value.

The six remaining subspecies probably are all more recent in their origin than those already discussed. This is evidenced by their narrowed leaves, which feature enables them to cope with their more arid environment, and especially by the reduction in the number of flowers in each head. It would be desirable to set off this group as a distinct species (thus preserving the established name of *howardi* in specific rank) were it not for *laticus*, which, although plainly a derivative of *bolanderi*, has the flower reduction of these. There is also some doubt as to the naturalness of the assemblage, as will be noted further on. The difficulties in the way of such a treatment are seen also in the key to the subspecies, where no clear-cut division can be made between these and the earlier subspecies. The migratory routes taken by *typicus* and *bolanderi* and their derivatives doubtless were followed by these later subspecies, but most of them did not get so far from the original center of distribution and at least two (*nevadensis* and *asper*) still occupy mountainous districts well within the Great Basin area.

The members of this second major division of *Chrysothamnus parryi* may be assembled into two apparently natural groups of three subspecies each. One of these groups constitutes what may be called the *asper* line, the other the *howardi* line, the two differing chiefly in the nature of the involucre, as indicated on the diagram (fig. 27). In the former subgroup, *asper* is given a central position, because it has undergone the least amount of reduction in the number of flowers in the head. Its intermediate geographic position is also to be taken into account. Farther to the west it divides into two branches. One of these is *vulcanicus*, a subspecies of the higher Sierra Nevada, which differs in the smaller average number of flowers and also in the loss of certain xerophytic features, notably the stalked resin-glands. There is evidence, however, that the two thoroughly intergrade along the east slope of the Sierra Nevada (see, for example, Congdon's numerous collections). The other branch has ascended even higher and culminated in subspecies *monocephalus*, which has all of the characteristics of a subalpine derivative, the stems being low and divergently branched, the inflorescence reduced to one or two heads among the upper leaves, and the foliage gray with a fine though sparse tomentum. It is not impossible that *monocephalus* is a subalpine derivative of subspecies *nevadensis*, and possibly it is polygenetic in origin.

The *howardi* line consists of three primary and several secondary derivatives. The subspecies *howardi* itself is a common form in the Rocky Mountains and differs from the others of its line by the presence of elongated upper leaves and involucre bracts that are only moderately attenuate. An unnamed modification, differing chiefly in the short congested inflorescence, occurs in Wyoming. It is discussed under minor variation 18. The connection between *nevadensis* and *howardi* is not direct, and possibly it passes through *attenuatus*; *nevadensis* belongs to the desert mountains and is itself polymorphous. The derivation of *attenuatus* from *howardi* is more easily demonstrated, since intermediate stages are represented by existing forms. Such, for example, is a form from Panguitch Lake, Utah (Jones 5994, 6002z) in which the bracts are almost as slender as in *attenuatus*, and another from South Park, Colorado, which is almost the same but with a reduced number of bracts (minor variation 7). Finally, there is to be noted a possible connection through *attenuatus* and its variation *newberryi* (minor variation 15) to *C. nauseosus bigelovi* and thence to other members of *C. nauseosus*.

The accompanying diagram (fig. 27) is intended to express graphically the ideas of relationships as above set forth. It is quite possible that the lines of evolution have been different from those here indicated; for example, *vulcanicus* and its derivatives may have arisen from a *bolanderi*-like ancestor after this was evolved from *typicus*. Even if this could be demonstrated, it would not greatly modify the position of the subspecies as given in the diagram and it is believed that those there brought near to one another are of close genetic relationship, even though the direction of the evolutionary current may be in doubt.

ECOLOGY AND USES.

Chrysothamnus parryi forms characteristic societies in climax grassland, its low stature, and dense growth suggesting certain subspecies of *C. viscidiflorus*, as well as *Gutierrezia*. Both *typicus* and *howardi* are frequent in the mixed prairie, the latter being found over wide stretches in the foothills, on elevated plains, and in the lower mountain parks, while the former occurs in the moister parks at higher altitudes. *Howardi* is also frequently found on rocky slopes and ridges, as an open subclimax community. This is in harmony with the fact that both forms are indicators of a somewhat greater water-content. They occur in the original mixture of *Bouteloua*, *Stipa*, and *Agropyrum*, but are most abundant in grama short-grass, owing to their increase under grazing. They are frequently associated with *Artemisia frigida*, *Antennaria dioeca*, *Chrysothamnus*

TABLE 22.—Variation in the subspecies of *Chrysothamnus parryi*.¹

	Herbarium.	Involucre.			Corolla.		
		Length.	No. of bracts.	No. of flowers per head.	Length, including lobes.	Lobe-length.	Ratio of lobe-length to total length.
Subspecies <i>typicus</i> :		<i>mm.</i>			<i>mm.</i>	<i>mm.</i>	<i>p. ct.</i>
Big Creek, Wyo.....	10663 R	10.0	14	17	8.0	2.0	25
Golden Gulch, Wyo.....	7580 R	10.0	11	12	9.5	2.2	23
Albany County, Wyo.....	69421 UC	9.0	12 13	10 11	9.0	1.9	21
Larimer County, Colo.....	69423 UC	9.5	12	11	8.0	1.2	15
Montrose, Colo.....	81867 R	11.6	12	10	10.1	2.2	22
Tolland, Colo.....	76070 R	12.0	16	18	10.2	2.4	23
Breckenridge, Colo.....	30580 R	10.0	10	15	9.0	2.0	22
Do.....	13221 R	10.0	11	11	9.2	2.0	22
Cumbres, Colo.....	22893 R	10.1	12	12	8.5	2.0	23
Leadville, Colo.....	11056 CI	11.0	14	18	10.0	2.0	20
Minturn, Colo.....	11054 CI	11.0	12	10	10.0	2.0	20
Near Del Norte, Colo.....	11101 CI	9.0	12	14	9.0	1.5	16
San Juan Mountains, Colo.....	205815 UC	9.1	15	19	9.0	1.8	20
Near Empire, Colo.....	31169 UC	11.0	10	12	9.6	1.5	16
West Central Colo.....	55160 UC	11.0	10	13	10.0	1.0	10
Southwestern Colo.....	172775 UC	9.0	12	10	8.0	1.7	21
Cerro Summit, Colo.....	55166 UC	11.5	12	13	9.9	1.4	14
Hayden, Colo.....	69422 UC	10.0	11 12	10	10.0	1.7	17
Sevier River, Utah.....	159880 UC	10.0	13	9 11	9.1	1.6	17
Average.....		10.3	12	12.5	9.4	1.8	19
Subspecies <i>bolanderi</i> :							
Mono Pass, Calif. (type).....	Gr	9.0	12	10	10.5	1.2	11
Duplicate type.....	31162 UC	9.0 10.0	13	8 10	10.0	1.2 1.5	13
Average.....		9.3	12	9	10.2	1.3	12
Subspecies <i>lactor</i> :							
Mount Eddy, Calif. (type).....	SF	13.0	11 15	5 6	11.0	2.5	23
Duplicate type.....	Gr	12.0 14.0	11 12	6 7	11.0 12.0	2.3	20
<i>Eastwood 2079</i>	205549 UC	13.0	11	5	12.0	2.2	18
Mount Shasta, Calif. <i>Grant 5162</i>	62938 UC	12.0	14	5 6			
<i>Canby 111</i>	Gr	13.0	13	5 6	11.0	1.5	14
Modoc County, Calif.....	75822 UC	12.0 14.0	12 14	5	Young.....		
Average.....		12.9	12	6	11.4	2.1	19
Subspecies <i>imulus</i> :							
San Bernardino Mountains, Calif. (type).....	Jones	12.0	16	11 12	10.0	1.5	15
Do.....	31177 UC	10.5	16	12 13 15	9.5	1.0	10
Average.....		11.3	16	12	9.7	1.2	12
Subspecies <i>asper</i> :							
Inyo County Calif. (type).....	206849 US	12.0	11 13	6 6	10.0	1.4	14
Bloody Cañon, Calif.....	31165 UC	10.5	12	6 8 10	8.0	1.5	18
Charleston Mountains, Nev. ²	171476 UC	11.0	10 9 12	5 5 4	8.9	1.4	16
Ventura County, Calif.....	68942 UC	11.0	10	9 10	9.0	1.5	17
Average.....		11.1	11	6.9	8.9	1.4	17
Subspecies <i>vulcanicus</i> :							
Mono Mills, Calif.....	203167 UC	11.5	9 12	5 7	9.0	1.5	17
Volcano Creek, Calif. (type coll.).....	Gr	12.0	9	5	11.0	1.1	10
Eastern Tulare County, Calif.....	126456 UC	11.0	9 10	6 6	10.2	1.6	16
Little Kern River, Calif.....	126547 UC	13.0	12	7	10.3	2.0	19
Tulare County, Calif.....	134760 UC	11.0	10	6	10.0	1.5	15
Average.....		11.7	10	6.1	10.1	1.5	15

¹ Except where otherwise mentioned the plants selected for measurement are normal and fairly representative of the subspecies to which they are assigned. The figure given is the average of a number of measurements, but the fluctuation usually is slight on any given plant. In the case of involucre and corollas only the larger ones were measured, on the assumption that the smaller ones were not fully developed.

² Minor variation 17.

TABLE 22.—Variation in the subspecies of *Chrysothamnus parryi*—Continued.

	Herbarium.	Involucre.			Corolla.		
		Length.	No. of bracts.	No. of flowers per head.	Length, including lobes.	Lobe-length.	Ratio of lobe-length to total length.
Subspecies <i>monocephalus</i>:							
Mount Rose, Nev., 3,320 m. alt.	76001 UC	mm. 11.0	12	5	mm. 7.6	mm. 1.0	p. ct. 13
Mount Rose, Nev., 3,170 m. alt.	176764 UC	10.5	10	5	9.3	1.5	16
Jessie Lake, Calif.	31166 UC	10.0	10	5	8.0	1.0	12
Mono County, Calif.	195489 UC	10.1	8	5	7.7	1.3	17
Average		10.4	10	5	8.1	1.2	14
Subspecies <i>howardi</i>:							
Bells Springs, Carbon County, Wyo. ¹	51498 UC	10	14	5	8.1	1.3	16
Encampment, Carbon County, Wyo. ¹	69420 UC	12	13	5	8.0	1.3	16
Tipton, Wyo.	CI	10.8	11	4	8.0	1.4	18
Point of Rocks, Wyo.	CI	12.0	15	5	8.0	2.0	25
Laramie River, Wyo.	23595 R	11.1	11	5	9.5	2.1	22
Albany County, Wyo. ¹	69419 UC	13	13	5	10.6	1.7	16
North Park, Colo.	47263 R	13.0	14	6	10.7	2.5	23
West of Palmer Lake, Colo.	CI	9.5	14	5	9.0	1.2	13
Palmer Lake, Colo.	CI	11.0	13	5	8.5	1.2	14
Near Florissant, Colo.	CI	9.8	11	5	8.0	1.1	14
Walsenberg, Eastern Colo.	203169 UC	12	19	5	10.0	1.5	15
West of Walsenberg, Colo.	11089 CI	11.0	15	5	10.1	1.4	14
Cañon City, Colo.	203168 UC	10	14	7	10.0	1.0	10
Buena Vista, Colo.	205813 UC	10.0	12	5	9.5	1.7	18
San Luis Valley, Colo.	205814 UC	9.9	12	5	9.1	1.5	16
Average		11.0	13.6	5.1	9.1	1.5	17
Subspecies <i>attenuatus</i>:							
Ute Pass, Colo.	CI	11.0		5	9.0	0.6	7
Rio Mancos, Colo.	187573 UC	10.5	13	5	10.1	1.5	15
Thurber, Utah.	159552 UC	10.0	13	5	10.0	0.7	7
Marysvale, Utah (type coll.)	159554 UC	11.5	14	5	10.0	1.1	11
Marysvale, Utah.	159553 UC	11.0	13	5	10.2	1.5	15
Near Panguitch Lake, Utah.	159789 UC	10.2	13	5	10.0	0.5	5
Star Peak, Nev. (off type)	179590 UC	10.5	12	6	10.6	1.7	16
Average		10.7	13	5	9.9	1.0	11
Subspecies <i>nevadensis</i>:							
West Humboldt Mountains, Nev.	US	13.3	13	6	10.5	1.5	14
Comet Peak, Nev.	179575 UC	12.0	13	5	9.5	1.3	14
Kings Cañon, Nev.	75412 UC	11.5	13	5	9.9	1.1	11
Washoe County, Western Nev.	176431 UC	14.0	15	5	10.1	1.3	13
Do ²	176855 UC	11.0	18	4	7.1	1.0	14
Ormsby County, Western Nev.	87228 UC	15.0	14	5	10.1	1.2	12
Verdi, Western Nev.	193101 UC	13.0	15	6	10.5	1.5	14
Truckee, Calif.	134301 UC	15.0	13	6	10.1	1.0	10
Portola, Calif. ³	203269 UC	14.0	13	6	10.1	1.5	15
Do.	203263 UC	12.0	14	5	9.8	1.1	11
Keddie, Calif.	203265 UC	13.0	14	5	9.1	1.2	13
Average		13.0	14	5	9.7	1.2	13

¹ Minor variation 18.² Minor variation 19.³ Minor variation 20.

v. pumilus, *Lupinus argenteus*, etc., while *howardi* is often in contact with *C. n. pinifolius*. *Nevadensis* likewise forms societies in the bunch-grass prairie and in the sagebrush association of western Nevada and adjacent California, but it also extends to timberline in open parks and savannahs. The remaining subspecies are all of less importance.

They are practically confined to the mountains of California from the chaparral belt upward, *monocephalus* in particular reaching timber-line.

While *Chrysothamnus parryi* is browsed more or less during drought periods, especially the abundant *typicus* and *howardi*, it is to be regarded as a range weed, valuable only as an indicator of the degree to which over-grazing has proceeded.

12. CHRYSOTHAMNUS NAUSEOSUS (Pallas) Britton, in Britton and Brown, Ill. Fl. 3:326, 1898. Plates 33 to 35.

Shrub usually 3 to 20 dm. high, but varying from mere dwarfs to arborescent forms 25 dm. high, commonly with several erect stems from the base, these branching to form rounded bushes; bark of main stems brown, fibrous; twigs flexible, erect, moderately leafy, covered with a closely packed gray-green or white felt-like tomentum, which is deciduous only after several years, striate when the tomentum is smooth-surfaced but the striae masked when the surface is loose and fluffy; leaves varying from nearly filiform to broadly linear, not twisted, acute, 2 to 7 cm. long, 0.5 to 5 mm. wide, 1- to 3-nerved, not rigid, more or less tomentulose but sometimes practically glabrous; heads in terminal rounded cymes, these sometimes compound and forming elongated round-topped thyrses; involucre 6 to 13 mm. high; bracts usually 20 to 25, in vertical ranks, lanceolate, acute or obtuse, firm, glabrous to densely tomentose, without herbaceous tips; flowers usually 5, rarely 6; corolla tubular-funnelform, passing imperceptibly from tube to throat, 7 to 10 or rarely 12 mm. long, either glabrous or puberulent or arachnoid-pubescent on the tube; lobes 0.4 to 2.5 mm. long, erect to spreading, glabrous or sparsely pubescent; anther-tips lanceolate, acute, 0.4 to 0.7 mm. long; style-branches long-exserted, the linear-filiform acute appendage nearly equaling or usually much exceeding the stigmatic portion; achenes narrowed below, 5-angled, 5 to 5.5 mm. long, densely strigose or subvillous to glabrous; pappus shorter than or slightly exceeding the corolla, comparatively rigid, dull white. (*Chrysocoma nauseosa* Pallas in Pursh, Fl. Am. Sept. 2:517, 1814.)

On the plains and in the mountains, chiefly of the Great Basin area, but extending from Saskatchewan and the Dakotas to Colorado, western Texas, northern Sonora, Lower California, the inner Coast Ranges of upper California, eastern Washington, eastern British Columbia, and Alberta.

SUBSPECIES.

The specific limits here set for *C. nauseosus* are somewhat more extended than those assigned in any previous treatment, excepting only a recent one by Hall (Univ. Calif. Publ. Bot. 7:159 to 181, 1919). The species comprises a multitude of forms, from among which 47 segregates have been technically described. All but eight of these have been accorded specific rank at one time or another. The difficulties encountered in an attempt to assign specific or even varietal rank to all of the forms is indicated by the following quotation from page 161 of the paper just referred to:

"Nothing can be more certain than that these forty-two [now forty-seven] attempts to recognize species and varieties do not by any means exhaust the resources of the group. Every autumnal excursion into a new district brings to light one or more forms not previously described. The only limits set to the number of new species or varieties which might be set up lie in one's ability to visit all parts of the field during the flowering period and the failure or disinclination to recognize minute variations. But the systematist should include in his ultimate object not only the recognition of this multitude of forms, but also their proper arrangement in a scheme which will display their natural relationships. Since this would entail an enormous amount of detailed labor, including extensive experiments, and since the results, even if attainable, would be of but little practical value at the present time, the writer has satisfied himself with the acceptance of twenty-two forms, all of which are treated as varieties. This is believed to provide for all of the principal forms, and it is quite certain that each of the described varieties is a natural unit, although in most cases it is itself made up of still smaller variants."

*Artificial Key to the Subspecies of Chrysothamnus nauseosus.*¹

- Involucres puberulent (at least the short outer bracts) or tomentulose to densely woolly; foliage mostly gray or even white with a rather copious pubescence (least pronounced in *speciosus* and sometimes yellowish-green in *turbinatus*, *bigelovi*, and *glareosus*).
- Achenes densely pubescent.
- Tomentum loose, copious, and nearly pure white on twigs and leaves, extending to the involucre; corolla-tube often arachnoid-pubescent.
- Inner bracts of involucre plainly tomentose or if nearly glabrous the bracts then acute.
- Corolla-lobes lanceolate, 1 to 2 mm. long; style-appendage longer than the stigmatic part. (e) *albicaulis* (p. 212).
- Corolla-lobes short-ovate, less than 1 mm. long; style-appendage shorter than the stigmatic part. (b) *hololeucus* (p. 211).
- Inner bracts smooth and glabrous or nearly so, very obtuse. (d) *latisquameus* (p. 212).
- Tomentum close, compact, smooth, and gray or white on twigs, the leaves gray or greenish and sometimes nearly glabrous; corolla-tube glabrous or puberulent, only rarely arachnoid-pubescent.
- Bracts gradually acute or somewhat obtuse.
- Involucre 6 to 9 or rarely 10 mm. high.²
- Shrubs only 2 to 6 dm. high; corolla 6.5 to 8 mm. long² (very rarely 9 mm.) (f) *typicus* (p. 213).
- Shrubs normally 4 to 20 dm. high; corolla 8 to 10 mm. long or rarely only 7 mm. in *gnaphalodes*² (*latisquameus* of Arizona and New Mexico, with broad and very obtuse and smooth inner bracts, might be sought here).
- Corolla-lobes 1 to 2 mm. long; style-appendage longer than stigmatic portion. Leaves 1 to 3 mm. wide, 1-nerved; bracts various but mostly acute. (c) *speciosus* (p. 211).
- Leaves 3 to 5 mm. wide, 3-nerved; bracts mostly obtuse. (g) *salicifolius* (p. 213).
- Corolla-lobes 0.5 to 1 mm. long; style-appendage shorter than stigmatic portion. (a) *gnaphalodes* (p. 211).
- Involucre 11 to 12 mm. or rarely only 10 mm. high.² (Involucres of *turbinatus*, if shorter, may be known by their cylindric shape.)
- Corolla-lobes about 0.5 mm. long, villous. (q) *turbinatus* (p. 217).
- Corolla-lobes nearly 2.0 mm. long, glabrous. (i) *bernardinus* (p. 214).
- Bracts abruptly acute. Far western. (h) *occidentalis* (p. 213).
- Achenes glabrous.
- Bracts of the involucre obtuse; corolla 10 to 12 mm. long. (r) *glareosus* (p. 217).
- Bracts of the involucre very acute; corolla 9 to 10 mm. long. (s) *bigelovi* (p. 217).
- Involucres perfectly glabrous, although sometimes viscidulous or glandular; foliage mostly greenish, the tomentum rather sparse or wanting on mature leaves.
- Achenes glabrous or nearly so. (t) *leiospermus* (p. 217).
- Achenes densely pubescent.
- Leaves linear, mostly more than 1 mm. wide,² mostly 1- to 5-nerved.
- Involucre 10 mm. or more long; corolla 9 to 12 mm. long; lobes 1.5 to 2.5 mm. long. Southern California. (i) *bernardinus* (p. 214).
- Involucre 6 to 8 mm. long, corolla 7 to 9 mm. long; lobes 0.5 to 1.5 mm. long. (j) *graveolens* (p. 214).
- Leaves linear-filiform or very narrowly linear, mostly 1 mm. or less wide (except in *occidentalis*), 1-nerved.
- Bracts of the involucre obtuse to acute, not abruptly pointed.
- Corolla-lobes glabrous; shrub leafy except sometimes in *mohavensis*.
- Involucre 7 to 9 mm. long, not sharply angled, the bracts moderately keeled, 5-rowed.
- Corolla 7 to 9 mm. long; lobes under 2 mm.; twigs and foliage slender.
- Lobes of corolla 0.5 to 1 mm. long, rarely more; inflorescence typically rounded to pyramidal. Rocky Mountain States. (k) *pinifolius* (p. 215).
- Lobes of corolla 1 to 2 mm. long, inflorescence typically cylindric to pyramidal. Great Basin. (l) *consimilis* (p. 215).
- Corolla 7 to 10 mm. long; lobes 1.7 to 2.5 mm. long; twigs and foliage stouter. Southwestern. (m) *viridulus* (p. 215).
- Involucre 9 to 10 mm. long, sharply 5-angled, the strongly keeled bracts in very distinct vertical rows. (o) *mohavensis* (p. 214).
- Corolla-lobes sparsely long-hairy in the bud; shrub nearly leafless. (p) *junceus* (p. 216).
- Bracts of the involucre abruptly pointed or some only acute. Far western.
- Tip of the bract short, erect. (h) *occidentalis* (p. 213).
- Tip of the bract about 1 mm. long, very slender, recurved. (n) *ceruminosus* (p. 216).

¹ A natural key has not been prepared, but the groupings according to a natural system are given in figure 28, page 223.² These measurements are of fully mature involucre and corollas, the latter either fresh or restored by boiling.³ Care must be exercised in making this measurement since the leaves are often longitudinally folded. The figures given are for the total width of the flat leaf.

The difficulties encountered in an attempt to assign specific rank to the more striking variations are indicated somewhat in table 23, where the principal characters are tabulated. The principal characteristics of the 20 subspecies are given in the key on page 210 and the subspecies themselves are given a diagrammatic presentation on page 223.

12a. *CHRYSOTHAMNUS NAUSEOSUS GNAPHALODES* (Greene).—Shrub 5 to 15 or rarely 25 dm. high, usually globose in outline, with very many short twiggy branches; twigs erect or spreading, not densely leafy, obscurely striate, yellowish green or gray with a closely packed tomentum; herbage usually very fragrant; leaves 2 to 4 cm. long, 1 mm. or less wide, those of the end twigs only 1 to 3 cm. long and often recurved, 1-nerved, gray-tomentose; inflorescence a rounded cyme terminating each of the twigs; involucre about 7 (6 to 8) mm. high; bracts rather obtuse, keeled, in 5 distinct vertical rows, tomentose, not ciliate; corolla 7 to 8 mm. long; tube sparsely pubescent with short crisp or rigid hairs; lobes ovate, acute, 0.5 to 1 mm. long, erect or even connivent around the stament-tube; style-appendage shorter than the stigmatic part; achenes densely pubescent. (*C. speciosus* var. *gnaphalodes*, Greene, *Erythea* 3:110, 1895.) Abundant on gravelly and sandy non-alkaline slopes and benches of western Nevada, eastern California (and northern Arizona?). Type locality, Pyramid Lake, Nevada. Collections: Pyramid Lake, Nevada, 1883, *Curran* (Univ. Calif. Herb. 87247, probably the type); Fallon, Nevada, *Heller 10680* (DS, Gr, NY); California: Benton, Mono County, *Hall 10655* (UC); White Mountains, Inyo County, *Hall 10631* (UC); west of Lancaster, Los Angeles County, *Hall 10585* (SF, UC); Banning, westerly edge of Colorado Desert, September 27, 1894, *Toumey* (UC); mesas near Colton, *Parish 2057* (DS).

12b. *CHRYSOTHAMNUS NAUSEOSUS HOLOLEUCUS* (Gray).—Shrub 6 to 18 dm. high and fully as broad, closely branched and usually of rounded outline; twigs erect, leafy to the top, not striate, white with a permanent dense tomentum; herbage exceedingly fragrant; leaves linear, 1 to 3 cm. long, about 1 but sometimes nearly 2 mm. wide, 1-nerved, permanently white-tomentose; inflorescence a rounded often compact cyme; involucre 6 to 7 mm. high; bracts very obtuse, plainly keeled and in 5 distinct vertical ranks, woolly but not ciliate; corolla 6.5 to 8 mm. long; tube minutely puberulent and also more or less cobwebby with loose hairs or these occasionally wanting; lobes ovate, acute, strictly erect, 0.5 to 1 mm. long; style-appendage shorter than the stigmatic part; achenes densely pubescent. (*Bigelovia graveolens* var. *hololeuca* Gray, *Proc. Am. Acad.* 8:645, 1873.) Gravelly or sandy well-drained slopes of western Nevada and eastern California extending southward as far as Antelope Valley. Type locality, Owens Valley, California. Collections: Sutcliffe, Pyramid Lake, Nevada, *Hall 10884* (UC); near Lida, Esmeralda County, Nevada, *Hall 10818* (UC); Benton, Mono County, California, *Hall 10643* (UC); Independence, Inyo County, California, *Hall 10615* (SF, UC); type collection, *Horn* (Gr).

12c. *CHRYSOTHAMNUS NAUSEOSUS SPECIOSUS* (Nuttall).—Shrub commonly 6 to 20 dm. high (or only 4 dm. in the far west), broad and rounded; twigs mostly erect, with long leaves to the summit, striate but the striae often obscure, greenish white, the tomentum comparatively smooth; herbage nearly inodorous; leaves linear, 2 to 6 cm. long, typically about 1 mm. wide but varying to 3 mm. (see minor variation 58); 1-nerved, usually erect or ascending, becoming dense toward the inflorescences and there scarcely reduced in size, gray, tomentose or the tomentum partly deciduous and the foliage then greenish; inflorescence a round-topped or somewhat elongated cyme, commonly loose; involucre 8 to 10 mm. high; bracts acute, strongly keeled, in obvious vertical rows, either tomentulose on the back or all but the very short outermost ones glabrous (as in the type), not ciliate; corolla 8 to 10 or rarely 11 mm. long; tube sparsely puberulent or glabrous; lobes 0.8 to 2 mm. long; style-appendage longer than the stigmatic part; achenes densely pubescent.

(*C. speciosus* Nuttall, Trans. Am. Phil. Soc. II, 7:323, 1840.) Sandy and clayey slopes and benches, where only moderately alkaline, Montana, Wyoming, and western Colorado to Utah, eastern California, Washington, and Idaho. Type locality, in the Rocky Mountain plains, near Lewis River. Collections: Type collection, Nuttall (Gr, Phila); Fremont County, Wyoming, Goodding 521 (NY, UC); Woods Landing, Wyoming, Nelson 3477 (R, type of *C. pulcherrimus* Nelson, minor variation 68); North Elk Cañon, Rio Blanco County, Colorado, September 3, 1902, Sturgis (Gr, leaves 3 mm. wide, tomentum dense and stopping abruptly with the outer involucre bracts exactly as in the type); North Park, Colorado, Osterhout 2266 (NY); near Hebron, Colorado, Shear 4341 (NY); Parleys Cañon near Salt Lake City, Utah, Jones 511 (UC); Ogden, Utah, September 28, 1917, Stilwell (UC); Fall Creek, Ormsby County, Nevada, Baker 1436 (Gr, UC, SF, minor variation 58); Mono Pass, California, Bolander 6145 (Gr, NY, US, same variation); Leevining Cañon, Mono County, California, Hall 10852 (UC, same variation); near Yreka, Siskiyou County, California, Butler 1824 (UC); Crater Lake, Oregon, 2,750 m. altitude, Heller 12945 (DS, SF, UC); near Echo, eastern Oregon, Leiberg 906 (DS, Gr, UC, tall, erect form with strongly pubescent involucres, minor variation 57); Cow Creek, mouth of Doe Creek, Douglas County, Oregon, Ward 43 (NY, typical).

12d. CHRYSOTHAMNUS NAUSEOSUS LATISQUAMEUS (Gray).—Shrub tall (perhaps rounded at top); twigs erect or ascending, leafy to the summit, the striae obscured by a white rather loose tomentum; herbage probably mildly fragrant; leaves 2 to 5 cm. long, less than 1 mm. wide; inflorescence a loosely branched rounded compound cyme; involucre about 8 mm. high (7 to 9 mm.); bracts very obtuse (at least the inner ones), carinate, in 5 distinct vertical rows, outermost ones tomentulose, inner ones usually glabrous; corolla about 8 to 9 mm. long; tube short-pubescent or glabrous; lobes ovate or short-lanceolate, 0.5 to 1 mm. long, erect; style-appendage longer than the stigmatic portion; achenes densely pubescent. (*Bigelovia graveolens* var. *latisquamea* Gray, Proc. Am. Acad. 8:645, 1873.) New Mexico, Arizona, and Sonora. Type locality, New Mexico. Collections: Type collections, October 2, 1853 or 1854, Bigelow, and on the Mimbrres, 1853, Henry (Gr); San Lorenzo, Grant County, New Mexico, Metcalfe 1462 (DS, Gr, NY, US); Burro Mountains, New Mexico, Rusby 202 (US); Santa Rita Mountains, Arizona, November, 1891, Brandegee (UC, type collection of *C. speciosus arizonicus* Greene, minor variation 73); Billings, Arizona, Jones 4511 (NY, US); Santa Cruz, Sonora, Mearns 2624 (US).

12e. CHRYSOTHAMNUS NAUSEOSUS ALBICAULIS (Nuttall).—Shrub 5 to 10 dm. high, of rounded outline; twigs erect, leafy to the top, not evidently striate, white with a permanent and dense tomentum; herbage not fragrant; leaves narrowly linear, 2.5 to 4 cm. long, 0.5 to 1.5 mm. wide or up to 3 mm. wide in occasional forms, 1-nerved, permanently and floccosely white-tomentose; inflorescence a rather loose round-topped cyme; involucre 7 to 9 mm. high; bracts mostly acute, plainly keeled, in 5 distinct vertical ranks, white-woolly but not ciliate; corolla 8 to 10 mm. long; tube usually arachnoid with long weak hairs; lobes lanceolate, 1.5 to 2 mm. long; style-appendage longer than the stigmatic part; achenes densely pubescent. (*C. speciosus* β . *albicaulis* Nuttall, Proc. Am. Phil. Soc. II, 7:324, 1840.) Upland slopes and benches, most plentiful in the basin of the Columbia River, extending into British Columbia, Montana, and Utah, also southward in a wide-leaved form to middle Nevada and middle eastern California; occurs mostly as scattered plants on areas where subspecies *speciosus* is more abundant. Type locality, not specifically given, but probably in the valley of the Snake River, for the habitat of *C. speciosus* is given by Nuttall as "in the Rocky Mountain plains, near Lewis' River," and *albicaulis* is then described as a form of this, with no other locality mentioned. Collections: Wawawai, Washington, Piper 1571 (Mo. Bot. Gard.); Prosser, Yakima Region, Washington, Cotton 897 (Gr); near forks of Cottonwood Cañon, eastern

Oregon, *Leiberg 884* (Gr, UC, US); Warm Springs, Cook County, Oregon, *Coville and Applegate 724* (US); Polson, Montana, *Umbach 227* (NY); Marysvale, Utah, *Jones 5967* (NY, UC); California: Modoc County, near the Oregon line, *Clements and Hall 11662* (UC); Big Meadows, August, 1880, *Austin* (Herb. Greene, type of *C. orthophyllus* Greene, minor variation 63); Honey Lake Valley, Lassen County, *Clements and Hall 11681* (UC); Truckee, Nevada County, *Heller 7192* (Gr, NY, UC, minor variation 25, *C. californicus* Greene); near Bridgeport, Mono County, *Bolander 6159* (UC, same variation); near Reno, Nevada, August, 1883, *Brandege* (UC, same variation).

12f. *CHRYSOTHAMNUS NAUSEOSUS TYPICUS*.—Low shrub 2 to 6 dm. high, woody only at the base, usually rounded and not as broad as high, often nearly prostrate; twigs mostly erect, very leafy, not striate, gray or at the most whitish with a smooth close tomentum (white in minor variation 64); herbage not strongly scented; leaves narrowly linear, 2 to 5 cm. long, 0.5 to 1.5 mm. wide, either spreading or ascending, white-tomentose; inflorescence cymose or elongated; involucre 6.5 to 8 mm. high; bracts rather obtuse, scarcely keeled, the outer ones tomentulose and somewhat glandular, ciliolate at least at summit, the innermost only puberulent or glabrous; corolla 6.5 to 8 mm. long (9 mm. in one collection); tube puberulent, rarely arachnoid; lobes linear-lanceolate, 1.2 to 2 mm. long; style-appendage longer than the stigmatic part or sometimes slightly shorter; achenes densely pubescent. (*Chrysocoma nauseosa* Pallas in Pursh, Fl. Am. Sept. 2:517, 1814.) Assiniboia and Montana to South Dakota, Colorado, Utah, and British Columbia; often on bleak or alkaline plains, especially common in Wyoming and eastern Colorado. Type locality, on the banks of the Missouri. Collections: Type collection, *Lewis* (Phila, see under *Chrysocoma nauseosa*, p. 219; Sedan, Gallatin County, Montana, August 12, 1902, *W. W. Jones* (Gr, UC);¹ Great Falls, Montana, *Anderson 89* (UC);² Pennington County, South Dakota, abundant in bad lands, *Over 1804* (US);² Douglas, Converse County, Wyoming, *Nelson 9001* (R, UC);² Howell Lakes, Wyoming, *Nelson 5315* (NY, UC);¹ Laramie, Wyoming, July 29, 1889, *Greene* (Herb. Greene, UC, US);¹ Huttons Lake, Wyoming, *Nelson 5300* (R, Gr, NY, UC, US, type collection of *C. frigidus concolor* Nelson, minor variation 36); near Laramie, Wyoming, *Nelson 5347* (R, Gr, NY, type collection of *C. pallidus* Nelson, minor variation 64); New Windsor, Weldon County, Colorado, *Osterhout 2335* (NY, R, UC);² near Kanab, Utah, *Jones 6047d* (US);¹ Milk River, Assiniboia, *Macoun 10871* (US).¹

12g. *CHRYSOTHAMNUS NAUSEOSUS SALICIFOLIUS* (Rydberg).—Shrub 3 to 10 dm. high, with erect branches; twigs erect or ascending, very leafy to the summit, plainly striate, gray with a thin loose tomentum or nearly green; herbage probably not fragrant; leaves broadly linear, 4 to 8 cm. long, 3 to 5 mm. wide, 3-nerved, minutely tomentulose; inflorescence cymose, dense; involucre 7 to 8 mm. high; bracts mostly obtuse, not keeled, the ranks obscure, the outer (more acute) ones slightly tomentulose, the inner glabrous or only ciliate; corolla about 10 mm. long, tube only minutely puberulent; lobes 1.5 to 2 mm. long; style-appendage longer than the stigmatic portion; achenes densely pubescent. (*C. salicifolius* Rydberg, Bull. Torr. Club 37:130, 1910.) Apparently rare and confined to Utah. Type locality, Strawberry Valley, Utah. Collections: Type collection, 2,150 m. altitude, *Leonard 288* (NY); near Salt Lake City, Utah, *Garrett 2455* (NY); Twelve-mile Creek, Utah, *Ward 659* (Gr).

12h. *CHRYSOTHAMNUS NAUSEOSUS OCCIDENTALIS* (Greene).—Shrub probably rather low, with numerous short, slender, erect branches; twigs ascending, leafy, striate, gray-tomentose, but not loosely or flocculently so; herbage not strongly odorous; leaves narrowly linear, 4 cm. or less long, mostly less than 1 mm. wide, but occasionally up to 3

¹ The form of *typicus* described as *C. frigidus* Greene, minor variation 35, p. 220.

² The form of *typicus* described as *C. plattensis* Greene, minor variation 67, p. 222.

mm., 1-nerved, tomentulose; inflorescence compactly cymose, rounded, 2 to 5 cm. across; involucre 7 to 10 mm. high; at least some of the bracts abruptly acute or cuspidate, keeled, 5-rowed, the outer ones more or less glandular-puberulent; corolla 8.5 to 10.5 mm. long; tube only puberulent; lobes lanceolate-linear, about 2 mm. long; style-appendage longer than the stigmatic part; achenes densely pubescent. (*C. californicus* var. *occidentalis* Greene, *Erythra* 3:112, 1895, in part. *C. occidentalis* Greene, Fl. Fran. 369, 1897.) Inner Coast Ranges and Sierra Nevada Mountains of California. Type locality, in the Coast Ranges of California, from Humboldt County southward and in the mountains of southern California. Collections: Mount Eddy, *Baker 3785* (UC); Grouse Creek, Humboldt County, August 2, 1888, *Chesnut* and *Drew* (UC); South Yolla Bolla, October, 1916, *Merriam* and *Bailey* (UC); Bloody Cañon, Mono County, August 13, 1898, *Congdon* (DS); Kaweah River Basin, *Hopping 52* (UC); Barton Flats, San Bernardino Mountains, *Wilder 597* (UC); Cleveland National Forest, San Jacinto Mountains, *de Forest 129* (S. F. office, U. S. Forest Service).

12i. CHRYSOTHAMNUS NAUSEOSUS BERNARDINUS (Hall).—Shrub probably low and with erect stems but habit not well known; twigs erect, simple, leafy, not striate, coated with a smooth gray or white pannose tomentum; leaves ascending, linear, very acute, often recurved at tip, 3 to 5 cm. long, 1 to 2 mm. wide, mostly conduplicate, 1-nerved, green and scabro-puberulent (white-tomentose in minor variation 51); inflorescence a loose rounded cyme, 3 to 10 cm. across, the lower branches 2 to 10 cm. long; involucre 10 to 13 mm. high; bracts sharply acuminate, keeled, in well-defined ranks, glabrous or slightly erose-ciliate or the outer ones obscurely puberulent (white-tomentose in minor variation 51); corolla 9 to 12 mm. long; tube sparsely crisp-puberulent; lobes linear-lanceolate, acute, 1.5 to 2.5 mm. long; style-appendage longer than the stigmatic part; achenes densely sericeous-pubescent. (*C. nauseosus* var. *bernardinus* Hall, Univ. Calif. Publ. Bot. 7:171, 1919.) Mountains of southern California. Type locality, hillsides at 2,250 m. altitude, Bluff Lake, San Bernardino Mountains, California. Collections: Type collection, September 2, 1905, *Grinnell* (UC); open pine woods near Acton, Los Angeles County, August 24, 1893 (DS, ex herb. Hasse); above Aroyo Seco, West Fork Divide, San Gabriel Mountains, September 4, 1915, *Grinnell* (SF); Pine Mountain Ridge, San Antonio Mountains, California, *Johnston 1652* (DS, UC); Round Valley, San Jacinto Mountains, California, *Hall 341* (UC, form with very compact cymes and elongated anther-tips and style-appendages, Hall, l. c.).

12j. CHRYSOTHAMNUS NAUSEOSUS GRAVEOLENS (Nuttall).—Shrub commonly 6 to 15 dm. high, robust, taller than broad, with erect branches; twigs erect, leafy, more or less evidently striate, yellowish-green to nearly white with a compact smooth tomentum; herbage mildly ill-scented; leaves broadly linear, 4 to 6 cm. long, 1 to 2 mm. wide, some of them usually 3- or 5-nerved, impunctate, smooth and green but often slightly tomentulose, especially beneath; inflorescence a round or flat-topped cyme, fastigiate, the heads crowded, involucre 6 to 8 mm. high; bracts acute, keeled, in rather well-defined vertical rows, glabrous; corolla 7 to 9 mm. long; tube puberulent or glabrous; lobes 0.5 to 1.5 mm. long, erect; style-appendage longer than the stigmatic part; achenes densely pubescent. (*Chrysocoma graveolens* Nuttall, *Genera* 2:136, 1818.) On plains in only slightly alkaline soil, North Dakota to Colorado, New Mexico, northern Arizona, Utah, and Idaho. Type locality, on the banks of the Missouri, in denuded soils. Collections: Washington County, North Dakota, August, 1886, *Hatcher* (UC); Platte Cañon, Wyoming, *Nelson 8642* (Gr, NY, R, UC); Colorado: New Windsor, Weldon County, *Osterhout 2336* (NY, UC, US); west of Trinidad, *Hall 10777* (UC); Cañon City, September 7, 1896, *Greene* (Herb. Greene, type of *C. virens* Greene, minor variation 79); Grand Junction, August 27, 1896, *Greene* (Herb. Greene, type of *C. laetevirens* Greene, minor variation 42); Grand

Junction, August 27, 1896, *Greene* (Herb. *Greene*, type of *C. falcatus* *Greene*, minor variation 33); vicinity of Farmington, New Mexico, *Standley 6884* (US); Adamana, Arizona, *Hall 11164* (UC); Green River, Utah, *Jones 516* (UC); Sierra La Sal, Utah, *Purpus 7071* (UC); mesa west of Pocatello, Idaho, *Eggleston 9936* (US).

12k. *CHRYSOTHAMNUS NAUSEOSUS PINIFOLIUS* (*Greene*).—Shrub of medium size (6 to 15 dm. high), taller than broad, with erect branches; twigs slender, erect, leafy, striate, green with a closely packed tomentum (rarely white and non-striate); herbage with a disagreeable odor; leaves linear-filiform, 3.5 to 6 cm. long, 1 mm. or less wide, 1-nerved, green to grayish puberulent, often densely tomentulose beneath; inflorescence a thyrsoid panicle of rounded or pyramidal outline, varying to short-oblong; involucre 6 to 8 or rarely 9 mm. long; bracts acute, keeled, in vertical rows, glabrous; corolla 6.5 to 9 mm. long; tube puberulent or glabrous; lobes 0.5 to 1 mm. long; style-appendage longer than stigmatic part; achenes densely pubescent. (*C. pinifolius* *Greene*, *Pittonia* 5:60, 1902.) Alkaline plains and plateaus, Colorado, New Mexico (and Utah?). Type locality, Gunnison, Colorado. Collections: Type collection, September 1, 1896, *Greene* (Herb. *Greene*); Alamosa, San Luis Valley, Colorado, *Hall 10784a* (UC); Iola, region of the Gunnison watershed, *Baker 668* (Gr, NY, US); Doyles, west central Colorado, *Baker 629* (Gr, NY, UC, US, twigs green in one specimen, white in another); above Datil, New Mexico, *Wootton 2494* (DS, Gr, NY, UC); White Mountains, Lincoln County, New Mexico, *Wootton 379* (Gr, *Greene*, UC, US, type collection of *C. confinis*, minor variation 30).

12l. *CHRYSOTHAMNUS NAUSEOSUS CONSIMILIS* (*Greene*).—Shrub commonly 6 to 15 dm. high, taller than broad, with erect branches; twigs erect, very leafy, striate, green, with a closely packed tomentum; herbage with a strong disagreeable odor; leaves nearly filiform, 2.5 to 5 mm. long, less than 1 mm. wide, 1-nerved, somewhat resinous and canescently tomentulose to nearly glabrous; inflorescence an elongated pyramidal or cylindrical thyrus; involucre 7 to 8 mm. high; bracts acute, keeled, in fairly distinct vertical rows, glabrous; corolla 7 to 8.5 mm. long; tube glabrous or only puberulent; lobes linear, 1 to 2 mm. long, spreading in age; style-appendages longer than the stigmatic part; achenes densely pubescent. (*C. consimilis* *Greene*, *Pittonia* 5:60, 1902.) Alkaline valleys and plains, western Wyoming and Colorado to New Mexico, northern Arizona, Nevada, northeastern California (and one collection from San Diego County), eastern Oregon, and Idaho. Type locality, Deeth, Elko County, Nevada. Collections: Evanston, Wyoming, *Nelson 4105* (Gr, NY, R, UC, US, type collection of *C. oreophilus* *Nelson*, minor variation 61); Marysvale, Utah, *Jones 5966* (UC, US); Tooele Valley, Utah, *Jones 502* (UC); eastern base San Francisco Mountains, Arizona, *Hall 11180* (UC); type, August 7, 1895, *Greene* (Herb. *Greene*); Goldfield, Nevada, *Hall 10808* (UC); Fallon, Nevada, *Heller 10679* (DS, Gr, NY, UC, US); California: Tantillas Mountains, San Diego County, 1875, *Palmer* (Gr); Bridgeport, Mono County, *Hall 10866* (UC); Shasta Valley, *Heller 12978* (DS, SF, UC); near Alturas, Modoc County, 1894, *Austin* (Herb. *Greene*, type of *C. angustus*, minor variation 21); Lake County, Oregon, *Leiberg 769* (UC); Boise, Idaho, *Clark 317* (Gr, NY, UC, US, type collection of *C. oreophilus artus* *Nelson*, minor variation 62).

12m. *CHRYSOTHAMNUS NAUSEOSUS VIRIDULUS* (*Hall*).—Shrub 5 to 20 or even 30 dm. high, robust, taller than broad, with ascending branches; twigs erect, leafy, rather stout, striate, densely covered with pannose yellowish-green smooth tomentum; herbage mal-odorous; leaves (at first erect or ascending, later inclined to droop) narrowly linear, acute, 3 to 5 cm. long, about 1 mm. wide, 1-nerved, channeled above, green but tomentulose on both sides; inflorescence a pyramidal to nearly globose thyrse; involucre 6.5 to 8.5 mm. high; bracts acute except the obtuse inner ones, keeled, in 5 vertical ranks, glabrous but viscid with a resinous exudation; corolla 7 to 9.5 mm. long; tube glabrous or sparsely

puberulent; lobes 1.7 to 2.5 mm. long, recurving in age; style-appendage longer than the stigmatic part; achenes densely sericeous. (*C. nauseosus* var. *viridulus* Hall, Univ. Calif. Publ. Bot. 7:177, 1919.) Alkaline flats of west central Nevada and in eastern California, from Mono County south to the desert side of the San Antonio Mountains. Type locality, Benton, Mono County, California, on sandy alkaline flats with *Distichlis*, at 1,720 m. altitude. Collections: Lida, Esmeralda County, Nevada, *Hall 10814* (UC); California: north side Mono Lake, *Hall 10846* (UC); type collection, November 3, 1917, *Hall 10642* (UC); Antelope Valley, *Hall 10580* and *10582* (UC, minor variation 59); San Antonio Mountains, *Johnston 1706* (UC); east of Bear Valley, San Bernardino Mountains, August 20, 1907, *Bailey* (UC); and a large series mostly from Owens Valley, in Univ. Calif. Herb.

12n. CHRYSOTHAMNUS NAUSEOSUS CERUMINOSUS (Durand and Hilgard).—Shrub 5 to 12 dm. high, rounded, fastigiately branched; twigs erect, short-leafy, striate, yellowish-green with a smooth compact tomentum; herbage scarcely odorous; leaves linear-filiform, 1 to 3 cm. long, less than 1 mm. wide, 1-nerved, tomentulose; inflorescence compactly cymose, rounded, 2 to 3 cm. across; involucre 7 to 8 mm. high; bracts abruptly narrowed to a filiform recurved mucro about 1 mm. long, keeled, somewhat ranked, glabrous and glutinous; corolla about 6.5 mm. long; tube puberulent; lobes 1.5 to 2.0 mm. long; style-appendages longer than the stigmatic part; achenes densely pubescent. (*Linosyris ceruminosa* Durand and Hilgard, Jour. Acad. Nat. Sci. Phila. II, 3:40, 1855; also Pacif. R. R. Rep. 3:9, plate 6, 1857.) Mojave Desert, California, and mountains to the west. Type locality, Tejon Pass, California. Collections: Type collection, September, 1853, *Heermann* (Gr, US); *Hesperia*, California, October, 1917, *Spencer* (UC).

12o. CHRYSOTHAMNUS NAUSEOSUS MOHAVENSIS (Greene).—Shrub of medium or large size, usually 8 to 16 dm. high and with elongated straight stems; twigs erect or ascending, often but not always nearly leafless and rushlike, striate, white or greenish-yellow; leaves filiform, very acute, 2 to 3 cm. long, 1-nerved, nearly glabrous; inflorescence a rounded or somewhat elongated thyrs; involucre narrow, 9 to 10.5 mm. long; bracts obtuse to acute, sharply keeled, in very distinct vertical ranks, glabrous; corolla 8 to 10 mm. long; tube puberulent; lobes 1.5 to 2.5 mm. long, spreading; style-appendage longer than the stigmatic part; achenes densely pubescent. (*Bigelovia mohavensis* Greene in Gray, Syn. Fl. 1:138, 1884.) In well-drained, scarcely alkaline soil, western part of the Mojave Desert, north in the inner Coast Ranges to Mount Hamilton, all in California. Type locality, Mojave Desert, California. Collections: Mojave Desert, July, 1884, *Brandege* (UC); Oak Creek, south of Mojave, *Hall 10570* (UC, flowering twigs leafless for 6 to 7.5 dm.); near Fort Tejon, 1,550 m. altitude, *Rothrock 271* (Gr); Mojave Desert, October 19, 1882, *Pringle* (Gr, US); Alamo Mountain, Ventura County, *Baldwin 102* (UC); Rock Creek, desert slopes of San Gabriel Mountains, *Abrams and McGregor 625* (DS); Priest Valley to Coalinga, San Benito County, *Abrams 7685* (DS); Mount Hamilton, *Hall 9894* (UC).

12p. CHRYSOTHAMNUS NAUSEOSUS JUNCEUS (Greene).—Shrub of unknown size, strict, fastigiately much branched; twigs slender, rush-like, mostly leafless, not striate, yellowish-green with a smooth compact tomentum; leaves linear-filiform; inflorescence fastigiate-cymose; involucre about 10 mm. high; bracts acute, 5 in each of the distinct vertical rows, glabrous; corolla about 9 mm. long; tube pubescent but not arachnoid; lobes about 1.5 mm. long, externally beset with long delicate hairs; style-appendage longer than the stigmatic part; achenes densely pubescent. (*Bigelovia juncea* Greene, Bot. Gaz. 6:184, 1881.) Known only from Arizona. Type locality, calcareous bluffs of the Gila River in eastern Arizona, very near the New Mexican boundary. Collections: Type collections, September 5, 1880, *Greene* (Gr, Jones, hairs on corolla-lobes wanting or deciduous in

specimen in Herb. Jones); same locality, October 29, 1880, *Greene* (NY); Bright Angel Trail, Grand Cañon, Arizona, *Eastwood 3703* (SF).

12q. *CHRYSOTHAMNUS NAUSEOSUS TURBINATUS* (Jones).—Shrub 5 to 15 dm. high, rounded, bushy, broader than high; twigs irregularly ascending, leafy, faintly striate, yellowish-green with a close, smooth tomentum; herbage not strongly scented; leaves linear, 1.5 to 2.5 cm. long, about 1 mm. wide, 1-nerved, merely tomentulose to densely white-tomentose; inflorescence a few-headed simple or compound cyme; involucre 9 to 11 mm. high, very narrow, cylindric; bracts obtuse, often shortly apiculate, not keeled, 4 or 5 in each vertical row, sparsely tomentulose or the inner ones only ciliate; corolla 10 to 11 mm. long; tube puberulent; lobes ovate, erect, scarcely over 0.5 mm. long, the tips villous with long hairs; style-appendage longer than the stigmatic part; achenes densely pubescent. (*Bigelovia turbinata* Jones, Proc. Calif. Acad. II, 5:691, 1895.) In mounds of clay or sandy soil built up in alkaline flats, southern Utah. Type locality, Canaan Ranch (near Kanab, Kane County), Utah, on clay soil on the borders of an old sink, at 1,540 m. altitude. Collections: Type collection, September 24, 1894, *Jones* (Herb. Jones); Champlain, August 14, 1911, *Jones* (DS, Herb. Jones); Lund, Iron County, *Hall 10786* (UC).

12r. *CHRYSOTHAMNUS NAUSEOSUS GLAREOSUS* (Jones).—Shrub said to be only about 3 dm. high, many-stemmed; twigs erect, sparsely leafy; leaves broadly to narrowly linear, slightly widened above, plane; inflorescence cymose; involucre about 11 mm. high; bracts obtuse, somewhat keeled, in obvious ranks, erose-ciliate, scurfy-tomentulose; corolla 10 to 12 mm. long, glabrous; lobes linear-lanceolate; style-appendage longer than the stigmatic part, 0.9 mm. long; achenes glabrous. (*Bigelovia glareosa* Jones, Zoe 2:247, 1891.) Gravelly mesas of central and southern Utah and northern Arizona. Type locality, Marysvale, southern Utah. Collections: Little Colorado River, Arizona, October 8, 1851, *Thurber* (?) (Gr).

12s. *CHRYSOTHAMNUS NAUSEOSUS BIGELOVI* (Gray).—Shrub 3 to 10 dm. high, densely branched; twigs short, erect, leafy or nearly leafless, striate, yellowish-green with a closely packed smooth tomentum; herbage scarcely odorous; leaves linear-filiform, 1 to 2.5 cm. long, 0.5 to 1 mm. wide, 1-nerved, tomentulose when young; inflorescence a lax few-headed cyme terminating each of the branches; involucre 10 to 11.5 mm. high; bracts acute or subacuminat, spreading in age, 4 or 5 in each row, tomentulose and sometimes ciliate; corolla 9 to 10 mm. long; tube glabrous or nearly so; lobes ovate, erect or spreading, 0.8 to 1.5 mm. long; style-appendage longer than the stigmatic part; achenes glabrous, 5-nerved. (*Linosyris* (*Chrysothamnus*) *bigelovi* Gray, Pacif. R. R. Rep. 4:98, plate 12, 1857.) On very dry hills and plains, southern Colorado to Texas and Arizona. Type locality, hills and arroyos, Cienegella, above Albuquerque, New Mexico. Collections: Buena Vista, Colorado, *Crandall 2735* (NY, US); Wet Mountain Valley, Colorado, August 29, 1893, *Brandege* (UC); Colfax, Colorado, October, 1877, *Brandege* (UC); type collection, 1853-54, *Bigelow* (Gr); south of Farmington, New Mexico, *Hall 11140* (UC, form with villous corolla-lobes); bad lands near Ojo Alamo, New Mexico, *Hall 11137* (UC); Las Palomas, Sandia Mountains, New Mexico, *Ellis 319* (NY, US); Painted Desert, Arizona, October, 1919, *Long* (UC, intermediate to subspecies *glareosus*, the bracts only acute); Navajo Indian Reservation, Arizona, *Standley 7373* (Gr, NY, UC, US); Moqui Indian Reservation, Arizona, August 22, 1897, *Zuck* (Herb. Greene, type of *C. moquiatus* Greene, minor variation 47).

12t. *CHRYSOTHAMNUS NAUSEOSUS LEIOSPERMUS* (Gray).—Shrub low (3 to 12 dm. high), with erect branches; twigs very many, crowded, erect, either moderately leafy or almost naked, scarcely at all striate, yellowish-green to white even on the same twigs (type

with a very close tomentum; herbage not noticeably odorous; leaves filiform or nearly so, acute, mostly 0.5 to 2 or 3 cm. long, under 0.5 mm. wide, often reduced and scale-like, tomentose or green and essentially glabrous; inflorescence a close terminal cyme of 2 or 3 cm. diameter; involucre 6 to 8 mm. high; bracts obtuse, not keeled, in vague ranks, glabrous; corolla 5 to 8 mm. long; tube very obscurely pubescent (or glabrous?); lobes ovate, erect, 0.5 mm. or less long; style-appendage longer than the stigmatic part; achenes completely glabrous in the typical form but often sparsely pubescent, especially along the prominent nerves. (*Bigelovia leiosperma* Gray, Syn. Fl. 1², 139, 1884.) On exceedingly arid slopes, southern Utah, southern Nevada, and the borders of California. Type locality, Saint George, southwestern Utah. Collections: Type collection, 1875, Palmer (Gr); southeastern Utah, Rydberg and Garrett 9435, 9940, both with bracts nearly as acute as in subspecies *bigelovi* but not pubescent (UC, US); Clear Creek Cañon, Utah, Jones 6105 (Herb. Jones, NY, UC, type collection of *Bigelovia leiosperma abbreviata* Jones, minor variation 14); 3 miles north of Salina, Utah, Jones 529 (UC, same variation); Panaca, Nevada, September 5, 1912, Jones (UC); Caliente, Nevada, Hall 10791, 10795 (UC); Candelaria, Nevada, Shockley 311 (DS, Gr); Providence Mountains, California, June 6, 1902, Brandegee.

MINOR VARIATIONS AND SYNONYMS.

The number of minor variations of *Chrysothamnus nauseosus* is exceptionally high. This list includes only those which have already received names and a few others of exceptional interest. Still smaller variations, many of which, however, are more significant than some of the named species of preceding taxonomists, have been indicated by parenthetical remarks in the citation of specimens under the subspecies or are left without mention. To list and describe all of these would occupy much space and would be of little value, unless accompanied by a close ecologic and genetic analysis.

All of the known synonyms under *Bigelovia*, *Chrysocoma*, *Chrysothamnus*, and *Linosyris* are here listed. The few that have been published under other genera are not of significance, since none of them take precedence over the names here given.

1. BIGELOVIA BIGELOVI Gray, Proc. Am. Acad. 8:642, 1873.—*C. nauseosus bigelovi*.
2. B. CERUMINOSA Gray, l. c. 643, 1873.—*C. nauseosus ceruminosus*.
3. B. COLLINA Nelson, Wyo. Exp. Sta. Bull. 28:122, 1896.—Based upon *C. collinus* Greene, which see.
4. B. DRACUNCULOIDES DeCandolle, Prodr. 5:329, 1836.—*C. nauseosus graveolens*. DeCandolle here makes a transfer of the specific name from *Chrysocoma dracunculoides* Pursh (Fl. Am. Sept. 2:517, 1814). Pursh's description was intended to include *graveolens*, although the reference to *Chrysocoma dracunculoides* Lamarck is an error, Lamarck's plant being an *Aster*.
5. B. GLAREOSA Jones, Zoe 2:247, 1891.—*C. nauseosus glareosus*.
6. B. GRAVEOLENS Gray, Proc. Am. Acad. 8:644, 1873.—*C. nauseosus graveolens*, in part. Several of the cited synonyms belong to other subspecies.
7. B. GRAVEOLENS VAR. ALBICAULIS Gray, l. c. 645, 1873.—*C. nauseosus albicaulis*.
8. B. GRAVEOLENS VAR. APPENDICULATA Eastwood, Proc. Calif. Acad. III, 1:74, plate 6, 1897.—An abnormal form of *C. nauseosus latisquameus*, with 1 to 4 linear appendages on the corolla-tube. The tube is arachnoid-pubescent and the lobes are very short, these characters suggesting a connection with subsp. *hololeucus*. Type locality, White Sands of New Mexico.
9. B. GRAVEOLENS VAR. GLABRATA Gray, Proc. Am. Acad. 8:645, 1873.—*C. nauseosus graveolens*, from the description, although this applies also to several other subspecies. The synonym cited has not been placed. (See No. 83 of this list.)
10. B. GRAVEOLENS VAR. HOLOLEUCA Gray, Proc. Am. Acad. 8:645, 1873.—*C. nauseosus hololeucus*.
11. B. GRAVEOLENS VAR. LATISQUAMEA Gray, Proc. Am. Acad. 8:645, 1873.—*C. nauseosus latisquameus*.
12. B. JUNCEA Greene, Bot. Gaz. 6:184, 1881.—*C. nauseosus junceus*.
13. B. LEIOSPERMA Gray, Syn. Fl. 1²:139, 1884.—*C. nauseosus leiospermus*.
14. B. LEIOSPERMA VAR. ABBREVIATA Jones, Proc. Calif. Acad. II, 5:693, 1895.—*C. nauseosus leiospermus*, but with scant tomentum and with leaves 1 cm. or less long. The type is from Clear Creek, Utah.
15. B. MISSOURIENSIS DeCandolle, Prodr. 5:329, 1836.—Based upon *Chrysocoma nauseosa* Pallas; therefore the same as *Chrysothamnus nauseosus typicus*.
16. B. MOHAVENSIS Greene in Gray, Syn. Fl. 1²:138, 1884.—*C. nauseosus mohavensis*.
17. B. TURBINATA Jones, Proc. Calif. Acad. II, 5:691, 1895.—*C. nauseosus turbinatus*.

18. *CHRYSOCOMA DRACUNCULOIDES* Lamarek, Encyl. 2:192, 1790.—The description is that of an *Aster*, but the name was later taken up by Pursh (Fl. Am. Sept. 2:517, 1814), who included under it a form of *Chrysotamnus nauseosus*, probably subspecies *graveolens*.

19. *C. GRAVEOLENS* Nuttall, Genera 2:136, 1818.—*Chrysothamnus nauseosus graveolens*.

20. *C. NAUSEOSA* Pallas, in Pursh, Fl. Am. Sept. 2:517, 1814.—*Chrysothamnus nauseosus typicus*. There is much misunderstanding as to the form that Pallas had in hand when his description was drawn. It is more than probable that an early mixing of labels of the Lewis and Clark collection is responsible for this. Although the type locality is stated by Pursh as "on the banks of the Missouri," the sheet at the Philadelphia Academy commonly taken as the type is labeled "15th October 1805 on the Columbia River." Because of this, *nauseosus* in the strict sense has been applied to a form most common in the Columbia River Basin (subspecies *albicaulis*). However, the two specimens on the sheet referred to are not like forms that grow on the Columbia. One, with glabrous involucre, long style-appendages, and green herbage, is one of the *graveolens* group and may be ignored; the other, mounted on the right-hand side of the sheet, has gray-tomentose herbage and involucre and is now identified with "*C. frigidus*," that is, subspecies *typicus* of the Missouri River region, the corolla being too short (7 to 7.8 mm.) for *albicaulis*. This right-hand piece probably is a part of the type collection, but fortunately the identification of *Chrysocoma nauseosa* need not depend upon this sheet. There is another in the Philadelphia Academy labeled "*Chrysocoma nauseosa* Pall. Missouri, Octbr." "Pursh's spec." "Herb.: Lewis & Clark." This specimen has been carefully examined by the present author and found to agree in every detail with Pallas's description, except that the innermost bracts are faintly pubescent instead of glabrous—a difference easily overlooked by one working without a magnifying glass. Mr. Bayard Long, of the Philadelphia Academy Herbarium, has kindly indicated evidence which shows almost certainly that this sheet came from the Lambert Herbarium, where Pursh's types were deposited. For example, the paper is very old and thin, and the data originally written on the back have been cut off and pasted on the front below the specimen, these features agreeing exactly with those of other specimens well known to have come from the Lambert Herbarium. Furthermore, the Lambert plants were distributed through the general Academy herbarium at Philadelphia and it was here that this "Missouri, Octbr." sheet was found, while the other was segregated in the "Lewis and Clark Herbarium" and therefore came from the American Philosophical Society, not from Lambert.¹

The conclusion, therefore, is that the plant labeled "Columbia River" probably came from the Missouri and that the right-hand specimen on the sheet is a part of the type collection; but that the true type is on the other sheet, that is, the one labeled "Missouri, Octbr." This brings both the locality and the plant into agreement with Pallas's description. The type as thus identified is a plant with ascending and rather straight leaves and minutely pubescent inner bracts, a form very common on the Missouri drainage, especially in Wyoming. *C. frigidus* Greene is exactly the same thing and *C. plattensis* Greene differs by characters so variable that it is included in *Chrysothamnus nauseosus typicus*.

21. *CHRYSOTHAMNUS ANGUSTUS* Greene, Pittonia 5:64, 1902.—*C. nauseosus consimilis*. Described as distinguishable by its canescent woolliness, but more abundant material proves that this character is exceedingly variable and can not be correlated with others nor with geographic distribution. The leaves in the type specimen are 5 to 6 mm. long, very slender and lax, and the inflorescence is elongated. All of these features occur also in the type of *consimilis*, except that the inflorescence in this is shorter. The type specimens of these two exhibit no differences in involucre and only slight variations in detail of floral structure. Type locality, sagebrush plains north of Alturas, Modoc County, California. The plants no doubt came from alkaline soil.

22. *C. APPENDICULATUS* Heller, Muhlenbergia 1:6, 1900.—*C. nauseosus latisquameus*. (See note under *Bigelovia graveolens appendiculata*.)

23. *C. ARIZONICUS* Greene, Pittonia 4:42, 1899.—Based upon *C. speciosus arizonicus* Greene, which see.

24. *C. BIGELOVI* Greene, Erythra 3:112, 1895.—*C. nauseosus bigelovi*.

25. *C. CALIFORNICUS* Greene, l. c., 111, 1895.—Here taken as a more southerly large-leaved form of *C. nauseosus albicaulis*. No type specimen was indicated, but Greene's notations at the University of California leave no doubt that the form represented by Bolander's 6159 from near Bridgeport, Mono County, California, were intended. These are stout plants with heavy leaves 2 to 4 mm. wide, and corolla-tubes only short-hairy. They connect with *albicaulis* through forms with similar leaves but arachnoid corolla-tubes (Heller 7192), and others with slightly narrower leaves, the corolla-tubes sparsely arachnoid or only puberulent (Hall 10853), and still others with leaves only 1 to 2 mm. wide and the corolla-tube not at all arachnoid (Hall 11662). The wide-leaved plants of *californicus* so closely resemble those of subspecies *speciosus* as it grows in the same district that their origin from this rather than from *albicaulis* is strongly suggested (see minor variation 58). Collections of the broad-leaved variation of *speciosus* (No. 58) have been labeled in herbaria by Greene as *californicus*, and he doubtless included this variation in his conception of his species, at least in later years.

26. *C. CALIFORNICUS* var. *OCCIDENTALIS* Greene, l. c., 112, 1895.—*C. nauseosus occidentalis*.

¹ It might be thought that the type specimen was sent to the British Museum of Natural History, but it is learned through the kindness of Dr. Rendle that no authentic material of *Chrysocoma nauseosa* is to be found there.

27. *C. CERUMINOSUS* Greene, l. c., 94, 1895.—*C. nauseosus ceruminosus*.
28. *C. COLLINUS* Greene, Pittonia 3:24, 1896.—A variation of *C. nauseosus typicus* in which the inflorescence is reduced and the bracts are exceptionally acute. Described as "not tomentose, only obscurely cinereous and notably gummy." The type in the Greene Herbarium has the twigs heavily coated with a compact tomentum, as in all of the subspecies. Type locality, Rock Springs, Wyoming.
29. *C. CONCOLOR* Rydberg, Fl. Rocky Mts. 856, 1917.—Based upon *C. frigidus concolor*, which see.
30. *C. CONFINS* Greene, Pittonia 5:62, 1902.—Here regarded as a southern variation of *C. nauseosus pinifolius*, notwithstanding its short-ciliate bracts (described as obtuse but decidedly acute in specimens of the type collection) and its occasionally longer heads. Type locality, White Mountains of southern New Mexico.
31. *C. CONSIMILIS* Greene, Pittonia 5:60, 1902.—*C. nauseosus consimilis*.
32. *C. DRACUNCULOIDES* Nuttall, Trans. Am. Phil. Soc. II, 7:324, 1840.—Based upon *Bigelovia dracunculoides*, which see.
33. *C. FALCATUS* Greene, l. c., 62, 1902.—*C. nauseosus pinifolius* with the twigs and upper (not lower) surface of the leaves coated with a white tomentum, which is deciduous in places. Other differentiating characters have been studied by Hall and found to be of no moment (Univ. Calif. Publ. Bot. 7:176, 1919). Type locality, plains about Grand Junction, Colorado.
34. *C. FORMOSUS* Greene, Pittonia 4:41, 1899.—Payson, Bot. Gaz. 60, 381, 1915. Very close to *C. nauseosus albicaulis* and probably to be accepted as a minor variation of this, although perhaps derived locally from subspecies *speciosus*, as *albicaulis* is supposed to have been elsewhere. Known only from Naturita, southwestern Colorado. A low, matted, white shrub with narrow spreading leaves, the involucre 10 mm. long and with 4 to 6 bracts in each row, the outer bracts puberulent. Type collected by Greene, August 27, 1896 (Herb. Greene 26614). Additional collection, Payson 605 (Gr. St. Louis).
35. *C. FRIGIDUS* Greene, Erythea 3:112, 1895.—In describing this, Greene did not indicate a type specimen, but his reference to its abundance about Laramie, Wyoming, leads to the assumption that specimens there collected by him July 29, 1889, and labeled by him as *frigidus* are the ones from which the description was drawn. These specimens are now in the Greene Herbarium and in the University of California, where Greene was working at the time. The evidence from these sheets and from the description leaves no doubt that *C. frigidus* is the same as *C. nauseosus typicus*. In fact, Greene himself suggested this possibility. A slightly different form, described by Greene as *C. speciosus* var. (?) *plattensis* and later raised to specific rank, is now also included in *typicus*. This differs from *frigidus* in having a lax foliage, the leaves spreading or recurved and the bracts glabrous except along the margins. Both forms are common on the Rocky Mountain plains, but their separation taxonomically is almost impossible. The inner bracts even in *frigidus* are never very pubescent and most specimens necessarily referred here because of their straight, ascending leaves, have the bracts exactly as in *plattensis*, that is, pubescent only on the margins, or the short outermost ones slightly pubescent also on the back (for example, *Goodding 1933* and *2069* and *Nelson 8786*). Furthermore, many plants with the lax, narrow foliage of *plattensis* have all of the bracts tomentulose as in *frigidus* (for example, *Goodding 588*, UC, and *Anderson 89* and *593*, UC). Therefore, the only satisfactory treatment is to include in *typicus* plants with either straight or curved leaves and with bracts varying from glabrous to puberulent. The type of the species is discussed under *Chrysocoma nauseosa* of this list.
36. *C. FRIGIDUS* var. *CONCOLOR* Nelson, Bot. Gaz. 28:371, 1899.—*C. nauseosus typicus* but with a pale yellowish-green herbage and somewhat elongated inflorescence. The leaves are straight, flat, and ascending, the bracts of the involucre mostly puberulent but the innermost only ciliate. Type locality, Hutton Lakes, Wyoming.
37. *C. GLAREOSUS* Rydberg, Fl. Rocky Mts. 858, 1917.—Based upon *Bigelovia glareosa*, which see.
38. *C. GNAPHALODES* Greene, Pittonia 4:42, 1899.—*C. nauseosus gnaphalodes*.
39. *C. GRAVEOLENS* Greene, Erythea 3:108, 1895.—*C. nauseosus graveolens*.
40. *C. GRAVEOLENS GLABRATA* Nelson, in Coulter and Nelson, Man. Rocky Mts. 496:1909.—Based upon *Bigelovia graveolens glabrata*, which see.
41. *C. JUNCEUS* Greene, Erythea 3:113, 1895.—*C. nauseosus junceus*.
42. *C. LAETEVIRES* Greene, Pittonia 5:61, 1902.—A light green form or state of *C. nauseosus graveolens* gathered at Grand Junction, Colorado.
43. *C. LATISQUAMEUS* Greene, l. c., 4:42, 1899.—*C. nauseosus latisquameus*.
44. *C. LEIOSPERMUS* Greene, Erythea 3:113, 1895.—*C. nauseosus leiospermus*.
45. *C. MACOUNT* Greene, Pittonia 5:63, 1902.—Best referred to *C. nauseosus albicaulis*, although the corolla-tube is not arachnoid and the habit suggests that of the *plattensis* form of subspecies *typicus*, as noted by Greene. But the corollas are 8.5 to 9 mm. long, therefore longer than in *typicus*, and the involucre also is longer (8.5 to 9 mm.). The type specimen gives no indication that the plants are low in stature. Type, Lytton, British Columbia, August 30, 1887, *Macoun* (Herb. Greene).
46. *C. MOHAVENSIS* Greene, Erythea 3:113, 1895.—*C. nauseosus mohavensis*.
47. *C. MOQUIANUS* Greene, Pittonia 5:60, 1902.—*C. nauseosus bigelovi*. Greene says "achenes not seen," but the specimen marked as the type in his herbarium has well-formed achenes and these are glabrous, as in

bigelovi. The habit and also the details of involucre and flowers are exactly as in the usual form of this subspecies. Type locality, Moqui Indian Reservation, northern Arizona.

48. *C. NAUSEOSUS* (Pallas) Britton, in Britton and Brown, Ill. Fl. 3:326, 1898.—This is the proper combination and authority for all of the subspecies here assembled under *C. nauseosus*, although Britton used the name in a more restricted sense. His first cited synonym is the same as *C. nauseosus typicus*, but subspecies *graveolens* is included among the other synonyms and in the description.

49. *C. NAUSEOSUS ALBICAULIS* Rydberg, Mem. N. Y. Bot. Gard. 1:385, 1900.—*C. nauseosus* subspecies *albicaulis*, at least as to synonymy.

50. *C. NAUSEOSUS* vars. *BERNARDINUS*, *BIGELOVI*, *CERUMINOSUS*, *CONSIMILIS*, *GLAREOSUS*, *GNAPHALODES*, *GRAVEOLENS*, *HOLOLEUCUS*, *JUNCEUS*, *LATISQUAMEUS*, *LEIOSPERMUS*, *MOHAVENSIS*, *OCCIDENTALIS*, *PINIFOLIUS*, *SALICIFOLIUS*, *SPECIOSUS*, and *VRIDULUS*, all Hall, Univ. Calif. Publ. Bot. 7:160 to 180, 1919, are here transferred to subspecies of *C. nauseosus* without change of name.

51. *C. NAUSEOSUS BERNARDINUS*, but the twigs, leaves, and involucres white with a floccose tomentum. Above the Mill Creek Falls, San Bernardino Mountains, California, *Parish 1153* (DS). Probably grows also on San Jacinto Mountain, as indicated by an incomplete specimen from the lower edge of the pine belt on the north side (*Hall 10701*). Apparently bears the same relation to *bernardinus* that *albicaulis* does to *speciosus* but the form is too little known to permit of final taxonomic treatment at this time. According to Parish, the white form is not rare in the San Bernardino Mountains, where it grows with the gray or greenish form.

52. *C. NAUSEOSUS* var. *CALIFORNICUS* Hall, l. c., 174, 1919.—As to synonymy, this is the same as *C. californicus* of the present list, and therefore a form of *C. nauseosus albicaulis*. However, the description and specimen cited belong to *C. parryi bolanderi*.

53. *C. NAUSEOSUS* var. *FRIGIDUS* Hall, l. c., 170, 1919.—Based upon *C. frigidus* Greene, which see.

54. *C. NAUSEOSUS* var. *GRAVEOLENS* Piper, Contr. U. S. Nat. Herb. 11:559, 1906.—Based upon *Chrysocoma graveolens* Nuttall, here transferred to *Chrysothamnus nauseosus* subspecies *graveolens*.

55. *C. NAUSEOSUS* var. *OREOPHILUS* Hall, l. c., 175, 1919.—Based on *C. oreophilus* Nelson, which see.

56. *C. NAUSEOSUS* var. *PLATTENSIS* Hall, l. c., 170, 1919.—Based on *C. speciosus plattensis* Greene, which see.

57. *C. NAUSEOSUS SPECIOSUS*, but the dense gray tomentum extending even to the inner bracts of the involucre; the variation not named. (Plate 33, fig. 1.) Waitsburg, southeastern Washington, *Horner 413* (UC); near Clear Creek, Butte County, California, *Brown 46* (DS, UC). These are very much like the type of *speciosus*, except that in this the tomentum stops abruptly with the lower bracts of the involucre. Specimens referable to this variation, but with the involucre less densely tomentose, are: *Leiberg 906, 910, 924, and 946*, all from eastern Oregon. Still less pubescent, the inner bracts nearly glabrous, is a plant from Ogden, Utah (*Stilwell*, UC). The heavily tomentose specimens have been sometimes identified as *gnaphalodes*, but differ in the very acute bracts and longer corolla-lobes and style-appendages.

58. *C. NAUSEOSUS SPECIOSUS*, but a form with heavy leaves 2 to 3 mm. wide and close rounded cymes; the form not named, except as included in the original *C. californicus* Greene. This is a common type in eastern and northern California, and western Nevada, and is very strikingly different in its full development. It is represented by the collections so indicated in the citations under subspecies *speciosus*. The abundance of this form toward the south indicates that it may be a geographic ead or race. Intermediates are plentiful in the intervening territory (*Butler 1824; Heller 12945*), and also to the eastward (Utah, *Jones 503*; Wyoming, *Bran-degee*). It is probable that some collections of this variation were included in Greene's conception of his *C. californicus* (No. 25 of this list).

59. *C. NAUSEOSUS VRIDULUS*.—A dwarf form of the alkali flats of Antelope Valley, southern California, is referred here provisionally. It has flexuous stems, short rounded inflorescences, and exceptionally small flowers (commonly 6 or 7 in a head), but the flowers, although reduced in size, have the narrow, elongated, and spreading lobes of *viridulus*. Representative collections are *Hall 10582 and 10587*, both from near Lancaster. More nearly typical specimens have been gathered in the San Antonio Mountains at an altitude of 2,440 m. (*Johnston 1706*).

60. *C. OCCIDENTALIS* Greene, Fl. Francisc. 369, 1897.—*C. nauseosus occidentalis*.

61. *C. OREOPHILUS* Nelson, Bot. Gaz. 28:375, 1899.—A low form of *C. nauseosus consimilis* with erect and slightly wider upper leaves. Perhaps intermediate to subspecies *graveolens*. The type is *Nelson 4105* from Evanston, Wyoming. Other specimens distributed under this name are mostly subspecies *speciosus* and *typicus*.

62. *C. OREOPHILUS ARTUS* Nelson, l. c., 54:413, 1912.—Not distinguishable from *C. nauseosus consimilis*. Type locality, Boise, Idaho.

63. *C. ORTHOPHYLLUS* Greene, Pittonia 5:62, 1902.—*C. nauseosus albicaulis*, but with the lobes of the corolla sparsely villous. The value of this character has been already discussed (p. 167). Type locality, Big Meadows, Plumas County, California.

64. *C. PALLIDUS* Nelson, Bot. Gaz. 28:372, 1899.—*C. nauseosus typicus*, but the herbage nearly white with a very smooth, close, persistent tomentum and the short leaves crowded near the top. The type is from alkaline flats near Laramie, Wyoming, and the form occurs elsewhere in alkaline soil of Wyoming and northern Colorado.

65. *C. PATENS* Rydberg, Bull. Torr. Club 31 : 652, 1904.—*C. nauseosus pinifolius*, but a form with spreading and more or less falcate leaves. Type locality, Colorado.
66. *C. PINIFOLIUS* Greene, Pittonia 5:60, 1902.—*C. nauseosus pinifolius*.
67. *C. PLATTENSIS* Greene, l. c., 4:42, 1899.—Based upon *C. speciosus plattensis*, which see in this list.
68. *C. PULCHERRIMUS* Nelson, Bot. Gaz. 28:370, 1899.—A variation of *C. nauseosus speciosus* recognized in the field by its usually more robust, tree-like habit, larger leaves, larger inflorescences, and more nearly glabrous involucre. It seems that as *speciosus* moved eastward it developed this fine form in favorable situations, while subspecies *typicus* came to occupy the less favorable ones. The connection between *pulcherrimus* and *speciosus* is found at so many places, both in the field and in the laboratory, that the former is looked upon as the result of ecologic conditions and not of taxonomic rank. Its characters are strongly suggested by No. 58 of this list, which is also a robust form with even larger leaves, but with a slightly different involucre. The type of *pulcherrimus* is a specimen from Woods Landing, Wyoming, Nelson 3477 (R).
69. *C. PULCHERRIMUS* var. *FASCICULATUS* A. Nelson, Bot. Gaz. 28:371, 1899.—The same as *pulcherrimus* (see preceding note), but with numerous short branchlets and crowded rigid leaves only 2 to 3 cm. long. The types came from Boulder Creek and Creston, Wyoming.
70. *C. SALICIFOLIUS* Rydberg, Bull. Torr. Club 37:130, 1910.—*C. nauseosus salicifolius*.
71. *C. SPECIOSUS* Nuttall, Trans. Am. Phil. Soc. II, 7:323, 1840.—*C. nauseosus speciosus*.
72. *C. SPECIOSUS* β . *ALBICAULIS* Nuttall, l. c., 324, 1840.—*C. nauseosus albicaulis*.
73. *C. SPECIOSUS* var. (?) *ARIZONICUS* Greene, Erythea 3:110, 1895.—*C. nauseosus latisquameus*. Although described by Greene on the same page as *latisquameus*, the only tangible differences there given are the longer leaves and rather deeply cleft corolla in *arizonicus*. The specimens at hand exhibit much too great a fluctuation in the length of the leaves to permit the use of this as a character, and the corolla-lobes are always short, as is indicated by the measurements given in table 23. A search for the type at the Greene Herbarium was unsuccessful, but a specimen at the University of California (Santa Rita Mountains, Arizona, November, 1891, Brandegee), doubtless of the type collection, has leaves 2 to 4 cm. long and corolla-lobes 0.8 to 1 mm. long. The herbage of this, and in fact most specimens, is very white, whereas the type of *latisquameus* is less notably so. It is believed, however, that this difference is too slight to be compared with that between other pairs of subspecies (see p. 170).
74. *C. SPECIOSUS* var. *GNAPHALODES* Greene, l. c.—*C. nauseosus gnaphalodes*.
75. *C. SPECIOSUS* var. (?) *LATISQUAMEUS* Greene, l. c.—*C. nauseosus latisquameus*.
76. *C. SPECIOSUS* var. (?) *PLATTENSIS* Greene, l. c., 111, 1895.—A form of *C. nauseosus typicus* discussed under *C. frigidus*, No. 35 of this list. No type was indicated, but the distribution was stated as alkaline plains of the Platte and elsewhere along the eastern base of the Rocky Mountains. No specimens collected by Greene prior to 1895 have been found in herbaria.
77. *C. TORTUOSUS* Greene, Pittonia 5:63, 1902.—Described from very immature specimens from Plumas County and Mount Shasta, California. Probably referable to *C. nauseosus consimilis*, because of the green and glabrous involucre of the only head on the type specimens (in Herb. Greene). The corolla-lobes in this young condition are about 2 mm. long, the bracts rather pungently acute (suggesting subspecies *occidentalis*), the leaves nearly filiform and more or less spreading, and the twigs tortuous.
78. *C. TURBINATUS* Rydberg, Fl. Rocky Mts. 859, 1917.—*C. nauseosus turbinatus*.
79. *C. VIRENS* Greene, Pittonia 5:61, 1902.—*C. nauseosus graveolens*. The type specimens (in Herb. Greene) are perhaps a little greener than in the usual form, but although a search was made at the type locality (Cañon City, Colorado) and in surrounding districts, no specimens were found that could be satisfactorily separated, either on color or on other features. The involucre is 7 to 8 mm. high in the type and the whole head, to the tips of the styles, 12 to 15 mm. The flowers thus protrude farther than usual, but this is an exceedingly variable character. The bracts, described as of more or less triangular outline and scarcely acute, are as in typical *graveolens*.
80. *LINOSYRIS ALBICAULIS* Torrey and Gray, Fl. N. Am. 2:234, 1842.—*C. nauseosus albicaulis*.
81. *L. BIGELOVI* Gray, Pacif. R. R. Rep. 4:98, 1857.—*C. nauseosus bigelovi*.
82. *L. CERUMINOSA* Durand and Hilgard, Jour. Acad. Nat. Sci. Phila. II, 3:40, 1855.—*C. nauseosus ceruminosa*.
83. *L. GRAVEOLENS GLABRATA* Engelm., in Gray, Proc. Am. Acad. 8:645, 1873.—A form of *C. nauseosus graveolens*, judging from the description. Dr. B. L. Robinson writes that there is a specimen in the Gray Herbarium collected in Nebraska by Henry Engelm. in 1856 and labeled "*L. graveolens, glabrata*, H. Engelm., 1860 (G. Engelm. in litt.)" but that no reference to the name can be found in any of Engelm.'s papers. It seems, therefore, that the combination was published only in Gray's paper as cited.

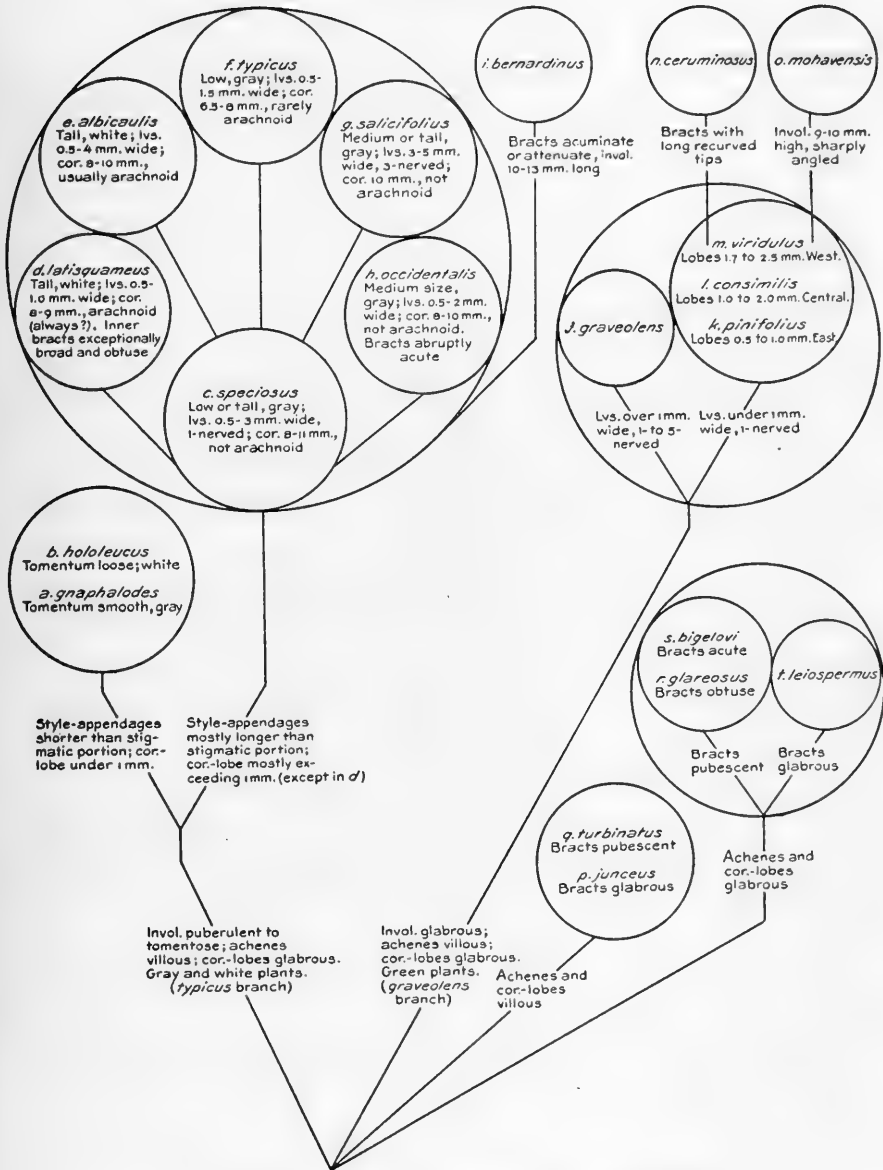


FIG. 28.—Phylogenetic chart of the subspecies of *Chrysothamnus nauseosus*

RELATIONSHIPS.

Chrysothamnus nauseosus is very distinct from all other species except *C. parryi*, but with this it has much in common. Indeed, reduced forms of the two, in which the type of inflorescence is difficult to make out, are sometimes mistaken for each other. These occur most frequently in the poor soils of western Wyoming and western Colorado. Often such forms can be placed with certainty only by giving close attention to neighboring plants in which the inflorescence may be better developed, and to any tendency toward elongated herbaceous tips of the involucre bracts, this latter a mark of *C. parryi*. A minor character, possibly indicative of the common origin of the two, is the growth of long weak hairs on the tips of the corolla-lobes in certain forms. This is so unusual in the Compositæ that its appearance in *C. parryi latior* and *C. pyramidatus*, and also in two subspecies of *C. nauseosus* (*junceus* and *turbinatus*) seems to have more than ordinary significance.

Variation within the aggregate here taken as *C. nauseosus* has been so marked that numerous striking forms have resulted. The difficulty in according specific rank to these has been indicated in the paragraph introductory to the key to the subspecies. The problem of organizing them into natural groups is a very complicated one because of the large number of characters involved and the exceptionally numerous combinations of these as represented in the copious collections already made. Furthermore, it is often impossible, in the absence of a detailed genetic analysis, to determine whether certain forms are merely ecologic variations or whether they are based upon inheritable factors. However, much time has been given to detailed field studies, to transplant experiments, and to a close analysis of herbarium material. The results of these studies are graphically set forth in the accompanying diagram. The statistical basis for some of the conclusions is given in table 23, page 223. According to the arrangement presented in the diagram, the species comprises two major assemblages of forms, three smaller groups representing lines of divergence which early separated from the parent stock, and three small assemblages which are believed to be marked developments from one or the other of the two principal groups. Each of the units indicated in the diagram by an ultimate circle is composed of one or more subspecies. Each subspecies, in turn, is usually composed of a number of still smaller units—strains, biotypes, ecads, etc.—which are not given taxonomic status, but the more noteworthy of which are discussed as minor variations.

All of the subspecies of *Chrysothamnus nauseosus* are so highly specialized that it is difficult to select any one as the most primitive. However, in some cases primitive traits have persisted in lines which exhibit a marked development in other features. Thus, conspicuously pilose corolla-lobes, found also in *C. pyramidatus* and in forms of *C. parryi*, here occur in subspecies *junceus* and *turbinatus*, occasionally also in *albicaulis* and *bigelovi*. With these and similar considerations as a clue, and recalling the close connection between *turbinatus* and *bigelovi*, the opinion is ventured that the first, third, and fourth primary diverging lines in the chart represent a past connection through primitive forms now extinct. The second or *graveolens* line is in more doubt, since this may have arisen directly from *speciosus*. Therefore, it should be understood that the placing of *turbinatus* and its allies at the end of the taxonomic sequence does not indicate that these are more highly developed than the others.

The two larger groups of the subspecies of *C. nauseosus* may be referred to as the *typicus* branch and the *graveolens* branch respectively. They differ from each other in a number of involucre and floral characters, so that after long acquaintance with the members one comes to have a fixed belief in the reality of the groups as natural units and is able unhesitatingly to place a majority of the specimens he encounters in either one or the other of the two assemblages. These characters, however, are so fluctuating and overlapping in some of the forms that they can not be used in keys, so for this purpose

it is better to fall back upon a distinction based upon the pubescence of the involucre. This character runs approximately parallel with what are believed to be natural lines and its use is thus very convenient, although, as is to be expected in a highly variable species like *C. nauseosus*, some forms plainly belonging by all other criteria to one group of subspecies will have a pubescence of the involucre which very closely approaches that of the other group. In fact, if this criterion alone is used, it will sometimes lead to an erroneous placing of a subspecies, especially if the pubescence is very scant or minute. Naturally, the pubescence of the involucre in the *typicus* group is only an expression of the general tendency toward an excess of pubescence in the whole plant. The herbage of all of the members of this group, with only now and then an exceptional form, is quite gray or sometimes even white as compared with the usually green or yellowish-green herbage of the *graveolens* branch. The two can not be accepted as distinct species, as is evidenced by the very nature of the character used for their detection and also by the frequent intergrading forms just mentioned. The contact seems to be between *speciosus* and *graveolens*, since forms are constantly recurring which can be about as satisfactorily placed in one as in the other of these subspecies. It seems probable that *speciosus* and *graveolens* come the nearest to representing the ancestral form in which the primary cleavage took place. This hypothesis finds some substantiation in the facts of geographic distribution. The subspecies *speciosus* is most abundant across the northerly part of the Great Basin, that is, west of the Rocky Mountains, while *graveolens* belongs chiefly to the plains and valleys of the Rocky Mountain States, but extends northwest to southern Idaho, thus overlapping the range of the former. Ecologically, *speciosus* belongs to mildly alkaline soil and runs up on slopes where there is perhaps no alkali. The other members of the *typicus* group are inhabitants of non-alkaline soils, except for occasional forms (especially *plattensis*) which have become adapted to moderately saline conditions. On the other hand, *graveolens* grows in soil quite strongly alkaline and among the other subspecies of its group are some which run down into strongly impregnated soils.

In following the *typicus* branch, it is first noted that two of the subspecies, *gnaphalodes* and *hololeucus*, differ so radically from the others that they are assigned to a group extraneous to the principal assemblage. They are very much like the others in superficial appearance, but differ from all of them in the very short, erect teeth to the corolla and especially in the comparatively short stylar appendages, although both of these structures are much shortened in occasional plants of other subspecies. By reference to table 23 it will be seen that in the 30 specimens examined the appendage is always shorter than the stigmatic portion, whereas in the 138 specimens of other subspecies the appendage is always longer than the stigma, except in a very few cases (see especially subspecies *typicus*). The measurements were made on specimens which had been previously determined as *gnaphalodes* and *hololeucus* because of their other characters. The short corolla-lobes furnish a useful criterion for the identification of these subspecies, but it is not always strictly applicable, for, as will be seen by reference to the table, the shortest lobes in others are not infrequently shorter than the longest ones in these. But the general parallelism between these two characters, together with the peculiarly aromatic odor of the herbage, and certain other considerations, leads to the conclusion that the two subspecies under consideration are closely related to each other and that they constitute an evolutionary group quite distinct from the others. Subspecies *gnaphalodes* is abundant on well-drained soils from middle Nevada and western Arizona to the Sierra Nevada, while *hololeucus* occurs only as scattered individuals or in small groups within this same area. The plants of the latter are so white as compared with the former that the two can be distinguished in the field without difficulty. The origin of *hololeucus* by mutation at different places and times seems quite probable.

Within the *typicus* group it is found that subspecies *speciosus* probably includes the plexus from which the others have arisen. As originally described, this is a rather low, narrow-leaved, gray plant with close, rounded inflorescences. This form is common in the basin of the Columbia River, extending south through eastern Oregon and east into Idaho, etc. Farther southward and southeastward it passes gradually into a more robust form with wider leaves (minor variation 58), while to the east it becomes taller, but with only a slight widening of the leaves. In the Rocky Mountain States it is commonly a tall, tree-like shrub with large, open inflorescences, the involucre more nearly glabrous, and the leaves slightly wider than in the typical form. This most easterly variation has been described as *C. pulcherrimus* Nelson (minor variation 68). It comes very close to connecting *speciosus* directly with *graveolens*. Thus, *speciosus* as here conceived includes a number of minor variations, which can be correlated roughly with geographic distribution, but none of which are sufficiently well marked to be given definite taxonomic status. In addition to these there are five stronger groups, each of which is given subspecific rank.

The subspecies *latisquameus*, a tall shrub of Arizona and New Mexico, is perhaps more distinct from *speciosus* than any of the others just mentioned. It is, however, given a position close to *speciosus*, because of its possible connection with a preceding subspecies, namely, *hololeucus*. In common with this latter it has a loose, white tomentum, exceptionally obtuse involucre bracts, short corolla-lobes, and a tendency toward an arachnoid pubescence on the corolla-tube (see minor variation 8). However, because of the proportionately longer style-appendages, it is provisionally referred to the *speciosus* group.

The subspecies *albicaulis* is perhaps the least distinct from *speciosus* of any included in this circle, having only its floccose and very white tomentum as a constant character. However, this difference holds without exception, there being no intermediates, even when the two grow side by side. The nature of this character difference has been discussed on page 170. Typical *albicaulis* grows with typical *speciosus* in the Columbia River Basin, while to the south it becomes more robust and the leaves are wider (minor variation 25), thus paralleling a similar variation found in southern plants of *speciosus*. This subspecies extends east only to western Montana and Utah. It is looked upon as a probable mutation from the western form of *speciosus*.

The subspecies *typicus* is now definitely restricted to certain low shrubs of the plateaus of the northern Rocky Mountain States. It has been frequently assumed that typical *C. nauseosus* was the northwestern plant here called subspecies *albicaulis*. The error of this application of the name is discussed under minor variation 20, where the identity of the original *Chrysocoma nauseosa* with the plant often known as *Chrysothamnus frigidus* is pointed out. Subspecies *typicus* is looked upon as an easterly derivative of *speciosus* which has undergone a reduction in the size of the heads and flowers and which has assumed certain vegetative characters that enable it to persist under the unfavorable conditions of its cold, bleak, and sometimes alkaline habitat. Its most important minor variations probably are ecads, since they are recognizable only by the size and direction of the leaves (minor variation 35, *C. frigidus*, and minor variation 67, *C. plattensis*).

The subspecies *salicifolius* is but little known, but seems to have split off from subspecies *speciosus* along the southeastern limits of the range of this latter. It is a robust plant with exceptionally wide, 3-nerved leaves.

The most unique feature in the *speciosus* group has been developed in the subspecies *occidentalis*. This is the abrupt narrowing of the tips to the involucre bracts. The narrowing is least noticeable in plants of northern California, where the two subspecies are in contact, but it becomes more and more pronounced toward the south. The bracts are only slightly puberulent or sometimes practically glabrous and the heads are in small, compact, globose cymes. The following note on *occidentalis* is from a recent paper by Hall (Univ. Calif. Publ. Bot. 7:168, 1919).

"The distribution of this variety was originally stated by Greene to be 'In the Coast Range, from Humboldt County (California) southward.' Later, this same author stated it as 'Kern and Santa Barbara counties' (Fl. Francisc. 369, 1897). This restriction in the adopted range was perhaps due to the fact that certain specimens from Humboldt and other northern counties do not meet the requirements of the description as well as those from farther south. The cuspidate bracts and long corolla-lobes, together with the habit (especially the small compact rounded inflorescence), are here taken as the most satisfactory characters for the variety. Accepting this definition, we find fairly typical collections from the dry inner north Coast Ranges and from the southern Sierra Nevada and San Bernardino Mountains. North and east of Trinity County it apparently passes into *speciosus*, from which it scarcely differs save in the more nearly glabrous and abruptly pointed bracts. At its southernmost stations it meets and perhaps merges into *bernardinus*."

A specimen in the Greene Herbarium collected by Miss Eastwood, September, 1894, and marked by Greene "*C. occidentalis*, type! in Fl. Fr.," may be considered the type. This is the narrow-leaved form of his later concept. There is here also a specimen labeled as "*C. californicus* var. *occidentalis*, Eryth. 3:112" (Siskiyou Mountains, September, 1889, Greene), but this is the broad-leaved plant now included in subspecies *speciosus* (minor variation 58). Its bracts are not especially acute, while abruptly acute bracts, united with narrow leaves and small compact cymes are characteristic of subspecies *occidentalis* as here defined.

Subspecies *bernardinus* is so distinct from the other members of the *typicus* branch that it is placed (in the diagram) in a special extruded circle. Because of the essentially glabrous involucre, this circle has also a tentative connection with the *graveolens* group, although it is extremely doubtful if these two are of common origin. On the other hand, *bernardinus* resembles certain Rocky Mountain forms of *speciosus* (once distinguished as *pulcherrimus*) both in general appearance and in technical characters, but the involucre is longer and the more strongly keeled bracts are acuminate instead of merely acute. Its wide geographic separation casts considerable doubt on the theory of its origin from such forms. It is more likely a descendant from *speciosus* as it occurs in northern California, the modifications being associated with its habitat on the mountains of the southern part of the State, and it is not at all impossible that the connection has been through *occidentalis*.

As previously indicated, the subspecies *graveolens* is considered as the beginning of the *graveolens* branch, all of the members of which are inhabitants of alkaline soil. The steps between it and the others are so gradual that except in a detailed monograph the whole group might be taken as constituting a single subspecies. The original *graveolens* is a plant with linear, partly 3-nerved, smooth leaves, as described by Nuttall and as indicated by the type at the Academy of Natural Sciences of Philadelphia. The leaves in the type are 1.5 to 2 mm. wide and the cymes 4 cm. across. This is the robust, green form with large rounded inflorescences that is so common in the easterly part of the range of the genus, especially in Wyoming, Colorado, and northern New Mexico. It presents many minor variations as to size and direction of leaf, height of involucre, etc. Similar variations occur in the other member of the group, and they are so numerous and so often intangible that their recognition as taxonomic units is not feasible. The several supposed species (*angustus*, *confinis*, *falcatus*, *laetevirens*, *oreophilus*, *patens*, *virens*) based upon such characters are included in the list of minor variations (p. 218), where they are briefly discussed. A majority of these have been studied at their type localities and in the herbaria where the type specimens are deposited. It is believed that most if not all of them are either ecologic or seasonal forms.

The three subspecies, *pinifolius*, *consimilis*, and *viridulus*, are of much more importance than the forms just mentioned. This is because they represent certain well-defined and fairly consistent tendencies, especially in floral structure, and also because each belongs to its own geographic area. There are, however, frequent intergradations in all of the characters, especially where the geographic boundaries meet, so that some

specimens can not be definitely assigned to a particular subspecies. Subspecies *pinifolius* most closely resembles *graveolens*, but has much narrower 1-nerved leaves. It is abundant on alkaline plains of the southern Rocky Mountain region. From western Wyoming and Colorado to Oregon and western Nevada, that is, almost throughout the Great Basin, the commonest subspecies is *consimilis*. This is a more slender plant than *pinifolius* and the corolla-lobes are 1 to 2 mm. long, as contrasted with 0.5 to 1 mm. for that subspecies. Perhaps because of their length, the corolla-lobes are inclined to spread or recurve. The inflorescence is often quite elongated, although in some cases, especially in dwarfed plants, it is as rounded as in the common form of *pinifolius*. To the southwest of the *consimilis* area, and especially in the alkaline valleys of west central Nevada and eastern California, is found the more robust subspecies *viridulus*, a form in which the corolla-lobes attain the length of 2 to 2.5 mm., this being the longest in the genus. The forms and relationships of this were discussed by its author as follows (Hall, Univ. Calif. Publ. Bot. 7:178, 1919):

"This is the common form on alkaline flats in southern Mono County and in Inyo County, California, and in western Esmeralda County, Nevada, although there are many slight variations from the type as described above. Almost every valley exhibits forms not exactly like those in any other. The variations are chiefly in habit, pubescence, leafiness, size and shape of inflorescence, shape of bracts, and length of corolla-lobes. The plants range in height from a few dm. to nearly 3 m., but are always taller than broad unless abnormal; the corollas vary from 8 to 10 mm. in total length; the corolla-lobes are seldom shorter than 2 mm., yet in two collections there are some flowers with lobes only 1.7 mm. long; although the involucre of the type are only 6 to 7 mm. long, they vary in other specimens to 8 or even 9 mm.; the mature pappus is 7 to 9 mm. long. * * * As to relationships, *viridulus* probably is a southwestern derivative of *consimilis* (or vice versa), from which it differs in the larger corollas with longer lobes, the thicker, more robust, and rigid twigs and leaves, the heavier and more rounded inflorescence, and the stronger odor of the herbage. These characters are far from constant at all stations. The length of the corolla-lobe is the most satisfactory. Of twenty-seven collections taken throughout the established range of the variety, only five have corolla-lobes 2 mm. or less long; of twenty-two collections from the range of *consimilis* none exhibit corolla-lobes of over 2 mm. in length; where the ranges meet, as around Mono Lake and at Sodaville, Nevada, intermediate sizes are frequent and here the other differentiating characters also intergrade."

It should not be inferred from the above that these varieties actually intergrade, because some of their characters do so. What appear to be intergrades may in reality be hybrids. On the other hand, the phylogenetic line from *graveolens* through *pinifolius* and *consimilis* to *viridulus* seems reasonably well established.

Two subspecies, both derivatives of *viridulus*, are indicated as lying outside of the *graveolens* circle, because of the marked development of certain features. In *ceruminosus* the tips of the involucre bracts are abruptly narrowed and recurved. No intermediate stages are known, but the form has been collected only twice. The subspecies *mohavensis* is a southern and far western derivative of *viridulus* and belongs to higher, less alkaline slopes. It is distinguished by an exceptionally long involucre, the sharply keeled bracts of which fall into very well defined vertical rows. It was first described as sparsely leafy or leafless, but there is a tendency throughout the *graveolens* group toward an early dropping of the leaves. Intermediates are sometimes found in which the habit is that of *mohavensis*, except for the more persistent leaves, the bracts are in sharply defined vertical rows, but acute as in *viridulus*, and the involucre and corolla-lobes are exactly intermediate in length (Oak Creek, westerly side of Owens Valley, California, Hall 10611).

In taking up the third main line, it is found to lead to a group of only two subspecies, namely, *junceus* and *turbinatus*. These are almost unique in the species in that their corolla-lobes are externally villous with long delicate hairs. This character reappears, however, in a form of subspecies *albicaulis* (see minor variation 63), in one subspecies of *C. howardi*, and in *C. pyramidatus*. Subspecies *junceus* is a nearly leafless, little-

known shrub of eastern Arizona. It is usually described as cinereous, or minutely canescent, but the twigs, even in the type, have the usual pannose tomentum. Subspecies *turbinatus*, also a rare plant, known only from Utah, is more striking because of its elongated, cylindrical involucre, but no character can be found as a basis for a distinct species. The original description reads "plants glabrous and a little glutinous even to the flowers." The type collection and two others have been examined. In all of these the copious tomentum of the twigs is so closely packed that it gives the appearance of a glabrous surface, the leaves are tomentulose, and the corolla-lobes hairy. *Junceus* and *turbinatus* are similar not only in the points mentioned, but also in habit and distribution. They appear to form an offshoot which sprang from the main stock at an early stage in the development of the genus. Their close connection with subspecies *glareosus* and *leiospermus* is evidenced by the variable nature of the pubescence on the corolla-lobes, by the erratic occurrence of this in *bigelovi* (see p. 167), and by transitions between glabrous and pubescent achenes, as will be indicated under *leiospermus*.

The last group to be considered is the one with glabrous achenes. The three subspecies that comprise it all come from the arid southerly portion of the Great Basin and are sufficiently alike in essential characters to lead to the conclusion that the group is probably a natural one. The absence of pubescence on the achenes is not of specific taxonomic significance, as is indicated by collections of *leiospermus* made near Caliente, Nevada (*Hall 10791, 10795*). In some of these plants the achenes are very sparsely pubescent on the edges, in others they are sparsely pubescent both along the nerves and on the intervening spaces. At this station the conditions are extremely xerophytic. This is reflected in the plants, which are quite leafless, thus resembling those of *junceus* in appearance. There is considerable variation in the color of the tomentum in *leiospermus*. The first specimen cited under the original description has twigs that are white in the inflorescence and for a distance of about 1 dm. below the heads, while from there down they are yellowish-green; in the other specimen cited the twigs are very white down to the old wood; in more recent collections, such as those from Caliente, Nevada, the twigs are green throughout. The subspecies *glareosus* and *bigelovi* differ from *leiospermus* not only in their pubescent involucre, but in matters of habit, in the more definite ranks of the bracts, and in the greater length of the involucre. All of these last five subspecies inhabit the southern part of the Great Basin. They have been greatly modified, especially in habit and foliage characters, and these modifications enable them better to cope with their very arid and often alkaline habitat.

ECOLOGY.

In general, the important subspecies of *Chrysothamnus nauseosus* are subclimax dominants of the sagebrush association. Forms of *graveolens* are abundant in the western portions of the mixed prairie, and of *speciosus* in particular in the bunch-grass prairie of the Northwest. They extend northward into Canada, but are found in the drier parts of the Southwest only in valleys in the mountains. As a rule, they mix and alternate with the sagebrush, except for such halophytes as *consimilis* and *viridulus*, which often form pure stands on alkali flats below it, in association with *Distichlis* and *Iva axillaris*. The *pinifolius* form of *graveolens* is also frequently halophytic, when it grows in mixture with *Sarcobatus*. All of these are seral dominants, and with drainage or shifting climate yield to the subclimax dominants, such as *speciosus*, *gnaphalodes*, *hololeucus*, *albicaulis*, etc. *Graveolens* is characteristic of the cliff edges and gullies of the bad lands of western Nebraska and the Dakotas.

This species reproduces readily from seed, and grows vigorously when transplanted, even when the crowns are divided. It forms basal sprouts after cutting, but only rarely when burned. Most of its forms are among the latest bloomers of the genus, the flowers appearing in September and often continuing into December.

TABLE 23.—Variation in certain subspecies of *Chrysothamnus nauseosus*.¹

	Herbarium.	Invo- lucre- length.	Corolla.			Style.		
			Length, including lobes.	Lobe- length.	Ratio of lobe-length to total length.	Stig- matic portion, length.	Append- age, length.	Ratio of appendage- length to total length of branch.
Subspecies a. gnaphalodes:								
Pyramid Lake, Nev.	87247 UC	8.2	8.5	0.7	8.2	1.4	1.1	44.0
Reno, Nev.	65323 UC	8.0	8.2	0.9	10.9	1.5	1.1	42.3
Lyon County, Nev.	203114 UC	6.5	7.9	0.7	8.8	1.5	1.0	40.0
Candelaria, Nev.	203124 UC	7.0	8.0	0.5	6.2	1.3	1.0	43.4
Goldfield, Nev.	203117 UC	6.6	8.0	0.8	10.0	1.6	1.2	42.8
Carson Sink Region, Nev. Benton, Mono County, Calif.	128633 UC 203129 UC	7.0 7.0	7.9 7.7	0.7 0.6	8.8 7.7	1.4 1.1	1.0 1.0	41.6 47.6
Inyo County, Calif.	203118 UC	7.0	7.6	0.6	7.8	1.2	1.0	45.4
Bishop, Calif.	203120 UC	7.8	7.8	0.5	6.4	1.2	1.0	45.4
Kearsarge, Calif.	203119 UC	6.1	7.1	0.5	7.0	1.3	1.0	43.4
Rosamond, Kern County, Calif.	87246 UC	6.5	7.5	0.8	10.6	1.4	1.1	44.0
Lancaster, Calif.	203111 UC	6.0	7.0	0.6	8.5	1.2	1.0	45.4
Do.	203110 UC	7.5	8.0	0.5	6.2	1.5	1.2	44.4
Near Lancaster, Calif.	203112 UC	7.2	7.8	0.7	8.9	1.4	1.0	41.6
Do.	203113 UC	6.0	7.1	0.8	11.2	1.4	1.1	44.0
Do.	194547 UC	6.0	7.5	0.5	6.6	1.4	1.3	48.1
Saugus, Calif.	87243 UC	7.8	8.0	0.6	7.5	1.3	1.2	48.0
Bareto, Calif.	203116 UC	6.1	7.4	0.7	9.4	1.4	1.2	46.1
Banning, Calif.	134761 UC	6.9	8.0	0.8	10.0	1.3	1.1	45.8
Average.		6.9	7.7	0.6	9.0	1.3	1.0	44.3
Subspecies b. hololeucus:								
Pyramid Lake, Nev.	203104 UC	7.1	8.0	0.9	11.2	1.7	1.5	46.8
Do.	203103 UC	7.0	8.0	0.9	11.2	1.5	1.3	46.4
Do.	178984 UC	6.6	7.3	0.9	12.3	1.3	1.2	48.0
Esmeralda County, Nev., Benton, Mono County, Calif.	203102 UC 194546 UC	6.2 7.0	8.0 7.8	0.6 0.7	7.5 8.9	1.5 1.4	1.2 1.1	44.4 44.0
Do.	194533 UC	6.5	7.0	0.6	8.0	1.2	1.0	45.4
Bishop Creek, Inyo County, Calif.	194532 UC	7.0	6.9	0.7	10.1	1.2	1.0	45.4
Oak Creek, Inyo County, Calif.	194531 UC	6.8	6.7	0.7	10.4	1.3	0.9	40.9
Do.	201226 UC	6.5	7.0	0.6	8.0	1.4	1.2	46.1
Independence, Inyo County, Calif.	194534 UC	6.6	6.7	0.5	7.4	1.1	0.9	45.0
Inyo County, Calif.	31196 UC	6.1	8.0	0.5	6.2	1.5	1.3	46.4
Average.		6.6	7.4	0.9	9.2	1.3	1.1	45.3
Subspecies c. speciosus:								
Woods Landing, Wyo. ² ...	10662 R	9.0	10.0	2.0	20.0	1.4	1.9	57.5
Fremont County, Wyo. ² ...	51497 UC	8.0	8.0	1.3	16.2	1.3	1.8	58.0
Southeastern Utah ² ...	176844 UC	8.8	9.0	1.0	11.1	1.5	2.3	60.5
Boise, Idaho ² ...	168807 UC	9.0	8.5	1.8	21.1	1.5	2.4	61.5
Near Salt Lake, Utah....	203197 UC	9.5	10.0	1.0	10.0	1.8	2.0	52.6
Do.	203198 UC	8.0	8.0	1.0	12.5	1.0	1.5	60.0
Near Grantsville, Utah ³ ...	203196 UC	7.8	8.0	0.4	5.0	1.5	1.8	54.5
Eastern Oregon ⁴ ...	175221 UC	10.5	10.0	1.5	15.0	2.0	2.3	53.4
Do ⁴ ...	175223 UC	9.5	9.0	1.3	14.4	1.5	2.0	57.1
Siskiyou Mountains, Oreg. Ormsby County, Nev. ⁵ ...	CI 75408 UC	9.5 9.2	10.5 11.0	1.7 1.7	18.1 15.4	1.5 1.8	2.5 2.3	62.5 56.0
Glenbrook Nev. ³ ...	128752 UC	10.0	11.0	1.8	16.3	1.8	2.6	59.0
Do ³ ...	129585 UC	8.6	9.5	1.5	15.7	2.0	2.8	58.3
Lake Tahoe, Calif. ³ ...	195527 UC	10.0	10.0	2.0	20.0	1.6	2.0	55.5
Placer County, Calif. ³ ...	194094 UC	10.5	10.0	1.4	14.0	2.0	2.5	55.5
Modoc County, Calif. ³ ...	195526 UC	9.0	9.0	1.3	14.4	1.4	2.0	58.8
Yreka, Calif. ³ ...	165409 UC	8.8	9.5	1.4	14.7	1.6	2.2	57.8
Mono Lake, Calif. ³ ...	203095 UC	9.8	9.0	1.2	13.3	1.5	2.0	57.1
Lundy, Mono County, Calif. ³ ...	195540 UC	8.5	9.2	1.6	17.3	1.6	2.0	55.5
Upper San Joaquin, Calif. ³	87259 UC	10.0	9.0	1.7	18.8	1.8	2.2	55.0
Average.		9.2	9.4	1.4	15.6	1.6	2.1	57.1

For footnotes, see page 233.

TABLE 23.—Variation in certain subspecies of *Chrysothamnus nauseosus*—Continued.

	Herbarium.	Involucre-length.	Corolla.			Style.		
			Length, including lobes.	Lobe-length.	Ratio of lobe-length to total length.	Stigmatic portion, length.	Appendage, length.	Ratio of appendage-length to total length of branch.
Subspecies <i>d. latiscapus</i>:								
White Sands, N. Mex.	125334 UC	mm. 8.5	mm. 9.3	mm. 0.4	p. ct. 4.3	mm. 1.5	mm. 2.0	p. ct. 57.1
Burro Mountains, N. Mex.	US	7.5	8.2	0.6	7.3	1.2	1.2	50.0
San Lorenzo, N. Mex.	498228 US	7.3	10.0	0.7	7.0	1.7	1.3	43.3
Eastern New Mexico.	Gr	6.5	7.5	0.7	9.3	1.2	2.3	65.8
Mimbres R., N. Mex.	Gr	8.0	8.2	0.6	7.3	1.4	1.7	54.8
Santa Rita Mountains, Ariz.	87234 UC	9.0	8.7	0.9	10.3	1.3	1.5	53.5
Santa Cruz, Sonora.	234366 US	9.0	9.0	0.9	10.0	1.6	2.1	56.7
Average.		7.9	8.6	0.6	7.9	1.4	1.7	54.4
Subspecies <i>e. albicaulis</i>:								
Tranquille, B. C.	NY	9.0	10.0	1.9	19.0	1.9	2.0	51.2
Polson, Mont.	NY	7.5	8.5	1.6	18.8	1.5	1.9	55.8
Wawawai, Wash.	Mo. Bot. Gard.	9.0	8.0	1.6	20.0	1.1	1.7	60.7
Warm Springs, Oreg.	381002 US	9.8	9.0	1.3	14.4	1.8	1.7	50.0
Eastern Oregon.	179775 UC	8.0	9.0	1.7	18.8	1.3	1.8	58.0
Plumas County, Calif. ⁵	26296 Gr	9.0	9.5	2.2	23.1	1.4	2.5	64.1
Mimodoc County, Calif.	11662 CI	9.7	10.0	2.0	20.0	1.5	2.0	57.1
Lassen County, Calif.	11681 CI	7.5	8.3	1.4	16.8	2.0	2.5	55.5
Average.		8.7	9.0	1.7	18.8	1.5	2.0	56.5
Subspecies <i>f. typicus</i>:								
Missouri River (type)	Phila.	7.5	7.2	1.4	19.4	1.6	1.9	54.3
Douglas, Wyo. ⁶	146485 UC	8.0	7.0	1.3	18.6	1.1	1.6	59.2
Church Buttes, Wyo. ⁶	205537 UC	6.7	7.9	1.3	16.4	1.0	1.5	60.0
Sheridan, Wyo.	38382 R	8.2	7.6	1.7	22.4	1.6	1.5	48.4
Do.	78175 R	8.0	8.2	2.1	25.6	1.8	1.9	51.3
Howell Lakes, Wyo.	187661 UC	7.4	7.0	1.3	18.6	1.2	1.5	55.5
Tipton, Wyo.	CI	8.0	7.0	1.5	21.4	1.5	2.5	62.5
Laramie, Wyo. ⁸	CI	7.5	7.5	1.3	17.4	2.4	1.6	40.0
Do.	29415 R	6.5	6.9	1.4	20.3	1.4	1.3	48.1
Do.	15383 R	7.1	8.1	1.6	19.7	1.5	1.5	50.0
Do.	193529 UC	7.8	7.0	1.2	17.1	1.2	2.0	62.5
Do.	51773 UC	7.2	7.0	1.5	21.4	1.5	1.8	54.5
Do.	5692 R	8.2	7.9	1.8	22.8	2.1	1.8	46.1
Laramie Plateau, Wyo. ⁸	CI	6.5	6.6	1.2	18.4	1.3	2.1	61.8
Albany County, Wyo.	29414 R	7.7	7.8	1.7	21.8	2.3	1.3	36.1
Do.	52302 R	8.1	8.2	1.5	18.3	1.0	2.1	67.8
Do.	42089 R	8.1	9.0	2.0	22.2	1.9	1.9	50.0
Do.	37246 R	8.0	8.0	1.6	20.0	1.5	1.6	51.6
Colorado-Wyoming line ⁶	29429 R	7.7	7.7	1.7	22.1	1.6	1.9	54.3
Windsor, Colo. ⁸	31151 R	7.0	7.0	1.8	25.1	1.3	1.7	56.7
Do. ⁶	9396 R	7.0	6.5	1.5	23.1	1.6	1.7	51.5
Fort Collins, Colo. ⁶	CI	7.1	7.5	1.2	16.0	1.5	2.3	60.5
Boulder, Colo. ⁶	57235 R	7.0	7.0	1.8	25.7	1.5	1.9	55.9
East Denver, Colo. ⁶	CI	7.9	8.0	1.7	21.2	1.5	1.6	51.6
Aurora, Colo. ⁶	CI	6.5	6.2	1.6	22.8	1.0	1.5	60.0
Average.		7.5	7.4	1.5	20.7	1.5	1.8	54.0
Subspecies <i>h. occidentalis</i>:								
Sierra Nevada Mountains, Calif.	US		10.5	2.2	20.9	1.6	2.2	56.3
San Bernardino Mountains, Calif.	196667 UC	10.0	9.5	2.3	24.2	2.0	2.5	56.7
Southern Sierra Nevada, Calif.	195543 UC	9.0	9.0	2.0	22.2	1.5	2.0	57.1
North Coast Ranges, Calif.	196665 UC	9.5	8.8	2.1	23.9	1.8	3.3	64.7
Do.	69867 UC	9.0	10.0	1.7	17.0	2.0	2.4	54.5
Average.		9.4	9.6	2.1	21.6	1.8	2.5	57.9

For footnotes see page 233.

TABLE 23.—Variation in certain subspecies of *Chrysothamnus nauseosus*—Continued.

	Herbarium.	Involucre-length.	Corolla.			Style.		
			Length, including lobes.	Lobe-length.	Ratio of lobe-length to total length.	Stigmatic portion, length.	Appendage, length.	Ratio of appendage-length to total length of branch.
Subspecies <i>i. bernardinus</i>:								
San Gabriel Mountains, Calif.	SF	mm.	mm.	mm.	p. ct.	mm.	mm.	p. ct.
Do.	SF	12.1	10.7	2.2	20.6	2.0	2.8	58.3
San Bernardino Mountains, Calif. (type)...		11.2	10.2	1.8	17.7	2.0	2.7	57.4
Do.	149208 UC	12.0	9.5	1.9	20.0	2.0	3.0	60.0
Do.	69265 UC	11.0	9.0	2.0	22.2	1.3	3.2	71.1
Do.	111298 UC	12.0	10.0	1.8	18.0	1.7	3.8	69.1
Do.	64990 UC	10.0	10.0	1.5	15.0	1.5	3.5	70.0
San Jacinto Mountains, Calif.	62909 UC	11.5	12.0	2.5	20.8	2.0	2.5	55.5
Do.	31193 UC	10.5	12.0	2.4	20.0	2.4	2.8	53.8
Average.		11.2	10.4	2.0	19.3	1.9	3.0	61.9
Subspecies <i>j. graveolens</i>:								
Platte Cañon, Wyo.	51495 UC	7.0	8.0	0.7	8.7	1.3	1.6	55.2
New Windsor, Colo.	34342 UC	8.0	9.0	0.9	10.0	1.4	1.8	56.2
North Denver, Colo.	148163 UC	7.2	8.0	0.7	8.7	1.5	2.0	57.1
Fremont County, Colo.	87244 UC	7.0	7.2	0.6	8.3	1.5	2.0	57.1
Sierra La Sal, Utah.	135110 UC	8.0	8.0	1.2	15.0	1.6	1.9	54.3
South of Fort Collins, Colo.	CI	8.0	8.0	1.3	16.2	1.5	2.0	57.1
Do.	CI	8.0	8.0	1.3	16.2	1.5	2.0	57.1
Golden, Colo.	CI	6.8	8.9	1.3	14.6	1.3	1.8	58.1
North of Fort Collins, Colo.	CI	7.0	8.3	1.2	14.4	1.6	1.8	52.9
Do.	CI	8.0	9.0	1.3	14.4	1.7	2.0	54.0
Golden, Colo.	CI	6.5	8.0	1.3	16.2	1.6	1.9	54.3
North Denver, Colo.	CI	7.0	7.0	1.3	18.5	1.9	2.1	52.5
Gunnison, Colo.	8411 R	6.5	7.9	1.2	15.2	1.2	1.5	55.5
Farmington, N. Mex.	685894 US	8.0	8.2	1.4	17.1	1.3	1.8	58.1
Salida, Colo.	Gr	8.0	9.0	1.2	13.3	1.2	1.7	58.6
Average.		7.4	8.1	1.1	13.8	1.5	1.9	55.9
Subspecies <i>k. pinifolius</i>:								
Salida, Colo.	203157 UC	6.0	7.0	1.3	18.5	1.0	1.4	58.3
San Luis Valley, Colo.	203158 UC	6.3	6.3	1.1	17.4	0.9	1.0	52.6
Do.	203156 UC	6.5	5.7	0.8	14.0	1.0	1.3	56.5
Gunnison, Colo.	55167 UC	7.6	7.3	0.7	9.5	1.0	1.2	54.5
Do.	R	7.0	7.0	0.9	12.8			
Doyle's, Colo.	R	7.0	7.5	1.0	13.3			
West Central Colorado.	55168 UC	7.3	7.2	0.8	11.1	0.9	1.2	57.1
Do.	161363 UC	7.2	7.0	0.7	10.0	1.0	1.2	54.5
Iola, Colo.	412299 US	8.0	8.8	1.2	13.6	1.4	1.8	56.3
White Mountains, N. Mex.	Gr	9.0	9.0	1.3	14.4	1.5	1.5	50.0
Above Datil, N. Mex.	112410 UC	9.0	7.3	1.0	13.6	1.0	1.3	56.5
Gunnison, Utah (type)	26307 Gr	7.0	7.0	1.1	15.7	1.4	1.3	48.0
Do.	412455 US	8.0	8.0	0.9	11.2	1.1	1.1	50.0
Average.		7.3	7.3	0.9	13.4	1.1	1.3	52.8
Subspecies <i>l. consimilis</i>:								
Boise, Idaho.	164932 UC	8.2	8.1	1.3	16.0	1.5	2.0	57.1
Stockton, Utah.	203210 UC	7.8	7.0	1.3	18.5	1.5	1.6	51.6
Maggie Creek, Elko County, Nev.	65304 UC	8.0	8.0	1.4	17.5	1.5	1.7	53.1
Death, Nev. (type)	26603 Gr	7.8	7.9	1.4	17.7	1.4	1.5	51.6
Elko County, Nev.	175163 UC	7.5	7.0	1.2	17.1	1.3	1.8	58.0
Caliente, Nev.	203106 UC	8.0	8.0	1.1	13.7	1.0	2.0	66.6
Fallon, Nev.	176430 UC	7.2	7.2	1.6	22.2	1.0	1.8	64.2
Mountain House, Nev.	203146 UC	7.5	8.5	1.5	17.5	1.5	1.5	50.0
Reno, Nev.	87227 UC	8.0	7.6	1.3	17.1	1.3	1.5	53.5
Pyramid Lake Road, Nev.	203194 UC	7.0	7.1	1.3	18.3	1.1	1.4	56.0

For footnotes see page 233.

TABLE 23.—Variation in certain subspecies of *Chrysothamnus nauseosus*—Continued.

	Herbarium.	Involucre-length.	Corolla.			Style.		
			Length, including lobes.	Lobe-length.	Ratio of lobe-length to total length.	Stigmatic portion, length.	Appendage, length.	Ratio of appendage-length to total length of branch.
Subsp. <i>l. consimilis</i> —Cont.								
Shasta Valley, Calif.	201306 UC	8.1	8.0	1.4	17.5	1.3	1.6	55.1
Modoc County, Calif.	195494 UC	8.2	8.5	1.5	17.6	1.2	1.5	55.5
Near Alturas, Modoc County, Calif. ¹	26511 Gr	7.6	7.5	1.5	20.0	1.6	2.0	55.5
Do.	193100 UC	8.0	8.0	1.3	16.2	1.8	2.1	53.5
Eastern Oregon	31187 UC	7.6	7.0	1.2	17.1	1.3	1.8	58.0
Average		7.7	7.7	1.3	17.6	1.4	1.8	55.7
Subspecies <i>m. viridulus</i> :								
Esmeralda County, Nev.	203071 UC	8.0	7.2	1.7	23.6	1.2	1.6	57.1
Lida, Nev.	203072 UC	7.8	9.0	2.1	23.3	1.0	2.0	66.7
Mono Lake, Calif.	203067 UC	8.5	9.0	2.2	24.4	1.6	2.0	55.5
Near Benton, Mono County, Calif.	203074 UC	8.0	8.5	2.0	23.5	1.2	1.4	53.8
Benton Station, Mono County, Calif.	203077 UC	8.0	9.0	2.3	25.5	1.4	1.7	54.8
Benton, Mono County, Calif.	203139 UC	8.4	9.0	2.4	26.7	1.2	1.7	58.6
Do.	203134 UC	8.0	8.0	1.8	22.5	1.5	1.8	54.5
Deep Spring, Inyo County, Calif.	203144 UC	7.8	7.0	1.7	24.3	1.4	1.9	57.6
Laws, Inyo County, Calif.	203136 UC	7.0	7.2	2.3	31.9	1.4	1.6	53.3
Bishop, Inyo County, Calif.	203073 UC	8.5	9.0	2.3	25.5	1.2	1.8	60.0
Near Bishop, Inyo County, Calif.	203131 UC	7.0	8.0	1.8	22.5	1.2	1.6	57.1
Kearsarge, Inyo County, Calif.	203142 UC	8.0	7.5	2.3	30.7	1.3	1.6	55.2
Do.	203141 UC	8.0	7.5	2.2	29.3	1.4	2.0	58.8
Near Kearsarge, Inyo County, Calif.	203140 UC	7.4	7.5	2.1	28.0	1.5	1.8	54.5
Independence, Inyo County, Calif.	203075 UC	8.0	8.0	2.0	25.0	1.2	1.6	57.1
Lone Pine, Inyo County, Calif.	203070 UC	6.5	8.0	2.2	27.5	1.4	1.8	56.2
Do.	203069 UC	8.5	8.0	1.7	21.2	1.5	1.8	54.5
Panamint Mountains, Inyo County, Calif.	203132 UC	8.5	8.0	1.6	20.0	1.3	1.7	56.7
Average		7.9	8.1	2.0	25.3	1.3	1.7	56.8
Subspecies <i>o. mohavensis</i> :								
Near Mojave, Calif.	203078 UC	9.0	8.3	1.6	19.3	1.3	2.0	60.6
Mojave Desert, Calif.	87255 UC	10.8	9.2	1.5	16.3	1.1	1.7	60.7
Greenhorn Mountains, Calif.	63639 UC	10.0	10.5	2.4	22.8	1.2	2.1	63.6
Alamo Mountains, Calif.	73921 UC	9.3	9.5	1.7	17.9	1.3	2.7	67.5
Mt. Hamilton, Calif.	177561 UC	9.5	10.5	2.3	21.9	1.7	2.1	55.3
Near Fort Tejon, Calif.	Gr	9.6	9.8	2.0	20.4	1.6	1.8	52.9
Mojave Desert, Calif.	Gr	9.9	8.0	2.7	33.7	1.7	1.6	48.5
Average		9.7	9.4	2.0	21.7	1.4	2.0	58.4

¹ Except where otherwise mentioned the plants selected for measurement are normal and fairly representative of the subspecies to which they are assigned. The figure given for corolla and style characters is the average of a number of measurements, but the fluctuation usually is slight on any given plant. The involucre is more variable. Usually several of the larger and fully mature involucre were selected and these averaged. The measurement is from the base of the lowest row of bracts to a point on a level with the top of the longest bract, assuming the involucre to be in a vertical position. Thus no allowance was made for the slope of the sides.

² Minor variation 68, *C. pulcherrimus* Nelson.
³ Minor variation 58, with wide and thick leaves.
⁴ Minor variation 57, with pubescence covering the involucre.

⁵ Type of *C. orthophyllus* Greene, minor variation 63.
⁶ Minor variation 67, *C. plattensis* Greene.
⁷ Type of *C. angustus* Greene, minor variation 21.

USES.

The value of this shrub as a browse plant for animals depends largely upon local conditions. Throughout most of its range it is never browsed, except under very unusual circumstances. Toward the north, however, especially in Idaho and neighboring States, the stems and leaves of subspecies *speciosus* are eaten to a considerable extent by sheep, according to reports from the Forest Service, and even in eastern California this form is sometimes preferred to sagebrush by sheep. In northern regions it furnishes an important winter browse for elk and perhaps also for moose. On the other hand, reliable reports indicate that this species is poisonous to stock under certain conditions, at least in Nevada. If poisonous at all, it is probable that serious results follow only when it is eaten to the exclusion of other foods, or when the animal is in an underfed or weakened condition.

The possible utilization of *Chrysothamnus nauseosus* as a supply of rubber has been recently investigated by Hall and Goodspeed (Univ. Calif. Publ. Bot. 7:183-264, 1919). Rubber was found to be present in the cortex and medullary rays in all of the 12 varieties examined, the amount present running as high as 6.57 per cent in individual plants, but averaging only 2.83 per cent even for the best variety. The most constant producers were the varieties inhabiting alkaline soils, especially *viridulus*, *consimilis*, *pinifolius*, and *turbinatus*. Field surveys indicated that perhaps 300,000,000 pounds of rubber of good grade are present in the wild shrub of this species in the western United States and that this supply could be drawn upon in case of a national emergency, such as an extensive war during which time overseas importations might be curtailed. The percentage content of the shrub is much too low to render the extraction of the rubber a profitable undertaking under normal conditions. Even in wartime the total amount obtainable would be insufficient for more than a supplementary supply. It would seem wise, therefore, to carry the investigation of this and other rubber plants still further in the hope of so increasing the yield through breeding, selection, and various other methods of treatment that a permanent rubber-growing industry could be established within the boundaries of the continental United States.

The herbage of certain subspecies, notably *hololeucus* and *gnaphalodes*, is so pleasantly fragrant that the preparation of an essential oil from it would seem to be among the possibilities.

EXPLANATIONS OF PLATES 24 TO 35, GENUS CHRYSOTHAMNUS.

PLATE 24.

Chrysothamnus paniculatus. (Drawn from fresh material from east side of Tehachapi Pass, Calif.)

- (1) Portion of the inflorescence, $\times 1$.
- (2) Habit sketch of an old plant, woody throughout, $\times 0.03$.
- (3) Surface view of the middle portion of a leaf to show the resin-pits, $\times 20$.
- (4) Head, $\times 3$.
- (5) Outer bract of the involucre, $\times 9$.
- (6) Inner bract, $\times 9$.
- (7) Flower with part of pappus removed, $\times 6$.
- (8) Style-branches, $\times 12$.
- (9) Anthers, $\times 12$.

Chrysothamnus teretifolius. (Material from Inyo and Kern Counties, Calif., 32917 and 194530 UC.)

- (10) Branch showing leaves and inflorescences, $\times 1$.
- (11) Branch with a narrow inflorescence, $\times 1$.
- (12) Sketch of plant growing among rocks at Benton, California, $\times 0.05$.
- (13) Head showing thickened tips to the bracts, $\times 3$.
- (14) Outer bract of the involucre, $\times 9$.
- (15) Inner bract, $\times 9$.
- (16) Flower with part of pappus removed, $\times 6$.
- (17) Style-branches, $\times 12$.
- (18) Anthers, $\times 12$.
- (19) Surface view of the middle portion of a leaf to show the resin-pits, $\times 20$. (See fig. 24a, p. 160, for cross-section.)

PLATE 25.

Chrysothamnus gramineus. (Drawn from the type specimen.)

- (1) Upper portion of the stem showing the arrangement of the heads and the broad leaves, $\times 1$.
- (2) Head showing the broad truncate bracts, $\times 3$.
- (3) Outer bract of the involucre, $\times 9$.
- (4) Inner bract, $\times 9$.
- (5) Flower with part of pappus removed and showing elongated glabrous achene, $\times 6$.
- (6) Style-branches showing the very short stigmatic portion and the long appendages, $\times 12$.
- (7) Anthers, $\times 12$.
- (8) Habit sketch showing part of plant, $\times 0.12$.

Chrysothamnus vaseyi. (Material from Panguitch Lake, Utah, 159879 UC.)

- (9) Portion of plant showing the erect leafy shoots and the inflorescences, $\times 1$.
- (10) Head, $\times 3$. The bracts are greenish and slightly thickened near the tip.
- (11) Outer bract of the involucre, $\times 9$.
- (12) Inner bract, $\times 9$.
- (13) Flower with a portion of the pappus removed and showing the short glabrous achene, $\times 6$.
- (14) Style-branches showing the elongated stigmatic portion and the short appendages, $\times 12$.
- (15) Anthers, $\times 12$.

PLATE 26.

Chrysothamnus viscidiflorus lanceolatus. (Material from Cerro Summit, Colorado, 55164 UC.)

- (1) Branch showing leaves and inflorescence; herbage puberulent; $\times 1$.

Chrysothamnus viscidiflorus puberulus. (Material from Northern Nevada, 175448 UC.)

- (2) Branch showing leaves and inflorescences; herbage puberulent; $\times 1$.
- (3) Head, $\times 3$.
- (4) Outer bract of the involucre, $\times 9$.
- (5) Inner bract, $\times 9$.
- (6) Flower with part of pappus removed, $\times 6$.
- (7) Style, $\times 12$.
- (8) Anthers, $\times 12$.

PLATE 26—continued.

Chrysothamnus viscidiflorus humilis. (Drawn from material of the type collection, 87252 UC.)

- (9) Portion of plant showing leaves and inflorescences; herbage puberulent; $\times 1$.

Chrysothamnus viscidiflorus elegans. (Material from Gunnison Valley, Colorado, 193530 UC.)

- (10) Summit of branch with inflorescence; herbage puberulent; the leaves in this and other subspecies may be either twisted, as here shown, or straight, bracts greenish-tipped; $\times 1$.

Chrysothamnus viscidiflorus stenophyllus. (Drawn from specimen of type collection, Watson 566, NY.)

- (11) Summit of branch with inflorescence; herbage glabrous; $\times 1$.

Chrysothamnus viscidiflorus pumilus. (Material from Pocatello, Idaho, 193103 UC.)

- (12) Summit of branch, with inflorescence; herbage glabrous; $\times 1$.

PLATE 27.

Chrysothamnus viscidiflorus linifolius. (Drawn from fresh material from Point of Rocks, Wyo.)

- (1) Leafy stem and inflorescence; herbage glabrous; $\times 1$.

- (2) Head showing the slightly thickened greenish tips to the bracts of the involucre, $\times 3$.

Chrysothamnus viscidiflorus typicus. (Drawn from material from Weber Cañon, Utah, preserved in liquid.)

- (3) Inflorescence and leaves; glabrous; $\times 1$.
- (4) Head, $\times 3$.
- (5) Outer bract of the involucre, $\times 9$.
- (6) Inner bract, $\times 9$.
- (7) Flower with part of pappus removed, $\times 6$.
- (8) Style-branches, $\times 12$.
- (9) Habit-sketch of a plant at Buena Vista, Colorado; $\times 0.1$.

PLATE 28.

Chrysothamnus greenei filifolius. (Material from Lund, Utah, 203159 UC.)

- (1) Leafy shoot with inflorescence, $\times 1$.
- (2) Anthers, $\times 12$.
- (3) Head, $\times 3$.
- (4) Outer bract of the involucre, $\times 9$.
- (5) Inner bract, $\times 9$.
- (6) Flower with part of pappus removed, $\times 6$.
- (7) Style-branches, $\times 12$.

Chrysothamnus abidus. (Drawn from fresh material from the type locality.)

- (8) Leafy shoot with inflorescence, $\times 1$.
- (9) Habit sketch of a plant growing on an alkali flat; *C. nauseosus consimilis* and *Elymus condensatus* in the background; $\times 0.05$.
- (10) Surface view of middle part of leaf to show resin-pits, $\times 20$. (See fig. 24b, p. 160, for cross-section.)
- (11) Anthers, $\times 12$.
- (12) Flower with a portion of the pappus removed; the curved corolla is characteristic; $\times 6$.
- (13) Outer bract of the involucre, $\times 9$.
- (14) Inner bract, $\times 9$.
- (15) Style, $\times 12$.
- (16) Head, $\times 3$.

PLATE 29.

Chrysothamnus pulchellus typicus. (Material from Chihuahua, 87217 UC.)

- (1) Branch, $\times 1$.
- (2) Outer bract of the involucre, $\times 9$.
- (3) Inner bract, $\times 9$.
- (4) Habit sketch of a plant growing in northwestern New Mexico, $\times 0.1$.

EXPLANATIONS OF PLATES 24 TO 35, GENUS CHRYSOTHAMNUS.

PLATE 29—continued.

- (5) Head, $\times 3$.
- (6) Flower with part of pappus removed, $\times 6$.
- (7) Anthers, $\times 12$.
- (8) Style, $\times 12$.

Chrysothamnus depressus. (Drawn from fresh material from northern Arizona.)

- (9) Branch, $\times 1$.
- (10) Head, $\times 3$.
- (11) Flower with a part of pappus removed, $\times 6$.
- (12) Outer bract of the involucre, $\times 9$.
- (13) Inner bract, $\times 9$.
- (14) Style, $\times 12$.

PLATE 30.

Chrysothamnus pyramidatus. (Drawn from material collected above Oaxaca, Mexico, 87304 UC.)

- (1) Branch showing the characteristic fasciated leaves and the raceme-like inflorescence, $\times 1$.
- (2) Head showing the loosely arranged bracts, $\times 3$.
- (3) Accessory bract from just beneath the involucre, $\times 9$.
- (4) Outer bract of the involucre, $\times 9$.
- (5) Inner bract, $\times 9$.
- (6) Flower with part of pappus removed, $\times 6$.
- (7) Style-branches, $\times 12$.
- (8) Anthers, $\times 12$.

Chrysothamnus parryi latior.

- (9) An erect stem showing the broad leaves and the inflorescence, $\times 1$.

PLATE 31.

Chrysothamnus parryi typicus. (Main drawing from fresh material from San Juan Mountains, Colorado, 205815 UC; the details are from a plant collected at Leadville, Colorado.)

- (1) Erect flowering stem showing ample foliage, $\times 1$.
- (2) Style-branches showing the elongated appendages, $\times 12$.
- (3) An outer bract of the involucre, $\times 9$. Inner bracts less attenuate, as shown in fig. 6.
- (4) Anthers, $\times 12$.
- (5) Flower with part of pappus removed, $\times 6$.
- (6) Head showing the loose arrangement of the involucre bracts, $\times 3$.

Chrysothamnus parryi imulus. (Drawn from the type specimen.)

- (7) Portion of a plant showing the low spreading habit, $\times 1$.
- (8) Anthers, $\times 12$.
- (9) Flower with part of pappus removed, $\times 6$.
- (10) Outer bract of the involucre, $\times 9$.
- (11) Inner bract, $\times 9$.
- (12) Head, $\times 3$.
- (13) Style-branches showing the elongated appendages, $\times 12$.

PLATE 32.

Chrysothamnus parryi vulcanicus.

- (1) Inflorescence and upper leaves, $\times 1$. (Material from the southern Sierra Nevada, California, 126456 UC.)
- (2) A narrower inflorescence, $\times 1$. (Material from upper San Joaquin River, Calif., 87221 UC.)

Chrysothamnus parryi nevadensis. (Material from near Verdi, Nevada, 193101 UC.)

- (3) Inflorescence and upper leaves, $\times 1$.

Chrysothamnus parryi asper. (Material from Charleston Mountains, Nevada, 171476 UC.)

- (4) Inflorescence and upper leaves, the latter rough-pubescent with stalked glands; $\times 1$.

Chrysothamnus parryi howardi. (Drawn from fresh material from near Buena Vista, Colorado.)

- (5) Upper portion of plant with inflorescences, $\times 1$.

PLATE 32—continued.

- (6) Head, $\times 3$.
- (7) Style, $\times 12$.
- (8) Flower with part of pappus removed, $\times 6$.
- (9) Outer bract of the involucre, $\times 9$.
- (10) Inner bract, $\times 9$.
- (11) Anthers, $\times 12$.

PLATE 33.

Chrysothamnus nauseosus speciosus.

- (1) Branch and inflorescence of a form with broad, heavy leaves (minor variation 58, p. 221); $\times 1$. (Material from Honey Lake Valley, northeastern California.)
- (2) Leaf and heads of robust form (minor variation 68, p. 222, *C. pulcherrimus*), $\times 1$. (Material from Woods Landing, Wyo., 10662 R.)
- (3) Leafy shoot and inflorescence of typical *speciosus*, $\times 1$. (Material from Crater Lake, Oregon, 20317 UC.)

Chrysothamnus nauseosus gnaphalodes. (Drawn from living material in the Botanical Garden of the University of California, grown from seed collected at Benton, California; fig. 5 from a photograph taken at Benton.)

- (4) Leafy branch and inflorescence, $\times 1$.
- (5) Habit sketch of a normally developed plant of sandy, well-drained soil; $\times 0.04$.
- (6) Head, $\times 3$.
- (7) Outer bract of the involucre showing the woolly pubescence, $\times 9$.
- (8) Inner bract, woolly on the exposed tip; $\times 9$.
- (9) Flower with a portion of the pappus removed showing the pubescent corolla-tube and the very short corolla-lobes, $\times 6$.
- (10) Anthers, $\times 12$.
- (11) Style-branches showing the very short appendages, $\times 12$.

PLATE 34.

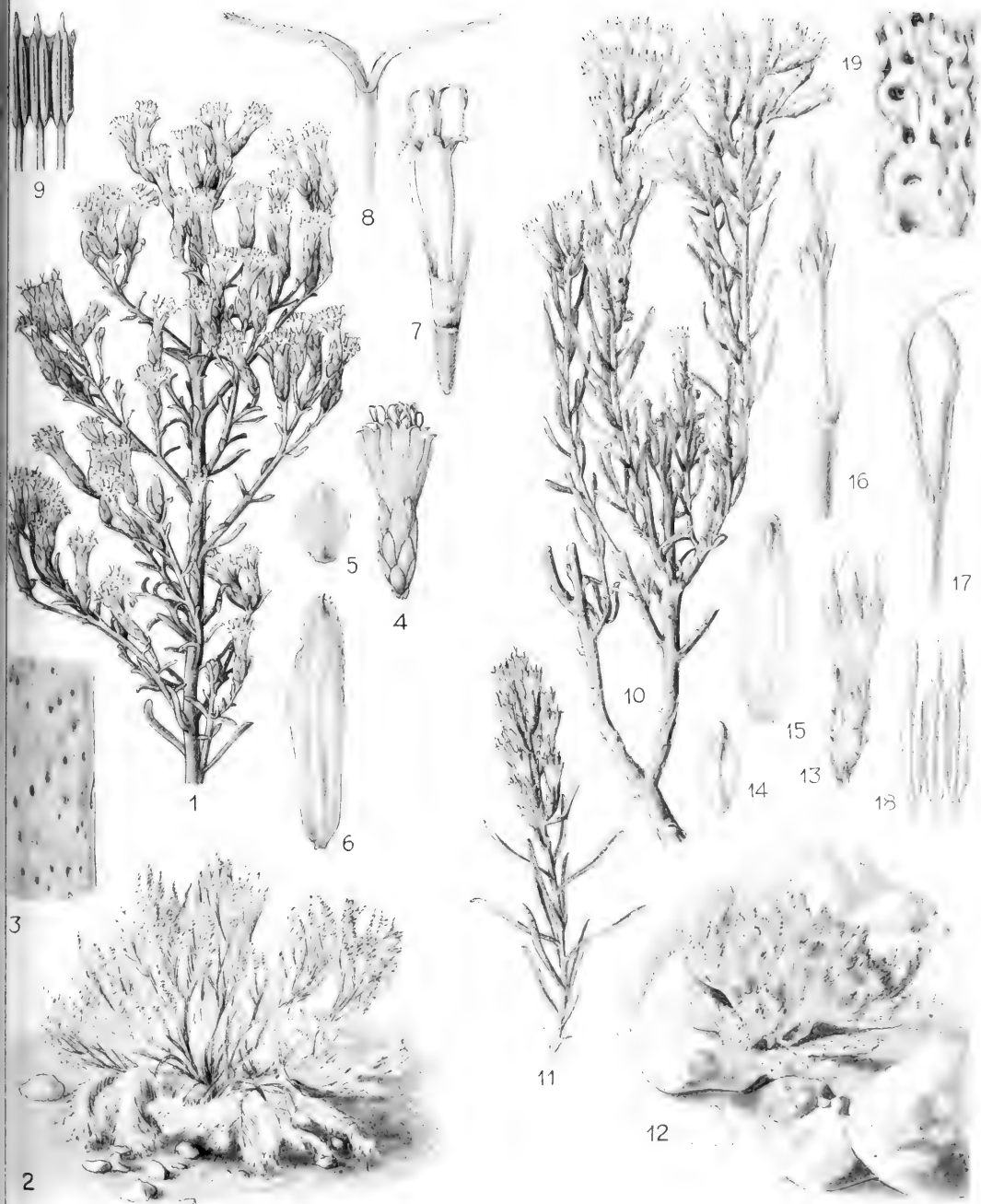
Chrysothamnus nauseosus typicus.

- (1) A branch of the genuine form from Laramie, Wyoming (July 29, 1889, Greene, UC., labeled *C. frigidus*), $\times 1$.
- (2) A branch with longer and slightly curved leaves (minor variation 76, p. 222, *C. speciosus plattensis*), $\times 1$. (Drawn from fresh material from East Denver, Colorado.)
- (3) A more widely branched inflorescence from the same collection as 2, $\times 1$.
- (4) Head from the branch shown in 3, $\times 3$.
- (5) Outer bract of involucre of same head, $\times 9$.
- (6) Inner bract of the same involucre, $\times 9$.
- (7) Style-branches of the flower figured in 9, showing the long appendages, $\times 12$.
- (8) Anthers from the same flower, $\times 12$.
- (9) Flower from the head shown in 4, a portion of the pappus removed; $\times 6$.
- (10) Habit sketch of a plant growing near Laramie, Wyoming; $\times 0.08$.

PLATE 35.

Chrysothamnus nauseosus graveolens. (Drawn from fresh material and photographs from eastern Colorado.)

- (1) Inflorescence and upper leaves, $\times 1$.
- (2) Habit sketch of normal plant of good soils, more spreading and regular in outline than in most specimens; $\times 0.03$.
- (3) Flower with part of pappus removed, $\times 6$.
- (4) Style, $\times 12$.
- (5) Anthers, $\times 12$.
- (6) Outer bract of the involucre, $\times 9$.
- (7) Inner bract, $\times 9$.
- (8) Head, $\times 3$.



by J. Powell del.

Chrysothamnus paniculatus, figs. 1 to 9.

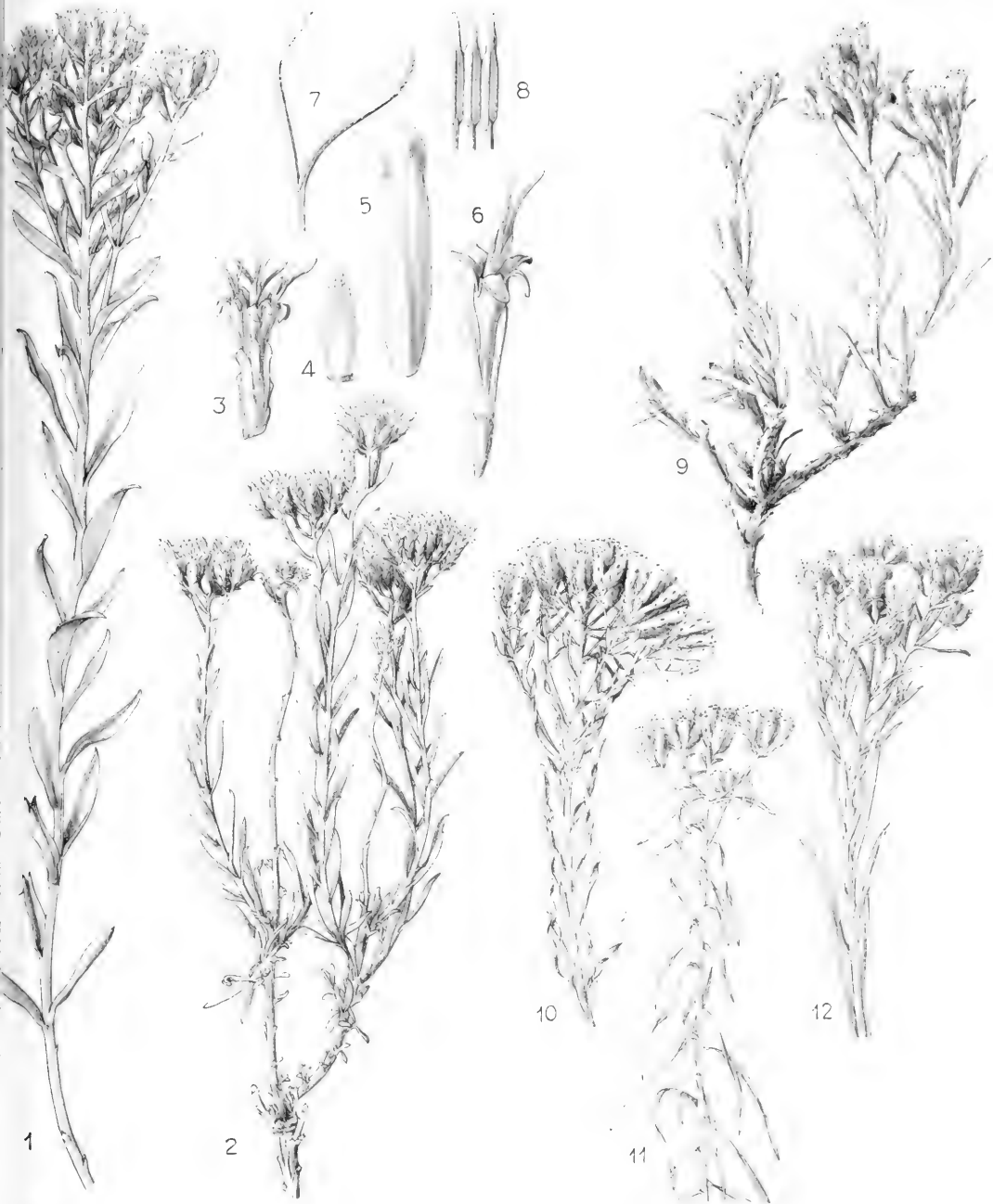
Chrysothamnus teretifolius, figs. 10 to 19.



Ruth J. Porsell del.

Chrysothamnus gramineus, figs. 1 to 8.

Chrysothamnus vaseyi, figs. 9 to 15.



J. Poirell del.

Chrysothamnus viscidiflorus lanceolatus, fig. 1.

Chrysothamnus viscidiflorus puberulus, figs. 2 to 3.

Chrysothamnus viscidiflorus humilis, fig. 9.

Chrysothamnus viscidiflorus elegans, fig. 10.

Chrysothamnus viscidiflorus stenophyllus, fig. 11.

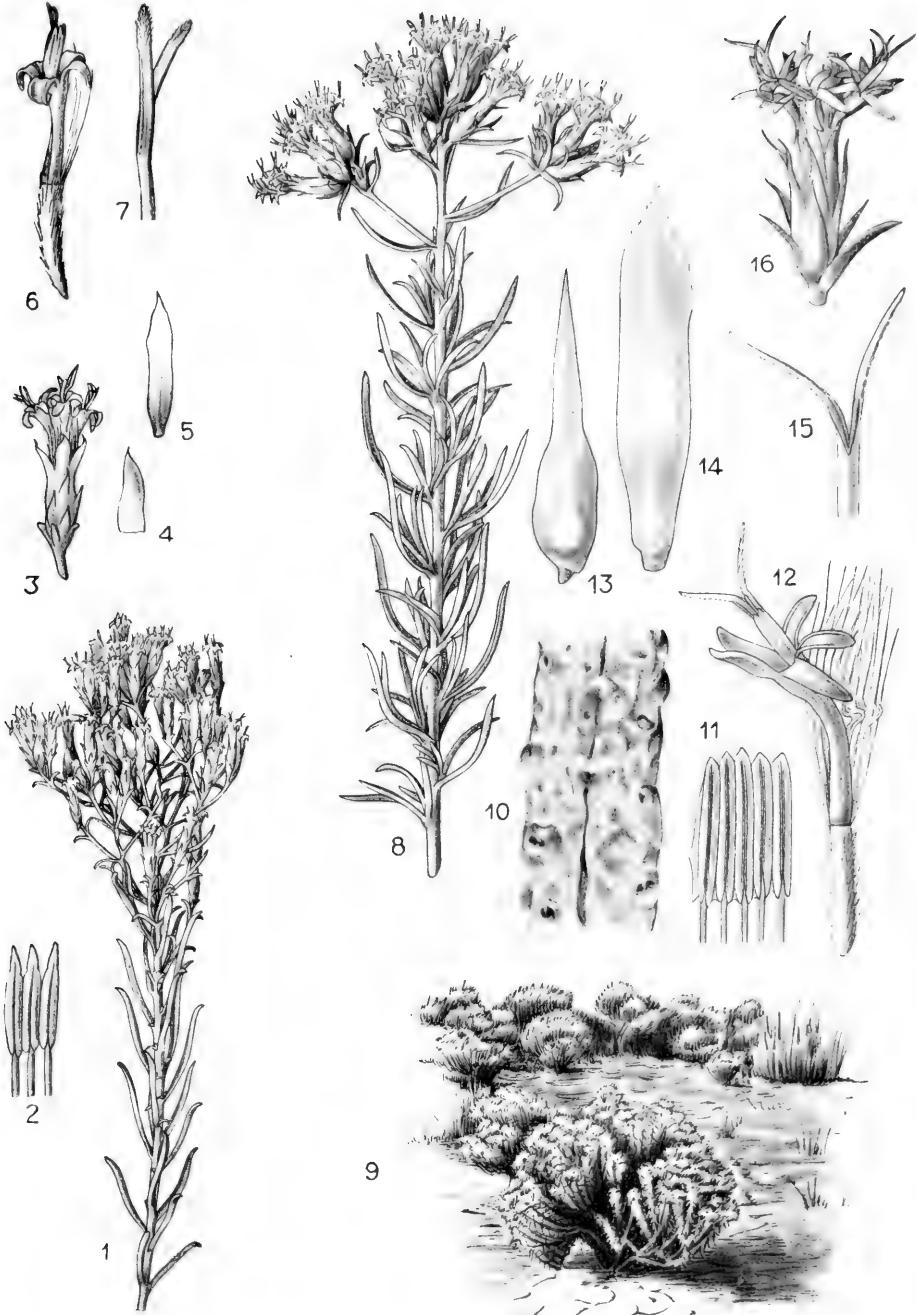
Chrysothamnus viscidiflorus pumilus, fig. 12.



Ruth J. Powell del.

Chrysothamnus viscidiflorus linifolius, figs. 1 and 2.

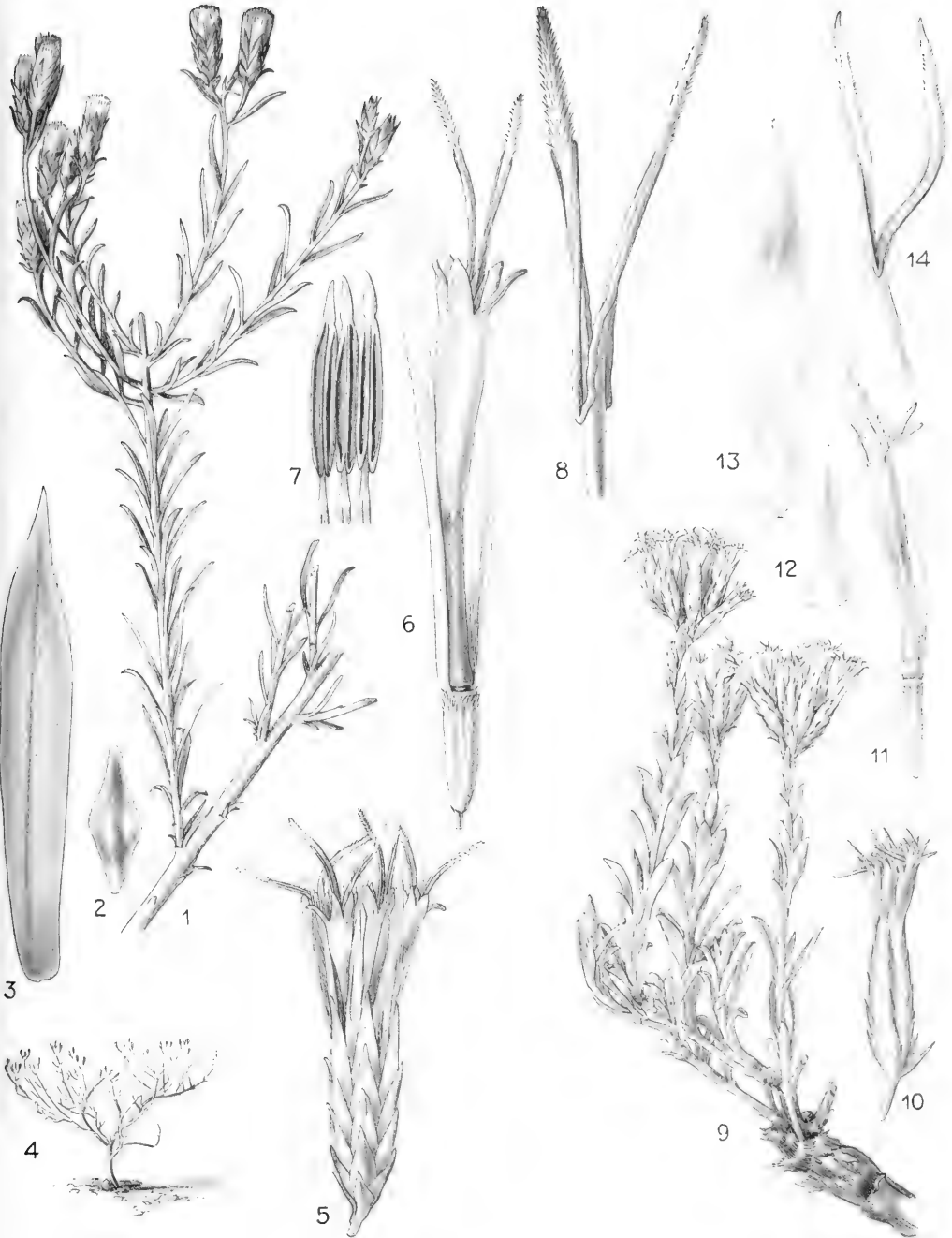
Chrysothamnus viscidiflorus typicus, figs. 3 to 9.



Ruth J. Powell del.

Chrysothamnus Greenei filifolius, figs. 1 to 7.

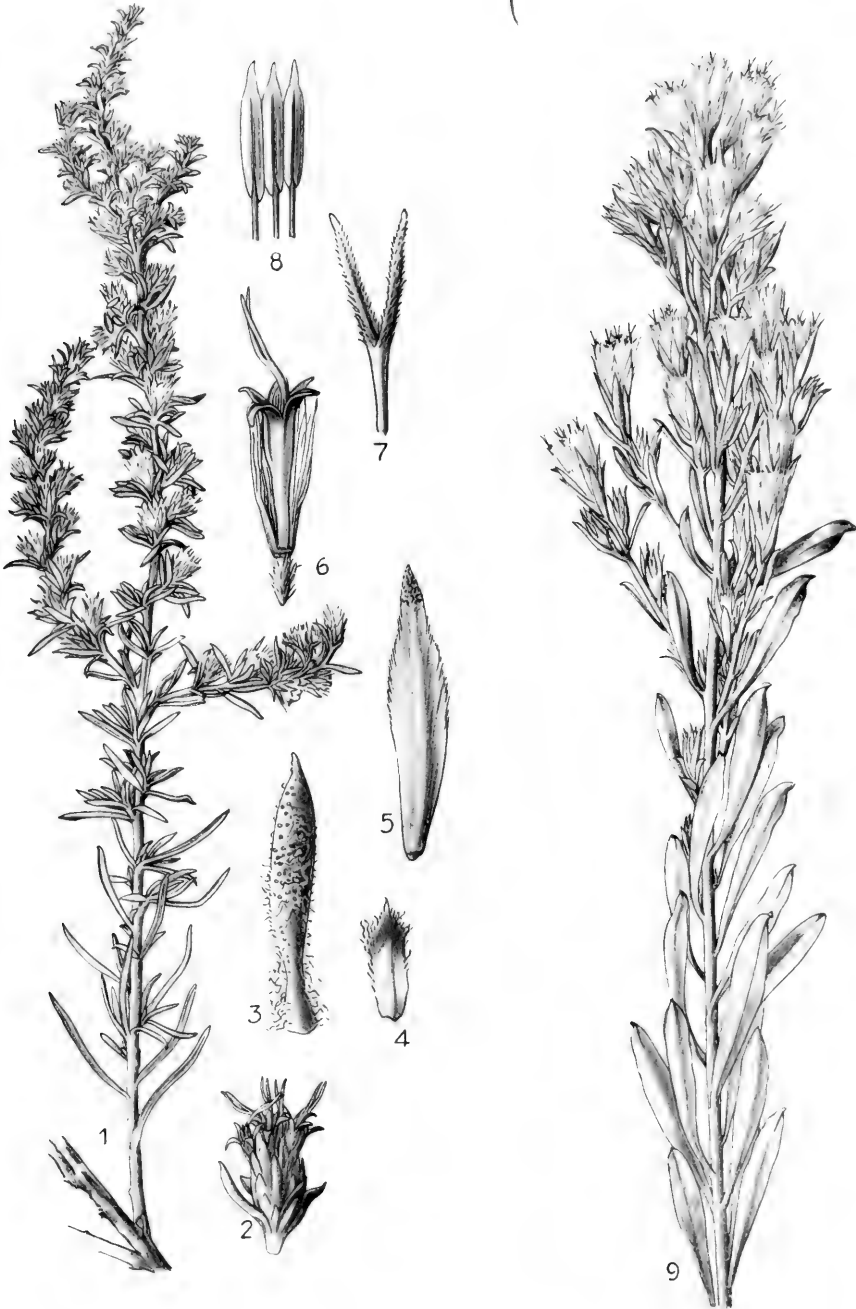
Chrysothamnus albidus, figs. 8 to 16.



Ruth J. Powell del.

Chrysothamnus pulchellus typicus, figs. 1 to 8.

Chrysothamnus depressus, figs. 9 to 14.



Ruth J. Powell del.

Chrysothamnus pyramidatus, figs. 1 to 8.

Chrysothamnus parryi latior, fig. 9.



Powell det.

Chrysothamnus parryi typicus, figs. 1 to 6.

Chrysothamnus parryi imulus, figs. 7 to 13.



Chrysothamnus parryi vulcanicus, figs. 1 and 2.
Chrysothamnus parryi nevadensis, fig. 3.

Chrysothamnus parryi asper, fig. 4.
Chrysothamnus parryi howardi, figs. 5 to 11.

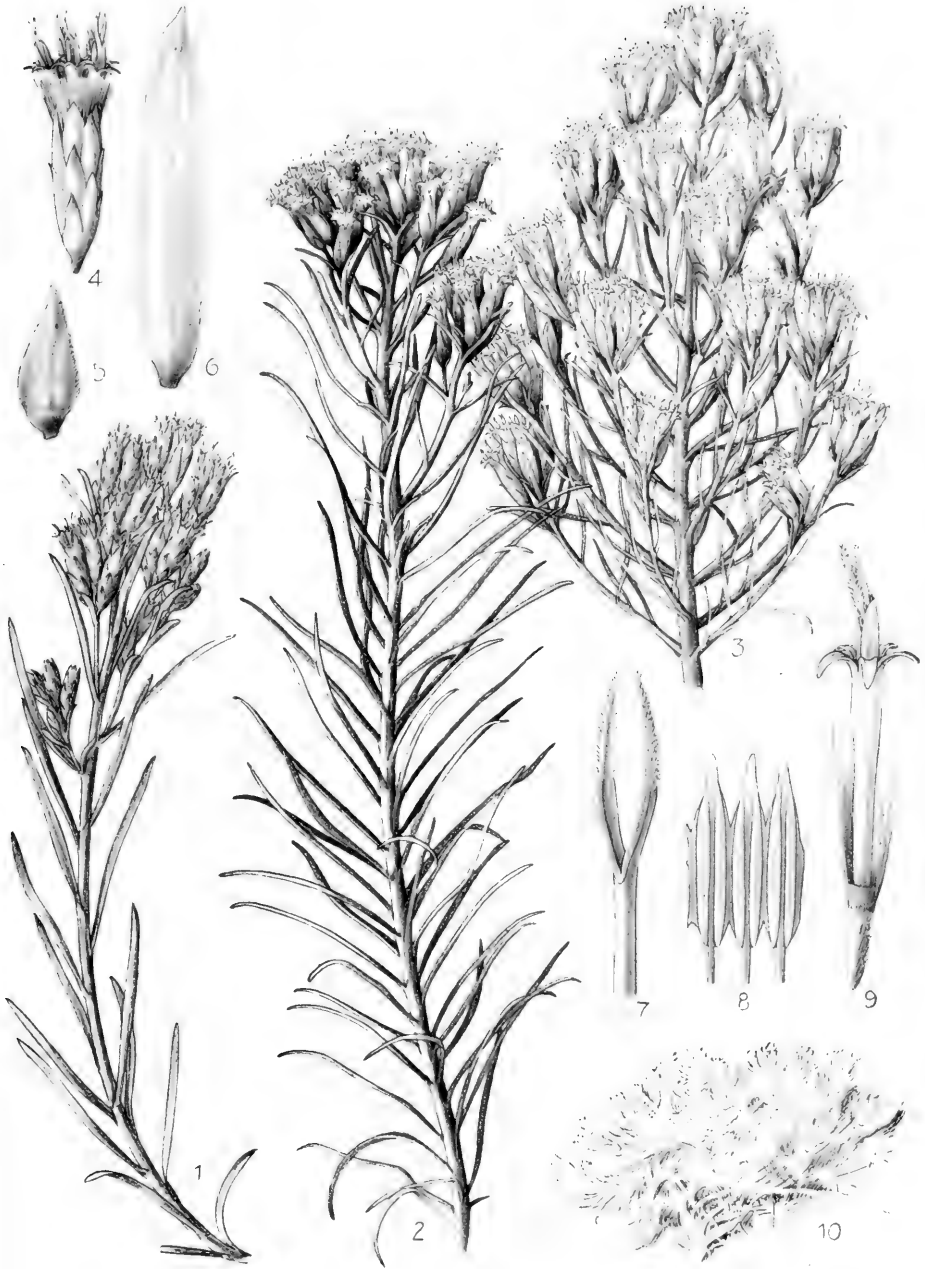
10. J. Powell, d.l.



J. Howell d.L.

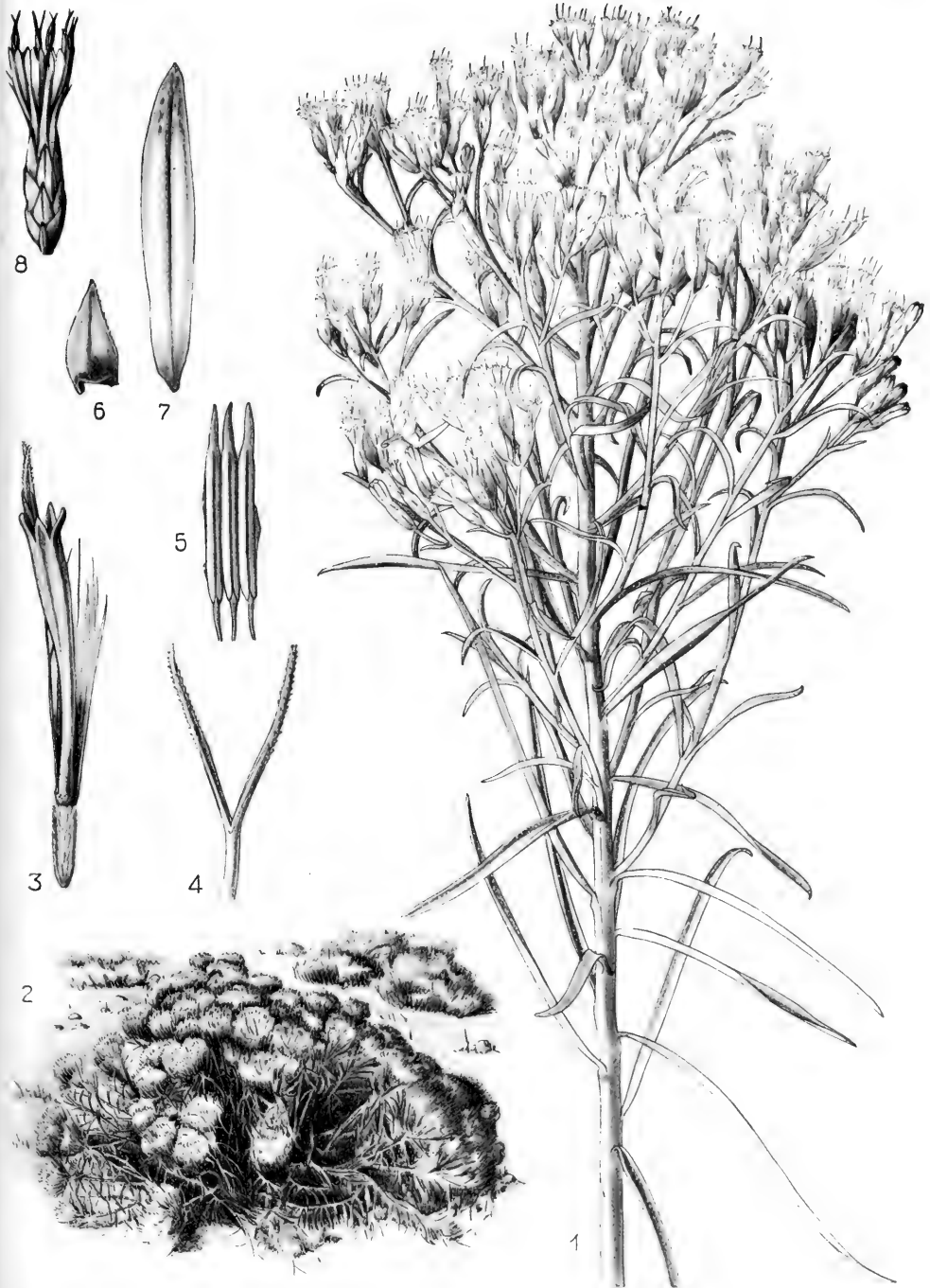
Chrysothamnus nauseosus speciosus, figs. 1 to 3.

Chrysothamnus nauseosus gnaphalodes, figs. 4 to 11.



Ruth J. Powell det.

Chrysothamnus nauseosus typicus.



Ruth J. Powell del.

Chrysothamnus naucosus graveolens.

GENUS ATRIPLEX

HISTORY AND GENERIC LIMITS.

Up to recent times the history of the genus *Atriplex* has been one of taxonomic segregation. According to many pre-Linnaean botanists, it included practically all of what is known as the family *Chenopodiaceae*, and apparently even a few species of *Polygonaceae* found their way into the genus. Linnaeus drew the generic lines much more closely, following in this respect a growing tendency among European taxonomists. Thus there came to be established by the middle of the eighteenth century such well-known genera as *Chenopodium*, *Beta*, *Spinachia*, *Blitum*, and *Salsola*.

After the time of Linnaeus there was no further division of the genus until 1791, when Gaertner described *Obione* (Gaertner, Fruct. 2:198), with a single species, *O. muricata* (= *Atriplex siberica* Linnaeus). This genus was accepted by Moquin-Tandon in his monograph of the *Chenopodiaceae* (*Chenopodearum monographica enumeratio* 1840), and to it have been referred a majority of the American species now included under *Atriplex*. The single constant character of *Obione* is the inverted embryo, the radicle of which thus comes to assume a superior position in relation to the plumule. The importance of this character of the embryo is fundamental. By reference to the chart of relationships (fig. 29, p. 238) it will be seen that it is used in the present treatment as indicating the phylogenetic separation of all of the American *Atriplexes* into two principal stocks, or subgenera. However, its acceptance as a generic criterion sunders groups of close affinity, with the result that the relationships between them are no longer expressed. Furthermore, there is no positive evidence that the result is a natural classification. For example, while it is probable that *A. rosea* and *A. argentea*, the former a true *Atriplex*, the latter an *Obione*, have been derived from widely separate stocks, yet they are so closely alike in many features that their distribution into distinct genera is likely to be misleading. It is possible that these are no more widely separated from each other phylogenetically than either of them is from *A. hortensis* or from *A. patula*. As far as the American species are concerned, this character serves for the primary division of the genus better than any other, and therefore it is used as a basis for the recognition of two subgenera. In one introduced species, namely, *A. semi-baccata*, the radicle lies to one side of the embryo. Such lateral radicles, which occur in a number of other foreign species as well, may be taken as representing an intermediate stage, the presence of which greatly weakens the status of *Obione* as a genus. It is retained by a few European botanists, e. g., Ascherson and Graebner (*Syn. Mitteleur. Fl.* 5:109, 1913), but it was not given generic standing by Bentham and Hooker (*Gen. Pl.* 3:54, 1880) nor by Volkens (in Engler and Prantl, *Natürl. Pflanzenfam.* 3^{ia}:64, 1893), nor by Moss and Willmott (in Moss, *Cambridge Brit. Fl.* 2:168, 1914). In America *Obione* was accepted as a genus by Torrey but not by Nuttall, Gray, nor any of the more recent writers. Watson treated it as a genus in his Report on the Botany of the King Exploration of the Fortieth Parallel (1871), but when he came to his revision of the North American *Chenopodiaceae* (*Proc. Am. Acad.* 9:82-126, 1874) he reduced *Obione* into *Atriplex*.

The next generic proposal was *Pterochiton* Torrey and Fremont (in Fremont, *Rep. Rocky Mts. Ore. Calif.* 318, 1845). This was based upon a form now referred to *A. canescens*. Its most distinguishing feature is the development of 4 pronounced wings to the fruiting bracts. Aside from the fact that bract characters are of doubtful value as a basis for genera, it is to be noted that in this case the wings are sometimes simulated by flattened appendages in other groups. Furthermore, certain specimens to be mentioned under *A. canescens* are either intermediate in this respect or are hybrids between some genuine

species of *Atriplex* and *A. canescens*. *Pterochiton* was recognized by Nuttall (Jour. Acad. Phila. II, 1:184, 1848), but otherwise it has been considered as not more than a section or subgenus of *Atriplex*.

Endolepis was proposed by Torrey (in Gray, Pacif. R. R. Rep. 12:47, 1860) on the basis of a peculiarly shaped perianth in the staminate flowers and the presence of a calyx in the pistillate flowers. But a calyx is sometimes present even in the type species of *Atriplex* (*A. hortensis*). It will be demonstrated under *A. phyllostegia* (p. 267) that this structure is vestigial and that in at least one species it may be found in all stages of suppression. Therefore, its presence or absence can not be used for the separation of genera. *Endolepis* was merged into *Atriplex* by Watson in his revision of the family above referred to. Recently it has been revived as a genus by Rydberg (Bull. Torr. Club 30:248, 1903) and by Standley (N. Am. Fl. 21:72, 1916), while Macbride (Contr. Gray Herb. n. s. 53:11, 1918) insists that it should not be given generic standing.

Additional segregate genera have been proposed by European botanists, but they include no American species.

None of the above-mentioned proposals are maintained in the present paper. Instead, they are all referred to the genus *Atriplex*, which, notwithstanding their inclusion, remains a natural and easily defined group. But in order to maintain this unity it is necessary to exclude one segregate formerly referred to *Atriplex*. This is the genus *Suckleya* Gray (Proc. Am. Acad. 11:103, 1876), based upon *Obione suckleyana* Torrey. This is a nearly prostrate annual herb with a habit unlike that of any true *Atriplex*. Its generic standing is maintained on its peculiar fruiting bracts, which are strongly obcompressed, i. e., flattened in a plane contrary to that of the original position of the faces. The resulting fruit is winged dorsally, but these wings are not homologous with the four prominent wings of *Pterochiton*. *Suckleya* has been accepted as a genus by Bentham and Hooker, by Volken, and by all of the more recent workers on the group.

The American species of *Atriplex* have received monographic treatment by but three authors. The first of these was Moquin-Tandon, who published his *Chenopodearum monographica enumeratio* in Paris in 1840. This was followed, in 1849, by a monograph by the same author in De Candolle's *Prodromus* (vol. 13, part 2, pp. 90 to 115) where 98 species of *Atriplex* and *Obione* are described, this number comprising all of the species of the world known at that time. As indicated above, the genera just mentioned now constitute the two subgenera of the genus *Atriplex*. The enormous amount of labor involved in bringing together the scattered facts regarding the genus at that early date, and the masterly way in which the species were organized and described, places all later workers under deep obligation to this early specialist.

No account covering the entire genus has appeared since the work of Moquin-Tandon. The North American species, however, were given a new treatment in 1874 by Watson in his *Revision of the North American Chenopodiaceae* (Proc. Am. Acad. 9:82-126, 1874). Here *Obione* is definitely reduced to *Atriplex*, which is then divided into three sections, the first comprising annuals with the radicle inferior or subsessing, the second annuals with the radicle usually superior, and the third perennials with the radicle usually superior. This treatment by Watson, which includes a key to the 40 accepted species, but in which only the new species are described, has served as a basis for all accounts given in regional, State, and local floras up to 1916. In this year there appeared an account of the North American *Chenopodiales* by Standley (N. Am. Fl. 21:1-93). Standley follows Watson in the reduction of *Obione* to *Atriplex*, but restores *Endolepis* as a distinct genus, to which 3 species are referred. His account of *Atriplex* includes 103 species grouped into 29 sections. The comparatively large number of species recognized is due in part to the adoption of a narrow species-concept; in part to the dependence, as it seems to the present authors, upon certain characters since

found to be too variable to serve as taxonomic criteria. Other revisions, covering portions of North America, will be found in the various floras. The most notable of the recent contributions of this nature will be found in Jepson's Flora of California (pp. 433 to 442, 1914) and in Rydberg's Flora of the Rocky Mountains and Adjacent Plains (pp. 245 to 250, 1917).

The present authors have greatly benefited from the monographs and revisions just enumerated. Especial attention, however, has been given to the assembling of previously unknown facts regarding the plants, more particularly through field studies and cultural experiments. The result is that the forms can now be more accurately described and their phylogeny worked out in a manner much more satisfactory than was previously possible.

ORIGIN AND DEVELOPMENT OF THE SECTIONS.

The American species of *Atriplex* can not be assembled into natural groups and the origin of these satisfactorily determined until those of other parts of the world have also been studied in some detail. Therefore, aside from the two subgenera almost universally accepted, no formal classification into sections will be here presented. The group names proposed by Standley (N. Am. Fl. 21:33-72, 1916) will be sometimes used for convenience, as will also other sectional and subgeneric names which have been proposed by European workers without much regard to American forms.

The primitive stock from which *Atriplex* has developed was almost certainly of a type in which the radicle pointed downward in the embryo and in which the essential organ of the pistillate flower was subtended by some sort of a perianth. The inferior position of the radicle is so common in the *Chenopodiales* that any modification from this indicates a divergent phylogenetic line. Similarly the absence of a perianth is looked upon as a case of suppression and therefore a mark of advance. With these postulates in mind it becomes impossible to select any one *Atriplex* as the common ancestor. The one most nearly meeting the requirements is *A. hortensis*, the taxonomic type of the genus. Therefore, this species is placed at the beginning of the subgenus *Euatriples*, i. e., the branch in which the radicle is always inferior and the perianth either present or absent in the pistillate flowers. In the only other subgenus, namely *Obione*, the embryo always is inverted, so that the radicle points upward (superior) and a much reduced perianth is found only in a few primitive species.

Of the American species of *Euatriples* only *hortensis*, itself introduced, exhibits a true perianth in the pistillate flowers. Even here a partial suppression has taken place, since only a portion of the flowers possess this structure. This species, together with a few minor derivatives, comprises the section *Dichospermum* Dumortier. Next to *hortensis*, but probably not a derivative from it, comes the section *Teulliopsis* Dumortier, which includes *A. patula* (section *Hastatae* Standley) with a long series of subspecies and minor variations widely distributed in both hemispheres. It has a perianth only in the staminate flowers and has developed features of the bracts which are quite distinctive. The absence of fusion between the bracts in some of the forms and the lack of complete fusion in any of them may be taken as indicating a low stage of development, while other considerations, especially the wide distribution and the abundance in a large variety of ecologic habitats, indicate this as a very successful type.

Atriplex californica is placed near to *patula* in the phylogenetic chart, but probably its connections are much more primitive. Its position is very doubtful as will be explained in discussing its relationships (p. 257). Also, *A. semibaccata* and *A. halimoides*, two species introduced from Australia and doubtless of a very different alliance, are given place in the taxonomic sequence as a matter of convenience. In the former the radicle is lateral, rather than inferior, suggesting a connection with the subgenus *Obione*.

The *rosea* group, consisting of three important species introduced from Europe, has had a development corresponding to that of *patula*. But here the fruiting bracts, instead of remaining soft have become more hardened and cartilaginous than in any other group. For this reason the name *Sclerocalymna* was proposed for the section by Ascherson. The similarity to other sections is expressed, on the other hand, by the taxonomically equivalent name of *Obionopsis* Lange. The shape as well as the degree of induration of the fruiting bracts is closely approximated in some forms of *A. argentea* and other members of *Obione*.

The most primitive American representatives of the subgenus *Obione* are *A. dioeca* and *A. monilifera*. They belong to the so-called genus *Endolepis* Torrey, which, however, is better received as a section of *Atriplex*. A much reduced but evident perianth is present in the pistillate flowers of these species, as also in those of the closely related *A. phyllostegia*. In this last, however, the perianth sometimes is completely suppressed, as it is in all of the succeeding species of *Atriplex*.

In order to arrange the remaining species in their proper phylogenetic sequence, it is necessary first to determine the evolutionary significance of the characters which differentiate them. Of these, the development of dioecism and of the shrubby habit seem to be the most important. There are no dioecious species in *Euatriples*. In *Obione* the tendency toward a complete separation of the sexes is noted at a number of places, especially in the species *phyllostegia* and *powelli*. Complete dioecism is attained, however, only in the truly shrubby species and two herbaceous ones, namely, *decumbens* and *matamorensis*. The nearly complete parallelism between these two characters is assumed to justify their use as criteria for the assembling of the large number of species into two natural groups—the group of monoecious herbs and the group of dioecious shrubs. The two notable exceptions just mentioned form an intermediate group marked also by its opposite leaves, an almost unique feature in the genus. The transition between the group of monoecious herbs to that of the dioecious shrubs is found in some members of the *pentandra* subgroup with woody basal portions and in “shrubby” species (*barclayana*, *acanthocarpa*, *corrugata*) which are sometimes herbaceous nearly to the base. Of these latter, *A. barclayana* is but imperfectly dioecious, since at least a few fruiting bracts may be found on many of the pistillate plants. The connection between the *pentandra* group and *barclayana* is suggested also by the turgid bracts in certain forms of each and by striking similarities in other features. The trait of monoecism persists also in *A. lentiformis*, a truly shrubby species, for, although the individuals of this are for the most part either chiefly staminate or chiefly pistillate, plants are not rare on which the sexes are about equally represented. Occasional monoecism is found also in other shrubby species.

The derivation of the dioecious shrubby *Atriplexes* from a stock close to the *pentandra* group, as just proposed, may appear to start them off too far along in the phylogenetic sequence. It should be noted, however, that while this gives them a high position on the chart of relationships (fig. 29, p. 238), it is possible that *pentandra* itself may be more primitive than might be assumed from its location. The evolutionary line, as charted in the diagram, does not pass through any group above *Endolepis*, so that the *pentandra* group may be considered, if so desired, as no higher in the scale than the others, each of which terminates a divergent line. *A. pentandra* may be even basal to these others, as its center of distribution in Mexico would seem to indicate, but the tendency to an obovate shape of the fruiting bracts, which is a reversal of the usual leaf and bract shape, and the separation of the sexes into different inflorescences, which presages the dioecism of the shrubby species, furnish evidence opposed to this view.

Atriplex pusilla and its immediate allies form a natural group within the larger assemblage of monoecious herbs of the subgenus *Obione*. All are annuals with fruiting bracts

widest below the middle. Next to these comes a group in which the original shape of the bracts is cuneate, as best illustrated in *A. truncata*. But in two of the species (*graciliflora*, *saccaria*) the shape is so modified through the development of wing-like margins or appendages that the clue to relationships is supplied only by an exceptional unmodified pair. Close to these species, but perhaps even closer to certain of the *Pusillae*, is the small group of *A. argentea* and *A. coronata*. The latter has fruiting bracts so variable in shape that it is often confused with *A. cordulata* of the *pusilla* group. *A. powelli* is placed by itself on the chart because of its semi-dioecious habit, as already noted, and a peculiar shape and lobing of the fruiting bracts. Probably it is not far removed from *A. argentea*, with which it has in common triple-nerved leaves and other vegetative features.

Passing over the groups of *pentandra* and *decumbens*, which have been already discussed, there remain only the dioecious shrubs. There is abundant evidence that these had their origin far to the south, probably in Mexico. Their migrations to the north and northwest, where they have come to occupy arid saline valleys and foothill slopes, were accompanied by considerable modifications in habit and structure. This has resulted in the development of 11 species and a much larger number of subspecies and minor variations. The most primitive of these, as indicated by their partly herbaceous habit and evident connection with Mexican forms of *A. pentandra*, are *A. barclayana* and the group beginning with *A. acanthocarpa*. The former occupies the area from western Sinaloa and Sonora across Lower California. Evidence as to its former connection with the monoecious herbs is found in its only partial dioecism, in the herbaceous branches, and in having certain subspecies with non-compressed bracts. *A. acanthocarpa* also is only a subshrub. Although it has evolved certain features of its own, probably it best represents the ancient stock which has culminated in the well-known and polymorphous *A. nuttalli*, a species which has reached to beyond the Canadian boundary in its northward migration.

The truly shrubby American *Atriplexes*, that is, those in which even the twigs are woody, now occupy extensive areas in the Great Basin Region and westward, a few of them reaching the saline shores of the Pacific in California. Beginning near *A. polycarpa*, which is most like *A. barclayana* in the character of its bracts, each has developed features so unique that a natural grouping into units larger than the species itself seems impossible. In *polycarpa* the fruiting bracts and seeds are much reduced in size; in *hymenelytra* and *lentiformis* the bracts are strongly compressed; in *confertifolia*, *spinifera*, and *parryi* there appears a spiny habit in addition to certain peculiarities in the bracts. The most divergent species is *A. canescens*, in which the fruiting body is provided with 4 wing-like outgrowths. The connections between these species will be further discussed under the heading of relationships as each is reached in the taxonomic treatment. Their differentiating characters are illustrated in figure 43 (p. 314).

CRITERIA FOR THE RECOGNITION OF SPECIES AND SUBSPECIES.

Seed.—The most nearly constant character used in the classification of the species of *Atriplex* is found in the seed. This has to do with the position of the seed within the pericarp. When the former is erect, the radicle points downwards, thus occupying an inferior or basal position in relation to the plumule, which either points upwards or is curved to one side. In a few species (*semibaccata*, *californica*, and others) the inferior radicle is turned to one side and takes up a lateral position beneath the tip of the plumule. But in most American species the seed is inverted, so that the radicle points upwards. Such radicles are said to be superior in relation to the plumule, although the latter also curves upwards and its tip is sometimes as high as that of the radicle. In many cases the superior radicle curves inward at tip and thus comes to occupy a position truly superior

to the plumule. These various positions are illustrated in the plates accompanying the descriptions of the species. The position of the radicle, whether inferior or superior, is utilized in the assembling of the species into two subgenera, *Euatriplex* and *Obione*, as already discussed.

In addition to the vertical seeds just described, there are also horizontal seeds in one species, namely *A. hortensis*. In this species the vertical seeds are borne naked between the bracts, whereas the horizontal seeds are produced only in those flowers in which a calyx is present. According to Eichler (*Bluthendiagr.* 2:84, 1875), only the flowers with horizontal seeds are a regular part of the inflorescence, the others occurring as adventitious shoots. Furthermore, a few introduced species (*patula*, *rosea*, etc.) produce two kinds of vertical seeds: (1), small black seeds with convex sides, the tip of the radicle scarcely produced; and (2), larger, brownish seeds with flat sides and a shallow groove near the margin, the radicle strongly produced. Only the latter are included in most descriptions. Details as to the different kinds of seeds have been discussed by Collins (*Seeds of Commercial Saltbrushes*, U. S. Dept. Agr. Div. Bot. Bull. 27, 1901).

Additional seed characters doubtless would be very useful in the classification of *Atriplex*, if consistently applied. The paucity of mature seeds in herbaria precludes the extensive use of size and color as criteria until further field studies and collections can be made. The samples preserved in seed laboratories are not very helpful in this connection, since they are but rarely accompanied by full specimens necessary to their accurate identification. It is believed that size of seed will prove to be a more reliable criterion than size of fruiting bracts, since the latter often depends largely upon the extent to which such purely vegetative structures as free margins and appendages are developed. The dimensions and color of the seeds as described in the present paper apply to these bodies only in their fully mature condition. Much confusion would result from measurements or colors determined from juvenile material.

Flowers.—The flowers of *Atriplex* are of two sorts, staminate and pistillate. Thus far the former have been scarcely utilized for taxonomic purposes, except as to their arrangement, as will be described under inflorescence. The depth to which the calyx is lobed or cleft is much greater in some species than in others, but there is also much variation within single species. The number of calyx-lobes is sometimes given in descriptions, but it is of doubtful value and never to be depended upon as a criterion unless checked by the examination of a large series of specimens. Field studies indicate that the staminate flowers may be either 4-merous or 5-merous in the following species: *patula*, *rosea*, *semibaccata*, *pusilla*, *parishi*, *truncata*, *argentea*, *coronata*, *powelli*, *leucophylla*, *elegans*, and *lentiformis*. The variation holds even within single subspecies of these, and in most of them it has been found on individual plants. On the other hand, only 5-merous flowers have been found on *bracteosa*, although a large series from different localities was examined. Similarly, *graciliflora* and *saccaria* yielded only 5-merous flowers, but only a limited number of plants were studied. Usually the number of stamens is the same as the number of calyx-lobes in the same flower. Cases of 5 stamens accompanied by a 4-merous calyx have been found in *truncata* and *leucophylla*. The number of stamens and lobes is sometimes reduced to 3 each in *elegans* and probably also in other species. Cases of a double calyx, that is, with 10 lobes, are not rare. The original number of calyx-lobes and stamens doubtless was 5, but it would be unsafe to assume that when this number is found the species in hand is primitive. This would lead to the placing of species like *bracteosa* at the bottom of the phylogenetic tree, while by all other criteria they are classed as among the most highly specialized forms.

Reference has thus far been made only to staminate flowers. The pistillate flower is so simple as to yield but little of value in addition to the pistil itself, which has been described under the heading of seeds. Obviously the perianth is a mark of primitiveness

when it occurs in pistillate flowers. It has been found only in *hortensis*, *dioeca*, *monilifera*, and *phyllostegia*, all of which exhibit other features of a primitive nature. In *phyllostegia* the perianth may be either present or absent, even in flowers of the same plant, and various degrees of suppression have been noted (see table 25, p. 269).

Fruiting bracts.—These structures have been almost universally considered as modified upper leaves. Evidence for this belief was given by Moquin-Tandon (Chenop. Enum. 1840), and recently the case has been stated by Collins (U. S. Dept. Agr. Div. Bot. Bull. 27:10, 1901). After reviewing the Australian species, Bentham (Fl. Austral. 5:166, 1870) came to the conclusion that the so-called bracts were homologous with the male perianth. The regular occurrence of an undoubted perianth between the bracts and the pistil in several of the species (*hortensis*, *dioeca*, *phyllostegia*, the first the type of the genus) clearly demonstrates that the structures under consideration are true bracts and not a part of the flower proper. This view was later adopted by Bentham (in Bentham and Hooker, Gen. Pl. 3:53, 1880).

More reliance has been placed upon the bract characters by nearly all writers on the genus than upon any other set of criteria, and very much more than their value warrants. The bracts vary to so great an extent that the extremes seem to present ideal criteria for the recognition of species. But over and over again these extremes are found on individual plants, not in such a manner as to indicate hybridization, but rather as a mark of variation between the individual bracts. Thus, smooth to strongly tuberculate or long-appendaged bracts very frequently are found on single plants of some species, as also are both sessile and long-stalked ones. Examples of this are shown in some of the illustrations (plates 41, 43, 44). Many more are mentioned in the descriptions of the species and subspecies and under the minor variations. It is, of course, possible that such qualities as those just mentioned are heritable and that the mingling of different types of bract on the same plant is merely the outcome of a heterozygous condition. If this is the case, then the utilization of such features for purposes of classification is futile, unless all of the forms are first subjected to a close genetical analysis, and at present this would serve no useful purpose. The grouping of these minor variations into closely defined subspecies and species will provide a classification adequate to all ordinary needs. An alternate explanation of these variations is that they are ecologic and perhaps correlated with the food-supply. This probably is the case when variation occurs in the same small cluster or between the bracts of a single pair, as often happens. In *Atriplex parishi* it has been noted that in some plants the upper bract of each pair, that is the one facing the stem, is always muricate, whereas the bract facing downward toward the subtending leaf is always smooth. The significance of this is not known.

Although the sculpturing of the bracts and the length of their stalks are characters of but little value, much use can be made of certain other features connected with these structures. Often the size is so different in even closely related species that this may be safely employed as a criterion. Only fully mature bracts should be measured for this purpose. The size character would be more definite if the dimensions of the body, exclusive of appendages, wings, or free margins could be determined, but this seems impracticable. It is therefore sometimes necessary to make allowance for unusual surface outgrowths. An extreme case of variation in the size of bracts is illustrated in figure 31 (p. 252). The shape is also helpful. It is assumed that the bracts in primitive forms were broadest below the middle, as in ordinary foliage leaves, and that bracts broadest near or above the middle are indicative of derived groups. United bracts are more highly specialized than distinct ones, since these structures are modifications of distinct leaves of the inflorescence. The extent of fusion is helpful in working out phylogenies, but it is difficult to express in the form of a proportion, since the thin margins, often unequally toothed, should first be eliminated. Bracts of ordinary leaf-like texture

precede both exceptionally hardened and unusually fleshy ones. The definitely winged bracts in *A. canescens* are the result of a development quite different from that represented by irregular appendages and indicate a divergent phylogenetic branch, as will be further noted when this species is reached in the taxonomic sequence.

Inflorescence.—All stages in the development of complete dioecism are present in *Atriplex*, beginning with the condition in which the sexes are mixed in small axillary clusters. As the two kinds of flowers began to separate, the staminate came to occupy the upper axils, the pistillate the lower ones. The staminate inflorescence is sometimes very long and branched (*bracteosa*, *wrightii*, etc.), sometimes much reduced and yet nearly or quite pure (*fruticulosa*, *leucophylla*, and some forms of *pentandra*). Partial dioecism has been attained at several places in the evolution of the species (*phyllostegia*, *powelli*), but it becomes complete only in two herbaceous species (*decumbens*, *matamorensis*) and in the shrubs. In the latter group, incomplete dioecism is not rare in several of the less highly evolved forms (*barclayana*, *nuttalli*, *lentiformis*).

The size of the staminate inflorescence and its degree of branching are useful as specific and subspecific criteria in only a few cases. At other times there is considerable variation even within a single subspecies (*A. pentandra typica* and *A. p. muricata*) and hybrids are suspected between species with long inflorescences and others with short ones (*A. davidsoni*, p. 306).

Leaves.—As in most large genera, the leaves are of much value in that they furnish corroborative evidence useful in the identification of species, but not to be relied upon in making the major groupings. They are usually alternate, but in a few species (*decumbens*, *matamorensis*) they are mostly opposite. In *A. parishii* the position varies independently of other characters. It has been determined by field observation and verified by garden experiment that the lower leaves in most and probably all of the species of the *argentea* and *pusilla* group are always opposite. Therefore the separation of species in these groups on the basis of their "alternate" lower leaves, as has been sometimes done, is not warranted. Such errors doubtless are the result of the incomplete nature of many herbarium specimens, but it is not safe to assume that all of the leaves on a plant were alternate merely because the remaining ones happen to be so. In some species the leaves are closely sessile, in others decidedly petioled. The chief difficulty in using this feature lies in the frequent interposition of intermediate species or minor forms in which the leaves are narrowed below to a petiole-like base. A strong tendency is noted in some of the more primitive herbaceous species to the formation of hastate and cordate bases to the leaves, and this recurs in a few of the shrubby species. All gradations from a strongly narrowed to a broadly hastate base are found in *A. patula* and nearly all stages are represented also in *A. phyllostegia* and *A. truncata*. The amount of dentation or lobing, the size, the shape, and the texture are useful in some cases for purposes of classification.

Pubescence.—All of the North American *Atriplexes* are glabrous, except for a more or less dense scurf consisting of modified trichomes. When the scurf is sparse or early deciduous, the herbage is greenish in color. This condition is pronounced only in the subgenus *Euatriples* (especially *A. hortensis* and *A. patula*), in the more primitive species of subgenus *Obione* (notably *A. dioeca* and *A. phyllostegia*) and in *A. bracteosa*. The remaining species are densely scurfy, at least on the lower surface of the leaves, and the herbage is therefore gray or whitish in appearance. This difference in color is an aid in distinguishing on sight between some species otherwise much alike in all but minute technical characters. However, it must be used with due regard to the presence of at least a sparse scurfiness on the juvenile herbage of all forms.

Habit.—With the exception of the anomalous *A. californica* and the two introduced Australian species, all of the subgenus *Euatriples* and all of *Obione* up to the *pentandra* group, as diagrammed in the chart of relationships (p. 238), consists of herbaceous annuals.

The transition between the annual and the perennial habit is found in the *pentandra* group, where the change takes place within several of the subspecies. The character is here useful as adding to the characters which separate the annuals, *A. bracteosa* and *A. wrightii*, from the similar but strictly perennial *A. linifolia*; also as an additional criterion for separating the annual *A. microcarpa* from the perennial *A. coulteri*. The two dioecious herbs following this group are perennials with a somewhat woody base. From here on to the end of the genus all of the species are classed as shrubs, although some of the earlier ones are only subshrubs with herbaceous branches. The distinction between herbs and shrubs is here more useful than in many other genera, because this character runs approximately parallel with the dioecious habit.

Other features of the habit, such as the method of branching, direction assumed by the stems and twigs, size of plant, and degree of leafiness are of some assistance in distinguishing the species and smaller units, but fail as criteria when groups of species are involved.

GENERIC DIAGNOSIS.

ATRIPLEX Linnaeus, Sp. Pl. 1052, 1753.

Annual and perennial herbs and shrubs, more or less pubescent with inflated scurf-like hairs. Leaves alternate, or the lower opposite, rarely all opposite, sessile or petioled, entire to dentate or irregularly and deeply lobed. Flowers monoecious or dioecious, solitary or in glomerules, the single or clustered flowers in the leaf-axils and often also in terminal spikes or panicles, the staminate and pistillate flowers often mixing in the same cluster, but the staminate usually confined to the upper axils or to terminal inflorescences. Staminate flowers without bracts or bracteoles; perianth 3- to 5-parted, the segments obovate or oblong and obtuse; stamens 3 to 5, inserted on the base of the perianth, the filaments either united at the base or distinct, the anthers 2-celled; rudiment of the ovary conical or wanting. Pistillate flowers each subtended by 2 bracts; bracts accrescent, distinct or usually united at least at the base and inclosing the fruit, entire or the margins variously dentate, sometimes fleshy-thickened or spongious; perianth none or rarely present and then consisting of a 3- to 5-lobed membranous calyx or of 1 to 5 squamellae; disk and rudimentary stamens wanting; ovary ovoid or depressed-globose; stigmas 2, nearly filiform, or slightly thickened or compressed near the base, where also shortly connate; ovule oblique or erect and with a short funicle, or inverted and suspended from the end of an elongated funicle. Utricle inclosed between the bracts, the pericarp membranaceous and usually free from the seed. Seed erect or inverted, rarely horizontal, the coats membranaceous, coriaceous or almost crustaceous; embryo annular, surrounding the farinaceous albumen, the radicle inferior, lateral, or superior.

Artificial Key to the Species of *Atriplex*.¹

Plant an herb, sometimes slightly woody at base, but not shrubby.

Foliage green or greenish on both surfaces, sparsely mealy and therefore sometimes grayish when young.

Bracts orbicular or rounded-ovate, 10 mm. or more broad.

Staminate flowers mixed with the pistillate; leaf-blades 4 to 12 cm. long. 1. *A. hortensis* (p. 247).

Staminate flowers in terminal panicles, the pistillate in the leaf-axils; leaf-blades 1 to 2 cm. long. 19. *A. graciliflora* (p. 279).

Bracts not orbicular, less than 5 mm. broad.

Fruiting bracts united only near the base; staminate flowers mixed with the pistillate or in very short spikes.

Bracts hastate to rounded or cuneate at base; radicle pointing downwards. 2. *A. patula* (p. 248).

Bracts mostly with rounded ear-like lobes near the base; radicle pointing upwards. (Interior species.) 11. *A. phyllostegia* (p. 266).

Fruiting bracts united to above the middle; staminate flowers mostly in glomerules of elongated terminal spikes or panicles.

Leaves strictly entire; calyx-lobes crested on the back. Rocky Mountains to Nebraska and northward. 9. *A. dioeca* (p. 264).

Leaves mostly sharp-toothed; calyx-lobes smooth. Nevada and California. 29. *A. bracteosa* (p. 305).

¹ A natural grouping of the species is given in a series of phylogenetic charts to be found on pages 238, 270, 278, 293, and 314.

Artificial Key to the Species of Atriplex—Continued.

- Foliage gray or whitish, with a fine scurf, at least on the lower surface.**
- Introduced perennials; bracts thickened, either fleshy and turning red or spongy.**
- Bracts fleshy, strongly nerved, ovate 7. *A. semibaccata* (p. 262).
- Bracts spongy, dry, fibrous, turbinate or apparently globoid 8. *A. halimoides* (p. 263).
- Native annuals and perennials; bracts neither fleshy-thickened nor spongy.**
- Fruiting bracts broadest below the middle.**
- Staminate glomerules in long naked terminal spikes.**
- Leaves alternate.
- Staminate and pistillate flowers on separate plants; plant woody at base 38. *A. nuttalli* (p. 322).
- Staminate and pistillate flowers on the same plant; plant an herbaceous annual 10. *A. monilifera* (p. 265).
- Leaves mostly opposite. A Pacific Coast perennial with staminate and pistillate flowers on separate plants 33. *A. decumbens* (p. 311).
- Staminate glomerules in the upper leaf-axils or in spikes 1 cm. or less long.**
- Leaves coarsely toothed; bracts becoming hard and indurated (see also *A. tatarica* and *A. maritima*) 5. *A. rosea* (p. 259).
- Leaves entire; bracts not becoming hard.
- Plant prostrate; root perennial, fusiform; bracts distinct to the base 3. *A. californica* (p. 257).
- Plant erect or spreading; root annual, slender; bracts united to the middle or above.
- Stem simple or with a few virgate branches, the plant usually 2 to 10 dm. high; fruiting bracts 2.5 to 5 mm. long.
- Leaves cordate at base; bracts 4 to 5 mm. long 12. *A. cordulata* (p. 269).
- Leaves rounded at base; bracts 2.5 to 3.5 mm. long 13. *A. tularensis* (p. 271).
- Stem intricately branched throughout, the whole plant rounded, often depressed, usually 0.5 to 3 dm. high; fruiting bracts 1 to 3.5 mm. long.
- Fruiting bracts 1 to 1.5 mm. long, very smooth, pungently acute 14. *A. pusilla* (p. 272).
- Fruiting bracts 2 to 3.5 mm. long, at least some of them tuberculate or appendaged, obtuse to merely acute at apex.
- Branches ascending, slender, not especially brittle; fruiting bracts 2 to 3 mm. long. Rocky Mountains 15. *A. tenuissima* (p. 273).
- Branches widely spreading, often horizontal and the lower ones decumbent, brittle, breaking into joints when dry; fruiting bracts 2.5 to 3.5 mm. long. California 16. *A. parishi* (p. 274).
- Fruiting bracts broadest at or above the middle.**
- Leaves cordate at base or the bracts cuneate in shape and truncate at summit. (All strictly annuals. *A. corrugata* and *A. nuttalli*, both dioecious subshrubs, might be sought here.)
- Base of leaf not cordate.
- Leaves deltoid to elliptic, 0.8 to 2 cm. wide; bracts 2 to 3 mm. long 17. *A. truncata* (p. 276).
- Leaves linear, 0.2 cm. or less wide; bracts 1.5 to 2 mm. long 18. *A. wolfi* (p. 279).
- Base of leaf cordate.
- Bracts orbicular to oblong, with broad flat margins 19. *A. graciliflora* (p. 279).
- Bracts globoid or cuneate, not margined but mostly long-appendaged 20. *A. saccaria* (p. 280).
- Leaves not cordate at base and the bracts not cuneate and with truncate summit.
- Bracts becoming hard and almost bone-like; radicle pointing downwards or to one side in the embryo. Introduced weeds.
- Terminal staminate inflorescences 1 cm. or less long; leaves sinuate or repand-dentate, usually gray on both surfaces.
- Plant spreading or prostrate; bracts 6 to 9 mm. long 4. *A. maritima* (p. 258).
- Plant erect; bracts 4 to 6 or rarely 8 mm. long 5. *A. rosea* (p. 259).
- Terminal staminate inflorescences 3 to 15 cm. long; leaves deeply lobed or subpinnatifid, greenish above 6. *A. tatarica* (p. 261).
- Bracts not becoming especially hard; radicle pointing upwards in the embryo. Native species.
- Staminate and pistillate flowers mostly mixing in the clusters.
- Bracts irregularly toothed at summit, without wing-like crown.
- Leaves ovate to deltoid, broad and often subhastate at base, mostly 1 to 4 cm. wide; bracts 4 to 8 mm. long 21. *A. argentea* (p. 282).
- Leaves narrowly ovate to mostly elliptic, narrowed at the base, 0.3 to 1 cm. wide; bracts 3 to 4 or rarely 5 mm. long 22. *A. coronata* (p. 288).
- Bracts crowned with a broad smooth wing-like appendage 23. *A. powelli* (p. 290).
- Bracts flat, exactly orbicular, evenly toothed all around 26. *A. elegans* (p. 300).
- Staminate and pistillate flowers mostly in separate clusters, the staminate terminal or on separate plants.
- Leaves strongly 3-nerved from the base, ovate; bracts crowned by a horizontal wing-like lobe 23. *A. powelli* (p. 290).
- Leaves 1-nerved or the nerve obscure.
- Pistillate and staminate flowers on the same plant; leaves chiefly alternate.
- Bracts not compressed, elliptic-globose, 5 to 7 mm. long; seed 2.5 to 3 mm. long. Perennial of the Californian coast 24. *A. leucophylla* (p. 292).

Artificial Key to the Species of *Atriplex*—Continued.

- Bracts more or less compressed except when under 4 mm. long; seed 1.5 mm. or less long.
- Fruiting bracts exactly orbicular, toothed all around. Desert annual. 26. *A. elegans* (p. 300).
- Fruiting bracts cuneate-orbicular to obovate, entire near the base.
- Inflorescence of staminate glomerules 5 to 30 cm. long.
- Plant annual; leaves mostly dentate.
- Leaves broadest above the middle, lower surface white. 28. *A. wrighti* (p. 304).
- Leaves broadest below the middle, lower surface greenish. 29. *A. bracteosa* (p. 305).
- Plant perennial; leaves all entire. 30. *A. linifolia* (p. 308).
- Inflorescence of staminate glomerules 3 cm. or less long, or flowers all axillary.
- Length of fruiting bracts 1 to 2 mm. Pacific Coast annual with entire leaves. 27. *A. microcarpa* (p. 303).
- Length of fruiting bracts 2.5 mm. or more.
- Fruiting bracts globoid, not compressed. Californian perennial. 31. *A. fruticulosa* (p. 309).
- Fruiting bracts obovate, compressed but sometimes thickened by numerous appendages. Forms of the Californian *A. bracteosa* with reduced staminate inflorescences might be sought here, but distinguished by its evil odor and from No. 32 by the dentate leaves.
- Branches erect or spreading but always with erect or ascending ends, thickish, from an annual or herbaceous-perennial base; leaves entire or toothed, commonly larger than in the next, often obtuse. Mexico and Texas to the West Indies and New England. 25. *A. pentandra* (p. 294).
- Branches mostly prostrate at least at first, slender, from a short woody perennial base; leaves all entire, 1 to 2 cm. long, 0.2 to 0.4 cm. wide, acute. Californian coast. 32. *A. coulteri* (p. 310).
- Pistillate and staminate flowers on separate plants; leaves chiefly opposite.
- (Here might be sought also *nuttalli*, *corrugata*, *obovata*, and *acanthocarpa*, all dioecious subshrubs with alternate leaves. See under next heading.)
34. *A. matamorensis* (p. 312).
- Plant a shrub or subshrub.
- Bracts never with 4 conspicuous longitudinal wings. (Irregular flattened appendages are not to be mistaken for wings.)
- Plant not spiny.
- Mature bracts 4 to 8 mm. or more long, either narrower or broader than long.
- Margin of leaf entire or only undulate.
- Leaves narrowed at base, 0.5 to 3.5 cm. long, or longer.
- Tall shrubs, 10 to 30 dm. high; bracts orbicular. 43. *A. lentiformis* (p. 334).
- Low shrubs, 1 to 10 dm. high; bracts never exactly orbicular.
- Bracts longer than broad.
- Bracts lanceolate to elliptic or cuneate-oblong, entire or toothed at summit. 38. *A. nuttalli* (p. 322).
- Bracts narrowly fan-shaped, ending above in a broad free transverse lobe. 39. *A. corrugata* (p. 330).
37. *A. obovata* (p. 321).
- Bracts broader than long.
- Leaves sagittate-clasping, 0.2 to 0.4 cm. long. 41. *A. julacea* (p. 333).
- Margin of leaf dentate.
- Bracts globoid, not compressed. 36. *A. acanthocarpa* (p. 320).
- Bracts orbicular, strongly compressed. 42. *A. hymenelytra* (p. 333).
- Mature bracts 2 to 4 mm. long, about as broad as long or broader.
- Leaves medium-sized or large, 0.5 to 5 cm. wide, 1 to 5 cm. long.
- Stems herbaceous above; bracts not truly orbicular. Mexican. 35. *A. barclayana* (p. 313).
- Stems woody throughout; bracts orbicular. 43. *A. lentiformis* (p. 334).
- Leaves small, 0.2 to 0.4 cm. wide, 0.3 to 1.5 cm. long (longer only on sterile shoots). 40. *A. polycarpa* (p. 331).
- Plant spiny, the spines consisting of slender rigid sharp-pointed twigs from which the leaves or fruiting bracts have fallen.
- Bracts orbicular, or broader than long in one form with wing-angled twigs. . . . 43. *A. lentiformis* (p. 334).
- Bracts not orbicular; the twigs terete or obtusely angled.
- Leaves not cordate at base; bracts 6 to 15 mm. long.
- Body of bract small, not contracted beneath the free terminal wings; leaves strictly entire. 44. *A. confertifolia* (p. 338).
- Body of bract large, thick, contracted to a neck beneath the free terminal wings; some of the leaves subhastate at base. 45. *A. spinifera* (p. 340).
46. *A. parryi* (p. 341).
- Leaves cordate at base; bracts 3 to 4 mm. long. 47. *A. canescens* (p. 342).
- Bracts with 4 conspicuous longitudinal wings extending the whole length of the body and often beyond.

1. ATRIPLEX HORTENSIS Linnaeus, Sp. Pl. 1053, 1753. Plate 36. GARDENSCALE;
GARDEN ORACHE.

Mostly erect but often half-decumbent coarse annual herb, 5 to 20 dm. high, widely branched from the base, the upper twigs ascending; branches slender or stout, strongly angled, lightly furfuraceous when young but soon glabrous and green, the old bark white; leaves alternate except the lower, petioled, ovate varying to somewhat triangular and to lance-oblong, truncate, cordate or subhastate at base, or the upper slightly rounded to the petiole, obtuse at apex, 4 to 12 or rarely 20 cm. long, 3.5 to 9 cm. wide, the margins entire to sinuate-dentate, rather thin, farinose when young, bright-green and usually glabrous in age (all densely whitish furfuraceous beneath in minor variation 5, *A. sagittata* Borkhausen); flowers monoecious, spicate along the branches of an elongated terminal panicle, the staminate and pistillate flowers somewhat mixed in the inflorescence but the former often also in pure terminal spikes; perianth 3- to 5-lobed, wanting in most of the pistillate flowers (the fruit then vertical, but horizontal when the perianth is present); fruiting bracts short-pedicellate, strongly compressed, united only at the base, nearly orbicular or rounded-ovate, always slightly narrowed above, becoming chartaceous, 8 to 18 mm. long, nearly as wide, the broad, thin margins entire or obscurely denticulate, the faces smooth but strongly reticulate-veiny; seed 2 to 4 mm. long and brown, or only 1.5 mm. long and black when horizontal; radicle inferior.

Apparently of garden origin, but perhaps native in central Asia (see further under Relationships), introduced in many widely separated parts of the United States and Cuba. Type locality, Siberia. Collections: South Boston, Massachusetts, 1878, *Faxon* (Gr); ballast grounds, Gowans, Long Island, New York, September 17, 1879, *Brown* (NY, form is *A. sagittata* Borkhausen); Jersey City, New Jersey, 1878, *Brown* (NY, same form); Santiago de las Vegas, Cuba, *van Hermann 789* (NY); Naperville, Illinois, August 3, 1895, *Umbach* (US); Benson County, North Dakota, August 4, 1890, *Lunnell* (US); Bozeman, Montana, September 5, 1901, *W. W. Jones* (Gr, UC, US); Boulder, Colorado, *Osterhout 2421* (NY); Ephraim, Utah, *Tidestrom 548* (US); Salmon, eastern Idaho, *Hall 11554* (UC); Ontario, southeastern Oregon, *Griffiths 913* (NY, US).

MINOR VARIATIONS AND SYNONYMS.

A considerable number of forms have been described in Europe and Asia, mostly as varieties. Only the following seem to apply to American plants. The color, used to distinguish some of these, appears to be a fluctuating character as far as American plants are concerned, but in Europe some color forms apparently are fixed (according to Miller, Gard. Diet., ed. 8, 1768, as quoted by Moss, Cambr. Brit. Fl. 2:169, 1914). Perhaps these permanent races have not been introduced into this country.

1. *A. HORTENSIS* MICROSPERMA Moquin, Chenop. Enum. 52, 1840, consists of plants with small fruits, the bracts and leaves green.

2. *A. HORTENSIS* OBTUSIFOLIA Moquin, in DeCandolle, Prodr. 13:91, 1849, is the common green form, with very obtuse leaves and large bracts.

3. *A. HORTENSIS* RUBRA Linnaeus, Sp. Pl. 1053, 1753, has leaves and bracts becoming reddish. Specimens from Golden, Colorado, and especially the collection from Idaho cited above, have reddish bracts, and other American collections exhibit tendencies in this direction.

4. *A. NITENS* Schkuhr, Handb. 3:541, 1803.—This is the name usually applied to the earlier *A. sagittata* Borkhausen (No. 5 of this list). The taxonomic equivalence is indicated by Schkuhr's citation of *sagittata* as a synonym. Schkuhr also cites an *A. viridis* Ehrhart, but this doubtless refers to Ehrhart's erroneous identification of the plant with *A. viridis* Crantz, that is, *Chenopodium album* Linnaeus.

5. *A. SAGITTATA* Borkhausen, Rhein. Mag. 477, 1793.—The oldest name for the form which commonly passes in Europe as *A. nitens*. It has been sparingly introduced into America, as indicated among the above citations. The characters differ from those of *hortensis* only in the more shining upper surface of the leaves and a rather persistent furfuraceous coating on the under surface. Borkhausen described the leaves as shining green above and bluish-green beneath. He also indicated some leaf and habit characters which are now well known to be much too variable for use. The size of the seed has been used by others to distinguish between *hortensis* and *sagittata*, the seed of the former being given as about 2 mm. long, and of the latter as 3 to 3.5 mm., but seeds of undoubted *hortensis* from France are as much as 4 mm. long (borders of fields in the Maures, September 23, 1859, *Huet*, Gr. Hb.). If retained as a subspecies or variety, the name *nitens* is suggested as the more distinctive and at the same time more in accordance with usage when this variant is treated as a species.

RELATIONSHIPS.

The principal characters of this species indicate that it is close to the primitive type of *Atriplex*. The retention of the perianth in about 25 per cent of the pistillate flowers, the inferior radicle, and the herbaceous and monoecious habit all indicate an absence of specialized development, which, however, is noted in some minor details. It has no close relatives in America, where it is known only as an introduced plant. It has been suggested by Beck (Icon. 24:128, 1908) that it has originated in cultivation, and Moss (Cambr. Brit. Fl. 2:170, 1914) admits this as a possibility. However, these authors refer to the species exclusive of *A. nitens* (see 4 and 5 of the minor variations), and when so restricted *A. hortensis* is not positively known anywhere as a native plant. It seems quite probable that *A. nitens*, which is a native of Central Asia and especially of Tibet, is the original form and that the common *hortensis* has been derived as a consequence of the suppression of scurf on the under surface of the leaves. If this assumption is correct, the ancestral home of the genus probably was in central Asia. Furthermore, the true or phylogenetic type of the species is *A. nitens*, while the nomenclatorial type remains as the earlier *A. hortensis*. Throughout this discussion the well-established name of *nitens* has been used for a form which should be designated as *A. sagittata* if the rules of nomenclature are strictly followed (see Nos. 4 and 5 of the minor variations).

ECOLOGY AND USES.

Atriplex hortensis is an annual herb, which has escaped from gardens to become a weed in waste places, and especially along ditches and in depressions. As a temporary weed of infrequent occurrence it plays little part in vegetation, and its ecological behavior is negligible. The plants bloom from spring to late summer, and the showy colored fruits persist through the autumn.

Orache, as this species is commonly known, is much grown in Europe and also to a limited extent in America as a food plant. It is often called French spinach, this name indicating the use to which it is put. There are numerous garden varieties, differing from one another in habit, taste, and especially in color. Some have dark-red herbage and fruiting bracts, but the color disappears on cooking. A variety with white stems and pale foliage is said to be the one most commonly grown. A crimson-leaved variety (*atro-sanguinea* of the gardeners) is a favorite for ornamental purposes. These various color forms come true to seed in garden cultures. One authority states, after 40 years of observation, that he has never seen them to vary (Miller, Gard. Dict., ed. 8, 1768). Although the gardenscale frequently escapes in America and then becomes a weed, it will never cause much trouble. It grows only in moist, waste places and soon disappears when cultivation is practiced.

2. ATRIPLEX PATULA Linnaeus, Sp. Pl. 1053, 1753. Plate 37. SPEARSCALE;
SPEAR ORACHE.

Erect, decumbent, or prostrate annual herb, varying greatly in habit and size, usually 2 to 10 dm. high, but sometimes reduced to less than 1 dm. in simple-stemmed plants, sometimes up to 15 dm. when growing in thickets, simple to widely branched; branches slender or stout, rather rigid, smooth in small and young plants, but commonly grooved or with numerous vertical ribs, these white or pale, the intervals green; leaves perhaps always opposite below, usually alternate above, but sometimes all opposite, petioled or sometimes sessile, typically subdeltoid-lanceolate or ovate, but varying from broadly triangular-hastate to linear, attenuate to cordate or hastate at base, acute or obtuse at apex, exceedingly variable as to size, the margins entire or coarsely dentate, somewhat fleshy, sparsely or densely furfuraceous when young, usually glabrate and green at maturity; flowers monoecious, in glomerules the lower of which are sometimes in the leaf-axils, the upper glomerules commonly in simple or compound spikes, the staminate

and pistillate usually in the same small clusters; perianth 4- or 5-cleft, wanting in all of the pistillate flowers; fruiting bracts sessile or stalked, not much compressed, sometimes thickened and spongy (especially in subspecies *alaskensis*), united only near the base, broadly deltoid to linear, 3 to 12 mm. long, about as wide, herbaceous, becoming slightly hardened in only one variant (subspecies *glabriuscula*), the broad free margins entire or sparsely denticulate, the faces smooth or muricate or with clustered tubercles, often with prominent veins; seed 1 to 3 or rarely 4 mm. long, dark brown or black; radicle inferior.

In saline soil and in salt marshes throughout North America, except possibly in north-central Canada and southern Mexico; also in Europe, Asia, and northern Africa.

SUBSPECIES.

The variable characters in *A. patula* are so numerous that it is difficult to make a selection of those that lead to the assembling of the most closely related variations into natural subspecies. It is believed, however, that a primary division based upon the width and dentation of the margins of the fruiting bracts is the most reliable. While this feature is generally applicable, warning should be given that the teeth are sometimes so minute as to be easily overlooked, and occasionally the assemblage of other features indicates that a plant with entire bracts belongs to a subspecies with usually dentate bracts, and vice versa. There seems to be no method of escaping this condition in a species so given to individual variation. Shape of leaf, and its corresponding expression in the modified leaves called bracts, is a useful secondary character. Any considerable increase in the number of recognized subspecies doubtless would lead to a confusion comparable to that obtaining in the European literature on the species, since it would necessitate the use of single-character criteria. The most notable minor variation, and one which perhaps will require subspecific rank when the constancy of its characters are better known, is *A. carnososa* Nelson, which may be synonymous with the earlier names, *Chenopodium subspicatum* Nuttall and *Atriplex lapathifolia* Rydberg.

Key to the Subspecies of *Atriplex patula*.

- Bracts with narrow toothed margins, the teeth sometimes very small and sparse.
- Leaf-blades in part triangular-hastate or rhomboidal, with basal angles or lobes; bracts truncate or broadly rounded at base.
 - Inflorescence not leafy, spicate-paniculate; leaves mostly large..... (a) *hastata* (p. 249).
 - Inflorescence leafy, each glomerule in axil of a well-developed leaf; leaves small.. (b) *glabriuscula* (p. 250).
 - Leaf-blades lanceolate or oblong to linear, not hastate; bracts more often narrowly rounded or broadly cuneate at base.
 - Blades lanceolate or oblong; bracts usually smooth on the face..... (c) *typica* (p. 251).
 - Blades linear; bracts tubercled on the face..... (d) *litoralis* (p. 251).
- Bracts with wider entire margins.
- Bracts small, about 3 mm. long; leaves ovate-rhombic, coarsely toothed..... (e) *spicata* (p. 251).
 - Bracts larger, 4 to 12 or even 20 mm. long; leaves narrower, entire or shallowly toothed.
 - Base of bract not especially thickened nor spongy.
 - Bracts ovate or rhomboidal; leaves mostly lance-oblong or the upper ones linear..... (f) *obtusata* (p. 252).
 - Bracts linear; leaves linear..... (g) *zosteræfolia* (p. 252).
 - Base of bract much thickened, spongy..... (h) *alaskensis* (p. 253).

2a. *ATRIPLEX PATULA HASTATA* (Linnaeus).—Plant usually erect and the branches ascending, but the lower ones sometimes decumbent, strict and with few short branches in dwarf forms, widely branched and up to 15 dm. high in luxuriant forms of better soil or where protected; leaves large, petioled; blade deltoid or triangular, commonly hastate at base, sinuate-dentate to entire, rarely laciniate-dentate (thick, firm, and less obviously hastate in minor variation 3, *A. carnososa* Nelson); glomerules scattered along the spike-like branches of a terminal panicle (densely spicate and persistent in minor variation 3); fruiting bracts ovate or triangular, 3 to 7 mm. long, broadly rounded or truncate at base, the margins usually with a few tooth-like projections, rarely more deeply dentate, the face commonly tuberculate. (*A. hastata* Linnaeus, Sp. Pl., 1053,

1753.) Abundant in suitable places throughout the United States, except in the extreme southeast, north to Newfoundland, Saskatchewan, and British Columbia; also a common subspecies in the Old World. Type locality, Europe. Collections: Valley of Exploits River, Newfoundland, *Fernald and Wiegand 5368* (Gr); New Brunswick, *J. D. Smith 843* (US); Canso, Nova Scotia, August 10, 1901, *Fowler* (US); Gaspe County, Quebec, *Collins, Fernald, and Pease* (Gr); Milton, Ontario, October 12, 1900, *Moore* (UC); sea-beach of Massachusetts, *True 87a* (US); District of Columbia, *Canby* (US); Hyde County, North Carolina, *Kearney 2282* (US); Port Eads, Louisiana, on ballast, May 6, 1885, *Langlois* (US); Missouri, *Nuttall* (Gr, type collection of *Chenopodium subspicatum* Nuttall, minor variation 24); Iowa City, Iowa, *Somes 3645* (US); Pen Yan, New York, *Wright* (US); Denver, Colorado, *Eastwood 143* (Gr, UC, minor variation 3, *A. carnosa* Nelson); Laramie, Wyoming, *Nelson 8086* (R, NY, US, type collection of *A. carnosa* Nelson, minor variation 3); Colgate, Montana, *Sandberg 1018* (Gr, same variation); New Plymouth, Idaho, *Macbride 725* (DS, UC, same variation); St. George, Utah, *Jones 6098* (UC, US, same variation); Glendale, Washoe County, Nevada, *Kennedy 1200* (NY, UC, same variation); Winslow, Arizona, *Griffiths 5034*; California: Cienega, Los Angeles County, *Braunton 633* (DS, UC, apparently minor variation 3, *A. carnosa* Nelson); Ingomar, Merced County, September 27, 1921, *Kennedy* (UC); West Oakland, September 23, 1897, *Davy* (UC, genuine); Petaluma, September 1, 1888, *Greene* (UC, minor variation 3, *A. carnosa* Nelson); Grand Rond Valley, eastern Oregon, *Cusick 1759* (DS, UC, same variation); Coos Bay, Oregon, *House 4801* (US); near Victoria, British Columbia, *Macoun 1854* (Gr).

2b. *ATRIPLEX PATULA GLABRIUSCULA* (Edmonston).—Plant with widely spreading decumbent or prostrate branches forming circular patches; leaves rather small (blades of the lower ones 1.5 to 3 cm. long, 1 to 2 cm. wide), petioled; blade triangular with short lobes or only substately angled at base (the upper leaves lanceolate), dentate or sometimes entire; glomerules in the axils of the upper leaves; fruiting bracts ovate or triangular, 6 to 12 mm. long, broad at base, the margins sinuate or low-dentate, the face with small clusters of tubercles or smooth (fig. 30, *a* to *d*). (*A. glabriuscula* Edmonston, Fl. Shetland 39, 1845.) Sea-shores from Newfoundland to Maine and very locally to Rhode Island and casual on the ballast southward; also in Iceland, the British Isles, and continental Europe. The distribution given for America is quoted from Fernald (*Rhodora* 23:262, 1921), who cites a long series of collections.¹ Only two collections have been examined by the present writers, namely: Charnay, Labrador Peninsula, Quebec, *St. John 90408* (Gr); Sandy Beach, Miscou, Gloucester County, New Brunswick, *Blake 5564* (Gr).

2c. *ATRIPLEX PATULA TYPICA*.—Plant usually erect, the branches either ascending or widely spreading, strict and with few short branches in dwarf forms; leaves medium-sized, petioled; blade lanceolate or oblong, rounded or narrowed to the base, not hastate, entire or denticulate or rarely with a pair of basal lobes pointing forward; glomerules scattered along the spike-like branches of a terminal panicle or the whole inflorescence spike-like in reduced forms; fruiting bracts rhomboid or roundish, 3 to 6 mm. long or up to 8 mm. in plants of good soil, narrowed to the base, the margins sparsely denticulate, but the teeth sometimes very obscure, rarely entire, the face commonly smooth. (*A. patula* Linnaeus, Sp. Pl. 1053, 1753.) Newfoundland to the Gulf of Mexico, southern California, and British Columbia; common throughout the United States and southern Canada in a great variety of forms, also in Europe and Asia. Type locality, Europe. Collections:

¹ In the paper above referred to, Fernald records *A. patula* var. *bracteata* Westerlund, *Sveriges Atriplex* 57, 1861, as occurring in North America. The record is based upon a single specimen collected near the mouth of George River, Cape Breton. In this form the bracts are as long as or even longer than those of *glabriuscula*, but the inflorescence is not leafy-bracted. In many respects it is close to subspecies *obtusa*.

1753.) Abundant in suitable places throughout the United States, except in the extreme southeast, north to Newfoundland, Saskatchewan, and British Columbia; also a common subspecies in the Old World. Type locality, Europe. Collections: Valley of Exploits River, Newfoundland, *Fernald and Wiegand 5368* (Gr); New Brunswick, *J. D. Smith 843* (US); Canso, Nova Scotia, August 10, 1901, *Fowler* (US); Gaspé County, Quebec, *Collins, Fernald, and Pease* (Gr); Milton, Ontario, October 12, 1900, *Moore* (UC); sea-beach of Massachusetts, *True 87a* (US); District of Columbia, *Canby* (US); Hyde County, North Carolina, *Kearney 2282* (US); Port Eads, Louisiana, on ballast, May 6, 1885, *Langlois* (US); Missouri, *Nuttall* (Gr, type collection of *Chenopodium subspicatum* Nuttall, minor variation 24); Iowa City, Iowa, *Somes 3645* (US); Pen Yan, New York, *Wright* (US); Denver, Colorado, *Eastwood 143* (Gr, UC, minor variation 3, *A. carnosa* Nelson); Laramie, Wyoming, *Nelson 8086* (R, NY, US, type collection of *A. carnosa* Nelson, minor variation 3); Colgate, Montana, *Sandberg 1018* (Gr, same variation); New Plymouth, Idaho, *Macbride 725* (DS, UC, same variation); St. George, Utah, *Jones 6098* (UC, US, same variation); Glendale, Washoe County, Nevada, *Kennedy 1200* (NY, UC, same variation); Winslow, Arizona, *Griffiths 5034*; California: Cienega, Los Angeles County, *Braunton 633* (DS, UC, apparently minor variation 3, *A. carnosa* Nelson); Ingomar, Merced County, September 27, 1921, *Kennedy* (UC); West Oakland, September 23, 1897, *Davy* (UC, genuine); Petaluma, September 1, 1888, *Greene* (UC, minor variation 3, *A. carnosa* Nelson); Grand Rond Valley, eastern Oregon, *Cusick 1759* (DS, UC, same variation); Coos Bay, Oregon, *House 4801* (US); near Victoria, British Columbia, *Macoun 1854* (Gr).

2b. *ATRIPLEX PATULA GLABRIUSCULA* (Edmonston).—Plant with widely spreading decumbent or prostrate branches forming circular patches; leaves rather small (blades of the lower ones 1.5 to 3 cm. long, 1 to 2 cm. wide), petioled; blade triangular with short lobes or only subhastately angled at base (the upper leaves lanceolate), dentate or sometimes entire; glomerules in the axils of the upper leaves; fruiting bracts ovate or triangular, 6 to 12 mm. long, broad at base, the margins sinuate or low-dentate, the face with small clusters of tubercles or smooth (fig. 30, *a* to *d*). (*A. glabriuscula* Edmonston, Fl. Shetland 39, 1845.) Sea-shores from Newfoundland to Maine and very locally to Rhode Island and casual on the ballast southward; also in Iceland, the British Isles, and continental Europe. The distribution given for America is quoted from Fernald (*Rhodora* 23:262, 1921), who cites a long series of collections.¹ Only two collections have been examined by the present writers, namely: Charnay, Labrador Peninsula, Quebec, *St. John 90408* (Gr); Sandy Beach, Miscou, Gloucester County, New Brunswick, *Blake 5564* (Gr).

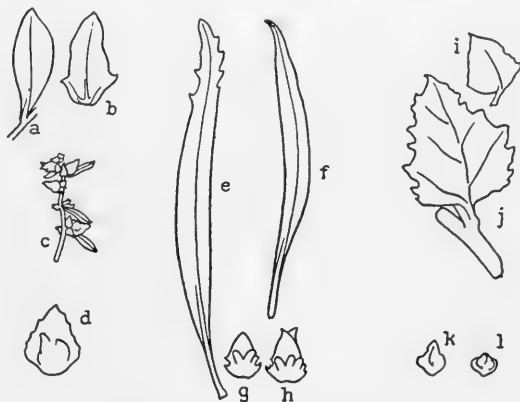
2c. *ATRIPLEX PATULA TYPICA*.—Plant usually erect, the branches either ascending or widely spreading, strict and with few short branches in dwarf forms; leaves medium-sized, petioled; blade lanceolate or oblong, rounded or narrowed to the base, not hastate, entire or denticulate or rarely with a pair of basal lobes pointing forward; glomerules scattered along the spike-like branches of a terminal panicle or the whole inflorescence spike-like in reduced forms; fruiting bracts rhomboid or roundish, 3 to 6 mm. long or up to 8 mm. in plants of good soil, narrowed to the base, the margins sparsely denticulate, but the teeth sometimes very obscure, rarely entire, the face commonly smooth. (*A. patula* Linnaeus, Sp. Pl. 1053, 1753.) Newfoundland to the Gulf of Mexico, southern California, and British Columbia; common throughout the United States and southern Canada in a great variety of forms, also in Europe and Asia. Type locality, Europe. Collections:

¹In the paper above referred to, Fernald records *A. patula* var. *bracteata* Westerlund, *Sveriges Atriplex* 57, 1861, as occurring in North America. The record is based upon a single specimen collected near the mouth of George River, Cape Breton. In this form the bracts are as long as or even longer than those of *glabriuscula*, but the inflorescence is not leafy-bracted. In many respects it is close to subspecies *obtusata*.

Birchy Cove, western Newfoundland, *Fernald and Wiegand 3319* (Gr); lower St. Lawrence River, August 13, 1880, *Pringle* (US); Black Lake, Quebec, *Fernald and Jackson 12084* (Gr); Little Harbor, New Hampshire, September 19, 1901, *Williams* (Gr); eastern North Carolina, July, 1885, *McCarthy* (US); Mobile, Alabama, June 4, 1893, *Mohr* (US); Oxford, New York, August 13, 1884, *Coville* (US); Toledo, Ohio, *Sanford 2355* (US); Joliet, Illinois, *Skeels 634* (US); Madison, Wisconsin, August, 1887, *Holzinger* (US); North Dakota, September 14, 1901, *Lunnell* (Gr); Fisher's Ranch, Wyoming, *Nelson 5323* (UC); Bay Farm Island, Alameda, California, *Jepson 5682* (Gr); near Victoria, British Columbia, *Macoun 1857* (Gr, US).

FIG. 30

Atriplex patula glabriuscula, *A. p. litoralis*, and *A. p. spicata*. a to d, *A. p. glabriuscula*, from New Brunswick (*Blake 5664*, Gr); a, b, leaves; c, fruiting branch; d, fruiting bract. e to h, *A. p. litoralis*, from Durham County, England (7182 UC), the bracts after Sowerby (Eng. Bot. pl 1200): e, f, leaves; g, h, fruiting bracts. i to l, *A. p. spicata*, from Main Prairie, California (205332 UC): i, j, leaves; k, l, fruiting bracts. All leaves $\times 1$; bracts $\times 2$.



2d. *ATRIPLEX PATULA LITORALIS* (Linnaeus).—Plant erect, the branches ascending, the lower ones from a decumbent base; leaves long but narrow, petioled; blade lanceolate to linear, attenuate to the base, never hastate, entire, as in the original description, undulate or sometimes acutely repand-dentate; glomerules in long, dense, rarely interrupted naked paniculate spikes and in the upper axils; fruiting bracts ovate or rhombic, 3 to 4 mm. long, narrowed at the base, the margins sharply denticulate, the face tubercled (fig. 30, e to h). (*A. litoralis* Linnaeus, Sp. Pl. 1054, 1753.) Northeast coast from Nova Scotia to New Hampshire and inland in Ontario, Ohio, etc.; common in Europe. Type locality, Europe. Collections: Portage Island, Northumberland County, New Brunswick, *Blake 5680* (Gr); Truro, Colchester County, Nova Scotia, *Fernald and Wiegand 4266* (Gr); North Berwick, Maine, September, 1893, *Parlin* (Gr); Little Harbor, New Hampshire, September 19, 1901, *Williams* (Gr); near Pittsburgh, Pennsylvania, August 18, 1869, *Porter* (Gr); Benton County, Indiana, *Deam 21542* (Gr); Kingston, Ontario, September 1, 1897, *Fowler*, (Gr).

2e. *ATRIPLEX PATULA SPICATA* (Watson).—Plant erect, not tall, the branches rather rigidly ascending; leaves medium-sized, petioled, the upper nearly sessile; blades triangular to ovate, usually rhombic, typically broad at base but shortly narrowed to the petiole, coarsely and irregularly sinuate-dentate; glomerules in very dense spikes terminating the branches; fruiting bracts ovate-oblong, about 3 mm. long, the margins entire, the face not appendaged but strongly ribbed or furrowed (fig. 30, i to l). (*A. spicata* Watson, Proc. Am. Acad. 9:108, 1874.) Middle western California. Type locality, San Joaquin Valley, California, according to Watson, but Livermore Pass, west side of San Joaquin Valley, according to the labels and field book. Collections (all in California): Hollister,

San Benito County, April 14, 1897, *Setchell* (UC); type collection, May 31, 1862, *Brewer 1190* (Gr, NY); Marsh Creek, Contra Costa County, May, 1884, *Greene* (UC); 6 km. west of Byron, Contra Costa County, *Hall 11801* (UC); Lagoon Valley, Solano County, September, 1891, *Jepson* (Herb. Jepson, type of *A. spicata lagunita* Jepson, minor variation 22); Maine Prairie, Solano County, July 5, 1891, *Jepson* (UC); near Dunnigan, Yolo County, *Stinchfield 357* (DS); near Williams, Colusa County, *Heller 12394* (DS, SF); rice fields near Willows, Glenn County, August 9, 1921, *Kennedy* (UC); west of Norman, Glenn County, *Hall 11009* (UC).



FIG. 31.—*Atriplex patula obtusa* and *A. p. alaskensis*. *a* to *e*, *A. p. obtusa* from the region of Humboldt Bay, California (146161 and 162361 UC); *a*, *b*, *c*, leaves; *d*, *e*, fruiting bracts. *f* to *h*, *A. p. alaskensis* from the type collection (Gr): *f*, twig; *g*, *h*, fruiting bracts. All leaves and twigs $\times 1$; bracts $\times 2$.

2f. ATRIPLEX PATULA OBTUSA (Chamisso).—Plant usually erect, with widely spreading upcurved branches, simple-stemmed in reduced forms; leaves long and narrow, short-petioled; blade lanceolate to linear, attenuate to the base (the lower obtuse at apex, hence the name), entire or crenulate, occasionally with 1 or 2 short ascending lobes from below the middle; glomerules in short dense panicle spikes and in the upper axils; fruiting bracts broadly ovate or rhomboidal, 4 to 12 mm. long, rounded to the base, the margins entire, the face smooth or rarely with a few minute appendages (fig. 31, *a* to *e*). (*A. angustifolia* var. *obtusata* Chamisso, Linnaea 6:569, 1831.) Pacific Coast from northern Alaska to middle California. Type locality, Eschscholtz Bay, Kotzebue Sound, Alaska. Collections: Fort St. Michaels, Norton Sound, Alaska, 1865–66, *Bannister* (Gr); near Karluk Village, Alaska, abundant on sandy and muddy beach near high-tide line, August, 1902, *Horne* (NY); Halibut Cove, Cook Inlet, Alaska, *Coville* and *Kearney 2451* (US, type of *A. drymarioides* Standley, minor variation 5); Loring, southwestern Alaska, *Howell 1655* (UC); San Juan Harbor, Vancouver Island, *Rosendahl 2060* (Gr, NY); Shoalwater Bay, Washington, August 17, 1907, *McGregor* (DS); California: near mouth of Mad River Slough, Humboldt County, not common, *Tracy 3555* (Gr, UC, US); mouth of Elk River, Humboldt County, *Tracy 2393* (UC); West Oakland, September 23, 1897, *Davy* (UC); Fitchburg, Alameda County, November 13, 1899, *Nott* (UC).

2g. ATRIPLEX PATULA ZOSTERAEFOLIA (Hooker).—Plant ascending, the branches mostly ascending but weak and slender, some decumbent; leaves 2 to 4 cm. long, or the lower probably much longer, petioled; blade linear, narrow at base, not hastate, entire;

glomerules in short axillary spikes and in the upper axils; fruiting bracts linear, 8 to 12 mm. long, the margins entire, the face smooth. (*Chenopodium* (?) *zosteraefolium* Hooker, Fl. Bor. Am. 2:127, 1838.) Southern Alaska and probably northwestern Washington. Type locality, British Columbia and Straits of Juan de Fuca. Collections: Type collection (Gr, fragment only); Prince of Wales Island, Alaska, *Walker 914* (Gr).

2*h*. *ATRIPLEX PATULA ALASKENSIS* (Watson).—Plant erect or ascending, stout (succulent?), the branches ascending from a spreading base; leaves large, petioled; blade ovate to oblong or lanceolate, cuneate at base, entire or with 1 or 2 short lobes from below the middle and then subhastate, or rarely repand-denticulate; glomerules in the leaf-axils; fruiting bracts oblong to ovate-orbicular, 6 to 20 mm. long, becoming thick and spongy at the rounded base, the broad margins entire, the face smooth (fig. 31, *f* to *h*). (*A. alaskensis* Watson, Proc. Am. Acad. 9:108, 1874.) Coast of Alaska. Type locality, Barlows Cove, Alaska. Collections: Type collection, *Kellogg 176* (Gr, US); Karluk Village, about high-tide line, August, 1902, *Horne* (NY); Kodiak, *Mytroe 142* (NY, young, but probably this).

MINOR VARIATIONS AND SYNONYMS.

1. *ATRIPLEX ALASKENSIS* Watson, Proc. Am. Acad. 9:108, 1874.—*A. patula alaskensis*.
2. *A. ANGSTIFOLIA* var. *OBTUSA* Chamisso, *Linnaea* 6:569, 1831.—*A. patula obtusa*.
3. *A. CARNOSA* Nelson, Bot. Gaz. 34:361, 1902.—A remarkable variation of *A. patula hastata*, perhaps to be admitted as a distinct subspecies. Stems stout, erect, with rigidly ascending branches; leaves thick, succulent, somewhat leathery on drying, seldom truly hastate, but the principal ones with a prominent spreading lobe from each of the basal angles; fruiting spikes dense, almost continuous, bracts more persistent than in the common coastal form, usually 4 or 5 mm. long, thick, fleshy. The type is *Nelson 8036* from Laramie, Wyoming. This form is common throughout the alkaline districts from the Rocky Mountains to the Pacific, in which area genuine *hastata* occurs only sporadically and perhaps as an introduction. In California *carnosa* grows also within reach of tide-water, but is not known to mix with *hastata*, although some collections can not be placed with certainty in either of the forms. In Nevada the fruiting bracts sometimes become much enlarged and vary also in their sculpturing (see No. 17).
4. *A. DIOECA* Rafinesque, Am. Mo. Mag. 2:176, 1818. Not technically published, since Rafinesque mentioned the name only incidentally in a review of Pursh's Flora. Applied to the plant here referred to *A. patula hastata*.
5. *A. DRYMARIOIDES* Standley, N. Am. Fl. 21:40, 1916.—Apparently a much reduced form of *A. patula obtusa*. The type specimens, from Halibut Cove, Cook Inlet, Alaska, are only 5 to 10 cm. high and have broadly oblong, obtuse lower leaves, which are so shortly cuneate at the base as to appear almost sessile. Another collection, from Peril Straits, Baranoff Island (*Stephens 69*, UC) is identical in habit and fruits, some of which, however, are more mature and hence more like those of *obtusa*. The leaves vary from nearly as broad and subsessile as those of the type to linear, and some are plainly petioled. This collection from Baranoff therefore establishes, almost beyond doubt, that *drymarioides* is a dwarf state of *obtusa*. Similar reductions of subspecies *hastata* and *typica* are well known.
6. *A. GMELINI* Meyer, Mem. Acad. St. Petersb. VI. 4^o:160, 1838.—The code name for *A. patula obtusa* when this is given specific rank. The name *obtusa* is here selected, since it was first used for this subspecies, although as a variety, and because of its descriptive value.
7. *A. GMELINI* β *ZOSTERAEOFOLIA* Moquin, in DeCandolle, Prodr. 13^o:97, 1849.—*A. patula zosteraefolia*.
8. *A. HALIMOIDES* Rafinesque, Am. Mo. Mag. 2:176, 1818.—Generally regarded as the same as *A. patula hastata*.
9. *A. HASTATA* Linnaeus, Sp. Pl. 1053, 1753.—*A. patula hastata*. Has place priority over *patula* in the Species Plantarum, but usage as well as descriptive value is in favor of this latter as the specific name, which furthermore is permissible under the International Code.
10. *A. HASTATA LITORALIS* Pons, Nuov. Giorn. Bot. Ital. II, 9:419, 1902.—*A. patula litoralis*.
11. *A. HASTATA PATULA* Pons, l. c., 417, 1902.—*A. patula typica*. (See note under No. 9.)
12. *A. JOAQUINIANA* Nelson, Proc. Biol. Soc. Wash. 17:99, 1904.—*A. patula spicata*.
13. *A. LACINIATA* β *AMERICANA* Torrey, Fl. U. S. 293, 1824.—*A. patula hastata*.
14. *A. LAPATHIFOLIA* Rydberg, Mem. N. Y. Bot. Gard. 1:133, 1900.—Probably the same as No. 3 of this list and therefore part of *A. patula hastata*. The type is a nearly leafless plant with bracts as in genuine *hastata*. It came from Fridley, Montana.
15. *A. LITORALIS* Linnaeus, Sp. Pl. 1054, 1753.—*A. patula litoralis*.
16. *A. PATULA* var. *HASTATA* Gray, Man. ed. 5, 409, 1867.—*A. patula hastata*.

17. *A. PATULA HASTATA*, but with much enlarged bracts, the other characters similar to those of *A. carnosa* Nelson (No. 3 of this list). In a collection from alkaline roadsides east of Sparks, Nevada (*Hall 11232*, UC), the mature bracts of one plant are in part of the usual type and 3 to 4 mm. long, while others on the same branches vary through all intermediate sizes up to 13 mm. long and nearly as wide. Some of these larger bracts are smooth on the faces, others tuberculate or cristate.

18. *A. PATULA* var. *LITORALIS* Gray, l. c.—Based upon *A. litoralis* Linnaeus, therefore the same as *A. patula litoralis*, although Gray's description includes also the lance-leaved *A. p. typica*.

19. *A. PATULA* var. *SUBSPICATA* Watson, Proc. Am. Acad. 9:107, 1874.—Based upon *Chenopodium subspicatum* Nuttall, No. 24 of this list.

20. *A. PURSHIANA* Moquin, Chenop. Enum. 55, 1840.—Referred by Standley (l. c.) to *A. hastata*.

21. *A. SPICATA* Watson, Proc. Am. Acad. 9:108, 1874.—*A. patula spicata*.

22. *A. SPICATA* var. *LAGUNITA* Jepson, Fl. W. Mid. Calif. 179, 1901.—The original description in full is as follows: "Very slender, simple, 5 to 8 in. high; fruiting bracts $1\frac{1}{2}$ lines long. Lagoon Valley, Solano County, California, September, 1891." The types are nearly leafless fruiting plants scarcely distinguishable from *spicata*, save by their small size and slender habit.

23. *A. ZOSTERAEOFOLIA* Watson, Proc. Am. Acad. 9:109, 1874.—Based upon *Chenopodium zosteræfolium* Hooker and therefore *A. patula zosteræfolia*.

23a. *A. SUBSPICATA* Rydberg, Bull. Torr. Club 33:137, 1906. Based upon *Chenopodium subspicatum*, which see.

24. *CHENOPODIUM SUBSPICATUM* Nuttall, Genera 1:199, 1818.—A form of *A. patula hastata* very close to, if not identical with, the later *A. carnosa* Nelson, of this list. A specimen in the herbarium of the Philadelphia Academy of Sciences is labeled "Upper Louisiana, Nuttall," which is probably a portion of the type collection. This has the usual moniliform staminate inflorescences and thick deltoid leaves characteristic of the *carnosa* form. The type locality is saline soils around the Mandan village, Missouri. This was included in the original Territory of Louisiana.

25. *C. (?) ZOSTERAEOFOLIUM* Hooker, Fl. Bor. Am. 2:127, 1838.—*A. patula zosteræfolia*. Hooker distinguished two forms in the type collection, one with leaves linear and scarcely 2 mm. wide, the other with leaves linear-oblong, broader, and shorter.

RELATIONSHIPS.

Atriplex patula evidences a considerable degree of evolutionary advancement along certain lines, notably the entire suppression of the perianth and the production of a large variety of forms adapted to diversified conditions. However, it retains the inferior position of the radicle and the monoecious habit, these traits indicating that it diverged from the main line at a very early period. The bracts also are still either distinct nearly to the base, or the margins are united only along the lower portion. The most closely related species seem to be of the *rosea* group, from all of which, however, it differs in the non-cartilaginous bracts and other characters. There is no direct connection with any other group.

The taxonomic segregates of *A. patula* are more numerous than those of any other species. The 16 species and varieties proposed by taxonomists from among the North American forms may be taken as only the beginning, since little attention has as yet been given to most of the characters and combinations of characters used as the basis for segregates in Europe, where the total number of these considerably exceeds 100. Something as to the difficulty of organizing these units was expressed by Ascherson and Graebner (Syn. Mitteleur. Fl. 5:123, 1913), who state that *A. patula*, even exclusive of *litoralis* and *hastata*, which they treat as distinct collective species, is so extraordinarily variable in almost all its parts that it appears impossible to bring the proposed forms into any sort of a classification except on the basis of single characters. These authors list 34 named variations of *A. patula*, the descriptions taken mostly from other sources, often with the remark that they have almost no value. Fourteen variations of *hastata* are also enumerated. The characters most commonly used in Europe are habit and color of plant, and size, texture, and dentation of the bracts and leaves.¹

A much more satisfactory treatment is given for the forms which occur in the British Islands, by Moss and Wilmott (in Moss, Cambridge Brit. Fl. 2:170-179, 1914). Here four species are recognized, *litoralis*, *patula*, *hastata*, and *glabriuscula*, each with a

¹ Turesson, G. Hereditas 3:211, 1922.

number of varieties and minor forms. The difficulties encountered and the unsatisfactory nature of the results are evidenced by the overlapping of the key characters, the occasional lack of concordance between these and the descriptions, the admitted difficulty of placing many of the forms, at least as to variety, and the frequency of supposed hybrids.

In order to avoid such confusion as exists in the European literature, it seems wise to retain all of the "*patula group*" in one collective species and to admit under this a limited number of closely defined subspecies. The precedents of Gray and Watson are followed in adopting *patula* for the specific name, notwithstanding the fact that *hastata* appears before it on the page where both were originally published. The distinctions between these two lie wholly in the shape of the leaves and of the bracts. Since these differences vanish when intermediate forms occur, and since the shape of the bract is looked upon only as another expression of the leaf-character, the criteria can have not more than subspecific value. On the other hand, these two subspecies are much more than ecologic forms. Over much of the area of distribution they remain entirely distinct and easily recognizable, even when growing side by side.

TABLE 24.—Variation in *Atriplex patula hastata* and *A. patula typica*.

	Herbarium.	Leaves.	Average size of mature bracts.	Margin of bracts.	Face of bracts.
Subspecies <i>hastata</i> :					
Bridgeport, Conn.	282946 US	Triangular-hastate.	3 mm. by 2.8	Dentate.	Some smooth, some bituberculate.
Maryland.	939158 US	Do.	4.6 4	Entire or few-toothed.	Smooth.
Ithaca, N. Y.	295716 US	Do.	6.5 6	Few-toothed.	Some smooth, some bituberculate.
Freeport, Ill.	647229 US	Do.	4 4	Do.	Sparsely muciculate.
Urbana, Ill.	490849 US	Do.	6 5	Crenate.	Smooth.
Laramie, Wyo.	267817 US	Ovate.	5 5	Do.	Do.
St. George, Utah.	271023 US	Triangular.	4 5	Sinuate.	Cristate.
Eureka, Calif.	161058 UC	Do.	5.5 5	Entire or low-dentate.	Cristate or smooth.
Subspecies <i>typica</i> :					
Canton, N. Y.	644691 US	Lanceolate.	4 3	Some denticulate.	Smooth.
Wilmington, N. C.	224223 US	Do.	6 6	Denticulate.	Do.
Fisher's Ranch, Wyo.	51223 UC	Do.	8 6	Sparsely dentate.	Do.
Berkeley, Calif.	7117 UC	Do ¹	6 4.5	Dentate.	Smooth or tuberculate.
Alviso, Calif.	75369 UC	Do ¹	4.5 4.5	Do.	Smooth.
Joliet, Ill.	646240 US	Linear.	4 3	Low-denticulate.	Smooth or bituberculate.

¹ Lower leaves wanting; probably referable to *typica* on the character of the shape of the bracts.

Various attempts have been made to differentiate these and other forms on the basis of size and sculpturing of the bracts. A hint as to the unreliability of these criteria is given in the subjoined table. The tabulation of a much more extended series has been made, but since it merely confirms the results of the first examination it is not given.

The subspecies *glabriuscula* is placed between the two just discussed because of its evident derivation from *hastata*, from which it scarcely differs, except in the larger upper leaves which persist throughout the inflorescence. It is much more abundant in Europe than on this continent and seems to be especially suited to boreal conditions. The close similarity in most characters to those of *A. maritima*, especially the tendency toward a hardening of the bracts, suggests that *glabriuscula* may represent the primitive stock of the group of species sometimes known as section *Obionopsis*. The subspecies *litoralis* may be looked upon as a development from *patula* in a direction opposite to that of *hastata*, since its leaves have undergone the greatest amount of reduction in width. In

North America it is apparently confined to the easterly part of the continent. Specimens from the Pacific Coast referred here are now found to belong to one or another of the following enumeration.

The remaining subspecies differ from all of the preceding in their fruiting bracts, the margins of which are narrower and strictly entire. (For a valuation of this feature see p. 242.) They belong entirely to the Pacific Coast and the connections with Asiatic forms indicate that, with the possible exception of *spicata*, all have reached America by way of Siberia. They are most abundant along the coast of Alaska and on the adjacent islands, becoming less common toward the south, none extending beyond middle California. The subspecies *spicata* is of doubtful origin, but it seems most like *hastata*, except for the bract differences just mentioned. Little is known of its variations or life history. The numerous salient teeth of the leaves are usually distinctive, but the same type of foliage is known also in subspecies *hastata* (for example, Newfoundland, *Wagborne 49*, Gr). Subspecies *obtusa* is much more widely distributed and ranges west well into Siberia, where it is usually known as *A. gmelini*. In the United States it has been unaccountably confused with both *patula* and *litoralis*, but differs from both in the bracts. These are not only entire, but also have a tendency toward the development of an elongated lanceolate tip, so that the whole bract is considerably longer than in those forms. It has also a characteristically strict or ascending habit of growth, which enables one to recognize it on general appearance. Little is definitely known concerning subspecies *zosteræfolius*, found only in a few collections made along the Straits of Juan de Fuca. Further field studies may demonstrate the wisdom of Hooker's suggestion, namely, that it is perhaps a luxuriant state of subspecies *obtusa* (Hooker, Fl. Bor. Am. 2:127, 1838). Fernald (*Rhodora* 23:264, 1921) recently has recorded *A. patula bracteata* Westerlund (Sveriges Atriplex, 57, 1861) from Nova Scotia. This is much like *obtusa* in the foliage and bracts, but the latter frequently are toothed.

The subspecies *alaskensis* is so luxuriant in its foliage and the margins of the bracts are so remarkably developed that it is the most outstanding of all of the forms here brought under *A. patula*. The bracts are usually described as spongy-thickened, but the thickening is perhaps no greater in proportion to the size of the body than sometimes takes place in other subspecies, notably *spicata*. The mature bracts are so large (6 to 20 mm. long) that this feature alone might seem to constitute a specific criterion, but other subspecies have bracts which not infrequently reach 10 or 12 mm. and even in *hastata*, where these structures are usually much smaller, occasionally plants are found in which they reach 12 mm. in length (minor variation 17). While this does not overthrow *alaskensis* as a valuable taxonomic unit, it does demonstrate the inherent capacity of other subspecies nearly to duplicate its most characteristic features. The radicle has been described as superior, but probably it is no more so than in the other subspecies. Dissections have been made of the type material, but the embryo was so deformed as to render impossible a positive determination of the position.

ECOLOGY AND USES.

Atriplex patula is typically a halophytic annual widely distributed in salt-marshes and on alkali-flats. The subspecies *hastata* and *typica* in particular often form pure consocieties in saline areas, though they are usually more or less mixed with other marked halophytes. They frequently invade fallow fields, especially in the arid regions, where they constitute a pioneer stage in the short subsera. The relation of *hastata* to the salt-content of the soil has been determined by Kearney and his associates to range from 0.33 to 1.33 per cent in the first foot and from 0.46 to 3.3 per cent in the third foot.

While the common forms of this species were formerly used for greens in the Old World, this is rarely if ever the case in this country. *Hastata* and *typica* are grazed to some extent, but are rarely abundant enough to be of much importance.

3. *ATRIPLEX CALIFORNICA* Moquin, in DeCandolle, Prodr. 13:98, 1849. Plate 39.

Prostrate perennial herb (the only North American *Atriplex* with a fusiform taproot, this slender, elongated, fleshy or spongioid), the stems spreading to form tangled mats or beds 1 to 2 dm. deep but up to 10 dm. or more across, the ultimate twigs erect or ascending; branches wiry, not angled, white-mealy, glabrate and then stramineous; leaves alternate or the lower opposite, crowded, sessile, lanceolate or ovate-lanceolate, all much narrowed to the base, acute at apex, 0.8 to 2 or rarely 3 cm. long, 0.2 to 0.4 cm. wide, entire, comparatively thin, heavily coated with a gray tomentum but the general hue often greenish, obscurely 1-nerved; flowers monoecious, the two kinds mixing in the leaf-axils, the staminate also in approximate glomerules arranged in nearly naked terminal spikes; perianth 4-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile, compressed, separate nearly to the base, ovate, acute, 3 to 5 mm. long, 2.5 to 4 mm. broad, entire, the faces not appendaged, 1-nerved under the dense scurf; seed 2 mm. long, black; radicle inferior or sometimes lateral, never superior.

Sandy coasts along the Pacific Ocean, from slightly north of San Francisco, California, to Cedros Island, Lower California. Type locality, California. Collections, all in California or Lower California: Bodega Point, Sonoma County, *Eastwood 4802* (SF); Point Reyes, Marin County, *Davy 6764* (UC); Mare Island, San Francisco Bay, September 7, 1874, *Greene* (Gr); West Berkeley, *Michener* and *Bioletti 561a* (US); Alameda Marshes, September 17, 1898, *Davy* (UC); Pillar Point, San Mateo County, *Baker 1748* (Gr, SF, UC, US); Santa Cruz, April 15, 1897, *Setchell* (UC); near Point Pinos, Monterey County, *Heller 6746* (DS, UC, US); San Simeon, San Luis Obispo County, August, 1885, *Brandegee* (UC); Santa Maria, June, 1894, *Alderson* (UC); Surf, Santa Barbara County, *Elmer 4011* (NY, US); Carpenteria, Santa Barbara County, *Hall 10953* (CI); Santa Rosa Island, June, 1888, *Brandegee* (UC); San Miguel Island (according to *Brandegee*, *Zoe* 1:144, 1890); Santa Cruz Island, 1919, *Swain* (SF); Anacapa Island, 1901, *Hemphill* (UC); Santa Catalina Island, rare, September, 1898, *Trask* (UC); San Nicholas Island, April, 1901, *Trask* (Gr, NY); San Clemente Island, *Mearns 4074* (DS, US); Redondo, Los Angeles County, *Braunton 267* (UC); La Jolla, San Diego County, *Clements 56* (UC, US); Initial monument, United States-Mexico line, July 1, 1899, *Brandegee* (UC); South Coronado Island, *Parish 8839* (DS, UC); Todos Santos Bay, *Orcutt 1269* (Gr, US); San Quentin Bay, *Palmer 718* (Gr, NY, US); El Rosario, March 21, 1889, *Brandegee* (UC); Cedros Island, April 30, 1885, *Greene* (US).

RELATIONSHIPS.

Atriplex californica is not closely related to any other species, at least not to any known in North America. It is primitive in its dioecious habit, inferior radicle, and the absence of cohesion between the bracts. Furthermore, the pistil is much less reduced in the staminate flowers than it is in the other species. Since no other exhibits this combination of fundamental characters, it is almost certainly a derivative of some ancestral stock not now here represented, and therefore belongs in a section or subgenus by itself. If *A. hortensis* is taken as the most primitive *Atriplex*, then *californica* represents an advance through the complete suppression of the perianth, but without the development of certain features which have been attained on the *hortensis* line. The *patula* and *rosea* groups are the only others in which the radicle is inferior, and these are far removed from *californica* in almost all other characters.

In appearance and in its ecologic relations this species is similar to *A. decumbens*, but probably there is no direct phylogenetic connection between them; the former differing in its fusiform root, monoecious habit, mostly alternate leaves, thin and distinct fruiting bracts, and inferior radicle, as well as in minor details.

The radicle in *A. californica* is described as inferior, and this is strictly true as far as most of the embryos are concerned. Occasionally, however, the radicle is carried

slightly above the normal position and thus becomes lateral. This appears to be the beginning of a tendency which has culminated in the superior position common in most species of the genus.

ECOLOGY AND USES.

Atriplex californica sometimes forms pure socies of limited extent in saline marshes, but it is usually associated with such dominants as *Distichlis* or *Haplopappus*, outside the *Salicornia* zone. It occurs also on the more stable strand and dunes, and especially in the saline valleys between inner dunes. It is unique in the genus in the development of a slender fusiform root for storage. The flowers bloom during an exceptionally long season, beginning in April and lasting to October.

This species is of little value for grazing, owing to its small size, its halophytic character, and its lack of abundance. The roots are said by Greene (*Pittonia* 1:207, 1888) to be sweet and well-flavored, but they are not used. Recent observations along the coast of middle California indicate that they are exceedingly bitter, at least in some cases.

4. ATRIPLEX MARITIMA Hallier, Bot. Zeit. 21, beilag 1:10, 1863. Plate 38.

Spreading or prostrate annual herb with stems 0.5 to 5 dm. long, branched from the base; branches thick but weak and with a tendency to droop, scarcely angled, nearly glabrous, stramineous, the bark smooth and persistent; leaves mostly alternate, the lowest opposite, petioled, suborbicular to ovate or rhombic-ovate, cuneate at base, very obtuse to acutish and mucronulate at apex, 2 to 4 cm. long, 1 to 2.5 cm. wide, irregularly repand-dentate with mostly obtuse teeth or some of the upper ones nearly entire, rather densely furfuraceous on both sides, soft; flowers monoecious, the staminate in small glomerules in the upper axils and in short dense terminal spikes, these 1 cm. or less long, the pistillate in axillary glomerules beneath the staminate, some of the intermediate glomerules with both staminate and pistillate flowers; perianth 5-cleft, wanting in the pistillate flowers; fruiting bracts sessile or subsessile, compressed, united to above the middle, rhombic-hastate, widest at the middle, 6 to 9 mm. long, 6 to 9 mm. wide, becoming hard and cartilaginous at least as to body, entire except at the angles, either with a few strong flattened tubercles or these wanting, strongly 3-nerved and reticulate; seed 3 to 4 mm. long, dull brown; radicle inferior, ascending.

On sandy beaches of Quebec and New Brunswick; also on shores of northwestern Europe. Type locality, England. Collections: Fox Island, New Brunswick, *Blake 5692* (Gr); Grindstone Island, Magdalena Islands, Quebec, *Fernald, Long, and St. John 7397* (Gr, UC, not mature but probably of this species). Additional localities are cited by Blake (*Rhodora* 17:86, 1915).

MINOR VARIATIONS AND SYNONYMS.

Little is known concerning the forms of this species in America, since it has been but little collected. A number of varieties have been named in Europe. The complicated synonymy of the species is discussed by Blake (l. c.)

1. *ATRIPLEX ARENARIA* Woods, *Phytologist* 3:593, 1849.—An older name for this species but antedated by *A. arenaria* Nuttall. Although Nuttall's species is reduced in the present paper to a subspecies of *A. pentandra*, Wood's name is not here taken up for *maritima*, as has been done by Ascherson and Graebner and other European botanists, because of its long use for the Nuttallian species.

2. *A. ROSEA* var. *ARENARIA* Westerlund, *Sver. Atr.* 32, 1861, and *Linnaea* 40:142, 1876.—An apparently necessary reduction of *A. maritima* to its most closely related species.

3. *A. SABULOSA* Rouy, *Bull. Soc. Bot. Fr.* 37:20, 1890.—*A. maritima*.

RELATIONSHIPS.

This is perhaps not more than a subspecies of *A. rosea*, since the differences are only those of habit and the size of the bracts and seeds. However, it is so little known in America that a decision as to its reduction may be left for the future, as this would

necessitate recognizing a subspecies *typica* in addition to the making of a new combination. It so closely simulates *A. patula glabriuscula* in most of its characters that its intermediate position between that and *rosea* is strongly suggested.

ECOLOGY AND USES.

Atriplex maritima is so local in America that nothing is known of its ecology and uses.

5. ATRIPLEX ROSEA Linnaeus, Sp. Pl. ed. 2:1493, 1753. Plate 38. REDSCALE; RED ORACHE.

Erect annual herb, 1 to 20 dm. high, branched from the base to form rounded bushy plants, or nearly simple and strict in small, starved forms, sometimes simple-stemmed below, but with divaricate branches above the middle; branches slender or stout, ascending, commonly a little angled, nearly glabrous, stramineous, the bark smooth and persistent; leaves alternate, except the lower, either sessile or petioled, ovate or rhombic-ovate to lanceolate, cuneate or rounded at base, acute or rarely somewhat obtuse at apex, mucronulate, 2 to 6 cm. long, 1 to 3 cm. wide, larger in occasional plants of rapid growth, remotely sinuate-dentate above the base with acute or obtuse teeth, thinly or densely furfuraceous, usually gray or whitish, rarely greenish, soft but persistent and becoming cartilaginous on drying; flowers monoecious, the staminate glomerules in the upper axils and often also in dense terminal spikes 1 cm. or less long, the pistillate also in axillary glomerules, but these beneath the staminate, many of the intermediate glomerules with both staminate and pistillate flowers; perianth 4- or 5-lobed, wanting in the pistillate flowers; fruiting bracts sessile, compressed, united usually to the middle, rhombic or ovate from a broad base, 4 to 6 mm. long, of about the same width, occasionally up to 8 mm. long and wide, becoming firm and strongly indurated in age, with wide greenish acutely dentate margins, the sides usually sharp-tuberculate, 3-nerved; seed 2 to 2.5 mm. long, dark brown, dull; radicle lateral.

Introduced and now abundant in all of the western United States, south to Chihuahua; also at various places along the Atlantic seaboard from Massachusetts to Florida; native and widely distributed in the Old World. Type locality, Europe. Collections: South Boston Flats, *Perkins*, according to Knowlton and Deane (*Rhodora* 17:176, 1915); Albany, New York, 1867, *Peck* (Gr, NY); Pensacola, Florida, *Mohr* (US); Sheffield, Missouri, *Bush* 7058 (Gr, NY, US); Laramie, Wyoming, *Nelson* 8961 (Gr, NY, UC, US); Granger, Wyoming, *Nelson* 8140 (R, types of *A. spatiosa* Nelson, see below); Murray, Salt Lake County, Utah, *W. W. Jones* 374 (Gr); Rio Arriba County, New Mexico, *Standley* and *Bollman* 10763 (US); Juarez, Chihuahua, August 23, 1909, *Wootton* (US); Needles, Mojave Desert, California, *Eastwood* 5967 (SF); Ballona, near Los Angeles, California, *Braunton* 687 (UC, US); Army Street Marsh, San Francisco, California, September 9, 1918, *Eastwood* (SF); Yreka, northern California, *Buller* 1066 (UC); Reno, Nevada, *Petersen* 464 and 465 (UC); Yakima County, Washington, *Cotton* 889 (US); Cañon County, Idaho, *Macbride* 736 (Gr, NY, UC, US). Numerous additional localities may be obtained by consulting any of the larger herbaria.

SYNONYM.

1. ATRIPLEX SPATIOSA Nelson, Bot. Gaz. 34:360, 1902. *A. rosea*.

RELATIONSHIPS.

The relationships of this species are with *A. maritima* and *A. tatarica*. All are introductions from the Old World, where they are classed as belonging to the section *Obionopsis*, or *Sclerocalymna* of Ascherson, best characterized by the hard or indurated nature of the body of the bracts at maturity. The foliage of *rosea*, and perhaps also of the others, likewise becomes hard and firm at maturity, the cartilaginous leaves persisting indefinitely on the dead and pale stems. The evolutionary lines between these species

and their allies of the Old World can not be satisfactorily worked out at this distance. It may be suggested, however, that because of its evident connection with *A. patula glabriuscula*, *A. maritima* is perhaps the most primitive, while *A. tatarica* evidences a higher degree of specialization than the others in the much more thorough separation of the two sexes in the inflorescence.

Because of its absence from all but the more recent American manuals, *Atriplex rosea* has been often wrongly identified. The inferior, or at least lateral position of the radicle is often overlooked and plants are then especially confused with *A. argentea*, *A. bracteosa*, and *A. pentandra arenaria*. It may be distinguished from the first by the narrower leaves, which taper to the base and are more sharply dentate; from *bracteosa* it differs in its much paler foliage and in the absence of the long, moniliform or spike-like staminate inflorescences; while *pentandra arenaria* may be easily recognized by the essentially entire and usually obtuse leaves. There are, of course, other and more constant although less obvious characters upon which these species are separated.

ECOLOGY.

Atriplex rosea, although an introduced weed, is so abundant in the West, especially in the arid portions, that it plays an ecological rôle of great importance. It is most characteristic of roadsides, fallow fields, and waste places, where it is often the pioneer consociates of the subseres, but it has also become abundant in alkaline valleys and plains, where it may form pure consociates, or may be mixed with native species of *Atriplex* or other halophytes. It is exceedingly variable in habit, ranging from typically branched forms a meter or more high to giant tumbleweeds 2 to 3 meters tall and wide. Under intense competition the plants are slender and unbranched and in extreme conditions they become dwarfs but a few centimeters in height. The tumbleweed habit has doubtless played a large part in the rapid migration of this species throughout the West, as it also explains its abundance in fenceways and roadsides. Owing to its size and abundance, this is one of the most important host-plants of *Eutettix tenella*, the leaf-hopper that carries the curly-top disease of the sugar-beet. In the West the plants bloom from July through September.

USES.

The herbage of the red orache has many uses in Europe, but none of them are of prime importance. Potash is obtained from it in Greece and it is utilized to a limited extent in medicine as an antiscorbutic and as a corrective for scrofula. No detailed study of the forage value of the plant has been made in America. In some parts of Nevada the young plants are highly prized for feeding to swine. It is said to be the cheapest and most satisfactory feed there available for fattening. On the other hand, recent experiments indicate that the plants are mildly poisonous to sheep when fed in large amount and to the exclusion of other material. An analysis is given by Suarez y Bermudez (Exper. Sta. Rec. 33:466, 1915). The plants grow so readily in the western States and on such poor soil that their possible utilization for stock-feeding, both direct and as silage, should be thoroughly tested.

The pollen has been found to be one of the causes of hay-fever of the late summer type in the West. Preliminary studies indicate that all species of the genus probably are potential causes of this malady, their relative importance depending more upon the abundance in which the plants grow in the populated districts than upon the specific properties of the different kinds. It does not follow, however, that an individual sensitive to one species is necessarily sensitive to all, since it is found that patients react differently to pollen of the various species. An extract of the pollen is used in making the tests, which consist of intradermal injections of extremely dilute solutions. If such

injection results in a definite reddened wheal, the conclusion is that the patient is super-sensitive to that particular pollen and treatment for desensitization is then begun by making injections at intervals with extracts of gradually increasing strength. When no further reaction is obtained, the patient is assumed to be immune from attacks of hay-fever from the species used. Although some people are sensitive to only one species of pollen, others react to two or more, in which case it is necessary to treat with all of these if perfect immunity is sought.

6. ATRIPLEX TATARICA Linnaeus, Sp. Pl. 1053, 1753. Plate 38.

Erect or spreading annual herb, 2 to 15 dm. or more high, widely branched from the base to form tangled masses or spreading plants; branches rather stout, obtusely angled, nearly glabrous, stramineous, the bark smooth and persistent; leaves alternate, except probably the lower, long-petioled or the upper nearly sessile, ovate or somewhat triangular, either subhastate or cuneate at base, acute or obtuse at apex, 3 to 6 cm. long, 2 to 4 cm. wide, deeply or shallowly sinuate-dentate or only undulate, the teeth acute or obtuse, thinly furfuraceous, usually greenish at least on the upper surface, soft and thin; flowers monoecious, the staminate glomerules in slender terminal spikes and panicles 3 to 15 cm. long, the pistillate fasciated in the upper leaf-axils; perianth 5-cleft, wanting in the pistillate flowers; fruiting bracts sessile, moderately compressed, united from the narrowed base to the middle, from broadly ovate to rhombic or nearly flabelliform, with wide foliaceous margins, 4 to 8 mm. long, 3 to 7 mm. wide, hard and indurated at maturity except for the broad foliaceous coarsely dentate margins, the sides tuberculate or smooth, strongly 3-nerved and reticulate; seed 1.5 to 2 mm. long, brownish; radicle inferior, ascending.

Introduced along the Atlantic and Gulf coasts from Connecticut to Alabama; widely distributed in the Old World. Type locality, Siberia. Collections: Connecticut, 1908, *Bissell* (Gr); on ballast, northern terminus of Eighth Avenue, New York City, 1879 and 1880, *Brown* (Gr, NY, US); on ballast, Greenwich Point, Philadelphia, Pennsylvania, 1874, *Parker* (Gr, NY); waste ground, Pensacola, Florida, *Curtiss 6865* (NY); Mobile, Alabama, July 22, 1896, *Mohr* (Gr, US).

RELATIONSHIPS.

The hardened fruiting bracts of this introduced species indicate that it is closely related to *A. rosea*. Its best distinguishing character is the wider separation of the two kinds of flowers, the staminate being assembled into elongated terminal spikes. The leaves are thinner than in *rosea*, not at all rigid, and are commonly subhastate and almost pinnatifid, so deep are the lobes, and the bracts are more nearly triangular because of the strong lateral angles. The introduced American plants, as far as seen, are fairly uniform in these characters. In the Old World is found a large series of forms, many of which have been named and described. These are based upon habit, color, shape of leaf, margins of bracts, and similar features. Twenty-one are described in Ascherson and Graebner's Synopsis of the Middle European Flora.

The misdetermination of certain collections of *A. tatarica* from the Southern States has led to the erroneous inclusion of *A. lampa* Gillies, a South American species, in the North American flora. The collections so referred are: Pensacola, Florida, *Curtiss 6865*, and Mobile, Alabama, July 22, 1896, *Mohr*. These specimens have monoecious flowers, the staminate in elongated spikes, the pistillate with triangular very acute bracts, while *A. lampa* is a shrub with dioecious flowers, the staminate in short rounded clusters, the pistillate with orbicular, very obtuse bracts.

ECOLOGY AND USES.

As an introduced ballast-plant of rare occurrence, *Atriplex tatarica* is unimportant, both ecologically and economically.

7. ATRIPLEX SEMIBACCATA Brown, Prodr. 406, 1810. Plate 39. FLESHSCALE;
AUSTRALIAN SALTBUUSH.

Prostrate perennial herb, becoming woody at base, the trailing stems sometimes as much as 15 dm. long; branches wiry, not angled, at first mealy, soon glabrate and then stramineous, the bark rough only on very old basal portions; leaves alternate, numerous, short-petioled, elliptic or elliptic-oblong, sometimes slightly spatulate, narrowed at base, acute or obtuse at apex, 1.5 to 3 or 4 cm. long, 0.3 to 1.2 cm. wide, irregularly and remotely repand-dentate or many entire, comparatively thin, gray with a fine dense scurf, or this thinner and the leaves then greenish especially on the upper surface, strongly 1-nerved from the base; flowers monoecious, the staminate in small terminal leafy-bracted glomerules, the pistillate solitary or in few-flowered clusters in the axils of nearly all but the uppermost leaves; perianth either 4- or 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile or on short stalks, convex and fleshy when fresh but compressed and nearly flat when dry, rhombic, 3 to 6 mm. long, 3 to 5 mm. broad across the middle, cuneate at base, acute at apex, united only below the middle, the margins denticulate or entire, the sides not appendaged but strongly 3- or 5-nerved (the nerves especially prominent when dry), fleshy-thickened and turning red in living plants; seeds of two kinds, one nearly black and only 1.5 mm. long, the other brown, about 2 mm. long, more convex, and with a groove near the margin; radicle lateral.

Native of Australia; introduced and naturalized in California, Arizona, and southern New Mexico; especially abundant in alkaline soil in the San Joaquin and Imperial Valleys and the coastal slope of southern California. Type locality, vicinity of Port Jackson, Australia. Collections, all from California, except as otherwise indicated: Rough and Ready Island, San Joaquin County, *Berg 28* (UC); Marin County, in a salt marsh, August, 1900, *Eastwood* (UC); near Bakersfield, October 23, 1919, *Hall* (CI); roadside near Ballona Lagoon, Los Angeles County, *Chandler 2020* (UC); Gardena, Los Angeles County, *Braunton 523* (UC); Avalon, Santa Catalina Island, *Millspaugh 4503* (UC); near Rincon, Riverside County, *Reed 374* (UC); La Jolla, *Millspaugh 4457* (UC); mesa near Otay, San Diego County, *Abrams 3522* (UC); Tucson, Arizona, *Jones* (Herb. Jones); Mesilla Valley, New Mexico (R); Alamogordo, New Mexico, according to Standley (Contr. U. S. Nat. Herb. 19:204, 1915).

SYNONYM.

1. ATRIPLEX FLAGELLARIS Wooton and Standley, Contr. U. S. Nat. Herb. 16:119, 1913.—Reduced to *A. semibaccata* by the authors of the proposed species (Contr. U. S. Nat. Herb. 19:204, 1915).

RELATIONSHIPS.

This is an Australian species the relationships of which have not been determined. The lateral position of the radicle and the nearly distinct fruiting bracts suggest that it is one of the more primitive forms.

ECOLOGY.

Although an introduced species, *Atriplex semibaccata* is now so thoroughly at home in California that it plays the ecological rôle of a native. Its habit of forming large spreading mats makes it an effective binder of sand and other bare soils, and hence it is a characteristic dominant of back-strands, sandy fields, and clay slopes, in the coast region especially. Its halophytic nature is indicated by nearly pure communities in saline flats and on sea-cliffs, where it is also often associated with *A. lentiformis breweri* and species of *Suaeda*. Owing to the protection it affords against erosion, this species regularly occurs as a relict along the eroding rim of bad lands of the Fernando formation, and is typical of the initial stages of such areas. It readily finds its way into roadsides, fallow fields, and other disturbed places, and it persists in annual grassland, where the dense mats are able to make headway in the competition with wild oats and the brome-grasses.

USES.

This species was introduced into America by the California Experiment Station in 1888 as a forage and hay plant for alkaline districts. Its cultivation was extended to all of the warmer parts of the State as rapidly as seed became available, and for more than a decade it was in high favor with stockmen, since it grew readily on land too poor for other crops. Although now much less highly prized, it is still useful as an adjunct to other browse and forage plants, especially for the purpose of carrying stock through unfavorable seasons. When other feed is plentiful, most animals avoid the Australian saltbush, as it is commonly known. Aside from its forage value for hogs, sheep, cattle, and horses, the foliage and seeds are eaten by poultry. In establishing the plant, the best results are obtained by first plowing and harrowing the land, after which the seed is sown broadcast or drilled, preferably just before a rain. The seed is regularly carried in stock by California seedsmen. The plants are killed by temperatures of about 14° F. and therefore can not be grown in cold regions. Further details and analyses are given in the reports and bulletins of the California Experiment Station (see especially Bull. 125, 1899). Analyses are given also by Headden (Colo. Exp. Sta. Bull. 135, 1908), who concludes with the following statement of facts, which he considers to have been established for this plant:

"First, when once established it will endure drought and even make a good crop with less than 5 in. of rainfall. Second, that stock will eat it or readily learn to eat it either green or as hay. Third, that it will produce very heavily under favorable conditions. Fourth, that it will, when fed alone, maintain the animals, and even better results are claimed for it. Fifth, that the hay is rich in protein, as rich or even richer than alfalfa. Sixth, that its coefficients of digestion are excellent, except for the fat or ether extract and crude fiber. Seventh, that it has no injurious effects on the animals even when they have no other fodder with it. The following facts, however, remain, that it has not become popular, and that when fed alone it does not produce the results that its composition and coefficients of digestion would seem to warrant us in expecting."

The most recent bulletin dealing with the culture and uses of this species in North America is one by McKee (U. S. Dept. Agr. Bull. 617, 1919).

The Australian saltbush is of economic interest also as a host plant for *Eutettix tenella*, the insect that carries the disease of the sugar-beet known as curly-top (see under *A. bracteosa*, p. 307). It is especially important in the Imperial Valley, California, where it serves to carry the insect over the autumn. Other autumn host plants are here almost wanting, so that if it were not for this *Atriplex*, the *Eutettix* would be much less plentiful or perhaps not able to persist.

8. *ATRIPLEX HALIMOIDES* Lindley, in Mitchell, Three Exped. East. Austral. 1:285, 1838.
Plate 39.

Erect spreading or procumbent perennial subshrub or herb, 1.5 to 4 dm. high; branches brittle, not angled, at first slightly white-mealy but soon glabrate and pale; leaves alternate, crowded, petioled, oblanceolate to rhomboid with a much narrowed base, acute at apex, 1 to 3 cm. long, 0.3 to 1.5 cm. wide, remotely repand-dentate or some entire, rather thin, white with a fine dense mealy scurf or less scurfy and greenish, 1-nerved; flowers monoecious, the staminate in short spikes in the upper axils, the pistillate solitary or in few-flowered clusters in the axils below; perianth 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile, not compressed but loose and spongy, the open tissue held together by strong web-like fibers, broadly turbinate or nearly hemispheric with a much depressed or flattened summit (apparently globoid in some pressed specimens), 6 to 12 mm. in diameter, united except at the minute valve-like apical tips, sparsely scurfy; seeds of 2 sorts, one kind 1.5 mm. long and dark reddish-brown, the other slightly smaller and black; radicle inferior.

Introduced from Australia; incompletely naturalized in southern California. Type locality, eastern Australia. Collections: Cockatoo Ranch, near El Nido, San Diego County, California, *Abrams 3527* (DS, Gr, NY, UC, US).

SYNONYM.

1. *ATRIPLEX LINDLEYI* Moquin, in DeCandolle, Prodr. 13: 100, 1849.—This name was given to the present species because of the earlier *A. halimoides* Tineo, which, however, has never been otherwise published than as a name in a garden catalogue (according to Bentham, Fl. Austral. 5: 179, 1870). There is also an *A. halimoides* Rafinesque (Amer. Mo. Mag. 2: 176, 1818), but this is universally regarded as the same as *A. patula hastata*.

RELATIONSHIPS.

This is not related to any American species. It differs from all native *Atriplexes* in the highly spongy bracts. This peculiar development is characteristic of several other Australian species, notably *A. holocarpa* and *A. vesicaria*. Both of these have been grown in American gardens with the thought of using them as forage plants, but neither has been found suitable for general planting.

ECOLOGY AND USES.

Atriplex halimoides is a native of the deserts of Australia, where it grows under extremely xerophytic conditions. It was introduced into California about 1885 and at first seemed to give much promise as a browse plant for alkaline districts. Seeds formed within a few months after sowing and when the plants were cut or pastured down a compact mass of soft new growth was formed (according to Wickson, Calif. Agr. Exp. Sta. Rep. for 1897-8:244, 1900). But this species did not become popular with farmers. The garden experiments were made mostly at Berkeley and in the Sacramento and San Joaquin Valleys, but the only known locality where *A. halimoides* escaped to wild conditions is in San Diego County. Chemical analyses of cultivated plants are reported by Shepard, Saunders, and Knox (S. Dak. Agr. Exp. Sta. Bull. 69:42, 1901) and by Knight, Heppner, and Nelson (Wyo. Agr. Exp. Sta. Bull. 65:50, 1905).

9. *ATRIPLEX DIOECA* (Nuttall) Macbride, Contr. Gray Herb. n. s. 53:11, 1918. Plate 40.
RILLSCALE.

Erect or spreading annual herb, 1 to 3 dm. high, branched from the base to form rounded plants usually 1 to 3 dm. broad, the twigs erect; branches rather stout, smooth, lightly furfuraceous when young but soon glabrous and dull green, the old bark whitish; leaves alternate, sessile, lanceolate or lance-ovate, either rounded or tapering to the base, acute or subacuminate at apex, 1 to 2.5 cm. long, 0.2 to 0.8 cm. wide (rarely up to 3.5 cm. long and 1 cm. wide), the upper ones moderately smaller, the margins entire, thickish and succulent, sparsely farinose when young, but soon glabrous and glaucous; flowers monoecious, the staminate in small glomerules which are widely separated in nearly naked terminal spikes and also in the upper leaf-axils, the pistillate solitary or few in the axils of the middle leaves, the two sexes mixing in some of the axils; perianth of staminate flowers cup-shaped, cleft into 4 or 5 lobes each with a fleshy crest on the back, of pistillate flowers minute, the 3 or 4 sepals distinct to the base; fruiting bracts sessile by a narrow base, compressed, united to the apex, ovate, about 2 mm. long, 1.5 mm. wide, herbaceous, not margined, the faces not appendaged but rough with a coarse scurf; seed 1.5 mm. long; radicle superior. (*Kochia dioeca* Nuttall, Genera 1:200, 1818.)

Alberta and Saskatchewan to western Nebraska, Wyoming, and Montana; the Nebraska plants were probably introduced, the seed having been brought in by stock cars, according to Bates (Asa Gray Bull. 6:35-37, 1898). Type locality, near Fort Mandan, North Dakota. Collections: Rosedale Trail, Alberta, *Moodie 1116* (DS, Gr, NY, US); southern Saskatchewan, *Macoun 1501* (US); Glen Allen, North Dakota, *Holzinger 30* (US); Owl Butte, South Dakota, *Griffiths 338* (US); Pennington County, South Dakota, *Over 1808* (US); Cretaceous hills below Fort Pierre, Nebraska Territory, June, 1853-54, *Hayden* (NY); South Fork Powder River, Johnson County, Wyoming, *Gooding 254* (DS, Gr, R, NY, UC, US); north of Baggs, Carbon County, Wyoming,

Osterhout 2637 (NY); Rock Creek Station, Wyoming, August 26, 1881, *Ward* (US); Teton River country, Montana, *Scribner 225* (Gr). Additional localities represented by specimens at the Rocky Mountain Herbarium include Wallace Creek and Sweetwater, Wyoming, northwestern Harding County, North Dakota, and Falls River County, South Dakota.

MINOR VARIATIONS AND SYNONYMS.

1. *ATRIPLEX ENDOLEPIS* Watson, Proc. Am. Acad. 9:110, 1874.—The same as *A. dioeca*.
2. *A. OVATA* Clements and Clements, Rocky Mts. Fls., 61, 1917.—*A. dioeca*.
3. *A. SUCKLEYANA* Rydberg, Mem. N. Y. Bot. Gard. 1:134, 1900.—This combination was proposed to avoid a conflict with *A. dioeca* Rafinesque (Am. Mo. Mag. 2:176, 1818). However, this latter was only incidentally mentioned by Rafinesque. In any event it would not interfere with the use of the name *dioeca* by those following the International Code, since Rafinesque had in mind a minor form of *A. patula*. *A. suckleyana* Watson, l. c., 111, 1874, is an entirely different plant, now referred to the genus *Suckleya*.
4. *ENDOLEPIS DIOECA* Standley, N. Am. Fl. 21:73, 1916.—*A. dioeca*.
5. *E. OVATA* Rydberg, Bull. Torr. Club 30:248, 1903.—The form with ovate 3-nerved leaves usually less than 1 cm. long. Type locality, Buffalo, Wyoming. The *Ward* specimen cited above belongs here, as also Goodding's 254. In the latter the leaves are 1 to 2 cm. long, mostly 3- or 5-nerved at the base, but some only 1-nerved, and is therefore somewhat intermediate to typical *dioeca*.
6. *E. SUCKLEYI* Torrey, in Gray, Pacif. R. R. Rep. 12:47, plate 3, 1860.—Exactly the same as *A. dioeca*, as indicated by the description and the excellent plate.
7. *KOCHIA DIOECA* Nuttall, Genera 1:200, 1818.—The first description of the species.
8. *SALSOLA DIOECA* Sprengel, Syst. Veg. 1:923, 1825.—*A. dioeca*.

RELATIONSHIPS.

The primitive position of *A. dioeca* is indicated by the presence of a well-formed perianth in the pistillate flowers. This perianth consists of 3 or 4 scales about as long as the ovary and apparently is never wanting. Because of its presence and the unusual shape of the calyx in the staminate flowers, Torrey, Standley, and others would make this species the type of a distinct genus, namely, *Endolepis*. The unreliability of the character of the perianth scales is seen in the related *A. phyllostegia*, where they may be either present or wanting, as will be more fully indicated under that species. These two and *A. monilifera* constitute a small group of succulent annuals of western North America. They are well separated geographically from one another and none of them is at all abundant.

ECOLOGY AND USES.

Atriplex dioeca is a characteristic pioneer in the bad lands of the West. Usually it occurs as small families in rillways or on tiny alluvial fans, but it is also associated with species of *Eriogonum* or *Atriplex* to form open colonies. Less commonly it makes a carpet of considerable extent on alkaline soils derived from the Mancos and other shales. The plants bloom from midsummer to fall. This species is usually too sparse and low to be of value even for grazing.

10. *ATRIPLEX MONILIFERA* Watson, Proc. Am. Acad. 9:111, 1874. Plate 40.

Spreading annual herb, the size not known but probably small, branched from the base, the twigs decumbent or ascending; branches leafy, hoary-farinoso, doubtless glabrate; leaves alternate, sessile, broadly elliptic or broadly ovate, 0.5 to 1.5 cm. long, 0.3 to 1 cm. wide, the upper ones scarcely reduced, broad at the base, obtuse or sometimes acute at apex, the margins entire or somewhat repand-dentate, thickish, densely gray-farinoso; flowers monoecious, the staminate in approximate glomerules forming terminal moniliform naked spikes, the pistillate flowers solitary in the leaf-axils; perianth of staminate flowers 5-cleft to the middle, each lobe with a thickened ridge down the back, of pistillate flowers described as consisting of 2 minute scales alternating with

the bracts; fruiting bracts and seeds probably as in *A. dioeca* but not known in mature condition.

Known only from the original collection from the dried bed of a lake in Bolson de Mapimi, Chihuahua, April 13, 1847, *Gregg* (Gr).

SYNONYM.

This species has been transferred to *Endolepis*, taking there the name *E. monilifera* Standley (N. Am. Fl. 21:73, 1916).

RELATIONSHIPS.

This species is so close to *A. dioeca* that on the basis of known characters the two might almost be united. It differs principally in the proportionately wider leaves, the dense staminate spikes, the more open and spreading perianth of the staminate flowers, and the densely mealy foliage. The wide geographic separation of the two suggests that further differences may be found when more abundant and fully mature material is available for study. The status of the genus *Endolepis*, to which this species has been referred, has been mentioned under *A. dioeca*.

ECOLOGY AND USES.

Nothing is known of the ecology and uses of this species.

11. ATRIPLEX PHYLLOSTEGIA (Torrey) Watson, Proc. Am. Acad. 9:108, 1874. Plate 40. ARROWSCALE.

Erect annual herb, 1 to 4 dm. high, branched throughout to form a rounded or pyramidal bushy plant, in some cases less widely branched and the plant then narrow and nearly columnar; branches slender, nearly terete, faintly striate, sparsely furfuraceous or glabrate, the pale bark persistent; leaves all alternate except one or two lower pairs, petioled or sessile, rhombic-triangular or hastate to broadly ovate or lanceolate, the terminal portion commonly elongate-lanceolate and acute or acuminate, obtuse or cuneate at base, 1 to 4 cm. long, 1 to 3 cm. wide, entire, thick and succulent when fresh, green, sparsely furfuraceous but glabrate, chartaceous when dry; flowers monoecious or the plants wholly pistillate, the staminate in small axillary glomerules near the ends of the branches, the pistillate clustered in all of the axils except the upper when these bear staminate flowers; perianth 5-cleft in the staminate flowers, sometimes present in pistillate flowers and then consisting of 1 to 4 scales as long as the seed or often much shorter; fruiting bracts sessile or subsessile or sometimes on stalks up to 15 mm. long, compressed, united only near the base, lanceolate or lance-oblong, often from a hastate cordate or winged base, the free tips attenuate and widely separated, 5 to 20 mm. long, 3 to 5 mm. wide at base, entire or deeply lacinate, the sides smooth, except for the 3 prominent ribs and cross-veinlets, or variously appendaged, the appendages sometimes linear and up to 4 mm. long; seed 1.2 mm. long, brown; radicle superior. (*Obione phyllostegia* Torrey in Watson, Botany King's Expl. 291, 1874).

Sandy soil, western Utah, Nevada, southeastern Oregon, and eastern California, extending across Tehachapi Pass and northward in the San Joaquin Valley nearly to Tracy. Type locality, between the Truckee and Humboldt Rivers, western Nevada. Collections: Gate of Gibraltar, Utah, June 3, *Engelmann* (NY); Dairy, Klamath County, Oregon, alkali basin, *Applegate 452* (Gr); Margin of Silver Lake, Lake County, Oregon, *Cusick 2787* (Gr, UC); Steamboat Springs, Nevada, *Lemmon 1142* (Gr); Truckee Pass and Hot Spring Mountains, Nevada, *Watson 986* (Gr, types); Wadsworth, near Clarks, Nevada, June 15, 1897, *Jones* (Herb. Jones, type of *A. draconis* Jones, minor variation 2); California: near Keeler, Inyo County, *Coville* and *Funston 875* (US, type of *Endolepis covillei* Standley, minor variation 3); Antelope Valley, *Davy 2196* (UC); Kern Lake, San Joaquin Valley, *Davy 2139* (UC); Chowchilla, Madera County, *Hall 11788* (UC). Additional localities are cited in table 25.

MINOR VARIATIONS AND SYNONYMS.

1. *ATRIPLEX COVILLEI* Macbride, Contr. Gray Herb. N. S. 53:11, 1918.—Based upon *Endolepis covillei*, which see in this list.

2. *A. DRACONIS* Jones, Contr. West. Bot. 8:40, 1898.—Characterized by an exceptional development of the basal lobes of the fruiting bracts. These lobes are wing-like and more or less lacinate, sometimes also with green ridges or teeth along their sides which "give the fruit a fantastic appearance, of halberd shape." These characters are exceedingly variable even on individual plants. In the type specimens many of the bracts have developed neither wings nor appendages, but are entirely smooth and narrowed to the base. The type of *draconis* was described as dioecious and the specimens exhibit a strong tendency to dioecism, but they are not purely so, the pistillate plants having a few staminate flowers, while at least some of the staminate plants are well supplied with pistillate flowers. The bracts of these latter, however, are only 2 to 4 mm. long and either arrested in their development or immature. The types came from between Wadsworth and Clarks, western Nevada, according to Professor Jones, the collector, who has himself made the reduction of his species to *phyllostegia* (Jones, Contr. West. Bot. 11:20, 1903).

3. *ENDOLEPIS COVILLEI* Standley, N. Am. Fl. 21:73, 1916.—The same as *A. phyllostegia*. Based upon plants in which a few scales, representing a reduced perianth, were found between the bracts of the pistillate flowers. Fully discussed under Relationships.

4. *E. PHYLLOSTEGIA* Rydberg, Bull. Torr. Club 39:312, 1912.—Based upon *Obione phyllostegia* Torrey (No. 5 of this list). Transferred because of the presence of a perianth in some pistillate flowers.

5. *OBIONE PHYLLOSTEGIA* Torrey, in Watson, Botany King's Expt. 291, 1874.—The original name for *A. phyllostegia*.

RELATIONSHIPS.

There is little doubt that *Atriplex phyllostegia* is very closely related to *A. dioeca*. It may, in fact, be a direct development from this, as is suggested by the frequent appearance of perianth scales in the pistillate flowers. These structures are only vestiges, apparently, even in *dioeca*, and *phyllostegia* may therefore be taken as the more advanced type, since they are sometimes present and sometimes entirely suppressed. The present species is the more highly specialized, as is shown by the remarkable development of unique features of the leaves and bracts, a notable tendency toward dioecism, and certain other details. (The other species is strictly monoecious, notwithstanding its name.) While *A. phyllostegia* is much like some forms of the *argentea* group in technical characters, there is no evidence that it was the starting point of these. The development of unusual features, especially the arrow-like foliage, indicates rather that it is the terminus of a short lateral branch of the evolutionary tree.

Perhaps nowhere in the three genera here treated is there a better example of the futility of attempts to establish and maintain genera on trivial characters than is furnished by the so-called genus *Endolepis*, to which a part of *A. phyllostegia* recently has been transferred. The unnecessary increase in synonymy and the resulting confusion which results from the incomplete examination of material is likewise well illustrated here. All of the opinions now to be cited are those of leading systematists. The differences in opinion and treatment may be taken, therefore, as an index of the efficiency of taxonomic methods, although it should be noted that the earlier workers were handicapped by a lack of abundant material.

Endolepis was first proposed as a genus by Torrey (in Gray, Pacif. R. R. Rep. 12²:47, 1860), with *E. suckleyi* as the only species. This is exactly the same as *Kochia dioeca* Nuttall, or *Atriplex dioeca*, as it is now called, the earlier Nuttallian name having been apparently overlooked. Torrey characterized his genus especially by "the remarkable calyx of the staminate flowers, and by the presence of a manifest 3-sepalous calyx in the fertile flowers." The feature of the staminate calyx still holds for *dioeca* and its close associate, *monilifera*. But the presence of a calyx in the pistillate flowers is of value as a character only as it furnishes a clue to relationships and shows how closely *Endolepis* is connected with *Atriplex*. The evidence of this is found in *A. phyllostegia*, described by Torrey 14 years after he established *Endolepis*. No calyx was found in the pistillate flowers at the time, but it is now well known that the calyx, which consists of a few

minute scales, may be either present or absent. These scale structures, or sepals, were first noted by Watson (Proc. Am. Acad. 9:108, 1874), who thereupon promptly reduced *Endolepis* to *Atriplex* (l. c., 110).

When Standley reached this group in his revision for the North American Flora, he attempted to sustain *Endolepis* on the basis of the perianth in the pistillate flowers, and he did this by the daring method of splitting *phyllostegia* into two species, assigning those plants without the perianth to *Atriplex phyllostegia*, while those with perianth were referred to his new *Endolepis covillei*, a species especially set up to receive them. An inconsistency resulting from this treatment was noted by Macbride (Contr. Gray Herb. N. S. 53:11, 1918), who pointed out that in the type species of *Atriplex* (*A. hortensis*) some of the pistillate flowers have a regular perianth, as called for in all modern descriptions, including that of Standley. Macbride then accepted *covillei* as a species and transferred

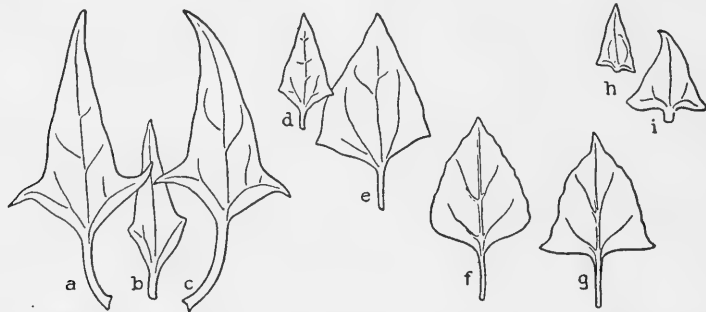


FIG. 32.—Leaves of *Atriplex phyllostegia* to illustrate variation in shape of blade and length of petiole; also to show lack of concomitance with flower characters: a, b, c, leaves from the type of the form called *A. covillei*, perianth present in pistillate flowers of this plant; d, e, f, g, leaves from the type of the form called *A. draconis*, perianth wanting in pistillate flowers; h, i, leaves as in genuine *A. phyllostegia* (Reno, Nevada, Curran, 185923 UC), perianth present as in *A. covillei*. All $\times 0.8$.

it to *Atriplex*, apparently without investigating the value of the character upon which it was based. As a result of the present study, *covillei* is found to be entirely devoid of substantiating characters and it can not be retained even in the most subordinate rank. An examination of the material in several herbaria shows conclusively that the perianth scales may be either present or absent, even on a single plant, and that when present the number varies from 5 to 1. The size also is variable, while the tendency toward complete reduction is not characteristic of plants of any particular geographic area, and can not be correlated with other characters. Most of these facts are perhaps sufficiently well brought out in table 25, which, however, lists only a portion of the collections examined. The others all point in the same direction. The lack of concomitance between width of leaf and the presence or absence of scales is incompletely shown by figure 32. Further evidence is furnished by plants from Fresno County, California, (Kearney 21, US), which although having comparatively narrow leaves, as in the type of *covillei*, have no perianth in the pistillate flowers. This collection carries genuine *phyllostegia* into middle California, while only *covillei* is accredited to this State in the North American Flora, a peculiarity in distribution to be taken into account by those who would retain the latter in specific rank.

The conclusion, therefore, is that *Atriplex phyllostegia* is in a fluctuating condition as far as the perianth of the pistillate flowers is concerned. This structure is to be looked upon merely as a vestige, sometimes consisting of several much reduced sepals, but

varying to a single minute scale and entirely disappearing in many cases. It possesses no value in classification and its presence or absence can not be used as a taxonomic criterion. Finally, many other features of this remarkable plant are also variable, giving to the species a degree of plasticity which enables it readily to adapt itself to varying ecologic conditions. Some of these additional variations were responsible for *A. draconis* Jones, a proposed species reduced to *A. phyllostegia* on evidence supplied by the type specimens, which were generously made available by Professor Jones. (See further under minor variation 2 of the above list.)

TABLE 25.—Variation in pistillate flowers of *Atriplex phyllostegia*.

Collection.	Herbarium.	Perianth.
Quinn River crossing, northern Nevada, <i>Griffiths and Morris 108</i>	402572 US	None.
Winnemucca, northern Nevada, <i>Griffiths and Morris 97</i>	402569 US	None.
Truckee Pass, western Nevada, <i>Watson 986</i> ¹	359070 US	None.
Hot Spring Mountains, western Nevada, <i>Watson 986 (type)</i> ¹	Gr	None.
Eagle Valley, western Nevada, <i>Baker 1251</i>	419436 US	4 scales.
Near Wadsworth, western Nevada, <i>Jones</i> ²	Jones	None.
Lovelock, western Nevada, <i>Griffiths and Hunter 542</i>	505740 US	3 scales.
Reno, western Nevada, September, 1887, <i>Curran</i>	185923 UC	5 scales.
Ash Meadows Ranch, southwestern Nevada, <i>Coville and Funston 370</i>	US	2 scales.
Amargosa Desert, southwestern Nevada, April 26, 1907, <i>Jones</i>	Jones	Varies, 0 to 2. ³
Near Keeler, Inyo County, Calif., <i>Coville and Funston 375</i> ⁴	48313 US	3 scales.
Mojave Desert, Calif., July 4, 1882, <i>Pringle</i>	Gr, US	Minute scales.
Rabbit Springs, Mojave Desert, Calif., <i>Parish 1346</i>	939200 US	3 with scales, 1 with no scales.
Bakersfield, interior Calif., August, 1885, <i>Leckenby</i>	468781 US	3 scales
Near Tulare Lake, Calif., <i>Palmer 2707</i>	278942 US	2 flowers with scales, 2 without.
Laton, Fresno County, Calif., <i>Kearney 21</i>	410815 US	None. ⁵

¹ Watson included two collections under his 986, either of which may be taken as the type. Both are from western Nevada and no perianth has been found in either of them.

² Type of *A. draconis* Jones, minor variation 2.

³ Ten flowers were examined of this collection; two of these were devoid of perianth, each of the others had 1 or 2 small scales.

⁴ Type of *Endolepis covillei* Standley, minor variation 3.

⁵ The result of 10 examinations.

ECOLOGY AND USES.

Atriplex phyllostegia may occur in clan-like groups in strongly saline soil, where it is associated with *Sarcobatus*, *Chrysothamnus nauseosus consimilis*, and *Distichlis*, or it may form families of some size in depressions in fallow fields and alkaline plains, especially where *Distichlis* has been plowed or otherwise disturbed. It is an indicator of strong alkali, to an amount of 3 to 4 per cent in the first foot, where the roots occur. The plants bloom for an unusually long period, namely, April to September, apparently in consequence of the relatively constant water-content.

This species is doubtless grazed, but it is too inconsiderable to be important.

12. ATRIPLEX CORDULATA Jepson, Pittonia 2:304, 1892. Plate 43. HEARTSCALE.

Erect rigid annual herb or spreading as the result of grazing, 1 to 5 dm. high, either simple or branched throughout; branches heavy, rigid, not angled, furfuraceous, glabrate in age, the bark then stramineous and exfoliating; leaves alternate except the lower, closely sessile, ovate, all cordate at base except the lowest which are merely rounded to a slightly narrowed base, acute at apex, 0.5 to 1.5 cm. long, 0.3 to 1 cm. wide, entire, rather thick, heavily coated with a furfuraceous tomentum which is only tardily deciduous, the veins then conspicuous; flowers monoecious, in dense glomerules in the axils of all but the few lowermost leaves, the staminate confined to the upper axils but not forming naked spikes; perianth 4-cleft or 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile or subsessile, lightly compressed, united to about the middle, typically ovate from a broad base, often slightly rounded to a very short stalk, usually broadest below but

sometimes at the middle or even slightly above (and then approaching flabelliform) by an exceptional development of the free margins, 4 to 5 mm. long, 4 to 5 mm. broad, the green foliaceous margins irregular and acutely dentate, the faces smooth (except for a dense scurf) or with only a few short protuberances; seed 1.5 to 1.8 mm. long, deep reddish-brown, nearly black, shining; radicle superior.

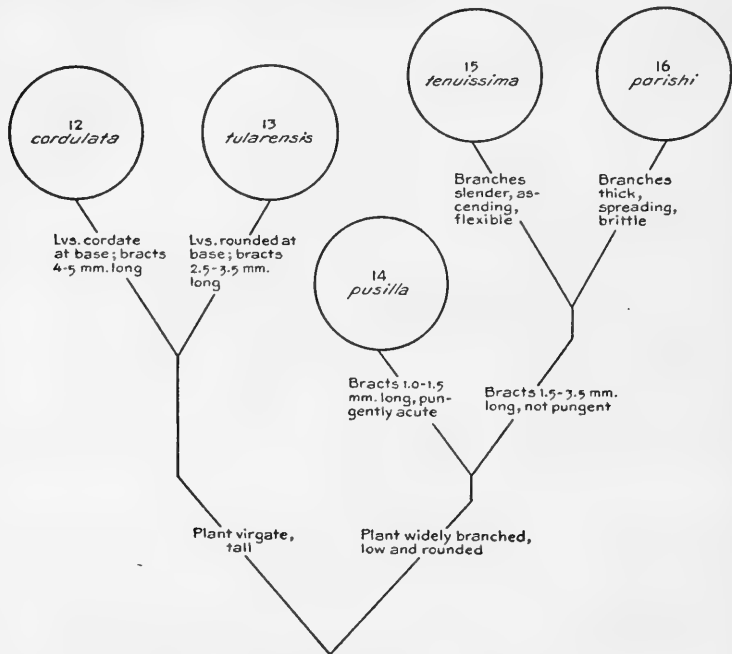


FIG. 33.—Phylogenetic chart of the *Atriplex pusilla* group.

Confined to California; Sacramento and San Joaquin Valleys; most common in the latter. Type locality, near Little Oak (just southeast of Vacaville), Solano County, California. Collections: North of Norman, Glenn County, scarce, *Hall 11007* (UC); type collection, August 16, 1892, *Jepson* (Herb. Jepson, NY, US); near Stockton, July 17, 1896, *Jepson* (Herb. Jepson); near Volta, Merced County, September 21, 1918, *Severin* (UC, strict, mostly simple-stemmed); same locality, July 20, 1920, *Hall 11017* (UC, both simple-stemmed and widely branched plants); 16 km. south of Merced, October 25, 1919, *Hall* (UC); near Chowchilla, Madera County, *Hall 11787*, *11790* (UC); Earlimart, Tulare County, *Hall 11786* (UC); between Tulare and Tulare Lake, *Palmer 2727* (NY, immature).

RELATIONSHIPS.

This species stands between *A. argentea* and the group of small-fruited species assembled by Standley under the sectional name *Pusillae*. In general appearance, especially the robust habit, it is more like the former. The bracts, however, are more like those of the latter, since they are for the most part widest below the middle. They are larger than any in the other species of the *Pusillae* and when the free margins are exceptionally

well developed the outline sometimes approaches obovate, the bracts then simulating those of the *argentea* group, even though the body itself is broadest at or below the middle. The bracts most closely resemble those of *A. coronata*, under which species the differentiating characters will be discussed.

The phylogenetic position of *cordulata* at the beginning of the *Pusillae* seems to be well established. It is less highly specialized than any of the others, each of which has undergone considerable reduction in the size of the foliage, flowers, fruiting bracts, and seeds. The development of certain other features will be pointed out later.

There has been no notable development of important variations within *A. cordulata*. This condition is associated with its restricted distribution. Two habit forms may be recognized, however. These are very unlike in their extreme development, yet all intervening stages are known and sometimes both are found at the same locality. They are illustrated even in the type material, which consists of three sheets with identical labels, except that one sheet is noted as the "small, strict form." This holds 2 plants, only 1.5 and 2 dm. high, respectively. One is simple-stemmed, the other has one very short branch. The other sheets have much taller and stouter plants, one with 5 branches from the base, each again forked, another with trunk-like leader and several strong lateral branches. Robust and much-branched bushy plants might easily be taken for a distinct species were it not for the close similarity to the simple-stemmed dwarfs in all essential characters and the presence of intermediate forms. Branching from the base is undoubtedly due to injury to the main shoot, most commonly as the result of grazing. The remarkably strict habit has been noted by Jepson (l. c.), who writes:

"The leaves on the virgate branches are much alike in size and form; they are triple-nerved and almost as broad as long; the lowest are rarely five lines long. The stem is sometimes absolutely strict, but usually the species is distinguished by its virgate branches. Sometimes the stems bear numerous very short branches which, however, rob the plant of nothing of its virgate aspect."

ECOLOGY AND USES.

Atriplex cordulata grows in hard, trampled soil that is only moderately alkaline. It may form pure stands in open spots in *Salicornia*, *Frankenia*, etc., or occur scattered in *Distichlis* turf with *Heliotropium curassavicum*, *Hemizonia pungens*, or *Helianthus annuus*. The flowers open from April to September.

This is a host-plant of *Eutettix*, the relations of which are described under *A. bracteosa*.

13. ATRIPLEX TULARENSIS Coville, Contr. U. S. Nat. Herb. 4: 182, plate 19, 1893.
Plate 41.

Erect rigid but slender annual herb, 2 to 10 dm. high, either simple or with strict ascending or erect stems, these sometimes from the base; branches rigid, brittle, terete or very obscurely angled, coarsely white-scurfy, early turning red, glabrate only near the root, many lateral branches of the upper parts arrested in their growth and forming very short imbricate-leafy shoots in the leaf-axils; leaves alternate except 2 or 3 lower pairs, sessile or subsessile, ovate to lanceolate, rounded to the base, acute or acuminate at apex, 1 to 2 cm. long, 0.4 to 0.8 cm. wide, entire, thin but firm, gray with a dense scurf, 1-nerved, sometimes with 2 additional faint nerves from the base; flowers monoecious, in small dense axillary glomerules, the lower of which are purely pistillate, the upper purely staminate, the sexes mixing in some of the intermediate axils; perianth 4-cleft in the staminate flowers, wanting in the pistillate, fruiting bracts sessile, lightly compressed, united nearly to summit, ovate in outline or some with narrowed base and then rhomboid and broadest at about the middle, 2.5 to 3.5 mm. long, 2.2 to 3 mm. broad, the thin margins few- to many-toothed, or only erose, the apex usually ending in a prominent ovate acute tooth, the faces neither tubercled nor appendaged but covered with a dense gray scurf; seed 1 to 1.2 mm. long, dark brown, shining; radicle superior.

Known only from alkaline plains of the southern part of the San Joaquin Valley, California. Type locality, about 25 km. south of Bakersfield, Kern County, California. Collections, all in California: type collection, July 13, 1891, *Coville 1235* (UC, US); same locality, *Severin and Hall 11782* (UC); plains 13 km. south of Bakersfield, *Severin and Hall 11783* (UC); plains south of Bakersfield, *Davy 2897* (UC).

SYNONYM.

1. ATRIPLEX CORDULATA var. TULARENSIS Jepson, Fl. Calif. 436, 1914.—*A. tularensis*.

RELATIONSHIPS.

This species is closely related to *A. cordulata*, as was expressed by Jepson in the above-quoted combination. Recent and detailed field studies of both species indicate, however, that they are not connected by intermediate forms. In judging from comparisons between the two as they grow under natural conditions, one would scarcely suspect them of being related. Also in detail there is sufficient difference for specific recognition. *A. tularensis* is a much more slender plant, the leaves are narrower in proportion to their length and never at all cordate at the base as in *cordulata*, but narrowed below. The shape of leaf is remarkably constant in both species. The fruiting bracts are sometimes very similar in shape, but those of *tularensis* typically end in an abrupt acute tooth not present in *cordulata* and both bract and seed are always smaller.

The small size of the bracts and their shape in some cases are very suggestive of a connection with *A. pusilla* and its allies. For these reasons *A. tularensis* was placed in the section *Pusillae* by Standley (N. Am. Fl. 21:50, 1916). It seems impossible to determine at the present time whether the direction of evolution was from *cordulata* through *tularensis* and then on to the true *Pusillae* by reduction in essentially all characters, or whether these last have developed from some entirely different source, such as *A. wolfei*.

ECOLOGY AND USES.

Atriplex tularensis grows typically in grassy alkaline flats in the southern portion of the San Joaquin Valley, where it is associated with *Distichlis*, *Elymus condensatus*, and *Sporobolus asperifolius*. It extends to the edge of the *Salicornia* belt, but is absent wherever *Salicornia* or *Spirostachys* occurs. It does not form distinct communities, but grows scattered among the grasses, apparently holding its own in the competition. The flowers occur from July to October.

The plants are grazed along with the grasses, repeated cropping giving them the branched form typical of pastures. They are also hosts of the beet leaf-hopper, but of restricted importance because of the limited range of the species.

14. ATRIPLEX PUSILLA (Torrey) Watson, Proc. Am. Acad. 9:110, 1874. Plate 41.
SMALLSCALE.

Erect annual herb, 0.5 to 2 dm. high, freely branched throughout but especially at the base; branches slender, not angled, sparsely furfuraceous, glabrate below, early becoming reddish; leaves all alternate, except 1 or 2 lower pairs, crowded and imbricate above, sessile, ovate or elliptic, narrowed or rounded to the base, acute at apex, 0.5 to 1.5 cm. long, 0.3 to 0.6 cm. wide, entire, thickish, somewhat fleshy, gray with a dense scurf or this sparse and the foliage then greenish, 1-nerved; flowers monoecious, usually 1 in each leaf-axil, sometimes 2, the staminate near the ends of the branchlets but never in naked terminal spikes; perianth either 4- or 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile, not compressed, united to the apex (united half their length, according to Torrey, but this apparently an error), ovate, abruptly acute, 1 to 1.5 mm. long, about 1 mm. broad, not margined, entire, the faces smooth; seed 0.8 mm. long, yellowish-brown (perhaps darker when mature); radicle superior. (*Obione pusilla* Torrey, in Watson, Bot. King's Expl. 291, 1871.)

Northern Nevada, southeastern Oregon, and northeastern California; range doubtless more extensive, but the plants easily overlooked. Type locality, near Carson City and on the edge of a dry alkali flat near the head of Humboldt Valley, Nevada. Collections: Nevada: Humboldt Valley, 1,220 m. altitude, *Watson 988* (Gr, NY, one of the type collections); Camp Halleck, Humboldt River Valley, *Palmer 454* (Gr); 4 km. west of Wells, Humboldt River Valley, *Hall 11033* (UC); 2 km. northeast of Wells, *Hall 11034* (UC); near Carson City, *Anderson 65* (Gr, NY, one of the type collections); same locality, June 4, 1897, *Jones* (Herb. Jones); Harney Valley, Oregon, *Howell 537* (Gr); same locality, *Cusick 1663* (DS, Gr, UC); Chat, eastern Lassen County, California, June 19, 1897, *Jones* (Herb. Jones); "California," August and September, 1872, *Torrey* (US).

SYNONYM.

1. *OBIONE PUSILLA* Torrey, in *Watson, Bot. King's Expl. 291, 1871.*—*Atriplex pusilla*.

RELATIONSHIPS.

This was the first described species of a small group of *Atriplex* characterized by the small size, slender branching habit, and minute ovate fruiting bracts borne singly or at least sparsely in the leaf-axils. It differs from the others, that is, from *A. tenuissima* and *A. parishi*, in the even smaller and uniformly smooth bracts, as well as in details of habit and leaf. These bracts are remarkably constant in their shape, which is ovate with abruptly narrowed tips, and in the total absence of teeth and appendages. These characters hold for all herbarium specimens examined and for several hundred plants studied in the field, mostly in the vicinity of Wells, Nevada.

The origin of *A. pusilla* is not known. In habit it is most like *A. wolfi*, a more easterly species, but the fruiting bracts of that are so highly specialized in shape that their modification into the more primitive ovate type seems scarcely probable. As far as the bracts are concerned, it might be looked upon as a derivative of the Californian *A. tularensis*, in which the bracts have lost their dentations and been much reduced in size. But in other features these two are very unlike. When compared with the other species (*tenuissima* and *parishi*) of its own small group, it is seen that *pusilla* can not be taken as the beginning of this branch, because of its greatly reduced and otherwise modified bracts and seeds. Neither can it be considered as a derivative of either of the other members, since each of these exhibits strongly specialized features. Thus, it becomes necessary to consider each of the three species as an isolated phylogenetic unit. Taken together they form a natural group which probably originated through a divergence from the main line somewhere near *A. cordulata* and *A. tularensis* and before either leaves or bracts had assumed the oblanceolate, obovate, or cuneate shape.

ECOLOGY AND USES.

Atriplex pusilla is a delicate annual that forms pure societies on alkaline flats between bushes of *Sarcobatus*, or grows in disturbed spots in communities of *Sarcobatus*, *Distichlis*, and *A. rosea*. The plants bloom from June through August.

This species is too delicate and too rare to be of economic importance.

15. *ATRIPLEX TENUISSIMA* Nelson, *Bot. Gaz.* 34:359, 1902. Plate 41.

Erect annual herb 1.5 to 3 dm. high, intricately branched throughout; branches slender, elongated, ascending, sometimes zigzag, not angled, moderately white-scurfy to the base, reddish except near the ends; leaves alternate except perhaps the lower, numerous, sessile, lance-ovate to linear (especially in minor variation 1, *A. greenii* Nelson), rounded to the base, acute at apex, 1 to 2 cm. long, 0.2 to 0.3 cm. wide, thickish, densely gray-scurfy, 1-nerved; flowers monoecious, several in each of the leaf-axils except near the base

of the plant, the staminate confined to a few of the upper axils; perianth 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile, thick, united nearly to apex, ovate, acute, 2 to 3 mm. long, 1.5 to 2.2 mm. broad, not margined, sparsely and minutely toothed along the edges, the faces bearing a few short acute tubercles, especially across the middle; seed, 1 to 1.2 mm. long, yellowish-brown; radicle superior.

Known only from southwestern Wyoming and eastern Utah. Type locality, Gunnison, Utah, altitude about 1,600 m. Collections: Type collection, September 15, 1900, *Jones 6525* (Herb. Jones, NY, St. Louis, UC); Rock Springs, Wyoming, August 9, 1896, *Greene* (R, NY, UC, type collection of *A. greenei* Nelson, minor variation 1).

MINOR VARIATION.

1. *ATRIPLEX GREENEI* Nelson, Bot. Gaz. 56:65, 1913.—Differs in having narrowly linear leaves, the larger of which are 1 to 1.5 cm. long by only 1.5 mm. wide, and in the bracts, which are described as appendaged at the middle or above. The leaves in the type of *tenuissima* are described as oblong to lance-ovate or broader, 1 to 7 mm. long; in the only material now at hand (duplicates of the type) they are mostly ovate to linear-oblong, the widest 5 mm. long by 2.5 mm. wide. But proceeding down the stem, the leaves progressively approach the linear shape of *greenei*, one measuring 6.6 mm. long by 2 mm. wide. The bract differences are as described as far as the general tendency is concerned. That the difference in the distribution of the appendages is not so sharp as supposed is indicated by the accompanying text-figures. The single collection thus far made of each of these forms does not furnish sufficient evidence for the final disposal of *A. greenei*, either as a distinct species or as a minor variation of *A. tenuissima*, but from the nature of the differentiating characters it is predicted that intermediate forms will be found, in which case the latter will be the preferred course.

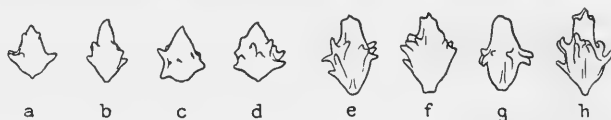


FIG. 34.—Fruiting bracts of *Atriplex tenuissima* to illustrate the distribution of appendages in the type and in a minor variation: a, b, c, d, bracts from the type specimen (Missouri Botanical Garden Herbarium); e, f, g, bracts from the type specimen of minor variation 1, *A. greenei* Nelson (Rocky Mountain Herbarium); h, bract from a duplicate of *A. greenei* (New York Botanical Garden Herbarium). All $\times 6$.

RELATIONSHIPS.

Atriplex tenuissima is most closely related to *A. pusilla*, but is sharply set off by its more numerous flowers in each of the glomerules and especially by its larger and constantly tuberculate fruiting bracts and larger seeds. The relationship to this species and the probable origin of the group are discussed under *A. pusilla*. In describing the type, which is at the herbarium of the Missouri Botanical Gardens, Nelson says that only the pistillate plant was seen. However, the species is not dioecious, for duplicates of the type collection bear both kinds of flowers. It is probable that the staminate flowers had all matured and dropped from the plant examined by Nelson. In the only other collection (Rock Springs, Wyoming, *Greene*) the plants are also monoecious.

ECOLOGY AND USES.

Nothing is known concerning the ecologic relations of this species, but probably they are similar to those of *A. pusilla*. It has no uses.

16. *ATRIPLEX PARISHI* Watson, Proc. Am. Acad. 17:377, 1882. Plate 41. BRITTLESCALE.

Erect but often seemingly prostrate rigid annual herb, 0.5 to 2 dm. high, widely branched throughout; branches numerous, rather stout, brittle, often horizontally spreading, coarsely white-scurfy, the scurf sometimes so long as to simulate a true pubescence, tardily glabrate, faintly tinged with red; leaves varying from all opposite to mainly alternate, numerous, the upper ones imbricate, closely sessile, ovate, the lower lanceolate,

broadly rounded to the base, acute at apex, 0.4 to 1 cm. long, 0.3 to 0.5 cm. wide, entire, rigid, gray or nearly white with a dense scurf, 1-nerved; flowers monoecious, several in each of the leaf-axils, the staminate in the middle and upper axils, the pistillate in the middle and lower axils; perianth of staminate flowers 4- or 5-cleft, wanting in the pistillate; fruiting bracts sessile, slightly compressed, united to a little above the middle, ovate or rhomboidal, often subhastately lobed, acute, 2.5 to 3.5 mm. long, 2.5 to 3 mm. broad, narrowly margined, entire or with a prominent tooth on each side, the faces smooth to muricate; seed about 1.2 mm. long, dark brown or nearly black when fully mature; radicle superior.

California, from the upper Sacramento Valley nearly to the southern border, east to the edges of the Mojave and Colorado Deserts. Type locality, Costa Station, Los Angeles County (now Almond, Orange County), California. Collections, all from California (all but the last 7 referable to minor variation 1, *A. depressa* Jepson, and some also to minor variation 2, *A. minuscula* Standley): Willows, Glenn County, *Hall 11005* (UC); near Norman, Glenn County, *Hall 11006, 11013* (UC); west of Vanden, Solano County, September 22, 1891, *Jepson* (Herb. Jepson, type of *A. depressa* Jepson, minor variation 1, also US); Altamont Pass, *Hall 10975* (CI); 2 km. north of Volta, Merced County, July 20, 1920, *Hall* (CI); Laton, Fresno County, *Kearney 33* (US, lower leaves opposite, the upper all alternate); same locality, *Kearney 34* (US, all leaves opposite); 20 km. east of Dos Palos, Fresno County, *Hall 11756* (UC); near Chowhilla, Madera County, *Hall 11769, 11789* (UC); Goshen, Tulare County, about the station, September 1, 1905, *Brandege* (UC); Visalia, Tulare County, October, 1881, *Congdon* (UC); between Tulare and Tulare Lake, *Palmer 2728* (US, type of *A. minuscula* Standley, minor variation 2); Cushenberry Spring, south edge of Mojave Desert, *Parish* (US); Bixby, Los Angeles County, *Brandege* (UC); type collection, October, 1881, *Parish 1119* (DS, Gr, US); Santa Monica, *Davidson 2936* (US); brackish flats near Cahuenga, Los Angeles County, *Hasse 5670* (NY); alkali flats, Laguna, Orange County, May, 1907, *Minthorn* (UC); southeastern base of San Jacinto Mountain, at Vandeverter Flat, *Hall 2146* (DS, NY, UC, US); Coahuila Hot Springs, San Diego County, *Parish 1119a* (Gr).

MINOR VARIATIONS.

1. *ATRIPLEX DEPRESSA* Jepson, *Pittonia* 2:304, 1892.—This has been reduced to *A. parishi* by Jepson (Fl. Calif. 436, 1914), a disposal with which the present authors agree. It was retained by Standley (N. Am. Fl. 21: 50, 1916) principally on three characters, namely, the branches not "copiously villous," the alternate leaves, and the slightly smaller fruiting bracts. A re-examination of the types and of extensive collections now at hand proves only the first of these to be of value and even this is of but minor importance. In the type of *parishi* and in three other collections from southern California the branches, especially near the ends, are apparently villous, while in all material from farther north, that is, from the area of *depressa*, the branches are merely scurfy. But this difference is one of degree only, for the "villosity" of the southern plants is due to the same transparent scurf as found in northern plants, except that the individual scales are more elongated and therefore hair-like. Since this elongation of the scurf is a constant feature of all of the southern plants, of which, however, there are only four collections, it may suffice for those who draw exceedingly fine lines between species. As to the opposite arrangement of the leaves, this can be associated neither with the character just mentioned nor with geographic distribution. For example, in Madera County, California, opposite-leaved and alternate-leaved plants grow side by side, and plants with leaves partly opposite and partly alternate are not uncommon in the San Joaquin Valley (e. g., *Hall 11756*, UC, and cf. plate 41, fig. 16). The type of *A. parishi* at the Gray Herbarium has mostly alternate leaves. A duplicate of the same collection at the United States National Herbarium has only opposite leaves, or an occasional leaf slightly displaced from its opposite position. Finally, as to size of bract, an examination of the type of *depressa* discloses the fact that mature bracts are 3 mm. long, exactly the size given for *parishi* (see plate 41, fig. 22). The average size of the bracts of northern plants is about the same as that of bracts from southern specimens. Thus *depressa*, if retained as a taxonomic unit, must be based solely upon the shorter scurf of the branches, a character which doubtless will be found to be variable as further collections become available for study. The type locality is "low saline spots, near the alkaline springs, point of the Pelevo Hills, west of Vanden," Solano County, California.

2. *A. MINUSCULA* Standley, N. Am. Fl. 21:51, 1916.—No characters can be found upon which to retain this proposal as distinct from *parishi*. The scurf of the branches consists merely of short scales, as in the preceding variation, under which the value of this feature is discussed. The leaves are mostly alternate, as in typical *parishi*, but leaf-scars and branches on the type indicate opposite leaves for about one-fourth the way up. The fruiting bracts are 2 to 3 mm. long and smooth on the sides, although the margins are dentate or crenulate. The presence or absence of appendages is much too variable a character to be used here. Both kinds of bracts are often found on the same plant and in some cases even in the same pair (see for example, plate 41, fig. 22). It has been noticed that on some plants one bract of each pair, namely, the one facing the adjacent leaf, is smooth, whereas the one on the stem side is muricate; thus, since the fruits are horizontal all of them appear to be muricate as one looks from above upon the living plant (*Hall 11005*). Type locality, between Tulare and Tulare Lake, California.

RELATIONSHIPS.

This species belongs to a group of three, the origin and relationships of which are but little known. The probable connections have been indicated under *A. pusilla*. In connection with the original description, Watson stated that *A. parishi* belonged to the *patula* group, but the superior radicle, as well as an absence of similarity in nearly all other features, indicates that this was an erroneous assignment. The short, stiff, scale-like leaves and the very rigid stems, which become brittle and break into short joints at maturity, are unlike those of any other *Atriplex*. The plants have been described as prostrate, but they are perhaps never truly so, except by injury to the main axis or through trampling. However, the lateral branches commonly spread horizontally, so that the lower ones recline on the ground and in some herbarium specimens all are flattened out and apparently prostrate. The outline of the whole plant when permitted to develop normally is approximately hemispheric, as shown in the thumb sketch (plate 41).

ECOLOGY AND USES.

Atriplex parishi forms families in areas of white alkali, often surrounded by *Distichlis*, or mixes with *A. fruticulosa* and *Distichlis* in similar areas. It also occurs on disturbed saline soil with *Frankenia*. It is evidently more resistant to alkali than is *Hemizonia pungens*, as it grows vigorously where the latter is small and sparse. The plants bloom from May to September.

This is an important host-plant of *Eutettix* in the San Joaquin Valley.

17. ATRIPLEX TRUNCATA (Torrey) Gray, Proc. Am. Acad. 8:398, 1872. Plate 42. WEDGESCALE.

Erect annual herb (somewhat decumbent in minor variation 2, *A. subdecumbens* Jones), 2 to 10 dm. high, with ascending branches throughout or unbranched (minor variation 1, variety *stricta* Gray); branches slender, angled, lightly furfuraceous, early glabrate, the bark then dull-white or reddish; leaves alternate or the lower ones perhaps opposite, mostly sessile, deltoid or triangular-ovate or rounded-ovate, rarely approaching oval, broad and truncate or subhastate or rarely rounded at base, acute or obtuse at apex, 1 to 3 or 4 cm. long, 0.8 to 2 cm. wide, entire or only undulate, thin, grayish furfuraceous especially beneath, tardily glabrate; flowers monoecious, in small glomerules of the middle and upper axils, the upper glomerules mostly or entirely staminate but a few staminate flowers often in the lower clusters also; perianth of 4 or 5 sepals in the staminate flowers, wanting in the pistillate; fruiting bracts sessile or on very short stalks, scarcely compressed, united to the summit, broadly cuneate, truncate at summit, 2 to 3 mm. long, 2 to 3 mm. broad, the green margins developed only across the summit and here with 2 to 4 minute teeth, the faces smooth or rarely with 1 or 2 minute tubercles, the scurf obscure and the veins and reticulations prominent; seed 1 to 1.5 mm. long, light brown

to dark amber, shining; radicle superior. (*Obione truncata* Torrey, in Watson, Bot. King's Expl. 291, 1871.)

Great Basin of western North America and adjacent territory; Montana to eastern Colorado, northwestern New Mexico (according to Standley), eastern California, eastern Washington, and British Columbia; apparently most plentiful in Idaho. Type locality, near Carson City and on the Truckee River, Nevada. Collections: Armstead, southwestern Montana, *Hall 11502, 11562* (UC); Bitter Creek, Green River, Wyoming, *Nelson 8141* (Gr); near Fountain, Geysers County, Wyoming, *Mearns 3170* (US); Laramie, Wyoming, *Johnston 2333* (UC); 3 km. east of Longmont, Colorado, not common, *Hall 11074* (UC); Argo, Denver, Colorado, *Eastwood 70* (UC, US, minor variation 1, var. *stricta* Gray); Fish Lake, Utah, *Jones 5745* (Herb. Jones, NY, UC, US, type collection of *A. subdecumbens* Jones, minor variation 2); Salt Lake City, Utah, *Jones 1306* (DS, Gr, US); Nevada: San Antonio Desert, *Purpus 6418* (UC, US, minor variation 1, variety *stricta* Gray, in part); Smoke Creek, *Griffiths and Hunter 509* (US); type collections, near Carson City, *Anderson 40* (Gr, NY) and northwestern Nevada, *Bailey 987* (Gr); Sparks, *Hall 11025* (UC); Palisade, August, 1885, *Brandege* (UC); Wells, Humboldt River Valley, *Hall 11035* (UC); California: Randsburg, 1913, *Brandege* (UC); Monache Meadows, southern Sierra Nevada, *Purpus 3007* (UC, minor variation 2, *A. subdecumbens* Jones); Benton Hot Springs, Mono County, *Hall 11699* (UC); Bridgeport, Mono County, *Hall 11693* (UC); Loyalton, Sierra County, *Eastwood 7859* (SF); eastern Oregon, *E. Hall 433* (Gr, type of variety *stricta* Gray, minor variation 1); Klamath Agency, Oregon, *Walpole 2310* (NY, US); Alma, Okanogan County, Washington, *Elmer 531* (NY, US); Idaho: Weiser, September 20, 1919, *Hall* (UC); Twin and Shoshone Falls, *Nelson and Macbride 1373* (DS, Gr, NY, UC, US, minor variation 1, variety *stricta* Gray); New Plymouth, Cañon County, *Macbride 323, 715* (DS, UC); Pocatello, *Palmer 412* (Gr, NY, UC, US); Leadore, *Hall 11507* (UC); near Egbert Spring, Douglas County, Washington, *Sandberg and Leiberg 372* (SF, UC); Donald, British Columbia, August 10, 1890, *Macoun* (Gr). Additional localities, mostly represented by specimens in the Rocky Mountain Herbarium, are Rawlins, Poison Spider Creek, Point of Rocks, Huttons Lake, Sheridan, Howell Lakes, Green River, Laramie River, and Granger in Wyoming; Windsor, Fort Collins, Boulder County, and Delta in Colorado; Marysvale and Gunnison in Utah; Wadsworth in Nevada; and Silver Lake, Ione, and Morrow County in Oregon.

MINOR VARIATIONS AND SYNONYMS.

1. *ATRIPLEX TRUNCATA* var. *STRICTA* Gray, Proc. Am. Acad. 8: 398, 1872.—Described from eastern Oregon plants as follows: foliis hastato-lanceolatis nunquam cordatis, inferioribus basi cuneatis; inflorescentia virgata minus foliata. This is an occasional development that appears at widely separated stations (e. g., Denver, Colorado, *Eastwood 70*, UC). Therefore it is doubtless an ecad. Perfectly simple-stemmed and rigidly erect plants are sometimes found, but along with them grow others with a few erect branches from the base. Along Green River, in Utah, the strict form grows on bottom-lands where partly shaded.

2. *A. SUBDECUMBENS*, Jones Proc. Calif. Acad. II, 5: 716, 1895.—Plants low, branched from the base and the short branches subdecumbent; leaves only 0.5 to 1.5 cm. long, mostly rounded or narrowed to the base. Type locality, Fish Lake, Utah, 2,750 m. altitude in gravelly meadows (*Jones 5745*). The extreme of this form is strikingly different from the rigidly erect plants characteristic of true *truncata*, but the difference is scarcely greater than between the extremes of *A. cordulata* or even of *A. argentea* (compare the minor variation of the latter listed as variety *hillmani*). The small narrow leaves are remarkable, but even in the type collection some are ovate from a broad base which is abruptly narrowed to a petiole. Still broader leaves are found on plants in which the habit is decidedly decumbent (Monache Meadows, California, *Purpus 3007*, UC). Intermediate, both in habit and foliage are: Randsburg, California, 1913, *Brandege* (UC); Palisade, Nevada, August, 1885, *Brandege* (UC). Prostrate and erect plants, both with subhastate leaves, sometimes grow together (Leadore, Idaho, *Hall 11507*, UC). Decumbent plants are produced by injury to the main stem, as by grazing (Bridgeport, California, *Hall 11693*, UC).

3. *OBIONE TRUNCATA* Torrey, in Watson, Bot. King's Expl. 291, 1871.—*A. truncata*.

RELATIONSHIPS.

Atriplex truncata is closely related to *A. argentea*. The fruiting bracts have undergone a greater reduction in size and the free herbaceous margins have almost disappeared. The latter are represented by only a narrow and minutely dentate fringe across the summit. The strictly cuneate shape is quite different from anything known in *argentea*. In some specimens of the latter the margins of the bracts are so greatly reduced as to produce an appearance similar to the bracts of *truncata*, but the shape of the body, the size, and the foliage still indicate the form as only a deviation from true *argentea* (e. g., Hanford, California, Kearney 154 US). The connection with *A. wolffi* will be considered later (p. 279).

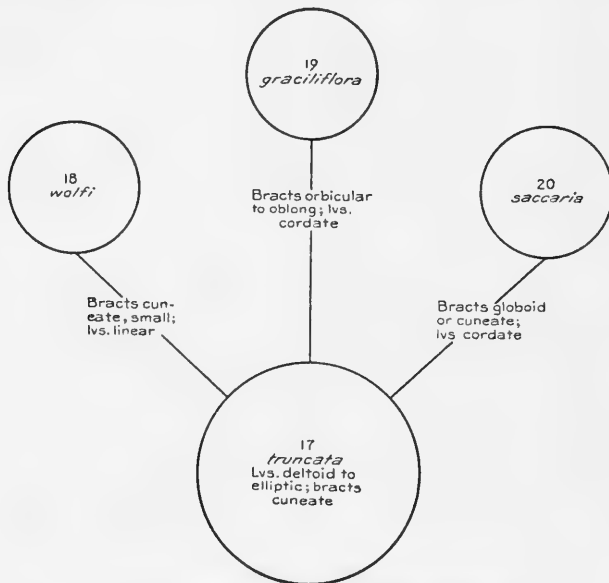


FIG. 35.—Phylogenetic chart of the *Atriplex truncata* group.

ECOLOGY AND USES.

Atriplex truncata resembles the other vigorous annuals of the genus in ecological behavior. It is primarily a halophyte, often growing in depressions white with alkali, where it is associated with *Distichlis* and *Chrysothamnus n. consimilis*, or it may occur in less alkaline soil with *Sporobolus airoides*. The range as to the salt-content of the soil is from about 0.2 to 3 per cent. It is most vigorous in low salt-contents, becoming dwarfed in soils with high amounts. In consequence it readily invades fallow fields and disturbed soils of low alkalinity, where it often forms a stage of the subsera. It is exceptional among related annuals in ranging to 9,000 feet in the mountains of Utah, and nearly as high in those of California as the depressed form, *subdecumbens*. It blooms early in the summer, and usually sets fruit by the middle of July.

In spite of its ruderal habit, this species never becomes a serious weed. It is grazed throughout its range, but furnishes a considerable amount of forage only in restricted localities.

18. ATRIPLEX WOLFI Watson, Proc. Am. Acad. 9:112, 1874. Plate 42.

Erect annual herb, 1 to 2 dm. high, branched from the base to form an obpyramidal ramose plant; branches ascending or spreading, very slender, tough, scurfy-canescens, glabrate, turning reddish with age; leaves alternate, except 1 or 2 lower pairs, numerous, sessile, linear or the lowest oblong-linear, obtuse or acutish at apex, 0.5 to 1.5 cm. long, 0.1 to 0.2 cm. wide, entire, thin, pale gray with a dense fine scurf, 1-nerved, often conduplicate; flowers monoecious, all axillary, the two kinds mixed in some of the axils but the staminate mostly toward the ends of the branches; perianth of staminate flowers 5-cleft, wanting in the pistillate flowers; fruiting bracts sessile or subsessile, compressed, united to the summit, cuneate-oblong, truncate and with 3 minute teeth at summit, 1.5 to 2 mm. long, about 2 mm. broad, the faces either smooth or with a few minute scattered tubercles, the veins obscured by the scurf; seed 1.5 mm. long, pale brown; radicle superior.

Southern Wyoming, Colorado, and Utah. Type locality, alkaline flats at Saguache, central Colorado. Collections: Fort Steele, southwestern Wyoming, *Tweedy 4495* (NY); type collection, September, 1873, *Wolf and Rothrock 277* (Gr, NY); North Park, Colorado, August 31, 1897, *Osterhout* (R); Grand Junction, Colorado, May, 1891, *Eastwood* (UC); Gunnison, Utah, 1,600 m. altitude, *Jones 6525* (US); Circle Valley, Utah, 2,140 m. altitude, *Jones 5987* (NY, UC, US). Other localities represented by collections in the M. E. Jones Herbarium, Salt Lake City, are Green River, Wyoming; Marysvale, Utah; and Ortons, Utah.

RELATIONSHIPS.

Atriplex wolfi is nearest to *A. truncata*, notwithstanding its very different appearance. The fruiting bracts are almost exact miniatures of some found on this species. Reduction has taken place also in the size and shape of the leaf and in the suppression of the petiole. The dainty habit and the small bracts suggest a connection with the *pusilla* group, and possibly it represents the beginning of this line. It is unlikely, however, that after a line had once developed the unusual shape of bract so familiar in *truncata* and in this species, there should be a reversion to the common type found in the *Pusillae*. Moreover, this group seems to have originated by an entirely different route, namely, through *argentea* and *cordulata*, as pointed out under the latter species. Whatever its origin, *A. wolfi* is now much restricted in its distribution and is not giving rise to new forms. Apparently it is especially adapted to peculiar conditions which it finds only in the easterly part of the Great Basin. It is probably much more common and occurs over a larger area than is indicated by the specimens cited, for the plants are small, delicate, short-lived, and easily overlooked by collectors.

ECOLOGY AND USES.

Atriplex wolfi occurs as a short-lived annual in saline areas, usually in the *A. confertifolia* consociation, often forming pure communities, but usually mixed with *Salsola*, and on lower areas with *Suaeda*. It is too delicate to be of value for grazing.

19. ATRIPLEX GRACILIFLORA Jones, Proc. Calif. Acad. II, 5:717, 1895. Plate 42.

Erect annual herb, 1 to 3 dm. high, widely branched from the base and also somewhat above, forming a flat-topped or more rounded plant 2 to 6 dm. across; branches curved-ascending, slender, brittle, not angled, sparsely furfuraceous, early glabrate, the bark then smooth and greenish-white; leaves alternate, except a few of the lowermost, all distinctly petioled, cordate-ovate or deltoid-ovate, cordate or broadly truncate at base, obtuse or acutish at apex, 1 to 2 cm. long exclusive of petiole, 0.8 to 1.6 cm. wide, entire, fleshy but drying thin, greenish, the scurf sparse, the veins evident; flowers monoecious, the staminate glomerules on short dense branches of terminal panicles, the pistillate all axillary (the plants fructiferous almost from the base); perianth of staminate flowers

5-cleft (as far as known), wanting in the pistillate; fruiting bracts long- or short-stalked or sessile, compressed, united to the summit, the body elliptic, but the whole bract orbicular through the development of marginal wings wider than the body, or these margins developing only above and the bract then oblong, 10 to 16 mm. long and broad, entire or undulate, the sides seldom appendaged, very sparsely scurfy, the midvein prominent and the reticulations of the margins sometimes evident; seed 3 mm. long, dull-white; radicle superior.

Known only from Utah. Type locality, Blue Valley, near the Henry Mountains. Collections, all in Utah: type collection, 1,220 m. altitude, in clay, July 30, 1894, *Jones 5697* (Herb. Jones, NY, R); Cainville, 1,370 m. altitude, *Jones 5656e* (according to Jones, l. c.); Price, September, 1888, *Jones* (Herb. Jones, many of the bracts with wings narrowed below the middle); near Moab, June 16, 1913, *Jones* (Gr); Emery, 2,140 m. altitude, *Jones 5443* (UC); foot of Book Cliffs, 16 km. north of Green River, *Hall 11042* (UC); near Bear Creek ranger station, Manti Forest, Utah, *Willey 284* (District Forest Herb. Ogden).

RELATIONSHIPS.

This species is too little known to justify positive statements as to its phylogeny. Jones has suggested a rank close to *A. canescens*, probably because of the remarkable wings to the bracts. But these wings are only expansions of the margins and there are no additional wing-like outgrowths from the middle line of each bract, as occurs in *canescens*. The herbaceous and monoecious habit, as well as all features of foliage and flowers, also indicates an absence of any direct connection. The shape of the bracts is very similar to that of *A. elegans*, but otherwise these two are very unlike.

A. graciliflora is more probably an offshoot from the *argentea-truncata-saccaria* line and is now restricted to peculiar soils where no other species can grow. Thus, it has become a relict without direct connections. It is more like *saccaria* than any of the other species, the similarity in habit, foliage, and inflorescence, being very close. Even the fruiting bracts are similar in shape when the wing fails to develop in *graciliflora*. However, even under these conditions the bracts are never strictly cuneate and they do not have the narrow terminal border of that species. The seed especially is unlike, being much larger and pale in color, a peculiarity that distinguishes *graciliflora* also from all other members of its group.

ECOLOGY AND USES.

Atriplex graciliflora resembles *A. saccaria* so closely that it appears to be a recent and local development of this, which has retained the vegetative structure and ecologic habits practically in their entirety. It forms small families in clay soils, and hence regularly grows in the Mancos and Mesa Verde shales of eastern Utah, where it behaves essentially like *saccaria* in habit and grouping. This species has no uses.

20. ATRIPLEX SACCARIA Watson, Proc. Am. Acad. 9:112, 1874. Plate 43. TWOSCALE.

Erect annual herb, 1 to 3 or 5 dm. high, copiously branched throughout to form a dense globoid bushy plant; branches stout, angled, roughly furfuraceous, glabrate only at the end of the season, the bark then white and cracking into flakes; leaves mostly alternate, all decidedly petiolate or the upper ones subsessile, broadly cordate-ovate or subreniform, cordate or some only broadly truncate at base, acute at apex, 1 to 3 cm. long exclusive of petiole, 1 to 2.5 cm. wide, entire, thick when fresh but drying thin, gray or nearly white with a rough scurf, rarely glabrate, the veins and reticulations prominent; flowers monoecious, the staminate glomerules in the upper axils and in open terminal panicles (these often lost in mature plants), the pistillate all axillary; perianth of stam-

inate flowers (always?) 5-cleft, wanting in the pistillate; fruiting bracts long-stalked to sessile, scarcely compressed, united to the summit, of two kinds, the smaller (normal?) ones cuneate, truncate at summit, 3 mm. long and nearly as broad, margined only at summit, the margin here undulate or with a few minute teeth, the sides smooth, the larger bracts (often in the same axils, sometimes scarce or reduced, as in the type), globoid through the development of numerous appendages, up to 6 mm. in diameter, thickly beset with flat or cristate appendages or some of these horn-like, all of the bracts densely scurfy and the veins not prominent; seed 1.8 to 2.3 mm. long, brown; radicle superior.

Middle and southerly parts of the Great Basin, in the warmer districts, in strongly alkaline clay soils; southwestern Wyoming and northern Utah to southwestern Colorado, western Texas, northern Arizona, and southern Nevada. Type locality, on the desert plains of southern Wyoming or northern Utah. Collections: Fort Bridger, Wyoming, July, 1873, *Porter* (Gr); type collection, "Wyoming-Nevada deserts," 1872, *Gray* (Gr); Marysville, Utah, June 5, 1894, *Jones* (UC); along San Juan River, near Bluffs, Utah, *Rydberg* and *Garrett* 9930 (NY, US); Green River, Utah, *Jones* 5481 (Herb. Jones, type of *A. cornuta* Jones, minor variation 2); near San Rafael River, Utah, *Hall* 11040 (UC); Naturita, southwestern Colorado, *Payson* 2327 (UC); El Paso, Texas, September 10, 1884, *Jones* (Gr); Ojo Alamo, San Juan County, New Mexico, *Hall* 11134 (UC); Billings, Arizona, October 8, 1884, *Jones* (Herb. Jones); Chalcedony Park, first and second petrified forests, Arizona, *Hall* 11155, 11163 (UC); Las Vegas, southern Nevada, June, 1915, *Brandegee* (UC); Caliente, southern Nevada, August 27, 1912, *Jones* (UC). Additional localities represented by specimens in the Jones Herbarium at Salt Lake City are the following, all in Utah: Marvine, Myton, Westwater.

MINOR VARIATIONS AND SYNONYMS.

1. *ATRIPLEX ARGENTEA* var. *CORNUTA* Jones, *Contr. West. Bot.* 11: 21, 1903.—This is merely a reduction of the earlier *A. cornuta*. The suggested connection with *A. argentea* can not be accepted, since the bracts, when not modified by appendages, are plainly of the *truncata* type and not at all like those of *argentea*. (See under *cornuta* of this list.)

2. *A. CORNUTA* Jones, *Proc. Calif. Acad.* II, 5: 718, 1895.—This is exactly the same as *A. saccaria*, as determined after an earlier comparison of the types, except that the fruiting bracts are covered with long appendages. Complete type material of *cornuta* is not at hand at this writing, but in specimens from the type locality, and indicated by Jones as *cornuta* (Green River, May 23, 1895), the bracts vary from large and bur-like, as described for *cornuta*, to narrow, cuneate, and smooth-faced. The presence of these cuneate bracts indicates very clearly that *cornuta* is the same as *saccaria* and that both have a connection with *truncata* rather than with *argentea*. Jones once reduced his species to a variety of the latter, but aside from the character just mentioned, it differs also in the cordate leaves and in the constantly better development of the staminate inflorescence.

3. *A. EXPANSA* *CORNUTA* Standley, *N. Am. Fl.* 21: 45, 1916, as synonym. This combination was due merely to an oversight. The combination intended by Jones is the one given under No. 1 of this list.

4. *A. TRUNCATA* var. *SACCARIA* Jones, *Contr. West. Bot.* 11: 20, 1903.—The reduction is made without comment. The reasons for retaining *saccaria* in specific rank will be given under Relationships.

RELATIONSHIPS.

Either this species is a direct development from *A. truncata*, or the two have evolved from a common stock after this had become separated from all other *Atriplexes*. This conclusion results from the close similarity in normal fruits. In the present species these fruiting bracts often are so densely covered with long, horn-like projections and cristate outgrowths that their original or primitive shape is entirely hidden. However, other bracts can be found, usually if not always on the same plant, which have not developed these appendages, and such bracts are practically identical with those of *truncata*. The peculiar cuneate shape occurs nowhere in the genus outside of the *truncata* group. The reduction of the free margin to a very narrow border across the truncate summit also is unique. On the other hand, the differences between *A. saccaria* and *A. truncata* are sufficient to justify the retention of both. The former never assumes

the open, strict habit of the latter; the leaves are for the most part cordate at base, always much broader in proportion to their length and hence more rounded-ovate; the staminate glomerules are always in well-developed, open, naked, graceful terminal panicles, instead of sessile in the upper axils, as they are in *truncata*.

A reduction to *A. argentea* has been suggested, as noted under the minor variations. But the differences here are even greater, for in addition to those just indicated as separating *saccaria* from *truncata*, the normal fruiting bracts are very unlike in shape and in the development of the free margins. However, there is a minor variation of *argentea* (*caput-medusae*) in which the bracts develop remarkably large appendages similar to those common in *saccaria*. Probably it was a comparison of plants in this condition that led to the taxonomic reduction just mentioned. The unappendaged bracts here furnish the dependable clue as to relationships, although the leaf and inflorescence characters also enable one to distinguish *saccaria* and *argentea* with certainty. It should here be noted that the latter occasionally develops an elongated staminate inflorescence. This, however, is rigid and spike-like, as compared with the slender, curving panicle of *saccaria*.

The original description of *A. saccaria* gives the bracts as "not at all appendaged." This was due to an oversight, for, while most of the bracts on the type-sheet are not appendaged, others, often in the same axils, bear a few appendages.

ECOLOGY AND USES.

Atriplex saccaria is the most typical indicator of bad-land shales. It is usually the first and often the pioneer in rillways and on the many small fans in Bad Lands, and not infrequently forms families on the crumbling slopes. The plants are typically low, compactly branched, and closely aggregated, both habit and grouping significant of the extreme xerophytic conditions and the precarious foothold. The salt-content usually ranges from 1 to 2 per cent, but is often much higher. In more stable spots this species is usually associated with *A. dioeca* or *Eriogonum divaricatum*. In ecological response it is practically identical with *A. graciliflora*, due to the fact that both grow in the same type of habitat.

This plant has rarely been found to be grazed, probably because of its high salt-content.

21. ATRIPLEX ARGENTEA Nuttall, Genera 1:198, 1818. Plates 43 and 44. SILVERSCALE.

Erect annual herb, 1.5 to 8 dm. high, freely branched from the base and globoid in outline, or rarely with few branches and more strict; branches stout, angled, furfuraceous when young, the whitish bark exfoliating in age; leaves alternate except the lowermost ones, sessile or subsessile or the lower ones decidedly petiolate, lanceolate, ovate or deltoid, 2 to 5 cm. long (exclusive of petiole), 1 to 4 cm. wide (smaller in minor variation 1), cuneate to subhastate at base (all narrowed to the base only in minor variation 9, *A. rydbergi* Standley), mostly obtuse or only slightly acute at apex, entire or repand-dentate, not exceptionally thickened, grayish-furfuraceous, glabrate; flowers monoecious, in axillary glomerules and in terminal interrupted spikes, the staminate and pistillate flowers usually mixing in the clusters, but the former mostly toward the ends of the branches and sometimes forming purely staminate spikes; perianth of 4 to 5 sepals in the staminate flowers, wanting in the pistillate; fruiting bracts sessile or subsessile, more or less compressed, united to the middle or above, obovate or cuneate-orbicular, 4 to 8 mm. long, 4 to 10 mm. wide, including the green foliaceous margins, which are subentire to variously lacinate, the faces smooth or appendaged or crested; seed 1.5 to 2 mm. long, brown; radicle superior.

Abundant in moderately alkaline soils of western North America and northern Mexico; southern Saskatchewan to western Texas, northern Chihuahua, California, and Idaho.

SUBSPECIES.

The characters of this species are subject to a wide range of variation, and it exhibits in consequence a considerable series of striking forms. This has led to the naming of 9 species and varieties segregated from what is here included under *A. argentea*. The characters used as bases for these segregates are themselves so variable and occur in so many combinations that many times this number would need to be accepted if one were to recognize all of the forms as they occur in the field. However, by the utilization of the features that seem to possess the greatest phyletic value, two principal stocks or subspecies may be distinguished. Other forms are better treated as minor variations.

Key to the Subspecies of Atriplex argentea.

Upper leaves short-petioled or subsessile. Distribution easterly from Nevada..... (a) *typica* (p. 283).
Upper leaves closely sessile. California to Texas..... (b) *expansa* (p. 284).

21a. *ATRIPLEX ARGENTEA TYPICA*.—Leaves all more or less petioled, the petiole from nearly as long as the blade on lower leaves to almost obsolete on upper ones; blades triangular-ovate or rounded-ovate, often subhastate. (*A. argentea* Nuttall, l. c.) In moderately alkaline soil, Saskatchewan to North Dakota, northern New Mexico, Nevada, northeastern California, eastern Oregon, and Idaho; also east to the Mississippi River, perhaps as an introduction. Type locality, on sterile and saline places near the Missouri River. Collections: Southern Saskatchewan, *Macoun 1496* (US); Glendive, Montana, September 2, 1892, *Sandberg* (DS, UC); Yellowstone Valley, Montana, August 19, 1898, *Setchell* (UC); Iroquois, South Dakota, August 11, 1894, *Thornber* (Gr, NY, UC); eastern Pennington County, South Dakota, *Over 1816* (US, minor variation 2, *A. caput-medusae* Eastwood); Upper Louisiana, *Nuttall* (Phila, "Pursh's specimen, ex-herb. Lambert"); Wyoming: Middle Fork Powder River, Johnson County, *Nelson 270* (UC); Seven-Mile Lake, *Nelson 2796* (R, type of *A. volutans* Nelson, minor variation 11); Fisher's Ranch, *Nelson 5319, 5320* (UC); Altamont, extreme southwest, *Johnston 2335* (UC); Albany County, *Nelson 8166* (Gr, NY, US); 5 km. east of Longmont, northeastern Colorado, not common, *Hall 11075* (UC); near Clear Creek and Sloans Lake, Denver, Colorado, *Eastwood 54, 104* (UC); Cañon City, Colorado, September, 1873, *Brandegee* (UC); Grand Junction, southwestern Colorado, *Baker 927* (Gr, UC, US); Kiowa Valley, western Nebraska, *Rydberg 325* (US, NY); salt-marsh, Lincoln, Nebraska (introduced?), September, 1890, *Rydberg* (US); Syracuse, Kansas (introduced?), *Thompson 145* (Gr, US); San Juan River, Utah, *Eastwood 116* (Gr, US, type collection of *A. caput-medusae* Eastwood, minor variation 2); Aztec ruins, northwestern New Mexico, *Hall 11125* (UC, same variation); south of Shiprock Station, northwestern New Mexico, *Hall 11145* (UC, same variation); Navajo Indian Reservation, northeastern Arizona, *Standley 7446* (US); Winslow, northern Arizona, *Hall 11175* (UC); Caliente, southern Nevada, August 7, 1912, *Jones* (DS); just east of Reno, Nevada, August 11, 1894, *Hillman* (Herb. Jones, type of *A. argentea hillmani*, minor variation 1); Peavine, western Nevada, July, 1913, *Brandegee* (UC, same variation); Truckee River near Vista, Nevada, *Hall 11027* (UC, same variation); Sierra Valley, northeastern California, *Leemmon 1206* (Gr, same variation); Malheur County, Oregon, *Cusick 1263* (Gr, US); Pocatello, Idaho, *Palmer 536* (US).

Additional localities in Nevada are cited under minor variation 1. Other stations represented mostly by specimens at the Rocky Mountain Herbarium include northwestern Harding County and Fall River County in South Dakota; Hanna, Gardiner River, Meadow Creek, Sheridan, Buffalo, Douglas, Glendo (Laramie County), Big Laramie River, Newcastle (Weston County), and Howell Lakes in Wyoming; Windsor,

Fort Collins, Pueblo, and Grand Junction in Colorado; Chadron in Nebraska; Wyandotte (rare, introduced) and Logan County in Kansas; Amedee in California; and Genoa in Nevada.

21b. *ATRIPLEX ARGENTEA EXPANSA* (Watson).—Lower leaves on petioles sometimes as long as the blade, the middle and upper leaves closely sessile, commonly erect or incurved through the axils; blades broadly cordate-ovate to lance-ovate, often subhastate but the lower sometimes tapering to the petiole. (*A. expansa* Watson, Proc. Am. Acad. 9:116, 1874.) In alkaline and often in fallow soil, northern Mexico to Arizona and California, most abundant in western Texas, southern New Mexico, and California, in the last-named State especially on alkaline areas of the coastal slope as far north as the region of San Francisco, and in the interior throughout the San Joaquin Valley, less plentiful in the Sacramento Valley. Type locality, not definitely stated, but the description drawn chiefly from specimens collected in the valley of the Rio Grande, western Texas. Collections: Valley of the Rio Grande, Paso del Norte, Chihuahua, *Pringle 1996* (Gr, NY, UC, US); "western Texas to El Paso, New Mexico," May to October, 1849, *Wright* (Gr, one of the types); El Paso, Texas, *Jones 4169j* (Herb. Jones); Barstow, western Texas, common, *Earle 631* (NY); Mesilla Valley, Doña Ana County, New Mexico, October 5, 1889, *Wooton* (US); California: National City, San Diego County, July, 1902, *Brandegee* (UC); Ramona, San Diego County, October, 1903, *Brandegee* (UC); San Bernardino, 1891, *Parish* (UC); Westminster, Orange County, September 10, 1901, *Byram* (UC); Ballona Lagoon, coast of Los Angeles County, *Chandler 2013* (UC); Los Angeles, *Braunton 138* (UC); Oxnard, Ventura County, *Davy 7822* (UC); Carpenteria, Santa Barbara County, October 18, 1919, *Hall* (UC); Lancaster, west end Mojave Desert, October 21, 1919, *Hall* (UC); dried bed of Kern Lake, San Joaquin Valley, *Davy 2910* (UC); west of McFarland, Kern County, October 24, 1919, *Hall* (UC); Earlimart, Tulare County, *Hall 11785* (UC); Hanford, Kings County, common in strongly alkaline soil, September 28, 1901, *Kearney* (US); south of Corcoran, Kings County, October 24, 1919, *Hall* (UC); south of Merced, very common, October 25, 1919, *Hall* (UC); Manteca, San Joaquin County, October 26, 1919, *Hall* (UC); fallow field at Livermore, Alameda County, *Hall 10964* (UC); Stockton, *Davy 1190, 1191* (UC); Brock Lane, near the Arequipa Hills, Solano County, September 22, 1891, *Jepson* (Herb. Jepson, type of *A. trinervata* Jepson, minor variation 10); west of Norman, Glenn County, Sacramento Valley, common, *Hall 11008* (UC).

MINOR VARIATIONS AND SYNONYMS.

A discussion of the value of the characters on which some of the following rest will be found under the heading of Relationships.

1. *ATRIPLEX ARGENTEA HILLMANI* JONES, Contr. West. Bot. 11:21, 1903.—This is a geographic form or race of *A. argentea typica*. It is common in northern Nevada, southeastern Oregon, and northeastern California. The only important character is the habit, the plants being low, rarely over 2 dm. high, although the branches are sometimes widely spreading. However, this trait is sometimes constant over extensive areas, as, for example, in the valley of the Humboldt River, especially along embankments. This variation appears to be a response to the more arid climate of those districts, which has left a sufficient impress upon the plant to make its character more or less permanent, or at least constant for that area. While the development of the plant is the most striking and constant character, the variety *hillmani* was based also upon other features. These were the crested bracts (which recur so frequently and without regularity in *argentea* as to be of no value as a criterion), together with the sessile character of these. It is only this last feature, and perhaps the size of plant, that separates *hillmani* from *caput-medusae* (No. 2 of this list), but this character has been demonstrated to be much too variable to be of significance. The following, the last four of which have both sessile and stalked bracts, the sides of which are both smooth and appendaged on the same plant, belong to this form: Nevada: East of Reno, August 11, 1894, *Hillman* (Herb. Jones, type); English Mill, near Reno, July 11, 1893, *Hillman* (US); Monitor Valley, *Watson 985* (Gr); Leonard Creek Ranch, northern Nevada, *Griffiths and Morris 346* (US); Battle Mountain, *Hitchcock 586* (US); same locality, *Kennedy 4001* (DS, US); Lemmon Valley, Washoe County, *Kennedy 2081* (DS, US); Sierra Valley, California, *Lemmon 1206* (Gr); Malheur County, Oregon, *Cusick 1263* (Gr, US).

2. *A. CAPUT-MEDUSAE* Eastwood, Proc. Calif. Acad. II, 6:316, plate 46, 1896.—The form or state of *A. argentea typica* in which the faces of most of the fruiting bracts are covered with flat, horny, acuminate, and often twisted processes, and the bracts themselves plainly stalked. Such plants are especially common in northern New Mexico, but field studies indicate that there is no dividing-line between this form and *typica*. The variability in the appendage character, also in the length of the stalks to the bracts, and in the distribution of the flowers is now well known (see, for example, plates 43 and 44). Similar but not identical bracts are sometimes encountered also in subspecies *expansa*. The type locality of *caput-medusae* is near Recapture Creek, along the banks of the San Juan River, southwestern Utah.

3. *A. EXPANSA* Watson, Proc. Am. Acad. 9:116, 1874.—*A. argentea expansa*.

4. *A. EXPANSA* var. *MOHAVENSIS* Jones, Contr. West. Bot. 11:20, 1903.—Differs from genuine *A. argentea expansa* only in the smaller and therefore sharper teeth along the margins of the practically sessile fruiting bracts. Principally Californian, although the other form occurs there also. Standley has added the smaller size of the bracts as a criterion (N. Am. Fl. 21:47, 1916). All of these differences are due to a reduction in the width of the herbaceous border in many Californian plants, so that the teeth are smaller and therefore seemingly more acute. These far-western specimens have bracts which are also more uniformly sessile or subsessile and with a less frequent tendency toward the formation of appendages. But as to dentation, the genuine *expansa* type of bract is also reproduced in western California on plants in which other bracts have only the narrow, finely dentate border (e. g., Redondo, *Piemeisel 3706*, US), and conversely, the *mohavensis* type sometimes occurs on plants from New Mexico (Mesilla Valley, October 5, 1889, *Wootton*, US), together with bracts of typical *expansa*. These conditions are illustrated in the accompanying plates and text-figures. As to the difference in the length of the stalk, it need only be said that the large series of specimens from Texas and New Mexico now in herbaria shows sessile about as often as stalked bracts, although in the *caput-medusae* type they are usually long-stalked, with ordinary sessile ones on the same plant (e. g., Archer County, Texas, *Reverchon 823*, US). Type locality of variety *mohavensis*, Mojave region to San Bernardino, California.



FIG. 36.—Fruiting bracts of minor variations of *Atriplex argentea expansa*: a, b, c, from western California (*Piemeisel 3706* US); d, e, f, from Mesilla Valley, New Mexico (*Wootton* US); g, h, i, from western Texas (*Earle 631* NY). All $\times 2$. (See under minor variation 4.)

5. *A. EXPANSA* *TRINERVATA* Macbride, Contr. Gray Herb. 53:9, 1918.—Based upon *A. trinervata*, which see.

6. *A. HILLMANI* Standley, N. Am. Fl. 21:48, 1916.—Based upon *A. argentea hillmani*, which see.

7. *A. MOHAVENSIS* Standley, l. c., 47.—Based upon *A. expansa mohavensis*, which see.

8. *A. NODOSA* Greene, Pittonia 1:40, 1887.—*A. argentea expansa*. An insect-stung monstrosity, according to Jepson (Fl. Calif. 436, 1914). A fragment of the type is preserved at the University of California. It seems to be a common form of *expansa* in which the long-stemmed bracts are covered with prominent appendages, as in *caput-medusae* (No. 2 of this list).

9. *A. RYDBERGI* Standley, l. c., 47.—A striking variation which perhaps should be treated as a distinct subspecies, but too little known and the distinguishing characters too subject to fluctuation to warrant a final disposal at this time. The leaves are all cuneate or acute at the base. Such leaves sometimes occur in true *argentea*, but always mixed in with a larger number with broad bases. The staminate glomerules are in slender interrupted spikes, these 2 to 6 cm. long. Such spikes are unusual in *A. argentea typica*. They occur, however, in some specimens, notably one from near Grand Junction, Colorado (*Hall 11045*). In this the leaves are exactly intermediate (fig. 37, d, e, f, g). Long, staminate spikes develop also in subspecies *expansa* (Westminster, Orange County, California, June 20, 1896, *McClatchie*, UC). The type specimen of *rydbergi*, which came from southeastern Utah, is young and but few of the lower bracts are well formed. These are compressed, flabelliform, the margins with 4 or 5 coarse teeth, the sides either smooth or slightly muricate. They suggest *A. powelli* in shape, but lack the broad entire summit of that species and the leaves have an entirely different venation. (See fig. 37.)

10. *A. TRINERVATA* Jepson, Pittonia 2:305, 1892.—*A. argentea expansa*, but the large leaves irregularly toothed and strongly 3-nerved from the base, the bracts also strongly nerved. The large size of the leaves is associated with vigor of growth and doubtless is responsible in turn for the dentations, which are seldom pronounced and never regular. All plants of *expansa* show a triple nerving of the leaves. The prominence of the nerves is exceedingly variable and can not be correlated with the other characters enumerated. Macbride (Contr. Gray Herb. 53:9, 1918) recently has attempted to sustain *trinervata* in varietal rank, calling distributional considerations to its support. But contrary to his assumption, it does not replace typical *expansa*

in central and northern California (where the entire-leaved form is exceedingly common), and on the other hand, it ranges to southern California, the best example of large, trinervate and dentate leaves coming from southern Santa Barbara County. Furthermore, the bracts in the type specimen are united well above the middle and most of them are short-stalked, so that these features can not be used for the separation of *trinervata*. It seems, therefore, that Jepson was correct in reducing his species to *expansa* (Jepson, Fl. Calif. 437, 1914) and that it represents only a common response to conditions favorable for exceptional growth. Type locality, near the Arequipa Hills, Solano County, California.

11. *A. VOLTANS* Nelson, Bull. Torr. Club 25:203, 1898.—The more globoid robust form of *A. argentea typica*, as indicated by Nelson (Bot. Gaz. 34:358, 1902). Type locality, Seven-Mile Lake, Wyoming.

12. *OBIONE ARGENTEA* Moquin, Chenop. Enum. 76, 1840.—*A. argentea typica*.

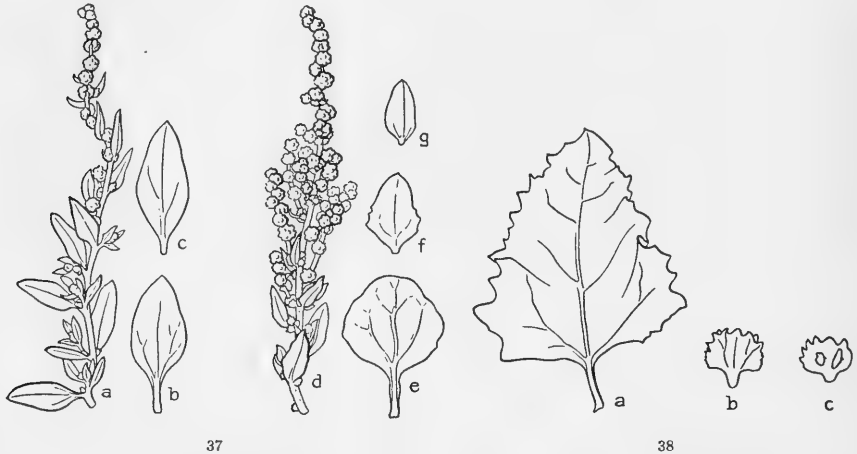


FIG. 37.—Minor variations of *Atriplex argentea*: a, b, c, from the type of *A. rydbergi* (minor variation 9); d, e, f, g, a form from Grand Junction, Colorado, intermediate to typical *argentea*. All $\times 0.8$.

FIG. 38.—*Atriplex argentea expansa*, minor variation 10 (*A. trinervata* Jepson): a, leaf, $\times 1$; b, c, fruiting bracts, $\times 2$. Drawn from the type specimen (Herb. Jepson).

RELATIONSHIPS.

This is looked upon as the central species of a large group that has progressed beyond *A. dioeca*, *A. phyllostegia*, etc., in a number of characters, but especially in the complete suppression of the perianth. Since each of the other species of the *argentea* group exhibit certain specialized features, the relation between them and *argentea* will be discussed as they are reached in the sequence.

There are here included within the species a considerable number of forms, certain of which represent diverging lines of development. However, all of the variations seem to belong to two principal branches, or stocks. These are treated as subspecies, namely *typica* and *expansa*. In the former, even the upper leaves usually exhibit at least a short petiole, while in the latter the upper leaves are very closely sessile and the blades commonly incurved between the stems (plate 44, figs. 1, 6, 7). The two are not widely separated geographically, but *typica* is chiefly a Mississippi Valley, Rocky Mountain, and Great Basin form, while *expansa* belongs to the southern borders of the United States and to California. They are therefore believed to be geographic types which are separating in their morphologic characters, although an overlapping along the boundaries has prevented a complete separation. The absence of a complete parallelism between geographic distribution and established characters is evidenced by the occasional appearance of plants of one subspecies well within the area assigned to the other. Examples

are specimens of typical *argentea* from Antioch and San Joaquin County, central California (July 4, 1902, *Congdon*, Gr, US; *Cusick 688*, Gr), and from San Bernardino, California (August 20, 1893, *McClatchie*, NY); also specimens of *expansa* from north-eastern Utah (*C. P. Smith 2073*, DS, SF).

In some keys and descriptions these two subspecies are also differentiated by their lower leaves, these being described as opposite in *typica*, alternate in *expansa*; but field studies in California have demonstrated that the lower leaves of *expansa* also are opposite. This finding has been verified by garden experiments in which the seedlings from several different collections of seeds had uniformly opposite lower leaves. The error as to the arrangement of the lower leaves doubtless has crept into the literature because of the incomplete nature of most herbarium specimens. Many other characters used in herbarium segregation of supposedly new species from *A. expansa* are now found to be so variable, even on individual plants, that they can no longer be used. Some such are almost certainly the result of a pathologic condition.

Especially unreliable features are those that have to do with the "pedicels" and sculpturing of the fruiting bracts. The former are of course only modified leaf-petioles and their length is therefore subject to much variation. Long-stalked and sessile bracts on the same plant is a common occurrence. The former condition is almost constantly associated with the development of appendages on the faces. In some cases this is almost a physical necessity, since the bracts are so compactly placed in the glomerules that any considerable outgrowth of appendages necessitates an elongation of the base in order to provide the space necessary for their development. If the appendage character is to be used specifically, it should be so employed throughout the group at least. The futility of such a course is demonstrated by a scrutiny of herbarium specimens, fully 50 per cent of which exhibit both smooth and appendaged bracts on single stems (plate 44, figs. 10 to 15).

Similar difficulties are encountered in an attempt to use the dentation of the leaves. Throughout the whole species, but especially in *expansa*, there is a general tendency of the leaves to be repand or sinuate-dentate. This shows even in dried specimens, through the unequal folding of the margins. Finally, the distribution of the staminate flowers is found to be far from constant. They are usually wanting in mature pistillate clusters, but this is often because they have matured ahead of the fruits and been crowded off. They sometimes form pure terminal spikes, although this can not be correlated with other characters. The most notable examples of elongated staminate spikes or panicles are found in a collection of *expansa* (Westminster, Orange County, California, June 20, 1896, *McClatchie* (UC) and in *A. rydbergi* (minor variation 9). The distribution of the staminate clusters is perhaps correlated with nutrition factors, and, if so, it can have no phylogenetic value. Since the characters just mentioned are thus found to be entirely unreliable, the only course open is to refer all species based upon them to the category of minor variations.

ECOLOGY.

Atriplex argentea is one of the most widely distributed annuals of its genus, occurring as a pioneer family or consociens in moderately alkaline areas throughout the West. While the two subspecies are complementary in distribution, they exhibit essentially the same ecologic behavior. Determinations of the salt-content by Kearney and his associates have given 0.27 per cent in the first foot, and 0.2 for the second. It grows frequently with *Salsola*, *Suaeda*, or *Distichlis*, as well as with other species of *Atriplex*. Both forms often leave their alkaline habitat to become weeds in fallow fields and disturbed places, usually constituting the initial stage of a short subseres. The plants bloom chiefly in June and July, but they begin in May and sometimes last as late as October in moist fields. The subspecies *expansa* is an important host-plant of *Eutettix tenella* (p. 308).

USES.

There is probably no commercial value to this saltbush, notwithstanding reports from Colorado that it is frequently fed as hay, and others from southern California that *expansa* makes good hay if cut in May and treated like wheat or barley hay (Calif. Agr. Exp. Sta. Rep. 1898-1901, 367). The difficulty of utilizing the wild growth is that it seldom forms solid stands, but usually grows sparsely on disturbed soils, especially in stubble. If it is really palatable to stock, as indicated in the reports referred to, it might be profitably used as a summer crop to follow hay on moderately alkaline soils, thus serving at once to supply food for stock and to remove the alkali. It is possible, too, that it might be used for ensilage. Detailed chemical studies and feeding experiments have been reported upon by Headden (Colo. Agr. Exp. Sta. Bull. 14:61-76, 1907); a description and chemical analysis are given by Knight, Hepner, and Nelson (Wyo. Agr. Exp. Sta. Bull. 65:48, 1905); and information on germination and growth under cultural conditions are supplied by Elias Nelson (Wyo. Agr. Exp. Sta. Bull. 63:1-19, 1904). The general experience of stock-feeders is that *Atriplex* furnishes only an inferior feed which animals will not eat, except in times of great need.

Since the pollen is a frequent cause of hay-fever, it is used by specialists in the preparation of extracts for the prevention of this disease. The methods employed have been described under *Atriplex rosea* (p. 260).

22. ATRIPLEX CORONATA Watson, Proc. Am. Acad. 9:114, 1874. Plate 43. CROWNSCALE.

Erect or spreading annual herb, 1 to 3 dm. high, branched from the base and bushy or sometimes simple below; branches stout or slender, not angled, furfuraceous, glabrate in age, the bark then stramineous; leaves alternate except the lower, all but the upper ones petiolate, mostly approaching elliptic, but nearly all broadest below the middle, the upper ones ovate (never deltoid nor with hastate base), middle and lower ones decidedly narrowed to the base, all acute at apex, 0.5 to 2.5 cm. long, 0.3 to 1 cm. wide, entire, thin, grayish furfuraceous, glabrate; flowers monoecious, in dense axillary glomerules, the pistillate in nearly all of the axils, the staminate mixing with them in the upper axils and perhaps forming pure glomerules near the ends of the branches (naked staminate spikes not thus far found); perianth of 4 or 5 sepals in the staminate flowers, wanting in the pistillate; fruiting bracts sessile, compressed, united to above the middle, broadly obovate or flabelliform, 3 to 4 or rarely 5 mm. long, 3 to 5.5 mm. broad, mostly broader than long, the green foliaceous margins irregularly dentate or lacinate, the faces smooth (except for the dense scurf) to cristate with numerous long appendages; seed 1 to 1.5 mm. long, dark purplish-brown or burnt umber, shining; radicle superior.

Interior of California, from the lower Sacramento Valley throughout the San Joaquin Valley, where common, to San Jacinto Lake, Riverside County, and perhaps to Lower California. Type locality given as San Joaquin Valley, California, in alkaline soil (*Brewer 1189*), and near Fort Mojave (*Cooper*); but Brewer states in his Field Book that No. 1189 came from an alkaline valley in Livermore Pass. This pass is on the westerly side of the San Joaquin Valley and just southeast of Mount Diablo. The Fort Mojave reference is probably an error. Collections (all from California): Collinsville, Solano County, May 13, 1892, *Jepson* (Herb. *Jepson*, type of *A. verna* *Jepson*, minor variation 5); 4 km. north of Collinsville, *Hall 11015* (UC, same variation); between Antioch and Marsh Creek, Contra Costa County, May 3, 1907, *Brandegee* (UC); type collection, *Brewer 1189* (Gr, UC, US); near Chowchilla, Madera County, *Hall 11758* (UC); Santa Fe Canal, near Los Banos, Merced County, July 9, 1921, *Kennedy* (UC); near Dos Palos, Merced County, *Hall 11020* (UC); near Kern Lake, *Davy 2135, 2138* (UC, minor variation 5, *A. verna* *Jepson*); dried bed of San Jacinto Lake, May 17, 1901, *Jepson 1240*

(Herb. Jepson, type of *A. coronata notatior*, Jepson, minor variation 1); same collection, *Hall 1800* (US, same variation); San Jacinto Valley, *Vasey 549* (Gr, US, type collection of *A. sordida* Standley, minor variation 4).

MINOR VARIATIONS AND SYNONYMS.

1. *ATRIPLEX CORONATA* var. *NOTATOR* Jepson, Fl. Calif. 437, 1914.—Sides of the bracts copiously toothed-crested, the fruits thus globose in outline, otherwise as in the typical form. Described from specimens gathered at San Jacinto Lake, California. These bracts exhibit the extreme development of appendages, but they are approached by bracts of other collections in which almost all degrees of intergradation occur (e. g., *Hall 11020*, UC). The variability of this feature in the closely related *A. argentea* is illustrated in plate 44.

2. *A. CORONATA* var. *VERNA* Jepson, Fl. W. Middle Calif. 179, 1901.—Based on *A. verna*, which see.

3. *A. ELEGANS* var. *CORONATA* Jones, Contr. West. Bot. 12:76, 1908.—Although *coronata* and *elegans* belong to the same major group, there is no apparent reason for assuming that they are any closer to each other than either one is to any of several other species. The bracts are much less strongly compressed and never approach the evenness of dentation so characteristic of *elegans*. The suggestion that the plants may sometimes be biennial does not receive support from extensive field observations.

4. *A. SORDIDA* Standley, N. Am. Fl. 21:47, 1916.—This is a very doubtful form because of the incomplete nature of the type, the middle and lower leaves being unknown. Possibly it is a variant from *A. cordulata* with exceptionally blunt bracts, but since these are broadest above the middle and there is a tendency in some of the lowest leaves present to be narrowed to the base, it is probably to be referred to *coronata*. The type is a piece from apparently a large bushy plant with many close ascending branches; the sides of the bracts smooth or with only a few small protuberances; the herbage loosely white-furfuraceous, as is common in *coronata* and *cordulata*. The type locality is San Jacinto Valley, Riverside County, California (*Vasey 549*, US). The distribution is given as Riverside and Los Angeles Counties, but no specimens from the latter can now be found in the herbaria.

5. *A. VERNA* Jepson, *Pittonia* 2:305, 1892.—A low, closely branched form with its type locality at Collinsville, Solano County, California. More recent collections around Collinsville include plants from 4 to 20 cm. high. Similar reduced forms come from as far south as the Upper San Joaquin Valley. Plants only 8 to 12 cm. high, but very stout and with numerous short, stout branches have been collected on Marsh Creek, east of Mount Diablo (May, 1883, *Brandege*, UC). All of these characters appear to represent only ecologic responses, although a similarly reduced form of the closely related *A. argentea* seems to be confined to a particular geographic area (*A. argentea hillmani*, minor variation 1 under *argentea*). Seasonal conditions seem to be responsible for the *verna* form only in part, since plants have been gathered as late as midsummer. The reduction of *verna* to *coronata* was first made by its author (Jepson, Fl. Calif. 437, 1914).

RELATIONSHIPS.

The natural position of this species is somewhere near *A. argentea* and *A. cordulata*, with both of which it has been confused at times. It differs from both in the more nearly elliptic leaves, most of which are much narrowed at base. As compared with *argentea*, the fruiting bracts are almost always smaller, although a few of the largest are larger than the smallest found on that species. The leaves, too, are much more reduced, except that in a minor variation under *argentea* (No. 1, *hillmani*) they are about as in *coronata*. If these two species are connected phylogenetically, the connection is probably through this reduced form of *argentea* rather than through its subspecies *expansa*, notwithstanding the overlapping geographic ranges of the latter and *A. coronata*.

The relationship with *A. cordulata* is less direct, although the morphologic differences are of such a nature that it is sometimes almost impossible to identify herbarium specimens as the one or the other. This is partly because the upper leaves are practically the same, being more or less ovate and subcordate in both, while the lower leaves are usually wanting at fruiting time, when most of the collections are made. The decidedly narrowed or rounded bases of the middle and lower leaves of *coronata* are very distinctive, when present. The upper leaves are more narrowly ovate than in *cordulata* and with less pronouncedly cordate bases. The fruiting bracts, too, are distinctive when carefully compared and when allowance is made for deception due to unequal development of the margins and appendages. In *coronata* the mature normal bracts are of the obovate type and are broadest at or above the middle; in *cordulata* they are of the ovate type

with a broad base and widest below the middle (exclusive of the stalk when this is present). The bracts in both are slightly broader than long. Differences in habit are of assistance at times. *A. coronata*, as far as known, never assumes the rigid, erect habit of *cordulata*, but this latter also has branched and spreading forms.

The type specimens of *A. coronata* are unsatisfactory in that they are both immature and incomplete. At this stage they display very clearly the subelliptic shape of the leaves, with the bases much narrowed. Some of the bracts are smooth on the sides, and some have low crests. The herbage is well developed and perhaps somewhat flaccid as compared with recent collections, but these latter are all from much overgrazed areas where they have suffered from trampling and hard soil as well as from grazing.

ECOLOGY AND USES.

Atriplex coronata behaves much like *argentea*, though it grows as a halophyte in more alkaline places, and it is not so strongly ruderal. In the original habitat it forms a pioneer consociety in soil containing 2 per cent or more of salt, even being found in the *Spirostachys* zone. The plants bloom from May to July.

This species is one of the important host-plants of *Eutettix*. It is grazed to some extent by cattle and sheep in the San Joaquin Valley of California.

23. ATRIPLEX POWELLI Watson, Proc. Am. Acad. 9:114, 1874. Plate 45. RIBSCALE.

Strictly erect annual herb, 1 to 10 dm. high, sparingly branched from the base to form an open pyramidal or columnar plant; branches ascending or erect, slender or moderately stout, somewhat woody and brittle in age, obtusely angled, whitish furfuraceous, glabrate, the old bark exfoliating in dull white patches; leaves all or mostly alternate, the lower on petioles often as long as the blades, the upper sessile, broadly ovate or rhombic-ovate, rounded or abruptly cuneate at base, acute at apex, 1 to 3.5 cm. long exclusive of petiole, 0.8 to 3 cm. wide, entire, firm, not fleshy, gray especially beneath with a fine scurf, prominently 3-nerved from the base; flowers imperfectly dioecious, some plants purely pistillate, some chiefly staminate, but with a few pistillate flowers in the lower axils, others chiefly pistillate below and staminate above, the flowers all in axillary glomerules which are exceeded by their subtending leaves; perianth of staminate flowers 4- or 5-cleft, wanting in the pistillate flowers; fruiting bracts sessile, thick, united to the summit, broadly spatulate or broadly oblong, ending above in a broad flattened usually truncate green terminal lobe, 3 to 4 mm. long and broad, the faces covered with prominent thickened ascending processes, or these sometimes nearly wanting; seed 2 mm. long, greenish-yellow; radicle superior.

Alkaline plains from Alberta to eastern Colorado, New Mexico, Arizona, and Utah. Type locality, Arizona. Collections: Rosedale, Alberta, *Moodie 4* (US); vicinity of Rosedale, Alberta, *Moodie 1182* (DS, NY); near Glendive, Montana, 1883 *Ward* (US); Shelby, Montana, September 11, 1909, *Jones* (Herb. Jones); Carson County, South Dakota, *Over 3425* (US); Wamsutter, Wyoming, *Nelson 3673* (R, UC, US); Howell Lake, Wyoming, *Nelson 5311* (Herb. Jones, type of *A. nelsoni* Jones, minor variation 1); Laramie River, Huttons Grove, Albany County, Wyoming, *Nelson 8171* (Gr, NY, R, US, type collection of *A. philonitra* Nelson, minor variation 2); Colorado: Montrose, *Shear 4929* (NY, US); Hotchkiss, *Coven 2185* (Gr, NY, R, US); east of Cañon City, *Hall 11032* (UC); Mancos Plains, *Brandegee 1277* (UC); Gunnison River, *Purpus 212* (UC); Grand Junction, *Baker 930* (UC, US); near Dulce, New Mexico, *Standley 8149* (US); south of Shiprock, northwestern New Mexico, *Hall 11146* (UC); type collection, cultivated from Arizona seed (Gr); Holbrook, Arizona, *Rusby 796* (US); 4 km. south of Adamana, Arizona, *Hall 11161* (CI); near Green River, Utah, *Hall 11037, 11039* (UC); 5 km. north of Emery, Utah, *Jones 5456* (UC). Other localities represented by collections in the M. E. Jones

Herbarium, Salt Lake City, include Marysvale, Sunnyside, and Cainville, all in Utah. Additional Wyoming localities represented at the Rocky Mountain Herbarium are Point of Rocks, Middle Fork of Powder River, and Claremont, Johnson County.

MINOR VARIATIONS.

1. *ATRIPLEX NELSONI* Jones, Contr. West. Bot. 11:21, 1903.—Described from plants in which the fruiting bracts are mostly smooth on the sides, the margins bearing a few large herbaceous lobes. The shape of the terminal lobe, the venation of the leaf, and other characters positively assign this to *powelli*, which species apparently was overlooked or misunderstood when the description of *nelsoni* was prepared.

2. *A. PHILONITRA* Nelson, Bot. Gaz. 34:358, 1902.—The description and the types are both as in genuine *powelli*. Type locality, Laramie River, Wyoming.

RELATIONSHIPS.

The characters of this species are so remarkably fixed that it can not be connected closely with any other. It appears to be not a modification of any existing form but the end of a branch from near the beginning of the *argentea* group. It is not primitive, as is indicated by the absence of a perianth in the pistillate flowers, the unusual development of the fruiting bracts, and the attainment of partial dioecism. In this last-named feature it has progressed far beyond its nearest allies. In the Green River district of eastern Utah the differentiation into pistillate and staminate individuals is so marked that the prevailing sex may be determined at a glance. Here the pistillate plants are strictly erect, with more numerous and larger leaves than occur on the staminate. They bear no male flowers. On the other hand, the staminate plants bear a few pistillate bracts in the lower axils of the inflorescence. The staminate flowers open before the pistillate on neighboring plants. At Green River Station some plants have about as many staminate as pistillate flowers, a proportion also found on herbarium sheets from other localities. Along the Laramie River, Wyoming, the axial branch of each plant is usually wholly staminate, according to Nelson (Bot. Gaz. 34:358, 1902, under *A. philonitra*). The type material at the Gray Herbarium consists of 3 plants, 2 purely pistillate, the third about half pistillate and half staminate. None of these are very leafy. Thus it seems that this species is in a progressive stage of evolution and that it is headed toward a complete dioecism like that obtaining in the shrubby species of *Atriplex*. The shape and venation of the leaves supply evidence that it is perhaps as close to *A. argentea* as to any other species.

Some taxonomic confusion has come about through a misunderstanding of *A. powelli*. Perhaps this resulted from the inadequate descriptions of the peculiar fruiting bracts. For some time collections were labeled as a form of *A. expansa*, with which it can not possibly be confused when attention is given to the bract characters or even to the venation of the leaf. This led Nelson to redescribe it as *A. philonitra*, and Jones, who had a slightly different form, as *A. nelsoni*. These names were reduced into synonymy by Standley (N. Am. Fl. 21:48, 1916), who, having access to the type specimens of *powelli*, noted the practical identity of all three.

ECOLOGY AND USES.

Atriplex powelli is a characteristic indicator of abundant surface alkali, usually occurring in pure stands in alkaline valleys and plains. It regularly forms the initial consocieties in such areas throughout most of southern Wyoming, Colorado, Utah, and northern New Mexico and Arizona. The perennial zone around is occupied by *A. nuttalli* and *corrugata*, by the first alone, or with *Sarcobatus* or *Sporobolus airoides*. While it may grow in depressions along roadsides, it rarely becomes a true ruderal, probably owing to the competition of more successful halophytes, such as *Salsola*. The plants flower from July through October.

Watson states that the fruits are collected by the Indians for food (Proc. Am. Acad. 9:115, 1874).

24. ATRIPLEX LEUCOPHYLLA (Moquin) Dietrich, Syn. Pl. 5:536, 1852. Plate 45. SEASCALE.

Prostrate perennial herb with ascending or erect leafy shoots from an often somewhat woody base, the above-ground portions 1 to 3 dm. high, sometimes forming open mats 3 to 10 dm. across; branches stout, obtusely angled when old, often pinkish, coarsely white-mealy, tardily glabrate and the bark then yellowish white; leaves alternate or those at the base of each shoot opposite, crowded, sometimes loosely imbricated, sessile, orbicular-ovate or broadly elliptic or rarely obovate, narrowed or rounded to the base, obtuse at apex, 1 to 3.5 cm. long, 0.5 to 1.5 cm. wide, entire, very thick, densely coated with a permanent brownish or gray scurf, 1- or 3-nerved, sometimes even the midnerve obscure; flowers monoecious, the staminate glomerules in dense stout terminal mostly simple spikes, the pistillate flowers few at a place in the upper axils; perianth 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile, spongy, not compressed, completely united except at apex, elliptic-globose, acutish, 5 to 7 mm. long, 4 to 5 mm. broad, entire or dentate, the faces at least lumpy and commonly with two or several wart-like projections, not nerved; seed 2.5 to 3 mm. long, very dark reddish brown; radicle superior. (*Obione leucophylla* Moquin, in DeCandolle, Prodr. 13²:109, 1849.)

Sea-beaches of California and Lower California and the adjacent islands, from Humboldt Bay to Viscaïno Bay; casual inland at Lake Elsinore. Type locality, California. Collections, all in California and Lower California: Sand hills of ocean beach at Samoa, opposite Eureka, *Tracy 1264* (UC, see minor variations); Bucksport, Humboldt Bay, *Tracy 4416* (UC, same variation); Point Reyes, Marin County, *Davy 6763* (UC); West Berkeley, December, 1896, *Davy* (UC); Alameda Marshes, September 24, 1898, *Davy* (UC); Point Lobos, San Francisco, August 20, 1891, *Jepson* (Gr, NY, UC, US); Tobin, San Mateo County, August 11, 1913, *Brandege* (UC); Monterey, *Heller 6858* (UC); Pacific Grove, *Elmer 4109* (UC); San Simeon, San Luis Obispo County, July, 1887, *Brandege* (UC); San Miguel and Santa Cruz Islands (according to Brandege, *Zoe 1:145*, 1890); Ventura Beach, October 19, 1919, *Hall* (CI); Avalon, Santa Catalina Island, at one locality only, April, 1896, *Trask* (US, see minor variations); San Nicholas Island, April, 1901, *Trask* (Gr); San Clemente Island, *Nevin and Lyon 29* (Gr); Santa Monica, *Davy 2733* (UC); Redondo, October 15, 1893, *Brandege* (UC); Lake Elsinore, *J. D. Abrams* (DS); La Jolla, San Diego County, *Clements 57* (Gr, NY, UC); South San Diego, *Chandler 4009* (UC); Enseñada, August 27, 1893, *Brandege* (UC); Todos Santos, June 2, 1883, *Fish* (US); Lagoon Head, *Palmer 812* (Gr, NY, UC); Coast near Ascension Island, April 17, 1897, *Brandege* (UC).

MINOR VARIATIONS.

This is one of the least variable of all the North American species. Such variations as occur are due chiefly to differences in size and habit and in the appendages of the bracts. Mrs. Trask has noted an exceptionally small-leaved form at Avalon, Santa Catalina Island. In this the leaves are only 1.2 by 0.5 cm. in size. It is doubtless the result of unfavorable soil conditions or perhaps of inbreeding, for the species is very rare on this island. A specimen with scarcely larger leaves comes from South San Diego (*Chandler 4009*, UC), while in two collections from Humboldt Bay (*Tracy 1264* and *4416*, UC), at the northern limit of the range of the species, the leaves are even smaller than in the Santa Catalina Island plant.

RELATIONSHIPS.

No direct connection can be traced between this species and any other. It certainly belongs, however, to the group best represented by *A. pentandra*, *A. coulteri*, etc. Each of these is more highly specialized than *leucophylla* in certain particulars, and all of the group have much more reduced and otherwise modified seeds and fruiting bracts. It seems probable, therefore, that *leucophylla* had its origin in Mexico and that it became

separated from the ancestral line during its northward migration. A close study of forms in Lower California and on the mainland of western Mexico may bring further evidence to bear on this question.

ECOLOGY AND USES.

Atriplex leucophylla may constitute the pioneer consocieties on the strand just beyond the reach of the waves, or it may form dunelets in moving sand farther back. It grows alone over much of its zone, but behind it is associated with *Abronia maritima*, *A. umbellata*, *Franseria bipinnatifida*, *Mesembryanthemum nodiflorum*, or *Distichlis*. The prostrate woody stems and the numerous erect branches enable it to resist erosion, and to accumulate wind-blown sand in small amounts. It is a marked halophyte, as indicated by its habitat, and the dense scurf of leaves and stems. The flowers appear from April to October.

No uses are known for this plant, though it is doubtless an occasional cause of hay-fever.

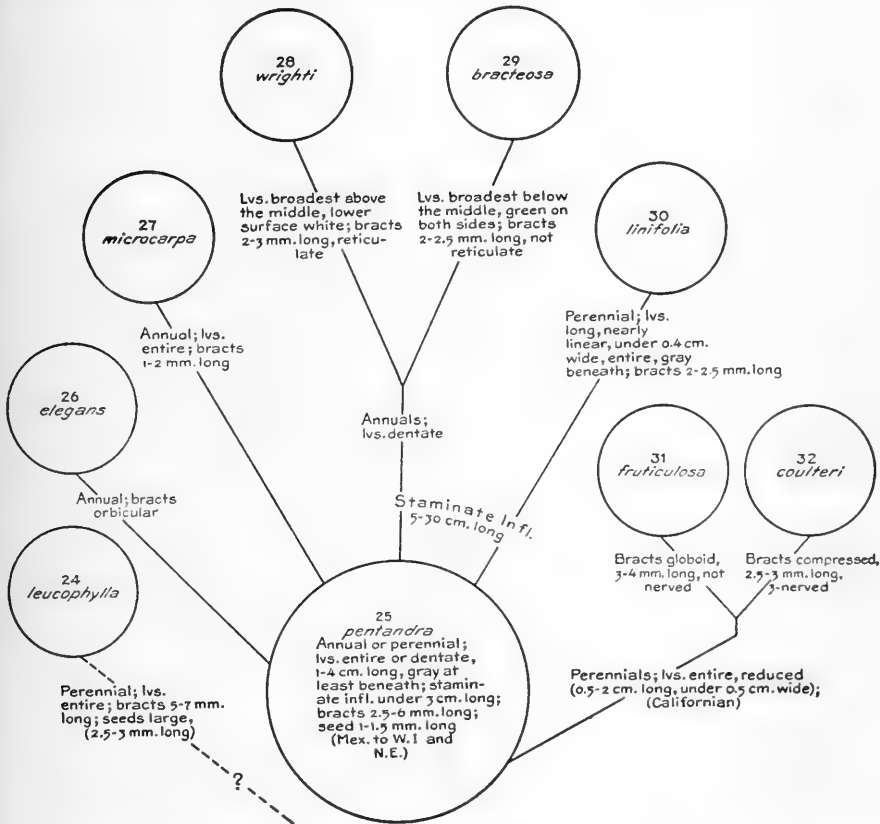


FIG. 39.—Phylogenetic chart of the *Atriplex pentandra* group.

25. ATRIPLEX PENTANDRA (Jacquin) Standley, N. Am. Fl. 21:54, 1916. Plate 46.

Decumbent or sometimes erect annual or perennial herb or the base suffrutescent, 1 to 8 dm. high, branched throughout to form a spreading bushy plant often of irregular outline; branches obtusely angled or nearly terete, not striate, sparsely scurfy but early glabrate and then stramineous, the pale bark persistent but breaking longitudinally on old stems; leaves all alternate, except probably the lower, with very short petioles or the upper ones sessile, elliptic to spatulate or obovate, rarely lanceolate, tapering or rounded at the base, obtuse or acute at apex, commonly mucronate, 0.5 to 4 cm. long, 0.2 to 1.5 cm. wide, entire or sinuate or acutely dentate, thin, sparsely scurfy and greenish on the upper surface, densely white-scurfy beneath, or white on both surfaces in some island forms (subspecies *confinis*), 1-nerved; flowers monoecious, the staminate glomerules either solitary or in terminal spikes up to 3 cm. (or more?) long, the pistillate flowers in small axillary glomerules and sometimes mixing with the lower staminate; perianth 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile or short-stalked, compressed, united to about the middle, obovate or orbicular-obovate, commonly with broad thin margins, 2.5 to 6 mm. long, 3 to 6 mm. broad, sharply and saliently dentate above the middle, the faces variously crested or tubercled or smooth, often reticulate-veined; seed 0.8 to 1.5 mm. long, brown; radicle superior. (*Azyris pentandra* Jacquin, Sel. Stirp. Am. 244, 1763.)

Mexico and States bordering the Gulf of Mexico to the West Indies and along the Atlantic Coast to New Hampshire, also in South America.

SUBSPECIES.

Artificial Key to the Subspecies of Atriplex pentandra.

Leaves sparsely scurfy and greenish on the upper surface; fruiting bracts mostly crested or tubercled.

Bracts 3 to 6 mm. long. Eastern.

Leaves broadly elliptic to obovate; bracts 4 to 6 mm. long. Virginia to New England. (a) *arenaria* (p. 294).

Leaves elliptic to lanceolate or linear; bracts 3 to 4 mm. long (rarely 4.5 mm.).

Eastern Mexico to West Indies and the South Atlantic States. (b) *typica* (p. 294).

Bracts 2.5 to 3 mm. long (rarely 3.5 mm.). Western. (d) *muricata* (p. 296).

Leaves densely and permanently white-scurfy on both sides; fruiting bracts (about 3 mm. long) not crested or tubercled. West Indies. (c) *confinis* (p. 295).

25a. ATRIPLEX PENTANDRA ARENARIA (Nuttall).—Stem erect from an annual taproot, or the lateral branches procumbent; leaves elliptic to broadly oblong or obovate, tapering to the base, obtuse or the upper acute at summit, 1.5 to 4 cm. long, 0.5 to 1.5 cm. wide, typically entire or undulate, but often saliently dentate, at first gray or whitish-scurfy on both sides, but soon greenish above; staminate spikes 3 cm. or less long; fruiting bracts 4 to 6 mm. long, 4 to 7 mm. broad, the sides with 2 dentate crests or tuberculate or rarely smooth, reticulate-veiny or the veins covered by the tubercles; seed about 1.5 mm. long. (*A. arenaria* Nuttall, Genera 1:198, 1818.) Sandy shores along the Atlantic Coast from New Hampshire to Virginia and perhaps farther southward. Type locality, sandy sea-coast of New Jersey. Collections: Hampton, New Hampshire, *Robinson 738* (Gr); Katama Bay, Marthas Vineyard, Massachusetts, *Fernald 75* (Gr, NY, UC, US); Groton, Connecticut, September 9, 1903, *Bissell* (Gr); Atlantic City, New Jersey, *Martindale 53* (US); type, *Nuttall* (Phila); Gardiners Island, Long Island, August 15, 1878, *Miller* (US); Piney Point, Maryland, 1874, *Vasey* (US); Franklin County, Virginia, *Brown* (Phila).

25b. ATRIPLEX PENTANDRA TYPICA.—Stems spreading or reclining, but usually with ascending or erect ends, from an annual or perennial root, often suffrutescent at base; leaves elliptic to narrowly oblong or lanceolate, acute at each end or obtuse and mucronate at summit, 1 to 3 cm. long, 0.3 to 1 cm. wide (short and broad in minor variation

13), entire to saliently and sharply dentate, greenish above, gray-scurfy beneath (gray on both sides in minor variation 13); staminate spikes either short, as in the type, or up to 2 cm. long; fruiting bracts 3 to 4 or rarely 4.5 mm. long, usually 4 to 5 mm. broad, each of the sides with 2 dentate crests or tubercled or rarely smooth, reticulate-veiny or the veins covered by the tubercles; seed 1.2 to 1.5 mm. long. (*A. pentandra* Jacquin, Sel. Stirp. Am. 244, 1763.) Coast of the South Atlantic and Gulf States and West Indies; also in northern South America. Type locality, seashores of Cuba. Collections: Indian River, Florida, *Curtiss 2357* (Gr, NY, US); shore of Upper Matecumbe Key, Florida, *Curtiss 5506* (NY, UC, US); Mon Louis Island, near Mobile, Alabama, August 15, 1879, *Mohr* (US); Horn Island, Mississippi, *Tracy 6395* (NY, US); Breton Island, Louisiana, *Tracy and Lloyd 42* (Gr, US); near Corpus Christi, Texas, *Heller 1819* (Gr, US); Atwood Cay, Bahamas, *Wilson 7422* (NY, form approaching subspecies *confinis*); Grand Turk Island, Bahamas, *Millspaugh 8998* (NY, similar form); Mariguana, Bahamas, *Wilson 7536* (NY); Ambergris Key, Caicos Group, Bahamas, *Millspaugh 9276* (NY); west of Playa Mariano, Havana, Cuba, *van Hermann 902* (NY); Playa del Vedado, Havana, Cuba, *Baker 1792* (NY); near mouth of Bueyvacca, Province of Matanzas, Cuba, *Britton and Wilson 53* (NY); Cuba, *Wright 3660* (Gr, US, as *A. aldamae* Grisebach, minor variation 1); Cayo Paredon Grande, Camaguey, Cuba, *Shafer 2741* (Gr, US); Pedro Bluff, Jamaica, *Harris 9932* (NY, minor variation 13); Morillos de Cabo Rojo, Porto Rico, *Britton, Cowell, and Brown 4714* (NY); near Guani Cay, Porto Rico, *Sintensis 3955* (Gr, NY); Pinetree Bay, St. Croix, *Rickesecker 327* (Gr, NY, US, form approaching minor variation 13); near Willemstad, Curaçao, *Britton and Shafer 2926* (NY, US, minor variation 13); Swan Islands, off the coast of Honduras, *Nelson 65* (Gr). Additional localities are mentioned under minor variations 16 and 18.



FIG. 40.

Atriplex pentandra typical. Tracing of the entire plate accompanying the original description (Jacquin, Sel. Stirp. Am. Pict. pl. 235).

25c. *ATRIPLEX PENTANDRA CONFINIS* (Standley).—Stems probably spreading at base from an annual or perennial root, the ends erect or ascending; leaves broadly elliptic or approaching rhombic, rounded to the base, obtuse at summit, 1.5 to 3 cm. long, 0.5 to 1.5 cm. wide (much smaller in minor variation 21, *Obione crispa* Moquin), typically low-dentate to entire but varying to acutely dentate in small-leaved forms, densely and closely white-scurfy on both faces; staminate spikes short (0.5 to 1 cm. long); fruiting bracts 2.5 to 3.5 mm. long, 3 to 4 mm. broad, the sides without appendages but with strong reticulations faintly visible through the dense scurf; seed about 1.5 mm. long. (*A. confinis* Standley, N. Am. Fl. 21:54, 1916.) The Bahamas to northern Venezuela. Type locality, Sombrero Island. Collections: Type collection, 1864, *Julien* (NY, US); Eastern Cay, Turks Islands, Bahamas, *Millspaugh 9369* (NY, minor variation 21, *Obione crispa* Moquin).

25d. *ATRIPLEX PENTANDRA MURICATA* (Humboldt and Bonpland).—Stems procumbent or ascending from an annual or perennial but short-lived root; leaves elliptic to spatulate or narrowly obovate, tapering to a mostly slender petiole-like base, obtuse and usually

mucronulate at summit, 0.5 to 2.5 cm. long, 0.3 to 1 cm. wide, acutely dentate to repandentate or the upper ones entire, densely white-scurfy beneath, greenish-gray on the upper surface; staminate spikes commonly shorter than the upper leaves and reduced to 1 or 2 glomerules each but varying up to 2 cm. long and subpaniculate (especially in minor variation 14, *A. pueblensis* Standley); fruiting bracts 2.5 to 3 or rarely 3.5 mm. long (exclusive of stipe-like base when this is present), 2.5 to 4 mm. broad, each of the sides with 2 dentate crests or smooth (especially in minor variation 9, *A. glomerata* Watson), 1- or 3-nerved, not obviously reticulated; seed 0.8 to 1.2 mm. long. (*A. muricata* Humboldt and Bonpland in Willdenow, Sp. Pl. 4:959, 1806.) Apparently throughout Mexico, except in the extreme south and southeast; known from Pueblo to Coahuila and Sonora. Type locality, Mexico. Collections: Near Tehuacan, Puebla, *Pringle 8577* (UC, US, type collection of *A. pueblensis* Standley, minor variation 14); Mexico City, *Pringle 8528* (Gr, NY, UC, US); San Luis Potosi, *Schaffner 287* (NY, US); near the City of Durango, *Palmer 295* (Gr); vicinity of Saltillo, Coahuila, *Palmer 290* (Gr, NY, UC, US); "States of Coahuila and Nuevo Leon," *Palmer 1156* (Gr, US, type collection of *A. glomerata* Watson, minor variation 9); Guaymas, Sonora, *Palmer 119* (US, doubtful).

MINOR VARIATIONS AND SYNONYMS.

1. *ATRIPLEX ALDAMAE* Grisebach, Cat. Pl. Cub. 282, 1866.—A form of *A. pentandra typica* in which the fruiting bracts are exceptionally large (4 to 5 mm. long) and without appendages. Apparently only an occasional plant is found, indicating that it may be the result of favorable local conditions. The type came from western Cuba and the form is not known elsewhere.
2. *A. ARENARIA* Nuttall, Gen. 1:198, 1818.—*A. pentandra arenaria*. This is not the same as *A. arenaria* Woods, Jour. Fl. 317, 1850, which is used in Europe for the plant properly known as *A. maritima* Hallier.
3. *A. CONFINIS* Standley, N. Am. Fl. 21:54, 1916.—*A. pentandra confinis*.
4. *A. CHRISA* Urban, Symb. Ant. 8:200, 1920.—Based upon *Obione crispa*, which see.
5. *A. CRISTATA* Humboldt and Bonpland, in Willdenow, Sp. Pl. 4:959, 1806.—Apparently identical with the earlier *Azyris pentandra* and therefore the same as *Atriplex pentandra typica*.
6. *A. CRISTATA* var. *ARENARIA* Kuntze, Rev. Gen. Pl. 546, 1891.—*A. pentandra arenaria*.
7. *A. CYCLOSTEGIA* Standley, l. c., 58, 1916.—Known from a single immature specimen collected near Hermosillo, Sonora (*Maltby 222*, US). Placed next to *A. elegans* by Standley, but the foliage and bracts indicate that it is close to *A. pentandra muricata* and perhaps a robust development of this. The leaves are large for the subspecies, the largest ones being 3.5 cm. long by 1.3 cm. wide. The larger and more nearly mature bracts are elliptic in shape, much longer than broad, and therefore not of the *elegans* type. The largest one is 5 mm. long by 3 mm. broad, including the dentate margins and large terminal tooth. It is this elongated apex that renders the bract, even at this immature stage, exceptionally large for subspecies *muricata*. Whether these marked vegetative characters are the result of especially favorable conditions under which this particular specimen grew, or whether they are characteristic of all plants of the Sonoran coast, and therefore worthy of taxonomic recognition, may be left for more extensive collections to determine.
8. *A. DOMINGENSIS* Standley, l. c., 55, 1916.—The same as *Obione crispa* Moquin, which see in this list.
9. *A. GLOMERATA* Watson, in Standley, l. c., 54, 1916.—*A. pentandra muricata* but the faces of the fruiting bracts not appendaged. Type locality, Parras, Coahuila.
10. *A. MUCRONATA* Rafinesque, Am. Mo. Mag. 2:176, 1818.—A name only incidentally mentioned where first used. Evidently intended to apply to *A. arenaria* Nuttall (No. 2 of this list), although *A. laciniata* Linnaeus is the name referred to. A more complete discussion is given by Blake (*Rhodora* 17:84, 1915).
11. *A. MURICATA* Humboldt and Bonpland, in Willdenow, Sp. Pl. 4:959, 1806.—*A. pentandra muricata*.
12. *A. PARVIFOLIA* Humboldt, Bonpland, and Kunth, Nov. Gen. Sp. 2:192, 1817.—There is nothing in the original description to indicate that this differs in any essential feature from *A. pentandra muricata*. Type locality, San Juan del Rio, south central Mexico.
13. *A. PENTANDRA TYPICA*.—In one West Indian variation the leaves are smaller, broader in proportion to their length, and with a more copious cinereous scurf than in the typical form. Common leaf-measurements are: 2.5 by 1.2 cm., 2 by 0.7 cm., 1.5 by 0.5 cm. Although grayish in color, the leaves are not so thick or so whitish as in subspecies *arenaria* and *confinis*. Both this and the typical form are abundant on many of the West Indian Islands, especially in Porto Rico. Recent collectors look upon them as only trivial and fluctuating variations and probably ecads. The following represent the gray, small-leaved form: Cayo

Muertos, Porto Rico, Britton, Cowell, and Brown 5036 (NY, US); Pedro Bluff, Jamaica, Harris 9932 (NY, US); near Willemstad, Curaçao, Britton and Shafer 2926 (NY, US).

14. *A. PUEBLENSIS* Standley, l. c., 56, 1916.—The same as *A. pentandra muricata*, but a form with unappendaged bracts (as in minor variation 9, *A. glomerata* Watson) and the staminate glomerules in naked terminal spikes. The leaves are described as entire, but this varies in the type collection (although not in the type specimen) as pointed out by Macbride (Contr. Gray Herb. 53:10, 1918). A duplicate of the type at the University of California has leaves mostly entire, but some with a few minute dentations, and the staminate inflorescences are 1 to 2 cm. long. Type, near Tehuacan, Puebla, Pringle 8577 (US).

15. *A. TAMPICENSIS* Standley, l. c.—There are no satisfactory characters upon which to separate this from *A. pentandra typica*. The leaves are entire, but the single collection thus far made consists only of the ends of the branches and the principal leaves are therefore unknown. In any event, this feature is much too variable in the group to be of taxonomic value. The staminate glomerules are in elongated terminal spikes and panicles, as is common in *pentandra*. The fruiting bracts are only 2.5 to 3 mm. long, not crested but faintly reticulated on the faces. The bracts are therefore undersized for *typica*, and in this respect the form is closer to subspecies *muricata*. Type, vicinity of Tampico, Tamaulipas, Palmer 332 (US).

16. *A. TEXANA* Watson, Proc. Am. Acad. 9:113, 1874.—A little-known form from southern Texas which may be referred to *A. pentandra typica* until differentiating characters can be found. Geographically it belongs between *typica* and *muricata*, but the bracts are much too large for the latter, 3 to 3.5 mm. long by 4 to 4.5 mm. broad in the type, which, however, was grown in the botanical garden at Cambridge, Massachusetts, from Texas seed. All of the few collections since made are from within 250 km. of the coast of the Gulf of Mexico. These localities may therefore represent the western limits of *typica*, which ranges thence both north and south along the Gulf. *A. texana* can not be separated from *typica* on the basis of its entire leaves as proposed by Standley (N. Am. Fl. 21:37, 1916), since these sometimes are sparingly dentate, as originally described by Watson and, moreover, typical *pentandra* varies in the West Indies to forms in which the leaves are nearly all entire. In addition to the type, the following belong here: Guadalupe, southwest of San Antonio, Texas, Palmer 1158 (Gr, US); Corpus Christi Bay, Texas, Palmer 1159 (Gr, US); Laredo, Texas, in sandy soil, Reverchon 3682 (Gr). An earlier name for this variation is given under No. 23.

17. *A. TUBERCULATA* Coulter, Contr. U. S. Nat. Herb. 2:368, 1894.—Based upon *Obione elegans tuberculosa*, which see in this list.

18. *A. WARDI* Standley, l. c., 56, 1916.—The types are nearly leafless plants with no characters to differentiate them from typical *A. pentandra*, except the absence of appendages on the faces of the fruiting bracts. These bracts were described as only 2 to 2.5 mm. long and longer than broad. Many of the mature ones of the type are fully 3 mm. long. The absence of the usually broad herbaceous margin is responsible for this small size. The faces are strongly reticulated, this indicating the close relationship with subspecies *typica* and *arenaria*. The root is annual and the few remaining leaves are entire. Type, Galveston, Texas, September 16, 1877, Ward (US).

19. *AXYRIS PENTANDRA* Jacquin, Sel. Stirp. Am. 244, 1763.—*Atriplex pentandra typica*. The original specimen is illustrated in figure 40.

20. *OBIONE ARENARIA* Moquin, Chenop. Enum. 71, 1840.—*A. pentandra arenaria*.

21. *O. CRISPA* Moquin, l. c., 73, 1840.—Referred to *A. pentandra confinis*, although both leaves and bracts are much smaller in true *crispa*. According to Moquin, the leaves in the type, which came from Haiti, are only 0.4 to 0.6 cm. long, 0.1 to 0.2 cm. wide, whitish farinose on both faces, and acutely dentate, while the bracts are only about 2 mm. long. This very small-leaved form is represented by plants from Eastern Cay, Turks Island, Bahamas (Millsbaugh 9369, NY), in which, however, the fruiting bracts are slightly over 3 mm. long. Possibly the type specimen was immature, which would account for the small size of the bracts. The name *crispa* is not here taken up because of the tenable *Atriplex crispa* Dietrich (Syn. Pl. 5:536, 1852) of Asia.

22. *O. CRISTATA* Moquin, l. c.—Based upon *Atriplex cristata*, which see.

23. *O. ELEGANS* var.? *TUBERCULOSA* Torrey, Bot. Mex. Bound. 183, 1859.—A form later described as *Atriplex texana* Watson (No. 16 of this list).

24. *O.?* *KUNTHIANA* Moquin, l. c., 72, 1840.—*A. pentandra muricata*.

25. *O.?* *MURICATA* Moquin, in De Candolle, Prodr. 13:109, 1849.—*A. pentandra muricata*.

RELATIONSHIPS.

This is believed to represent the plexus from which a large series of species has originated. At least 7 major species can be traced back with more or less certainty to this stock. They are all western and seem to have had their connection through the subspecies *muricata* of Mexico. Each has undergone essential modifications in one or more of the *pentandra* characters, and in every case the change has been in the direction of simplification or in the development of special features. These changes will be indicated under the heading of Relationships as each of the derived species is reached. The list includes: *elegans*, *microcarpa*, *wrighti*, *bracteosa*, *linifolia*, *fruticulosa*, and *coulteri*. It is

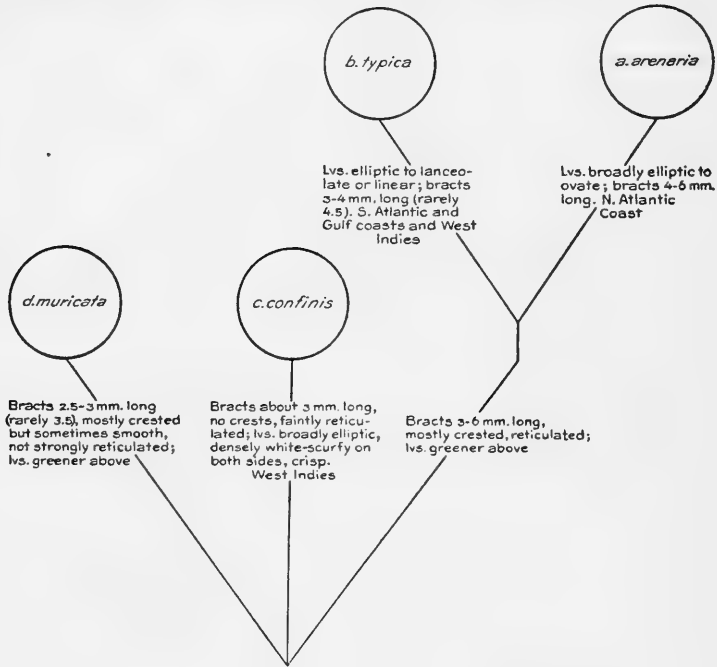


FIG. 41.—Phylogenetic chart of the subspecies of *Atriplex pentandra*.

probable that *A. barclayana* should be added to the list. If this is done *pentandra* will then stand near the base also of the large phylogenetic branch of dioecious shrubs, for *barclayana* seems to be a lateral branch which sprang from the common stock of this group. It is also possible that the present species is basal to the *pusilla*, *truncata*, and *argentea* groups, but for a number of reasons, the most important of which is a modification in the shape of the fruiting bracts combined with a rather well-developed separation of the sexes, it is given a position in the chart (fig. 29, p. 238) superior to these.

Evolution within the collective species *A. pentandra* has progressed to a high stage. The result is a number of subspecies well separated in their extremes, yet held together by a series of intergrading forms. Two principal branches are noted, an eastern and a western. The former comprises two groups of forms assembled under the subspecific

names *arenaria* and *typica*. Subspecies *arenaria* is perhaps the more primitive, as suggested by the absence of reduction in the leaves and bracts. It has migrated far northward and is now restricted to the proximity of the coast from the Carolinas, or somewhat farther southward, to New England. Every attempt made to separate this specifically has failed because of the large series of variations in all essential characters in subspecies

TABLE 26.—Variation in the fruiting bracts of the subspecies of *Atriplex pentandra*.

	Herbarium.	Length of bracts.	Breadth of bracts.	Surface of bracts.
Subspecies <i>a. arenaria</i> :				
		<i>mm.</i>	<i>mm.</i>	
Atlantic City, N. J.	NY	5.5 to 6.0	6.0 to 7.0	Smooth, reticulated.
Long Island, N. Y. (<i>Clute 324</i>)	NY	5.0	5.0	Crested, reticulated.
Groton, Conn. (<i>Bissell</i>)	Gr	4.5 5.0	4.0 6.0	Do.
Rhode Island (<i>Olney</i>)	Gr	4.0 5.0	4.0 6.0	Low-crested to smooth, reticulated.
Westport, Mass.	7151 UC	5.0 5.5	5.0 7.0	Crested, reticulated.
Seaview, Mass. (<i>Williams</i>)	Gr	4.2	4.2	Do.
Katama Bay, Mass.	78934 UC	5.0	4.0 6.0	Do.
Average		5.0	5.2	
Subspecies <i>b. typica</i> :				
Swan Island, Honduras	Gr	4.0	4.0	Not crested, reticulated.
Hort. Cantab. ¹	Gr	2.8 3.5	4.0 4.5	Crested, reticulations covered.
Near Tampico, Mex. (<i>Palmer 335</i>) ²	463276 US	2.5 3.0	3.0 3.5	Not crested, reticulated.
Breton Island, La. (<i>Tracy and Lloyd 42</i>)	Gr	3.5 4.0	3.5	Crested or smooth, reticulated.
Miami, Fla. (<i>Garber</i>)	Gr	4.0 4.5	4.0 5.0	Crested, reticulated.
Indian River, Fla. (<i>Curtiss 2357</i>)	Gr	3.5 3.7	4.0 4.8	Do.
Curaçao (<i>Britton and Shafer 2926</i>)	NY	4.0 4.5	5.0 5.0	Crests covering surface.
Porto Rico (<i>Britton 4714</i>)	NY	3.5	4.8	Do.
Porto Rico (<i>Sintensis 3955</i>)	Gr	3.5	4.5	Do.
Matanzas, Cuba (<i>Britton and Wilson 59</i>)	NY	4.0	4.0	Do.
Grand Turk, Bahamas (<i>Millspaugh 8998</i>)	NY	3.5	5.0	Crested or smooth, reticulated.
Little Creek, Andros, Bahamas (<i>Brace 5300</i>)	NY	4.0 4.5	5.0 6.0	Do.
Water Key, Bahamas (<i>Wilson 8156</i>)	NY	3.8 4.0	4.0 4.0	Do.
Atwood Key, Bahamas (<i>Wilson 7422</i>)	NY	3.5	4.2	Crested, reticulated.
Average		3.7	4.3	
Subspecies <i>d. muricata</i> :				
Mexico City	11037 UC	2.8	2.8	2-crested to smooth, not reticulated.
Mexico (<i>Palmer 1156</i>) ³	48301 US	2.8	3.0	Smooth, 3-nerved.
Near Tehuacan, Puebla ⁴	396697 US	3.0 3.5	3.5 4.0	3-nerved.
Saltillo, Coahuila	336285 US	2.8 3.0	3.0 4.0	2-crested to smooth, not reticulated.
Guaymas, Sonora (<i>Palmer 119</i>) ⁵	US	2.8	2.8	Nearly smooth, 3-nerved.
Average		2.9	3.2	

¹ Type of *A. texana* Watson, minor variation 16.² Type of *A. tampicensis* Standley, minor variation 15.³ Type of *A. glomerata* Watson, minor variation 9.⁴ Type of *A. publensis* Standley, minor variation 14.⁵ Doubtfully determined.

typica of the Gulf Coast and West Indies. The acceptance of *arenaria* as a species would necessitate the use of criteria so trivial that consistency would demand the setting up of a considerable number of other species from what is here described as subspecies *typica*. Those best acquainted with the variations of *typica*, especially in the West Indies, advise against treating these as species and the collections already available indicate that such a course would lead only to confusion. A few species have been described from this group. These are accounted for among the minor variations, where the value of their characters is briefly discussed. The type of *pentandra* is a small, den-

tate-leaved plant with the staminate glomerules much reduced, as will be seen from the tracing presented here of the rare original plate (see fig. 40). The only variation sufficiently distinct to justify particular mention is the one here described as subspecies *confinis* (Standley).

The western branch of *A. pentandra* constitutes the single subspecies *muricata*. This has undergone a reduction in the size of the bracts and the reticulations of these are less evident. But in all other characters its equivalent in the area of *typica* is frequently encountered. Even the size of the bracts overlaps in the two subspecies, as is indicated by the measurements given in table 26. It was through subspecies *muricata*, or some similar form perhaps now extinct, that the 7 or more far-western species of the *pentandra* group were derived.

ECOLOGY AND USES.

Atriplex pentandra and its subspecies are largely tropical and subtropical, and nothing is known of their ecology or uses.

26. ATRIPLEX ELEGANS (Moquin) Dietrich, Syn. Pl. 5:537, 1852. Plate 46. WHEELSCALE.

Erect or subdecumbent annual herb, 1 to 6 dm. high, branched from the base, the branches usually erect or ascending but sometimes shortly spreading and the ends erect, the whole plant rounded and bushy; branches slender or stout, more or less obtusely angled, coarsely furfuraceous, glabrate and then stramineous, the bark persistent; leaves alternate except a few basal pairs, sessile or short-petioled, elliptic-spatulate, oblanceolate or oblong or in small plants sometimes elliptic or obovate, narrowed to the base, obtuse or acute at apex, 0.5 to 2.5 cm. long, 0.2 to 0.7 cm. wide, entire or remotely and acutely short-dentate, thin, white-furfuraceous on both sides or sparsely furfuraceous and green above, only the midvein prominent; flowers monoecious, all in small axillary clusters the lower of which are purely pistillate, the upper mixed or perhaps some near the ends of the branches purely staminate; perianth of staminate flowers 4- or 5-cleft or exceptionally 3-cleft, of pistillate flowers wanting; fruiting bracts short-pedicellate, strongly compressed, united throughout (except the herbaceous margins), orbicular, 2 to 4 mm. in diameter, the margins acutely dentate all around, the terminal tooth sometimes more prominent than the others, the faces either flat and unappendaged or with a single low tubercle midway of the midvein or each face bearing 2 laciniate crests (only in minor variation 2, variety *thornberi* Jones), scurfy when young, glabrate, only the midvein prominent; seed 1 to 1.4 mm. long, pale to dark brown; radicle superior. (*Obione elegans* Moquin, in DeCandolle, Prodr. 13²:113, 1849.) Southwestern United States and northern Mexico.

SUBSPECIES.

Atriplex elegans exhibits a natural divergence into two subspecies, each occupying its own geographic area. In addition to these there is a form here listed as minor variation 2, which should perhaps be subspecifically treated.

Key to the Subspecies of *Atriplex elegans*.

- | | |
|---|----------------------------------|
| Fruiting bracts with broad deeply dentate margins; leaves often dentate. Southern Arizona and eastward. | (a) <i>typica</i> (p. 300). |
| Fruiting bracts with very narrow shallowly dentate margins; leaves entire. California and western Arizona. | (b) <i>fasciculata</i> (p. 301). |

26a. ATRIPLEX ELEGANS TYPICA.—Plant usually 1.5 to 6 dm. high; leaves elongated, 1 to 2.5 cm. long, entire to saliently denticulate; fruiting bracts with a broad herbaceous border which is sharply toothed or laciniate, the teeth 1 mm. long when well developed. (*Obione elegans* Moquin in De Candolle, Prodr. 13²:113, 1849.) Western Texas to southern Arizona, eastern border of California, Sonora, and Chihuahua. Type locality, Sonora. Collections: El Paso, Texas, Jones 4171 (Gr, US); Mesilla Valley, New Mexico,

September 29, 1906, *Wootton and Standley* (NY, US); Arizona: Tucson, *Thorner 131, 197a* (UC, form intermediate to subspecies *fasciculata*); Santa Cruz Valley, Tucson, August 16, 1901, *Thorner* (UC, minor variation 2, var. *thorneri* Jones); southern Arizona, near the Mexican Boundary, August 7, 1884, *Pringle* (US, same variation); Maricopa, *Hall 11202a* (UC, collected with *11202b*, which is minor variation 2, variety *thorneri* Jones); Phoenix, *Griffiths 4410* (US); Yuma, September 8, 1907, *Harter* (Gr, NY, US); Needles, eastern California, *Eastwood 5966* (SF); Guaymas, Sonora, *Palmer 122* (Gr, NY, UC); Gila River, northern Sonora, May, *Schott* (NY, type of *Obione radiata*, minor variation 8); plains near Chihuahua City, *Pringle 670* (Gr, NY); near Durango City, *Palmer 497* (UC).

26b. *ATRIPLEX ELEGANS FASCICULATA* (Watson).—Plant commonly small, 0.5 to 3 dm. high, rarely more; leaves 0.5 to 2 cm. long, entire; fruiting bracts with a very narrow herbaceous border which is minutely toothed or nearly entire. (*A. fasciculata* Watson, Proc. Am. Acad. 17:377, 1882.) Southern California, from central Inyo County south across the Mojave and Colorado Deserts to the borders of Lower California and western Arizona; abundant on the Colorado Desert. Type locality, near Fish Ponds, Mojave Desert. Collections: California: between Keeler and Darwin, Inyo County, *Coville and Funston 903* (DS, US); type collection, May, 1882, *Parish 1351* (Gr, US); Manix, San Bernardino County, *Parish 10368* (UC); Barstow, Mojave Desert, *Brandegee* (UC); Rabbit Springs, Mojave Desert, *Parish 5010* (DS, UC); Borregos Springs, western edge of Colorado Desert, May 28, 1894 and May, 1899, *Brandegee* (UC); Cameron Lake, Colorado Desert, March 29, 1901, *Brandegee* (UC); Cariso Creek, Colorado Desert, April, 1905, *Brandegee* (US); alkaline soil, about 60 m. below sea-level, Mecca, Colorado Desert, *Parish 8452* (DS, type of *A. saltonensis* Parish, minor variation 4); Niland, Imperial Valley, *Parish 10869* (UC); Blue Lake, Imperial Valley, *Davy 8019* (UC); bottom lands along the Colorado River, near Paloverde, *Hall 5924* (UC); Calexico, Imperial County, *Davy 7992* (UC); low hill near Volcano Lake, northern Lower California, *MacDougal 196* (NY); Phoenix, Arizona, *Eastwood 6147* (SF); Agua Caliente, Arizona, March 3, 1894, *Carlson* (SF); near San Xavier Mission, south of Tucson, Arizona, *Harris 14181* (US).

MINOR VARIATIONS AND SYNONYMS.

1. *ATRIPLEX ELEGANS* var. *FASCICULATA* Jones, Contr. West. Bot. 12:76, 1908.—*A. elegans* subsp. *fasciculata*.

2. *A. ELEGANS* var. *THORNERI* Jones, l. c.—Characters as in subspecies *typica*, except that each fruiting bract bears 2 prominent lacerate appendages on the face near the base. The margin also is more deeply toothed than usual. The presence of appendages is a more important character in this species than in most *Atriplexes*, where it is known to be extremely variable. Of 12 herbarium sheets examined, all have either uniformly smooth or uniformly crested bracts, with three exceptions, in which both forms were found on the same plant. At Tucson and at Maricopa, both in Arizona, the two forms grow intermingled, but apparently with no intergradation or with any mixing of the two kinds of bracts on the same plant. The three exceptions just mentioned are: (1) a sheet in the M. E. Jones Herbarium from Tucson (August 17, 1903, *Jones*) in which some of the bracts are smooth on the faces except for the strong midrib while others on the same stem are prominently two-crested; and (2 and 3) two sheets in the United States National Herbarium from Phoenix (*Griffiths 4410* and *6198*) in which the bracts are mostly crested, but a few on the same stems without crests (fig. 42, f, g). The type locality of variety *thorneri* is Tucson, Arizona.

3. *A. FASCICULATA* Watson, Proc. Am. Acad. 17:377, 1882.—*A. elegans fasciculata*.

4. *A. SALTONENSIS* Parish; Muhlenbergia 9:57, 1913.—This is a common depressed form of subspecies *fasciculata*, in which the short stems are subdecumbent and the leaves only 0.5 to 1 cm. long. The type specimens are 1 to 1.5 dm. long. Although *fasciculata* is often larger and more nearly erect than *saltonensis*, the two types are not very different. The type of the former, as at the Gray Herbarium, is 1 dm. high, the leaves are 0.8 to 1.3 cm. long, and the two main branches spread horizontally from the summit of the taproot to a distance of 1.5 cm., from which distance they are abruptly ascending. The type locality of *saltonensis* is in alkaline soil a little north of Mecca, California.

5. *A. THORNBERI* Standley, N. Am. Fl. 21: 57, 1916.—Based upon *A. elegans thornberi*, which see.
 6. *OBIONE ELEGANS* Moquin, in De Candolle, Prodr. 13: 113, 1849.—*A. elegans typica*.
 7. *O. ELEGANS* var.? *RADIATA* Torrey, Bot. Mex. Bound. Surv. 183, 1859.—The Thurber plant mentioned with the description has not been seen, but *Wright 571*, from western Texas, is *A. elegans typica* with rather deep incisions in the margins of the fruiting bracts. The original *radiata* of Torrey also included plants referable to *A. wrightii*, according to Coulter (Contr. U. S. Nat. Herb. 2: 368, 1894).
 8. *O. RADIATA* Torrey, l. c.—Not distinguishable from *A. elegans typica*. Type locality, alluvions of the Gila River, northern Sonora.

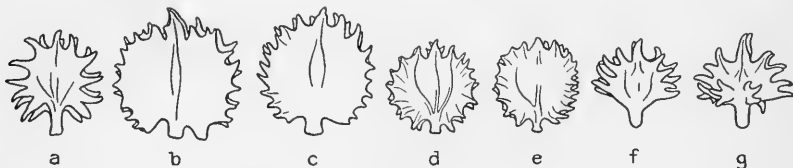


FIG. 42.—Fruiting bracts of *Atriplex elegans*: a, b, c, f, g, subspecies *typica*; d, e, subspecies *fasciculata*; a, from Durango (110218 UC); b, from Tucson, Arizona (128540 UC); c, from Tucson, Arizona (7167 UC); d, from the Colorado Desert, California (110328 UC); e, from the Mojave Desert, California (type of *fasciculata*, Gr); f, g, from a single plant from Phoenix, Arizona (424737 US). All $\times 6$.

RELATIONSHIPS.

The development of this species from the aggregate known as *A. pentandra* is quite certain. It appears to be a derivative of some form near to the primitive subspecies *muricata* which has become modified, especially in its bracts. These have been strongly compressed and the marginal dentations regularly spaced, while the staminate terminal spikes have been almost entirely suppressed, the flowers being confined in *elegans* to the leaf-axils. From this point of view, the present species is a northwestern derivative, which theory gains support from the close similarity between specimens of *muricata* from the northern borders of its area and some of *elegans* from adjacent territory (e. g., *Palmer 290*, representing the former, and *Palmer 497*, representing the latter, both from near Durango). Such plants are almost identical, except in the features mentioned. Furthermore, the differences become more pronounced at greater distances from the ancestral home in Mexico. Thus, the bract appendages, so peculiarly developed in *muricata*, are still present in a form of *elegans* known as variety *thornberi* (minor variation 2), which is most plentiful in northern Sonora and southern Arizona, while the bracts are always smooth in subspecies *fasciculata*, a form of the Californian deserts. Thus the connections with *pentandra* through its subspecies *muricata* (or possibly the little-known minor variation *cyclostegia*) may be traced along a line that is also the route over which the forms have passed in their northwestward migrations.

Although this species has given rise to no others, and is therefore represented as at the end of a line on the phylogenetic chart, it is by no means stationary. This is evidenced by several forms within the species, the best-marked of these being subspecies *fasciculata*, in which there is a notable reduction in the width and dentation of the margins of the fruiting bracts. The leaves and also the whole plant are often but not always much reduced in size. The leaves are always entire, as far as known, which has led to the use of this difference as a prime character for specific segregation. But it is quite untrustworthy, for not only are a portion of the leaves entire in typical *elegans*, but in some specimens with typical bracts apparently all the leaves are entire (Tucson, Arizona, August 12, 1901, *Thornber 7164*, UC). The bract character is therefore taken as the more reliable and the one which can best be correlated with features of habit and distribution. That it is not of specific value may be seen from an examination of the accompanying plate and text-figures, where it will be noted that all gradations may easily be found.

ECOLOGY AND USES.

Atriplex elegans typically forms pure or mixed societies in moderately saline areas in the valleys of southern Arizona, where it is associated with *A. canescens* or *A. polycarpa*, or both. Recently it has become a common weed in roadsides, fallow fields, and other disturbed places, serving as a pioneer of a short secondary succession. Kearney and his associates found as much as 1 per cent of salt in the first foot of soil, and 0.67 per cent in the second. It flowers regularly after the summer rains, but it may also bloom in late spring as a consequence of abundant rainfall.

This species furnishes excellent grazing, but is limited in amount. According to Thornber, it is used as greens by the Pima Indians, and it is probably a cause of hay-fever to some extent.

27. ATRIPLEX MICROCARPA (Bentham) Dietrich, Syn. Pl. 5: 536, 1852. Plate 48.
DOTSCALE.

Prostrate or procumbent annual herb, commonly much branched to form tangled masses 2 to 10 dm. across and 1 to 4 dm. high, the ultimate branches ascending or erect; sometimes less branched and all of the stems ascending; branches tough, flexuous, obtusely angled or terete, lightly furfuraceous when young, very soon glabrate and then stramineous, the bark persistent, breaking only on old stems; leaves alternate or a few lower ones opposite, numerous, sessile or the lower short-petioled, oblanceolate or spatulate-elliptic, narrowed at base, acute or obtuse at apex, often mucronulate, 0.5 to 2 cm. long, 0.3 to 0.6 cm. wide, entire, thin, sparsely scurfy and green above, more closely scurfy and gray beneath, 1-nerved; flowers monoecious, the staminate glomerules in the upper axils or rarely a few of the upper glomerules without subtending leaves and thus short-spicate, the pistillate also in axillary glomerules, but these beneath the staminate, many of the intermediate glomerules with both staminate and pistillate flowers; perianth deeply 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile or very shortly stalked, not compressed, united nearly to the summit, nearly orbicular, but with narrowed base and broad summit, obtuse, 1 to 2 mm. long, 1 to 2.2 mm. broad (larger in minor variation 3), entire, except for 1 to several minute teeth across the summit, faces smooth or with a few minute tubercles, 1-nerved, not obviously reticulated; seed 0.8 mm. long, light brown; radicle superior. (*Obione microcarpa* Bentham, Bot. Voy. Sulph. 48, 1844. Not *A. microcarpa* Waldstein and Kitaibel, 1812, nor *A. microcarpa* Bentham, 1870.)

Near the coast from Los Angeles County, California, to middle western Lower California, including the adjacent islands. Type locality, San Diego, California. Collections, all in California and Lower California: San Pedro Hills, near Rocky Point, Los Angeles County, *Abrams 3137* (DS, NY, UC, US); Redondo, Los Angeles County, October 15, 1903, *Brandege* (UC); Avalon, Santa Catalina Island, March, 1901, *Trask* (NY, US); San Clemente Island, April 26, 1912, *Wootton* (US); Laguna Beach, Orange County, May 5, 1916, *Crawford* (UC); La Jolla, near San Diego, *Clements 59* (Gr, UC); San Diego, *Palmer 330* (Gr, NY); San Quentin Bay, *Palmer 717* (Gr, US); Cedros Island, *Palmer 755* (Gr, NY, US). Other stations for Lower California are given under minor variation 3.

MINOR VARIATIONS AND SYNONYMS.

The characters of this species are remarkably constant, there being but little fluctuation, even in the vegetative features. This constancy is a common characteristic of species of limited distribution. The only variation of note is the large-bracted form found near the southernmost limits of the area inhabited and described under No. 3.

1. ATRIPLEX PACIFICA Nelson, Proc. Biol. Soc. Wash. 17:99, 1904.—The correct name for those who follow the American rules. According to these rules the name *A. microcarpa* (Bentham) Dietrich can not be used for this plant because of the earlier *A. microcarpa* Waldstein and Kitaibel (P. Rar. Hung. 3:278, 1812). This latter, however, is generally considered as synonymous with *A. patula hastata*, or at most only a minor variation of this.

2. OBIONE MICROCARPA Bentham, Bot. Voy. Sulph. 48, 1844.—*A. microcarpa* Dietrich.

3.—A very distinct form or subspecies, apparently connecting with *A. pentandra muricata*, of Mexico, comes from Lower California and the islands to the west. This is a small annual with prostrate lower branches, narrowly spatulate leaves, and fruiting bracts sometimes as much as 4 mm. long through the development of a prominent terminal lobe, or tooth. Most of the bracts, however, even on the same plant, are only about 2 mm. long and exactly like bracts of the common form of *microcarpa*. This variation apparently is well isolated geographically from the more northern type. Collections at hand include: Natividad Island, April 10, 1897, *Brandegee* (UC); San Benito Island, *Anthony* 277 (DS, UC, US); San Jose de Gracia, April 8, 1889, *Brandegee* (UC).

RELATIONSHIPS.

All available evidence indicates that this is a derivative of *A. pentandra* through its Mexican subspecies *muricata*. The two are identical in essential features, such as position of embryo, distribution of the two kinds of flowers, and general shape of bracts and leaves. *A. microcarpa* exhibits the greater specialization, especially in the almost constantly reduced staminate inflorescence, reduced size of bracts and leaves, more uniform suppression of bract-margins and bract-appendages, and constantly annual habit. These modifications apparently arose in connection with the northwesterly migration of the group. Genuine *muricata* stops at the western shores of the Sonoran Coast; *microcarpa* now begins about half-way up the peninsula of Lower California, on the Pacific side, and ranges thence northward. The connection between the two seems to be established by minor variation 3 of the latter species, which comes from that portion of the range of *microcarpa* which is nearest to that of *muricata*. The reductions indicated above are mostly quite evident in this, except that the staminate inflorescence sometimes is even more elongated than in any known form of *muricata* and some of the bracts also are as in *muricata*, while the leaves are intermediate and with their own peculiar shape. However, the elongated inflorescence is a feature of only one of the twelve plants at hand and may be either abnormal or a development representing a local strain. In other plants of the same collection (Natividad Island, *Brandegee*) the staminate glomerules are all axillary. The bracts on this intermediate form vary all the way from broadly winged, and therefore as large as in *muricata*, to nearly wingless and as small as in *microcarpa*. Most of them are of this latter type and the sides are not appendaged.

The phylogenetic connection just discussed was first suggested by Bentham in connection with his original description of the species. Bentham attempted to include also *A. barclayana* in the group, the material then available giving no indication that this species was chiefly dioecious, as has been since established. Other features also now indicate that, while *A. barclayana* belongs somewhere near, it is better considered as a divergent line which stands close to the beginning of a large group of species characterized by a shrubby and dioecious habit. There is now no reason to suppose that *microcarpa* evolved by the roundabout route of *barclayana*, and, moreover, there would be several insurmountable objections to such a theory.

ECOLOGY AND USES.

Atriplex microcarpa forms small clan-like groups in sandy soil back of the strand, and occurs also as a subruderal along roadsides. The flowers open for the most part from March to June, but have been found as late as October.

No uses are known for this species, though it is possibly an occasional cause of hay-fever.

28. ATRIPLEX WRIGHTII Watson, Proc. Am. Acad. 9:113, 1874. Plate 47.

Erect or ascending annual herb, 2 to 8 dm. high, the branches few and the plants bush-like; branches thick, deeply grooved, sparsely scurfy, soon glabrate and then stramineous or reddish; leaves alternate, numerous, mostly short-petioled, oblanceolate to elliptic-spatulate, all much narrowed to the base, obtuse and mucronulate or the upper ones

acute at apex, 2 to 7 cm. long, 0.5 to 2.5 cm. wide, coarsely sinuate-dentate or repand-dentate or many of the leaves entire, thin, sparsely scurfy but soon glabrate and green on the upper surface, permanently white-scurfy beneath, strongly 1-nerved; flowers monoecious, the staminate glomerules in naked terminal panicles 5 to 30 cm. long, the pistillate flowers in nearly all of the leaf-axils; perianth 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts short-stalked or sessile, well compressed, united to about the middle, cuneate-orbicular, 2 to 3 mm. long, 2.5 to 4 mm. broad, the conspicuous margins greenish above the middle and acutely gash-toothed, the faces usually not appendaged, but with 3 nerves from the base; seed 1.2 to 1.5 mm. long, brown; radicle superior.

Southwestern New Mexico, Arizona, and northern Sonora. Type locality, New Mexico. Collections: Type collection, *Wright 1743* (Gr, NY); Mangas Springs, Grant County, New Mexico, *Metcalf 639* (NY, US); Crain's Ranch, northwestern Grant County, New Mexico, July 18, 1900, *Wooton* (US); Old Camp Goodwin, Arizona, *Rothrock 343* (US); Clifton, Arizona, *Davidson 2937* (US); Williams, Arizona, *Griffiths 4924* (US); cultivated lands at Tempe, Arizona, *Kearney 96* (US); Santa Cruz Valley, Tucson, Arizona, *Thornber 134* (UC); Catalpa, Arizona, *MacDougal 749* (US).

SYNONYM.

1. *ATRIPLEX RADIATA* Coulter, Contr. U. S. Nat. Herb. 2:368, 1894.—Intended by Coulter to replace the name *A. wrightii*, because of the earlier *Obione elegans radiata* Torrey. But Torrey's name, in addition to having only varietal rank, is not now desirable, since it covered plants of *A. elegans* as well as of *A. wrightii*, and, moreover, its descriptive features are misleading for the present species.

RELATIONSHIPS.

Atriplex wrightii stands between *A. pentandra muricata* and *A. bracteosa*, both geographically and phylogenetically. Its origin from the former or from some slightly more primitive ancestral stock seems reasonably certain. It has a closely similar habit. The fruiting bracts are slightly reduced in size but retain the characteristic reticulate venation. The leaves have modified their shape and become for the most part broadest above the middle. This is looked upon as a later development from the usual lanceolate or ovate shape. On the other hand, the inflorescence exhibits no reduction, the elongated staminate panicles being especially well developed. Since the inflorescences usually are much reduced in *muricata*, it is probable that *wrightii* diverged from the common stock before the present characters of the former were firmly fixed. The connection with *bracteosa* will be discussed when this species is reached.

ECOLOGY AND USES.

Atriplex wrightii forms dense consociates in river valleys with somewhat alkaline soil, often making pure stands 3 to 4 feet in height and almost impenetrable, but usually associated with *Amarantus palmeri* and *Eriochloa polystachya*, and less commonly with *Kalstroemia grandiflora*. It grows sparsely along roadsides on the mesas, but becomes a weed in valley roads and in cultivated fields.

The vigorous growth and palatability of this species render it of considerable value for grazing, as indicated by the fact that it is grazed close to the ground in dry seasons. It gives promise of becoming a valuable forage plant under cultivation.

29. *ATRIPLEX BRACTEOSA* (Durand and Hilgard) Watson, Proc. Am. Acad. 9:115, 1874.
Plate 47. BRACTSCALE.

Erect or decumbent annual herb, 3 to 10 dm. high, the stems commonly spreading to form dense tangled mats 5 to 30 dm. across, from which arise slender erect or ascending twigs, or whole plant erect, slender, and sparsely branched in some forms (see minor variation 4); branches thick, obtusely angled or grooved, sparsely scurfy, soon glabrate

and then pale or stramineous, rarely reddish; leaves alternate, numerous, sessile or subsessile, lanceolate, narrowly ovate, or narrowly elliptic, all narrowed to the base, acute or acuminate at apex, mostly 2 to 4 cm. long, 0.4 to 1.5 cm. wide, or up to 8 cm. long by 4 cm. wide on vigorous sterile shoots, acutely and sparingly dentate or some entire, thin, scurfy only when young, equally green or greenish on both faces or only slightly paler beneath, strongly 1-nerved; flowers monoecious, the staminate glomerules in naked terminal panicles or spikes, these 5 to 15 cm. long or occasionally only 3 or 4 cm. (still more reduced in a hybrid form, minor variation 1), the pistillate flowers in small clusters in nearly all of the leaf-axils; perianth apparently always 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile or subsessile, slightly to moderately compressed, united to about the middle, cuneate-orbicular or fan-shaped with a narrowed summit, 2 to 2.5 or rarely 3 mm. long, 2 to 3 mm. broad, the margins greenish and acutely dentate above the middle, the faces tuberculate or sometimes smooth, 1-nerved and with also some faint secondary nerves but not reticulated, scarcely scurfy; seed 1 to 1.3 mm. long, brown; radicle superior. (*Obione bracteosa* Durand and Hilgard, Pacif. R. R. Rep. 5: 13, 1858.)

Alkaline valleys of California from the Sacramento Valley south to the borders of Lower California, very abundant in the San Joaquin Valley and on the coastal slope of southern California, rare east of the Sierra Nevada; grows also in west-central Nevada. Type locality, Poso Creek, Kern County, California. Collections, all in California except the last three: Chico, Butte County, *Heller 13350* (SF); Princeton, Colusa County, September 14, 1905, *Chandler* (UC); east of Maxwell, Colusa County, *Hall 11011* (UC); Manteca, San Joaquin County, October 26, 1919, *Hall* (UC); West Park, near Fresno, October 26, 1901, *Daves* (UC); near Hanford, Tulare County, *Kearney 153* (US); Tulare, August, 1902, *Pillsbury* (UC); Visalia, September, 1881, *Congdon* (UC); Rosedale, near Bakersfield, *Davy 2886* (UC); near Kernville, *Purpus 5537* (UC); Lancaster, western part of Mojave Desert, *Elmer 3984* (DS, Gr, NY, US); Summerland, Santa Barbara County, *Abrams 4142* (Gr, NY); near Piru, Ventura County, October 20, 1919, *Hall* (UC); Santa Catalina Island, *Eastwood 6529* (SF); Cienega, near Los Angeles, *Braunton 636* (UC, US); near San Bernardino, *Parish 21195* (UC); near Riverside, *Piemeisel 3765, 3767, 3647* (US); near Winchester, Riverside County, April, 1902, *Hall* (UC); Elsinore, July 8, 1896, *McClatchie* (UC); San Diego, *Vasey 554* (US); Needles, *Eastwood 5968* (SF); Tecate River, Lower California, *Mearns 3785* (US); Coronado Islands, on bluffs near the sea, Lower California, *Cowles 14* (Pomona, minor variation 1, *A. davidsoni*); Reno, Nevada, *Petersen 466* (UC).

MINOR VARIATIONS AND SYNONYMS.

This species exhibits a wide range of vegetative forms, most of which can be correlated with environmental conditions. These include variations in size, dentation, and succulence of leaf and a wide divergence in the habit, this ranging from nearly simple erect plants to widely branched forms which make tangled masses 2 meters or more across and sometimes 1 meter high. There is no indication that the root is ever perennial, as has been reported. Three forms which seem to be quite different from the fluctuating variations just mentioned are described under Nos. 1, 4, and 5.

1. *ATRIPLEX DAVIDSONI* Standley, N. Am. Fl. 21: 57, 1916.—This is exactly like a common small-leaved form of *A. bracteosa*, except that the terminal staminate spikes are reduced to very short, almost globose terminal clusters. The cause of this is not known, but the occurrence of the form only along the coast of southern California, where *A. microcarpa* also grows, suggest that possibly it may be a hybrid, with this species for the other parent. A rather more noticeable compression of the bracts and the presence of 3 faint nerves on each bract lend support to this view. The collections thus far made show no intergrading series between *davidsoni* and *bracteosa*, but a single collection is intermediate. This is *Parry 677* (US) in which the staminate inflorescence varies from a globoid cluster to spicate and 2 cm. long. Collections of *davidsoni* include: Type collections, labeled as Balboa, California, *Davidson 2951* (US) but said by Davidson to have been gathered between Balboa and Santa Ana; Temple Street, Los Angeles, *Braunton 630* (DS, UC, US); Long Beach, *Parish* (DS, US); Mesmer, *Abrams 206* (DS); San Pedro, *Eastwood 165* (SF); Abalone Point, Laguna Beach Bluffs, July 29, *Crawford* (Pomona, US); Coronado Islands, *Crawford 14* (Pomona).

2. *A. SERENANA* Nelson, in Abrams, Fl. Los Angeles, 128, April 5, 1904; Proc. Biol. Soc. Wash. 17:99, April 9, 1904.—This name has been adopted by some American botanists for *A. bracteosa* Watson because of the earlier *A. bracteosa* Trautvetter, Act. Hort. Petrop. 1:17, 1870. This latter is synonymous with the still older *A. dimorphostegia* Karelin and Kirilow, an Asiatic species. The name *bracteosa* is therefore available for the American plant, according to the International Code.

3. *OBIONE BRACTEOSA* Durand and Hilgard, Pacif. R. R. Rep. 5:13, 1858.—*A. bracteosa* Watson.

4.—A slender, strictly erect, early maturing form of *Atriplex bracteosa* is sometimes found in the San Joaquin Valley, California. It always grows, as far as known, in sod of *Distichlis spicata* and *Cynodon dactylon*. The foliage is yellow and sere by the middle of October, when the typical form in nearby fields is still green. No differences can be found in the fruiting bracts or other essential characters, and the assumption is that it is an ecologic or seasonal form. It is of some interest in connection with the curly-top disease of the sugar-beet, since the leaf-hopper that transmits this disease is not carried over so late on these slender plants as on the usual form. The following collections belong here: 5 km. northwest of Hanford, Hall 10970 (UC); near Fresno, October 25, 1919, Hall (UC); between Bakersfield and Rosedale, Hall 11780 (UC); Rosedale, Davy 2922 (UC).

5.—A supposed hybrid between *A. bracteosa* and *A. argentea expansa* has been collected near Ventura, California (Hall 10954, UC). It is a rounded, bushy plant 7 dm. high with staminate inflorescences of the former, but bracts as in the latter. The stems and branches are rigid, as in *expansa*. The leaves are similar to those of *bracteosa* in shape and dentation, but larger, especially broader, and therefore somewhat intermediate.

RELATIONSHIPS.

Atriplex bracteosa is the end of an evolutionary line which began somewhere near *A. pentandra* and threw off as short divergent branches *A. p. muricata*, *A. barclayana*, *A. linnifolia*, and *A. wrightii*. This process was accompanied by a migration of the group from the ancestral habitat in central or southern Mexico to the north and northwest. *A. bracteosa* is restricted in its distribution to California, with only slight invasions across the borders into Nevada and Lower California. It is thus well separated geographically from its nearest allies. *A. microcarpa*, which belongs to the same general group, occurs also along the coast of southern California, but this arose from another branch and reached its present location by way of Lower California, whereas *bracteosa* has its closest affinities with species of Arizona and New Mexico. Although these two species apparently hybridize, as is indicated under minor variation 1, no intermediates occur and their connection can be traced only through more primitive Mexican forms.

The nearest approach to the common phylogenetic stock is through *A. wrightii*, which, however, exhibits certain specialized features of its own. *A. bracteosa* differs from this in the still more reduced size of the bracts and seeds, in the much less or scarcely compressed fruits, and in having the leaves broadest below the middle and with smaller, acute dentations. The foliage is not white beneath and the fruiting bracts do not have the 3 nerves and fine reticulations which have been cited as evidence of the connection between *wrightii* and *muricata*.

ECOLOGY.

Atriplex bracteosa was originally a moderate halophyte of the *Distichlis* zone especially, but in recent years it has become the most characteristic weed of disturbed areas in the San Joaquin Valley. It often covers fallow fields, roadsides, fenceways, etc. with a dense pure community. The plants are exceedingly vigorous and produce abundant seeds, so that they maintain the initial consocieties for a longer period than usual. Kearney and his associates have found a range of no alkali to 0.32 per cent in the first foot of soil and 0.2 per cent in the second foot. The flowers appear from April to October.

USES.

This species is of no value, as it is not eaten by stock, but it is of some importance as a cause of hay-fever. Its greatest interest, however, is in connection with the curly-leaf disease of the sugar-beet. This malady has become so serious in some of the western

States that the production of sugar-beets has been abandoned over extensive areas, with the consequent closing down of sugar factories in some districts. The exact nature of the disease is not known, but since it is transmitted exclusively by the beet leaf-hopper (*Eutettix tenella* Baker), a knowledge of the habits of this insect is of prime importance. According to Severin, after the beets are harvested the leaf-hoppers pass to certain wild species, the most important of which are the annual *Atriplexes*. When these dry up in the autumn the insects pass over to the shrubby species, especially those of the foothill cañons, where they remain until after the first winter rains, when they leave these plants for the more tender annuals, particularly *Erodium cicutarium*. The annual *Atriplexes* are important as host-plants upon which *Eutettix* breeds from spring to autumn. Of these, the most important are *A. argentea expansa*, *A. bracteosa*, and *A. rosea*, because of their remaining succulent later in the season than most other species and because of their abundance. It is believed that the considerable increase in the number of these plants as a result of disturbances due to man is largely responsible for the enormous number of leaf-hoppers. The most important shrubby *Atriplexes* which serve as food plants for the insects in a dry season in California are *A. polycarpa* and *A. spinifera*.

The eradication of the *Atriplexes* is impracticable, because of their great abundance. It is therefore impossible to control the disease by the destruction of the host-plants of the carrier. However, a knowledge of the distribution and abundance of the different species is an aid in determining the districts where outbreaks of *Eutettix* are most likely to occur. Such information, therefore, should be used in selecting locations for the culture of the sugar-beet and for the erection of factories. This subject has been discussed in detail by many writers, more especially by Severin and Basinger (Journ. Econ. Ento. 15: 411-419, 1922).

30. ATRIPLEX LINIFOLIA Humboldt and Bonpland, in Willdenow, Sp. Pl. 4:958, 1806.
Plate 47.

Erect or decumbent perennial herb, 2 to 8 dm. high, the stems curving upwards from a short woody base; branches moderately thick, angled or grooved in the inflorescence, sparsely scurfy, soon glabrate and then stramineous; leaves alternate, crowded, sessile or short-petioled, linear or linear-oblong or some narrowly spatulate, cuneate to attenuate at the base, obtuse and mucronate or acutish at apex, 1 to 4 cm. long, 0.2 to 0.5 cm. wide, entire or the larger ones with a few spreading teeth, rather thin, glabrate and greenish on the upper surface, permanently gray-scurfy beneath, 1-nerved; flowers monoecious or partly dioecious, the pistillate flowers in the leaf-axils, the staminate glomerules in nearly naked terminal spikes and panicles, these 5 to 15 cm. long; perianth 5-cleft in staminate flowers, wanting in the pistillate; fruiting bracts sessile or short-stalked, compressed, united to above the middle, cuneate-orbicular, the summit always broadly rounded, 2 to 2.5 mm. long, 2.5 to 3 mm. broad, the margins obtusely or acutely dentate above the middle, the faces either tuberculate or crested or unappendaged on the same plant and reticulated or the reticulations masked by the appendages, scarcely scurfy; seed about 1.2 mm. long, brown; radicle superior.

Mexico, apparently rare. Type locality, Mexico. Collections: Vicinity of Durango, Palmer 349, 350, 495, 496 (Gr, NY, UC, US); alkaline meadows near Mexico City, Pringle 6892 (Gr, NY, UC, US).

SYNONYMS.

1. ATRIPLEX POLYGAMA Sesse, in Lagasca, Gen. Sp. Nov. 12, 1816. Apparently the long-leaved form of *A. linifolia*. Described from Mexican specimens.
2. OBIONE LINIFOLIA Moquin, Chenop. Enum. 74, 1840. Based upon *Atriplex linifolia*.
3. O. POLYGAMA Moquin, in De Candolle, Prodr. 13: 114, 1849. Based upon *Atriplex polygama*, which see.

RELATIONSHIPS.

Although sharply set off from all of its allies, this species clearly stands next to *A. pentandra muricata*, from which it differs especially in the elongated linear entire leaves, in the uniformly well developed staminate inflorescence, and in the marked tendency towards dioecism. In the last feature *linifolia* approaches *barclayana*, but in other respects, and especially in the bracts, these two are very unlike. It is probable that both stand near the phylogenetic connection between the group of monoecious herbaceous species and the dioecious shrubby ones.

ECOLOGY AND USES.

Nothing is known of the ecology and uses of this Mexican species.

31. ATRIPLEX FRUTICULOSA Jepson, Pittonia 2:306, 1892. Plate 43. BALLSCALE.

Spreading or nearly erect perennial herb from a woody base or rarely the stems also woody, the plant then suffruticose, 0.5 to 3 dm. high, the stems when procumbent a few cm. to 3 dm. long; branches slender, terete, not grooved or striate, coarsely furfuraceous, glabrate and then stramineous or reddish, the bark becoming dark and fissured on old woody stems; leaves all alternate, mostly short-petioled, the upper ones sessile, narrowly elliptic or linear-lanceolate, acute at each end, 0.5 to 1.5 cm. long, 0.2 to 0.4 cm. wide, entire, moderately thick but not succulent, gray on both faces with a dense permanent scurf, soft, 1-nerved; flowers monoecious, the staminate glomerules in short terminal interrupted spikes, these commonly reduced to 1 or 2 dense globose clusters at the end of each branch or the spike rarely up to 6 cm. long, the pistillate flowers mixing slightly with the lower staminate and continuing down the stems in the leaf-axils; perianth apparently always 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile or subsessile, not compressed or only slightly flattened, united to above the middle, orbicular-obovate or subglobose, 3 to 4 mm. long and nearly as broad, narrowly margined and acutely dentate from the middle upwards, the sides neither strongly nerved nor reticulated, tooth-crested or muricate or sometimes smooth and then with a suggestion of longitudinal nerves, indurate; seed 1.4 to 1.7 mm. long, dark brown; radicle superior.

Sacramento and San Joaquin Valleys, California. Type locality, alkaline soil near Little Oak, Solano County, California. Collections: South of Willows, Glenn County, *Hall 11003* (UC); near Norman, Glenn County, May 26, 1898, *Davy* (UC); type collection, August 16, 1892, *Jepson* (Herb. Jepson, herbaceous to the base); Wilson Creek, near Vacaville, September 30, 1893, *Jepson* (Herb. Jepson, suffruticose, the woody stems 4 mm. thick); Livermore Pass, May, 1898, *Davy* (UC); near Crows Landing, Stanislaus County, *Hall 11016* (UC); 10 km. south of Dos Palos, Fresno County, *Hall 11022* (UC); 5.5 km. south of Mendota, Fresno County, *Hall 11762* (UC); Laton, Fresno County, *Kearney 25* (US).

RELATIONSHIPS.

This and *A. coulteri* are very closely related, as will be explained more fully under the latter species. Taken together they represent a branch of the *pentandra* line which has reached farther to the northwest than any other, except perhaps *bracteosa*. They differ from other western members of the group in the notable reduction in the size of the leaves. These are consistently entire. The present species differs from *bracteosa* also in the perennial habit, absence of a pronounced odor, and other features.

The flower and fruit characters of *A. fruticulosa* are remarkably constant, as also are those of the foliage. On the other hand, the habit is extremely variable. The type collection includes plants that are so slender and erect that they appear to be annual and others in which the herbaceous stems arise from a short, woody base, the plant in

this case plainly perennial and suffrutescens, as described by Jepson. Other collections include plants with decidedly woody stems up to 4 mm. in diameter. The only specimens of this extreme woody form are Jepson's plants from Wilson Creek, Solano County, September 30, 1893. It is remarkable that all recent collections are of plants in which the leafy stems are spreading or prostrate, and herbaceous throughout except at the very base, where they are attached to a more or less woody crown. Although normally a perennial, *A. fruticulosa* flowers and seeds in the first season, at least under garden conditions. These one-year-old plants are herbaceous throughout.

ECOLOGY AND USES.

Atriplex fruticulosa grows more or less copiously in alkaline flats of the Great Valley of California, usually associated with *Distichlis*. It has become ruderal to some extent, where it is found on railway embankments. The plants flower most abundantly in midsummer, but bloom in some degree from March to November.

This species is much relished by cattle and sheep, and is kept grazed down to a mat-like form, but it is not large enough to be of importance as a rule.

32. ATRIPLEX COULTERI (Moquin) Dietrich, Syn. Pl. 5:537, 1852. Plate 48.

Spreading perennial herb, 1 to 3 dm. high, the stems sometimes 10 dm. long, branched from the base; branches slender, terete, not grooved or striate, sparsely furfuraceous, glabrate, stramineous or sometimes reddish, the bark pale and persistent but splitting near the base of the stems; leaves all alternate, on short petioles or the upper ones sessile, narrowly elliptic, narrowly oblong or lanceolate, tapering at base, acute at apex, 1 to 2 cm. long, 0.2 to 0.4 cm. wide, entire, rather thin, gray with a close fine scurf or slightly greenish above, soft, 1-nerved; flowers monoecious, the staminate glomerules in a few upper axils and in terminal spikes less than 3 cm. long, the pistillate flowers in small clusters in the upper leaf-axils, a few sometimes in the lower staminate clusters; perianth 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile or subsessile, moderately compressed, united to the middle, obovate but with narrowed summit, 2.5 to 3 mm. long and about as broad, sharply dentate from the middle upwards, the sides with 3 prominent raised longitudinal nerves or these obscure (as in the type specimen), also with cross-veinlets and a few sharp tubercles or the tubercles wanting (as in the type); seed 1.3 to 1.5 mm. long, brown; radicle superior. (*Obione coulteri* Moquin in DeCandolle, Prodr. 13²:113, 1849.)

Coast of southern California, including the adjacent islands, probably also in northern Lower California. Type locality, California. Collections: Type collection, *Coulter* (fragment in Herb. Gray, ex-herb. Hooker); Bixby, Los Angeles County, *Brandegee* (UC); Gardena, Los Angeles County, *Braunton 265* (US); Catalina Island, *Macbride* and *Payson 370* (Gr); Avalon, Santa Catalina Island, common at a single locality at 450 m. altitude, March, 1898, *Trask* (US); Chino Creek, south of Ontario, San Bernardino County, *Johnston 1275* (UC); Trabuco Cañon, near Capistrano, Orange County, *Abrams 3270* (DS, Gr, UC); La Jolla, San Diego County, *Grant* (UC); San Diego, near the shore, May, 1878, *Cleveland* (Gr).

RELATIONSHIPS.

This species is very closely connected with *A. fruticulosa*, but each has certain features so highly specialized that both are retained in specific rank. One belongs to the coastal slope of southern California, the other to the interior valleys of the same State. Neither the ranges nor the characters fully meet. The present species exhibits the greater reduction in the size of the fruiting bracts and seed and often also in the staminate

inflorescence. On this basis it might be taken as the less primitive, but, on the other hand, the bracts are almost always longitudinally 3-nerved and reticulate-veiny, these features indicating a connection with *A. pentandra muricata*, which represents the common ancestral stock. The texture and degree of compression of the bracts are about the same in *coulteri* and *muricata*, while in *fruticulosa* the bracts are but slightly if at all compressed, therefore subglobose, and firmly indurated. These thick and hard fruiting bracts furnish perhaps the best means of distinguishing *fruticulosa* from *coulteri*. Also, the strongly veined and reticulate bracts of the latter usually serve as a distinguishing feature, but in a few specimens, such as the types themselves, the nerves and reticulations are obscure.

ECOLOGY AND USES.

Atriplex coulteri is similar to *A. fruticulosa* in its ecological relations, but it occurs on the coastal slope and the islands of southern California. It has no known uses, apart from incidental grazing.

33. ATRIPLEX DECUMBENS Watson, Proc. Am. Acad. 12:275, 1877. Plate 49.

Prostrate perennial herb, slightly woody below, the stems much branched throughout and forming tangled mats often several meters across and 3 to 4 dm. deep; branches tough and flexuous, terete, densely white-scurfy and the scurf either persistent or deciduous, the stems then stramineous, the bark smooth, except on old portions near the base; leaves very numerous, nearly all opposite, sessile, broadly elliptic to ovate, narrowly rounded to the base, acute at apex, 0.8 to 2 cm. long, 0.4 to 1 cm. wide (rarely up to 3.5 cm. long by 1.5 cm. wide), entire, thick, somewhat succulent when fresh, white on both sides with a dense permanent scurf, soft, 1-nerved; flowers dioecious, the staminate glomerules in naked moniliform, terminal spikes 1 to 10 cm. long, the pistillate ones in small clusters in the leaf-axils; perianth 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile, compressed, united to the middle, ovate or rhombic, 5 to 8 mm. long, 5 to 6 mm. broad, with broad free margins above the middle, entire or erose-denticulate, the sides neither appendaged nor nerved; seed about 1 mm. long, light brown; radicle superior. Pericarp continued as a flat, broad sheath which incloses the thickened bases of the stigmas.

Proximity of the Pacific Ocean, from Santa Barbara County, California, to San Quentin Bay, Lower California, including the adjacent islands (except the Santa Cruz Islands, where the species is not known). Type locality, near San Diego, California. Collections, all from southern and Lower California: Santa Barbara, near the beach, September, 1882, *Bingham* (Gr); Long Beach, July, 1896, *McClatchie* (UC); Newport Bay, Los Angeles County, 1882, *Nevin* (Gr); Santa Catalina Island (Catalina Cove), *Pendleton 1427* (UC); San Clemente Island, *Trask 32* (US); San Nicholas Island, April, 1897, *Trask* (US); La Jolla, San Diego County, *Clements 58* (UC); type collection, near San Diego, 1875, *Palmer 334* (Gr, NY); borders of the bay near Old Town, San Diego, *Abrams 3454* (DS, Gr, NY, UC, US); National City, San Diego County, *Hall 11214* (UC); San Quentin Bay, Lower California, *Palmer 740* (NY).

SYNONYM.

1. *ATRIPLEX WATSONI* Nelson, in *Abrams*, Fl. Los Angeles, 12S, April 5, 1904; Proc. Biol. Soc. Wash. 17:99, April 9, 1904.—This name is in accordance with the American Code. According to the International Code, however, the name *A. decumbens* Watson is available for this species, since the earlier *A. decumbens* Roemer and Schultz is synonymous with the still older *A. prostrata* R. Brown, an Australian species.

RELATIONSHIPS.

This species and *A. matamorensis* constitute a small natural group, the relationships of which are not known. It seems that they have been long separated from the more primitive species and that they have not given rise to the more modern ones. The superior radicle, together with the dioecious habit, is suggestive of a starting-point for the large group of dioecious perennial species, but there is no direct connection with any of these. Moreover, the dioecious true shrubs can be more logically connected with the monoecious herbs through the *pentandra-barclayana* line, or it is not impossible that they have had an origin entirely independent of any of the present North American species.

A. decumbens and *A. matamorensis* possess certain features not present in any species that they resemble in other characters. The opposite leaves are noteworthy in this connection. Especially unique is the dilation of the pericarp around the thickened bases of the stigmas. It is such considerations that lead to the assembling of these two species into a single close group, notwithstanding their rather wide geographic separation.

Constancy in all essential characters is a feature of *A. decumbens*. The only notable exception, aside from the usual variation in the size of the fruiting bracts, is the presence of rather well-marked forms differing in the size of the leaf. The type specimen is from an average robust plant, the largest leaves measuring 1.5 cm. long by 1 cm. wide. In an extremely large-leaved form the leaves measure 3.5 cm. long by 1.4 cm. wide and in this the staminate inflorescence also reaches the maximum length of 10 cm. (Santa Barbara, Bingham, Gr). The opposite extreme is a form with crowded subimbricate leaves only 0.8 to 1.2 cm. long by 0.3 to 0.6 cm. wide. This comes from San Clemente Island (August 25, 1894, Brandegee, UC) and from the mainland at National City (Hall 11214, UC). Since these various forms can not be correlated with geographic distribution, and since there is evidence of partial intergradation, it is believed that they are ecads.

ECOLOGY AND USES.

Atriplex decumbens regularly forms dense mats one to several feet in diameter, from the back-strand, where it grows with *Distichlis* and *Oenothera bistorta*, to the adjacent slopes of *Stipa setigera* and *Avena fatua*, where also occur *A. semibaccata*, *Baeria chryso-stoma*, *Layia platyglossa*, *Eschscholtzia*, *Platystemon*, etc. It is distinctly halophytic, but less so than *A. leucophylla*. The plants bloom from April to July or later.

This species is grazed to a slight extent by cattle, though they find the associated *A. semibaccata* much more succulent.

34. ATRIPLEX MATAMORENSIS Nelson, Proc. Biol. Soc. Wash. 17:99, 1904. Plate 49.

Erect or ascending perennial, woody toward the base, 2 to 4 dm. high; branches rather slender, terete but irregular and often crooked, obscurely furfuraceous, the old bark breaking apart and exfoliating; leaves nearly all strictly opposite, sessile, lanceolate from a broad base, crowded and often imbricate, obtuse at base, acute at apex, 0.2 to 0.5 cm. long, 0.1 to 0.3 cm. wide, entire, thick, gray with a dense scurf, soft, 1-nerved; flowers dioecious, the staminate not known, the pistillate solitary or several in axillary glomerules, these in rigid leafy spikes; perianth wanting in the pistillate flowers; fruiting bracts sessile, strongly compressed, united to the middle or above, nearly orbicular, obtuse but sometimes with a short mucronate apex, 2.5 to 3 mm. long and wide, sharply and evenly dentate nearly to the base, the sides not appendaged but strongly 1- or 3-nerved; seed 1.2 mm. long, yellowish; radicle superior. Pericarp continued as a flat white sheath around the bases of the stigmas.

Southwestern Texas and Tamaulipas. Type locality, Rio Grande Valley, near Matamoras, Tamaulipas. Collections: Type collection, Matamoras to San Fernando, October, 1830, *Berlandier 3201* (Gr, NY); Corpus Christi Bay, southwestern Texas, *Palmer 1160* (Gr, US); vicinity of Corpus Christi, Texas, *Rose 18086* (US).

SYNONYM.

1. *ATRIPLEX OPPOSITIFOLIA* Watson, Proc. Am. Acad. 9:118, 1874. The original name for *A. matamorensis*, but antedated by *A. oppositifolia* Vilmorin, a European species which apparently still has taxonomic standing.

RELATIONSHIPS.

The relationships of *A. matamorensis* have been considered under *A. decumbens*. In addition to what is there said, attention should be called to the close similarity between the fruiting bracts of *matamorensis* and *elegans*, these organs being strongly compressed, nearly orbicular, and evenly dentate in both. The habit and foliage of the present species is more like that of *A. julacea* than any other. It is doubtful, however, if either of these similarities indicate anything more than a parallel development in species widely separated phylogenetically. As contrasted with *decumbens*, *matamorensis* is a more woody plant with greatly reduced foliage and with more nearly orbicular, closely dentate fruiting bracts.

ECOLOGY AND USES.

Nothing is known of the ecology and uses of this Mexican species.

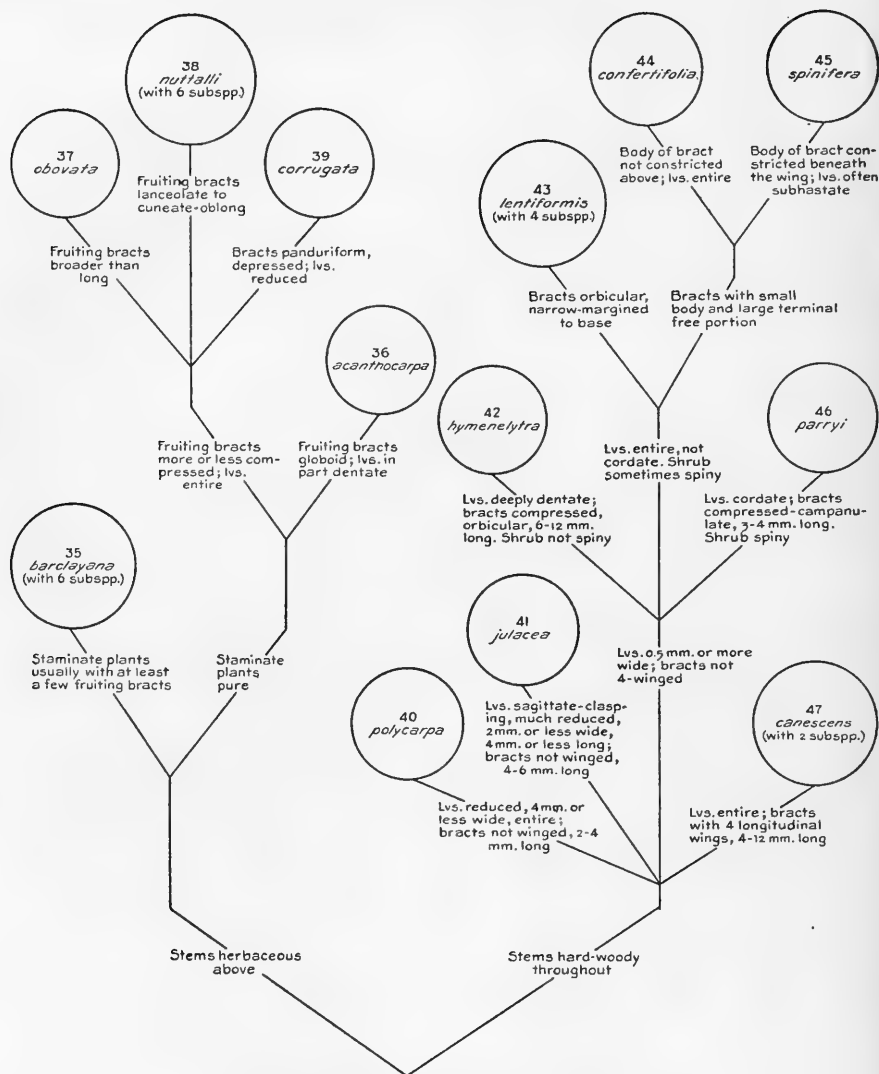
35. *ATRIPLEX BARCLAYANA* (Bentham) Dietrich, Syn. Pl. 5:537, 1852. Plate 49.

Erect or prostrate perennial shrub or herb, usually woody at least toward the base, 2 to 15 dm. high; branches stout, terete or rarely somewhat angled, sometimes striate after the fall of the scurf, densely white-furfuraceous or glabrate and reddish, the bark fissured on old plants; leaves alternate, except perhaps the lower, short-petioled or nearly sessile, obovate or broadly elliptic, tapering to the base, obtuse or mucronate at apex, 1 to 4 cm. long, 0.5 to 2 cm. wide, entire or undulate or dentate in one subspecies (*lurida*), thick, white with a dense scurf (the leaves thinner, less scurfy, and greenish in some specimens, particularly in minor variation 1); flowers dioecious, the staminate in glomerules scattered along the branches of a short spreading terminal panicle, the pistillate in small axillary glomerules of a narrow leafy-bracted terminal panicle, this 0.5 to 2 dm. long; perianth 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile or short-stalked, compressed and obovate or suborbicular to thickened and globoid, narrowed at base, united at least halfway up, usually only the margins distinct, the tip obtuse and dentate or ovate-acute or subulate, the whole bract 2 to 4 mm. long (occasional precocious bracts up to 7 mm. long), 2 to 5 or 8 mm. wide, with a few small teeth near the apex or dentate also down the margins, the sides either tuberculate or cristate or unappendaged, often irregularly thickened; seed about 1 to 1.5 mm. long, brown; radicle superior. (*Obione barclayana* Bentham, Botany Voyage Sulph. 48, 1844.)

Northwestern Mexico, from the coast of Sinaloa and Sonora across Lower California.

SUBSPECIES.

Eight species have been described from what is here included under *A. barclayana*. One is based upon leaf characters, the others upon the nature of the bracts and supported in some cases by quite unimportant features of habit or of the scurf. After assembling all of the available material, including a very fine series of specimens recently collected by Mr. I. M. Johnston on the California Academy of Sciences Expedition to the Gulf of California, it seems doubtful if any of these, with possibly the exception of *A. lurida*, can be advantageously retained even as subspecies. Much individual variation is apparent and single plants very frequently have fruiting bracts of two or more of the "species." However, the differences between the extremes are so striking that it seems desirable to give some kind of taxonomic recognition to the more frequently recurring forms. For this reason all of the variations have been assembled into the following 6 subspecies.

FIG. 43.—Phylogenetic chart of the shrubby dioecious species of *Atriplex*.

Key to the Subspecies of Atriplex barclayana.

Bracts compressed (sometimes appearing thickened by the tubercles when these are present), mostly as wide as long or wider except in *magdalanae*.

Leaves entire.

Bracts dentate from summit to middle or lower.

Length and width of bracts about equal..... (a) *palmeri* (p. 315).

Length of bracts much exceeded by their width..... (b) *dilatata* (p. 315).

Bracts 3-toothed at summit, sides entire..... (c) *magdalanae* (p. 315).

Leaves saliently dentate..... (d) *lurida* (p. 315).

Bracts much thickened, convex on the sides, mostly longer than wide.

Bracts lacinate around summit and well down the sides, the margin foliaceous above. (e) *sonorae* (p. 316).

Bracts entire except at summit, where there are only a few small teeth, the margin not foliaceous..... (f) *typica* (p. 316).

35a. *ATRIPLEX BARCLAYANA PALMERI* (Watson).—Leaves entire; fruiting bracts compressed, sometimes appearing thickish when tubercled, cuneate-orbicular or cuneate-obovate, about 3 mm. long, as wide or slightly wider; margins wing-like, coarsely lacinate-dentate nearly to the base of the bract; faces smooth or tuberculate. (*A. palmeri* Watson, Proc. Am. Acad. 11:146, 1876.) Islands off the west coast of Lower California; also on islands in the Gulf of California. Type locality, Guadalupe Island. Collections: San Luis Island, *Johnston 3320* (SF, minor variation 3, *A. insularis* Rose); Santa Inez Island, *Johnston 3653* (SF, same variation); Raza Island, *Palmer 155* (Gr, SF, US); same locality, *Palmer 158* and *159* (US, the former the type of *A. insularis* Rose, minor variation 3); Raza Island, growing among rocks, facing the lagoon, *Johnston 3210* (SF, with ascending herbaceous branches, 5 dm. high, minor variation 3, *A. insularis* Rose, but some bracts smooth); same spot, *Johnston 3211* (SF, shrubby, 1 meter high, staminate plant, a few mostly smooth bracts in the leaf-axils); Raza Island, on silty flat at southwest end, *Johnston 3214* (SF, nearly prostrate, stems woody, same variation in bracts as No. 3210); same but on south side, *Johnston 3213* (SF, with loosely ascending stems 3 to 5 dm. high, same variation in bracts as No. 3210); San Benito Island, March 27, 1897, *Brandege* (UC); Magdalena Island, *Orcutt 6* (US); type collection, 1875, *Palmer 83* (Gr); Guadalupe Island, *Palmer 862* (Gr, US) and *863* (Gr), also April 3, 1889 (UC); Guadalupe Island, April 24, 1885, *Greene* (UC, US); Guadalupe Island, March 20, 1897, *Brandege* (UC, plants mainly staminate, but with a few bracts in the leaf-axils); Seal Island, *Rose 16818* (NY, US, minor variation 3, *A. insularis* Rose).

35b. *ATRIPLEX BARCLAYANA DILATATA* (Greene).—Leaves entire or slightly sinuate or inclined to be dentate; fruiting bracts compressed, or somewhat thickened when strongly tuberculate, wider than long, 3 to 6 mm. long, 5 to 8 mm. wide; margins wing-like, thin, irregularly lacinate-dentate nearly to the base of the bracts; faces either smooth or low-tuberculate or conspicuously crested (in minor variation 4, *A. rosei* Standley). (*A. dilatata* Greene, Pittonia 1:264, 1889.) Guadalupe and San Benito Islands, off the west coast of Lower California. Type locality, San Benito Island. Collections: Guadalupe Island, *Rose 16022* (US, type of *A. rosei* Standley, minor variation 4); San Benito Island, *Palmer 907* (US); San Benito Island, *Anthony 269* (Gr, DS, NY, UC, US); San Benito Island, *Rose 16074* (NY, US).

35c. *A. BARCLAYANA MAGDALENÆ* (Brandege).—Leaves entire; fruiting bracts moderately compressed, cuneate-obovate, about 4 to 4.5 mm. long, 3.5 to 4 mm. wide; margins developed only around the summit, there deltoid and tridentate; faces smooth. (*A. magdalanae* Brandege, Proc. Calif. Acad. II, 2:200, 1889.) Magdalena Island, off the west coast of Lower California. Type locality, Magdalena Island. Collection: Type collection, February 20, 1889, *Brandege* (UC).

35d. *ATRIPLEX BARCLAYANA LURIDA* (Brandege).—Leaves (rather thin) acutely dentate with broad salient teeth or some only crenate, the upper mostly entire; fruiting bracts compressed, cuneate-orbicular, 2 to 3 mm. long, 2 to 4 mm. wide; margins wing-

like around the summit, deeply and acutely dentate to midway of the bract; faces smooth. (*A. lurida* Brandegee, l. c.) Mainland of Lower California. Type locality, San Gregorio. Collections: Sandy plains near Santa Gertrudis Island, *Purpus 2* (DS, UC); 25 miles north of San Ignacio, *Nelson 7206* (US); type, February 2, 1889, *Brandegee* (UC); Agua Verde, *Rose 16575* (US, staminate only); Los Dolores, 1892, *Bryant* (UC).

35e. ATRIPLEX BARCLAYANA SONORAE (Standley).—Leaves entire; fruiting bracts moderately thick and spongy, the body convex on the sides and commonly spindle-shaped (including the narrowed pedicel-like base), the whole bract 3 to 4 mm. long, 2.8 to 4 mm. wide, usually a trifle longer than wide; margins flat, herbaceous, lacinate from apex to halfway down the sides of the bract; faces with 2 or more sharp spine-like processes similar to the teeth of the margins. (*A. sonorae* Standley, N. Am. Fl. 21:62, 1916.) Coast of Sonora and Sinaloa, islands in the Gulf of California, Cape Region of Lower California, and Magdalena Island. Type locality, in alkaline soil near Empalme, Sonora. Collections: Type collection, Sonora, *Rose, Standley and Russell 12631* (US); Guaymas, Sonora, *Palmer 670 and 690* (US); same locality, *Palmer 671 and 672* (US, minor variation 1); San Luis Gonzales Bay, Lower California, *Johnston 3351* (SF); Gulf of California: Angel de la Guarda Island, *Johnston 4234* (SF); North San Lorenzo Island, *Johnston 4196* (SF); San Esteban Island, *Johnston 3189, 3191* (SF, UC, with some bracts as in subspecies *typica*); same locality, *Johnston 3192* (SF, UC, all bracts of subspecies *sonorae*); Santa Inez Island, *Johnston 3651* (SF); Altata, vicinity of Culiacan, Sinaloa, September 2, 1904, *Brandegee* (Gr, UC); Lower California: Espiritu Santo Island, 1892, *Bryant* (UC); San Jose del Cabo, *Anthony 358* (DS, UC, US, intermediate to subspecies *typica*); Magdalena Island, February 26, 1889, *Brandegee* (UC).

35f. ATRIPLEX BARCLAYANA TYPICA.—Leaves entire; fruiting bracts thick and spongy, the body globose, 2.5 to 4 or rarely 5 mm. long, 2.5 to 4 mm. wide; margins entire, except at the summit, where usually there are a few short teeth; faces irregularly swollen, often with a vertical furrow on each side of the enlarged midrib, nearly smooth, or with a few minute obtuse tubercles. (*Obione barclayana* Bentham, Botany Voyage Sulph. 48, 1844.) Seacoast of Sonora, Sinaloa, and Lower California and on the adjacent islands. Type locality, Magdalena Bay, Lower California. Collections: Tepoca Bay, Sonora, *Johnston 3284* (SF, UC); island in harbor of Guaymas, Sonora, *Rose 12564* (NY, US); Gulf of California: Angel de la Guarda Island, *Rose 16766* (NY, US); San Luis Island, *Johnston 3319, 3321* (SF); Patos Island, *Johnston 3242* (SF, UC, minor variation 2); Tiburon Island (north end), *Johnston 3259* (SF); Tiburon Island (south end), *Rose 16806* (US); Idefonso Island, *Johnston 3750, 3751, and 3752* (SF); Carmen Island, *Palmer 874* (Gr, US); Isla Partida, *Johnston 3228* (SF, UC, some undeveloped bracts resembling those of subspecies *palmeri*); same locality and collector, *3229* (SF, UC, typical); Sal si Puedes Island, *Johnston 3525* (SF); South San Lorenzo Island, *Johnston 4191* (SF); Lower California: Los Angeles Bay, *Johnston 3429* (SF); San Francisquito Bay, *Rose 16753* (NY, US); Santa Aueda, *Palmer 259* (US); Pichilique Island, *Rose 16519* (US); Santa Maria Bay, *Rose 16255* (NY, US); Lagoon Head, *Palmer 809* (Gr, NY, US); Cedros Island, *Palmer 754* (Gr, NY, US); Ascension Island, August 17, 1897, *Brandegee* (UC); Magdalena Island, *Rose 16318* (NY, US); Altata, Sinaloa, *Rose 1362* (US).

MINOR VARIATIONS AND SYNONYMS.¹

1. ATRIPLEX BARCLAYANA SONORAE, but with thin, greenish leaves of an oblanceolate shape, many of them slenderly cuspidate at apex. Represented by *Palmer 671, 672*, and a part of *677*, all at the United States National Herbarium, and collected at Guaymas, where grows also the usual form of *sonorae*. The plants are apparently more herbaceous than the usual type, in which the leaves are thicker and broader, obtuse, and

¹Additional synonymy is given in connection with the description of each of the subspecies.

white-scaly, but the bract characters assign the plants cited to this subspecies. Among the collections listed above as *typica* and *sonorae* are some with leaves that are narrow and elliptic, but still white or gray with a dense scurf.

2. *ATRIPLEX BARCLAYANA TYPICA*, but with dense subcylindric and pyramidal panicles 20 to 30 cm. long by 8 to 10 cm. broad, heavy with fruiting bracts. This form is from a protected draw on Patos Island, *Johnston 3243*. It is not even approached in density and size of the inflorescence by any of the other numerous collections.

3. *A. INSULARIS* Rose, Contr. U. S. Nat. Herb. 1: 80, 1890.—The form or state of *A. barclayana palmeri* in which the bracts are appendaged by two conspicuous toothed crests. The type is from Raza Island, in the Gulf of California. Since this character is unreliable in other species, it is not surprising to find that in nearly all of the collections in which most of the bracts are conspicuously crested there are some (on the same plant) with smooth sides. A number of such are cited under subspecies *palmeri*. An attempt was made in the North American Flora to use also the more fruticose branches and the more nearly sessile leaves as criteria for the separation of *insularis*. But the type specimens indicate that *palmeri* is perhaps as woody as *insularis* and the original descriptions ("shrubby at base" for the former, "woody below" for the latter) furnish no support for the distinction. Mr. Johnston, who collected abundantly on Raza Island, considered the plants as all closely similar in this respect, that is, all had a woody base and more or less herbaceous, ascending or decumbent branches. His plants are all of the *insularis* form as to most of the bracts, except No. 3211, which is a staminate plant with well-developed fruiting bracts in the leaf axils. These bracts are mostly smooth as in typical *palmeri*, yet this was one of the most woody plants found. Other plants referred to *insularis* on the characters of the bracts, such as Palmer's 862, are less than 3 dm. high and herbaceous nearly to the base. The length of petiole is equally unsatisfactory. On the type sheet of *insularis* some petioles are one-third the length of the blade, exactly the proportion stated for *palmeri*, and the large series of specimens now at hand shows conclusively that this feature is extremely variable, and that the variations do not parallel those of other characters. Therefore, if *insularis* is to be retained in any rank, it must be on the single character of the appendages, and even these are absent from some of the bracts.

4. *A. ROSEI* Standley, N. Am. Fl. 21: 60, 1916.—The extreme form of *A. barclayana dilatata* in which the bracts are 6 to 8 mm. wide and with conspicuous crests on the face, the seeds correspondingly large. The type collection from Gaudalupe Island includes a splendid series of bracts, some of which are nearly twice as wide as long. Others of the same collection are much narrower, and some, perhaps immature, are scarcely wider than long. For the most part, they are much thicker than in other collections of subspecies *dilatata* and *palmeri*, some apparently not at all compressed, but this is due to the exceptional development of the tubercles with thickened bases, as indicated by other bracts, also of the type specimen, which are strongly compressed and with only a few minute appendages on the face. Some of the leaves are slightly sinuate or subdentate.

RELATIONSHIPS.

This species stands near the beginning of that great phylogenetic branch of *Atriplex* characterized by a shrubby habit and dioecism. The evidence for this is found in the only half-shrubby nature of many of the plants and in the almost constant occurrence of at least a few pistillate flowers on the staminate plants. These female flowers are usually well formed and are protected by normal bracts which grow in clusters from the upper leaf-axils, that is, just below the long and dense staminate inflorescence. In a few cases no trace of fruiting bracts can be found, indicating that a complete separation has been effected in these individuals.

In assembling the numerous variations of *A. barclayana*, it is found that these fall into two groups, which may be conveniently referred to as the *palmeri* and the *typica* groups. These differ only in their fruiting bracts. In the former, the bracts are distinctly compressed, so that the body is more or less strongly flattened, that is, they are as in most *Atriplex* only slight modifications from the reduced foliage leaf. These compressed bracts are sometimes thickened by the enlarged bases of the appendages, or tubercles, but this is not to be confused with the swelling or thickening of the body proper. The bracts of the *typica* group are distinctly thickened and spongy, so that the body is strongly convex on each face, that is, approaching globose. The bracts of the *palmeri* group are usually wider in proportion to their length than are those of the *typica* group. In each the length and width are sometimes equal, and the subspecies *magdalenae* is an exception, but in the main the tendencies are as indicated. It seems that the loss of

tissue which goes to make up thickness in the one case is compensated by the greater lateral extension in the other. An earnest endeavor has been made to utilize these bract features as criteria for the retention of each group in specific rank, but the too frequent meeting of the characters, and the apparently total absence of correlated features seem to make this impossible. Furthermore, there are some collections, such as Johnston's 3228 from Isla Partida, in which both compressed and thickened bracts occur on the

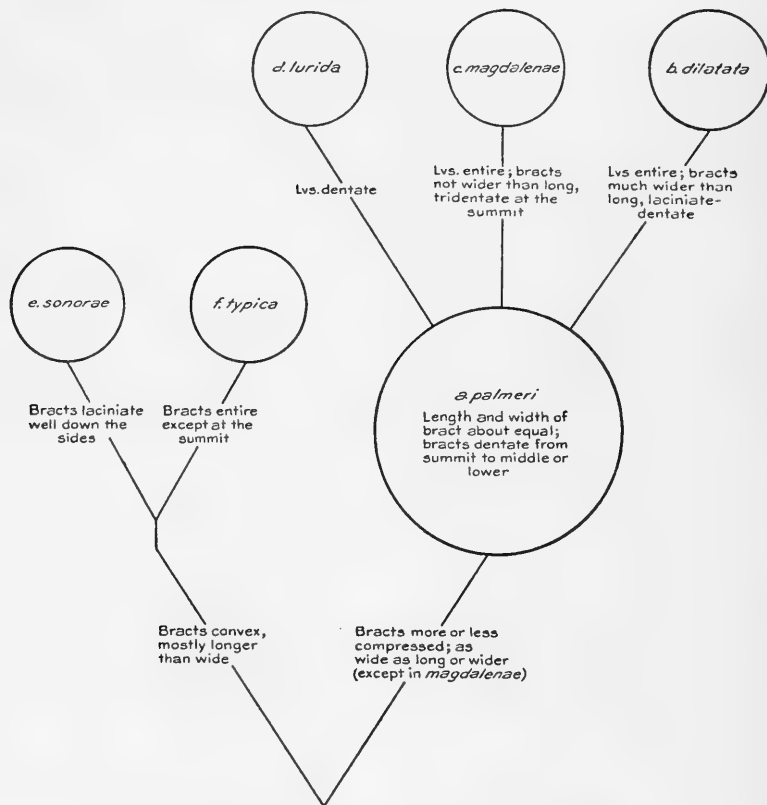


FIG. 44.—Phylogenetic chart of the subspecies of *Atriplex barclayana*.

same plant. This is possibly a case of hybridization, but, if so, the wide distribution of both types over the same area could be expected to result in such frequent crossing as to swamp the specific characters. As a final reason for merging the two groups may be cited a parallel pair of forms under *A. polycarpa*, one with compressed, the other with thickened bracts; yet here these characters are not concomitant with any others, nor can the forms be assigned to different geographic areas.

In considering these two groups of subspecies from an evolutionary viewpoint it seems that the *palmeri* group is the more primitive. This is because the bracts are more like

those common in the genus and less highly modified from the original leaf-like structure. The thickening of the bracts in *typica* has resulted in the almost complete loss of the thin, herbaceous borders. From these considerations it becomes necessary to place the *palmeri* group first in a phylogenetic arrangement, reserving the highly specialized taxonomic type of the species, that is, subspecies *typica*, for treatment at the end.

The subspecies *palmeri* exhibits no features indicative of a special development. On the other hand, the remarkable width of the compressed bracts, mentioned above as one of the characters of the *palmeri* branch of the species finds its greatest development in subspecies *dilatata* (especially the minor variation called *A. rosei* Standley). Although the shape fluctuates to such a degree that future studies may indicate the impracticability of the distinction, it seems helpful at present to retain a subspecies *dilatata* for this form. Possibly other substantiating characters will be found after the forms have received a more thorough field study. As far as now known, *dilatata* is confined to two islands off the west coast of Lower California (where true *palmeri* also grows), but one collection from Raza Island, in the Gulf of California, has bracts up to 5 mm. wide and is therefore to be classified as very close if not the same as *dilatata* (Johnston 3232, SF, UC), and other collections from Raza Island (*Palmer 155* and *156*), here cited as subspecies *palmeri*, were identified by *Rose* (Contr. U. S. Nat. Herb. 1:80, 1890) as *dilatata*.

The subspecies *magdalenae* is here maintained only because no direct intergradation with *palmeri* is known, although the two come from the same island. The herbaceous, prostrate habit and the less strongly compressed nature of the bracts will furnish characters substantiating those used in the key, if the former are found to be constant, which seems unlikely. Since the bracts are longer than broad and only lightly compressed, this subspecies should perhaps stand ahead of *palmeri*, connecting this with typical *barclayana*. Its rare occurrence, however, and this only on an outlying island, is evidence that it is a divergent type that did not give rise to the other forms.

The most easily distinguished subspecies and the one least subject to intergradation is *lurida*. This is the only one thus far found to be generally distributed on the mainland of Lower California, exclusive of the Cape Region the flora of which is more like that of the southern islands. It has not been collected on any of the islands. Two collections of *typica* have been made on the west coast, opposite Cedros Island. Aside from this, the other subspecies occur only in Sonora and Sinaloa and on the islands off both sides of the peninsula. In some cases a single subspecies is known both from the gulf and from islands off the west coast, yet none of them are known to mingle with *lurida*. The nearest approach is at Agua Verde and Los Dolores, where *lurida* grows on the mainland and other subspecies on the adjacent islands. Further field studies and also experiments are needed to determine whether *lurida* is an ecologic response to the mainland environment or an hereditary type held true by isolation.

The *typica* branch has produced but two subspecies, *typica* itself and *sonorae*. This latter is characterized by having the margin of the bract more fully developed around the summit, where it is deeply cut into a number of sharp teeth. This commonly leaves the lower portion as a spindle-shaped structure, the base of which is pedicel-like. In the original diagnosis, Standley differentiated this form also on the failure of the bracts to unite above the middle. However, this lack of union applies in most cases only to the marginal wings and therefore may be looked upon as another expression of a single character. A careful examination of the much more copious material now at hand indicates that the extent of fusion varies too greatly in both subspecies to be of taxonomic value. After all of the available material has been classified into *typica* and *sonorae* on the basis of the bracts, it is found that, while they have the same general area of distribution, they seldom occur at the same station. This is indicated by the above citation of collections. The distribution indicates that they may be genetic types preserved in their charac-

ters by isolation. Much more intensive field studies will be necessary before this can be determined. In this connection it must be pointed out that, although each plant usually can be placed in one or the other of the subspecies, this is done by ignoring a small number of bracts which may come closer in characters to those of the other form. Something of the variation found on single plants is indicated in plate 49. When bracts of the *sonorae* type occur on plants with typical *barclayana* bracts, the latter fall off much more easily in the press, indicating an earlier maturity.

ECOLOGY AND USES.

Atriplex barclayana grows commonly in the sandy or gravelly soil of back-strands and of alluvial fans at the mouths of cañons, as well as on dunes. It also grows inland in gravelly washes, always preferring soil that is slightly or not at all saline. In all such situations it occurs as a scattered secondary species. However, on the guano islands of the Gulf of California, where the soil is discolored with guano salts, it is a dominant, usually associated with *Amarantus watsoni*, which is equally important. These two species constitute the initial associates, which forms 95 per cent of the vegetation of such islets. Nothing is known of the uses of this species.

36. ATRIPLEX ACANTHOCARPA (Torrey) Watson, Proc. Am. Acad. 9:117, 1894.

Plate 50. BURSACLE.

Erect subshrub or herbaceous perennial with a woody base, 1 to 10 dm. high, freely branched from the base; branches stout, obtusely angled or nearly terete, densely furfaceous or those of the staminate plants nearly naked, glabrate in age, the bark exfoliating in layers from the old woody portions; leaves mostly alternate but the lower ones opposite, tapering to a short- or long-winged petiole, varying from lanceolate to oblong-elliptic or obovate, narrowed at base, obtuse at apex, 2 to 5 cm. long, 0.5 to 2.5 cm. wide, more or less sinuate-dentate or some of the leaves entire, rather thick or thinnish, white with a dense and permanent scurf; flowers dioecious, the staminate in glomerules along the branches of elongated nearly leafless terminal panicles, the pistillate in more leafy panicles or racemes; perianth 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts on stalks 2 to 20 mm. long (or a few sessile), thick and spongy, united nearly to the apex, subglobose or broadly elliptic in outline, 8 to 14 mm. long and nearly as broad, the free tips often beak-like, the faces bearing numerous flattened, irregular, often toothed appendages, these commonly longer than the body; seed 1.5 to 2 mm. long, brown; radicle superior. (*Obione acanthocarpa* Torrey, Bot. Mex. Bound. 183, 1859.)

Western Texas to southern Arizona, Chihuahua, and San Luis Potosi. Type locality, plain between the Burro Mountains, New Mexico. Collections: Guadalupe, 105 miles southwest of San Antonio, Texas, *Palmer 1157* (Gr); "western Texas to El Paso, New Mexico," *Wright 573* (Gr, NY, US); Franklin Mountains near El Paso, Texas, *Rose 17891* (NY, US); banks of the Gila River, New Mexico, August, 1880, *Greene* (Gr); Winslow, Arizona, *Jones 102* (Gr); vicinity of Torreon, Coahuila, *Palmer 473* (Gr, NY, UC, US); southwest of Parras, Coahuila, *Palmer 1161* (US); Sapio, Sierra Madre Mountains, Chihuahua, September 10, 1903, *Jones* (US); Chihuahua State, *Hartman 723* (Gr, NY, UC, US); alkaline plains, Hacienda de Angostura, San Luis Potosi, *Pringle 3775* (Gr, NY, UC, US, type collection of *A. pringlei* Standley, minor variation 2).

MINOR VARIATIONS AND SYNONYMS.

1. A peculiarly slender-stemmed and thin-leaved form has been collected in Texas and New Mexico. The stems in this are but obscurely farinose and even the leaves are only thinly covered with scales and therefore greenish. The absence of complete fruiting specimens would render taxonomic recognition impossible at this time, even if it could be demonstrated that the form is other than an ead. Representative collections are: southwest of San Antonio, Texas, *Palmer 1157* (US); New Mexico, *Wright 1737* (US).

2. *ATRIPLEX PRINGLEI* Standley, N. Am. Fl. 21: 68, 1916.—Stems erect to horizontally spreading from the base, the whole plant only 1.5 to 3 dm. high; leaves spatulate or narrowly obovate, densely and coarsely white-furfuraceous, mostly entire but a few with obscurely sinuate-dentate margins. Type, Hacienda de Angostura, San Luis Potosi, *Pringle 8775* (US). This was placed in the *Nuttallianae* by Standley, and there is no question that in foliage it is intermediate between that group and *A. acanthocarpa*. No leaves can be found on the type specimen that are certainly dentate, but that the tendency is present is indicated by duplicates of the types at the University of California in which some of the leaves are plainly sinuate-dentate. The body of the fruiting bracts is thicker and more spongious than in any of the forms of *nuttalli*, and in this respect the specimens are like *acanthocarpa*. Possibly the habit and foliage characters may be linked with others of greater importance when these little-known Mexican forms are studied in the field and *pringlei* may then be reestablished as a species or at least as a subspecies.

3. *OBIONE ACANTHOCARPA* Torrey, Bot. Mex. Bound. 183, 1859.—*A. acanthocarpa*.

RELATIONSHIPS.

Together with *A. barclayana*, *A. obovata*, and *A. nuttalli*, this represents an early Mexican stock from which many of the shrubby, dioecious *Atriplexes* have developed. The connection with the first-mentioned of these is seen in the very much thickened fruiting bracts, while in nearly all of its other features, except the dentate leaves, it is more like *nuttalli*. In the extreme form the fruiting bracts firmly unite to form a spherical body 6 or 7 mm. in diameter, the surface of which is covered with short spinose processes. In other forms the body is smaller but the processes are longer and much flattened, resembling, except for arrangement, the wings on the bracts of *A. canescens*, which species may have been connected with *acanthocarpa* at some remote period.

ECOLOGY AND USES.

Atriplex acanthocarpa resembles *A. obovata* somewhat, but is more open and branched. It likewise grows in alkaline flats, but is of less importance, usually mingling with the more dominant *polycarpa* or *canescens*.

While it is doubtless grazed to a slight extent, nothing definite is known of its uses.

37. *ATRIPLEX OBOVATA* Moquin, Chenop. Enum. 61, 1840. Plate 50. BROADSCALE.

Erect subshrub, woody at least at the base, 2 to 5 dm. high; branches rigidly erect from a much-branched spreading base, not angled, gray-furfuraceous, the bark exfoliating in strips from the old basal portions; leaves mostly alternate, the lowest opposite, short-petioled, obovate or broadly elliptic, tapering to the base, very obtuse or even retuse at summit, 1 to 3.5 cm. long, 0.5 to 2 cm. wide, entire or only undulate, thick, firm, nearly white with a smooth, compact permanent scurf; flowers dioecious, the staminate in small glomerules along the spike-like branches of oblong terminal nearly naked panicles, the pistillate in small clusters in the axils of elongated terminal more leafy spikes, these sometimes slightly paniculate; perianth 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile or short-stalked, compressed or only slightly convex, united at least to the middle, obovate or cuneate-orbicular, 4 to 5 mm. long, 5 to 7 mm. broad, the summit and margins sharply toothed, the sides smooth or with a few small tubercles or crests (tubercles more numerous and elongated in variety *tuberata* Macbride, minor variation 4); seed 2.4 to 2.8 mm. long, light (or reddish?) brown; radicle superior.

Northern Arizona, southern Colorado, and western Texas to Chihuahua and Zacatecas. Type locality, San Luis Potosi, Mexico. The type locality was originally given as Peru, but the Berlandier specimen, which is the type, came from San Luis Potosi, according to Moquin (in De Candolle, Prodr. 13²: 99, 1849) and according to a label with a portion of the type in the Gray Herbarium, which label reads: "Hacienda del Salad, Saint Louis Potosi, 1827." Collections: Arizona: Adamana, *Griffiths 5121, 5125, 5126, 5128, 5129* (US); Navajo Reservation, rather common in valleys, *Vorhies 27* (UC); Winslow, *Jones 4109* (Herb. Jones, type of *A. sabulosa* Jones, minor variation 3); north end of Carrizo Mountains, *Standley 747* (US); Holbrook, *Rusby 795* (UC); El Sauzal, September

5, 1858, *Hayes* (Gr); Aztec ruins, northwestern New Mexico, *Hall 11126* (UC); near Tiznitzin, northwestern New Mexico, *Wooton 2775* (UC); southwestern Colorado, 1875, *Brandegee* (UC); Tornillo Creek, western Texas, *Haward 103* (Gr, type of variety *tuberculata* Macbride, minor variation 4); El Paso, Texas, *Jones 4183* (Gr, US); Comacho Plains, Zacatecas, *Lloyd 253* (US); type collection, Hacienda del Salad, San Luis Potosi, 1827, *Berlandier 1346* (Gr); Mexico, *Gregg 462* (Gr, NY, type collection of *A. greggi* Watson, minor variation 1).

MINOR VARIATIONS AND SYNONYMS.

1. *ATRIPLEX GREGGI* Watson, Proc. Am. Acad. 9:118, 1874.—Based upon Gregg's No. 462 from Mexico, which is the typical small-leaved and small-bracted form of *A. obovata* Moquin, the type collection of which was also cited by Watson as representing his species. Quite probably Moquin's name was overlooked by Watson.

2. *A. JONESI* Standley, N. Am. Fl. 21:65, 1916.—Based upon *A. sabulosa* Jones, which see.

3. *A. SABULOSA* Jones, Contr. West. Bot. 11:21, 1903.—When originally described this was not compared with *A. obovata*, which doubtless was overlooked, but it is a northern large-leaved and large-bracted form of this species. Genuine *obovata* has leaves only about 1 cm. long by 0.5 to 0.7 cm. wide and bracts correspondingly small. In the type of *sabulosa* the leaves are about 2.5 cm. long by 1 cm. and more wide, the bracts 6 mm. broad. The two forms are not entirely geographic, for in specimens from as far south as Zacatecas (*Lloyd 253*) there are leaf-blades as large as 1.7 by 0.9 cm. and bracts 5 mm. broad; while in some from El Sauzal, Arizona (September 5, 1858, *Hayes*) the largest blades are only 1.2 by 0.5 cm. and the bracts 5 mm. broad. As intermediate in size of leaf and bracts may be cited: El Paso, Texas, *Jones 4183* (Gr); western Texas, *Wright 572* (Gr). After changing the name of *sabulosa* to *jonesi* (because of the earlier *A. sabulosa* Rouy), Standley characterizes this as having bracts smooth or rarely slightly tuberculate on the sides, while *obovata* is described as having crested, sparsely tuberculate, or rarely smooth bracts (Standley in N. Am. Fl. 21:38 and 66, 1916). The decidedly unreliable nature of this character is now well known (see under *Criteria*, p. 242, and compare Macbride, Contr. Gray Herb. N. S. 53:10, 1918). Moreover, the original description of *obovata* reads: "bracteis * * * disco inappendiculatis." It is true that most of the large-leaved northern plants have broad fruiting bracts which are smooth or with only 2 small thickenings on the side, but not infrequently there may be found on single plants all variations from smooth to as strongly crested as in any yet collected in Mexico (e. g., Winslow, Arizona, at the type locality of *sabulosa*, *Hall 11174*, UC). It seems, therefore, that *sabulosa* is, at the most, only an ecologic form of *obovata*. This conclusion was predicted by Standley at the time he made the above-mentioned transfer of names (see Bull. Torr. Club 44:425, 1917).

4. *A. OBOVATA* VAR. *TUBERATA* Macbride, Contr. Gray Herb. 53:11, 1918.—Marked only by having some of the fruiting bracts copiously tuberculate. Type locality, Tornillo Creek, Texas. The negative value of the tubercle character as a taxonomic criterion is indicated under No. 3.

RELATIONSHIPS.

This species is most closely related to *A. nuttalli*. Both seem to have originated in Mexico, where the present species still maintains a foothold. The fruiting bracts are broader in proportion to their length than in any other *Atriplex* of this group and the seeds are considerably larger.

ECOLOGY AND USES.

Atriplex obovata is similar to *A. nuttalli* in ecological behavior, but it is less adaptable, and hence is more restricted in range and habitat. It is taller and looser in growth and in consequence is usually not a mound-former. It sometimes makes a pure consociation on alkaline flats, but is more often associated with *Sarcobatus*, *Suaeda*, or *Sporobolus airoides*, and such annuals as *A. powelli*, *A. argentea*, and *Salsola*.

This species has much the same grazing value as *nuttalli*, but is eaten less because it grows in a region where grass is more abundant.

38. *ATRIPLEX NUTTALLI* Watson, Proc. Am. Acad. 9:116, 1874.¹ Plate 51.
MOUNDSCALE.

Erect or slightly spreading subshrub, woody at the base, but the erect or ascending stems mainly herbaceous, 2 to 5 dm. high; branches rigid, not angled, gray or whitish with

¹The reasons for retaining this name instead of *A. gardneri*, as called for by the botanical codes, are stated under minor variation 18 (p. 327).

a dense scurf, the bark becoming dark and rough only on the old basal portions; leaves all alternate except the lower ones of young stems, short-petioled (sessile in subspecies *buzifolia*), oblong oblanceolate or spatulate to elliptic or ovate (rarely obovate), mostly tapering to the base, obtuse at apex, 1.5 to 5 cm. long, 0.2 to 2 cm. wide, strictly entire, thick and firm, gray or greenish-white with a dense and permanent scurf; flowers dioecious (rarely monoecious, see note under Relationships, p. 329), the staminate in glomerules of terminal spikes or narrow panicles a few centimeters long, this inflorescence leafy in the lower part, the pistillate in long, compact terminal spikes and spike-like panicles leafy below; perianth 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile or stalked (especially in subspecies *falcata*), thick and somewhat spongy, united nearly to summit, lanceolate to broadly elliptic or cuneate-oblong, 4 to 7 mm. long, 2 to 5 mm. broad (slightly larger when long-appendaged), the free tips sometimes beak-like, more or less dentate across the summit and often also down the sides, the faces smooth or tuberculate or with variously shaped appendages; seed 1.5 to 2 mm. long, brown; radicle superior.

Saskatchewan and South Dakota to western Nebraska (where introduced?), New Mexico, Arizona, northwestern California, eastern Washington, and Alberta.

SUBSPECIES.

All of the following subspecies, with the exception of *falcata*, are based upon characters which are not constant. It must be expected, therefore, that some specimens can not be definitely placed.

Key to Subspecies of Atriplex nuttalli.

- Fruiting bracts orbicular-ovate or oblong to cuneate-oblong, often globoid when appendaged, terminal tooth sometimes beak-like but never attenuate.
- Leaves oblong-linear to spatulate or nearly obovate, usually elongated and broadest above the middle.
- Fruiting bracts broadest at or below the middle.
- Leaves oblong, spatulate, or obovate; bracts usually appendaged..... (a) *typica* (p. 323).
- Leaves narrower, linear-oblong, sides nearly parallel except at the narrowed base; bracts usually smooth..... (b) *tridentata* (p. 324).
- Fruiting bracts broadest above middle, usually smooth. (Leaves narrow.)..... (c) *gardneri* (p. 324).
- Leaves broadly elliptic or ovate, short, usually broadest at or below the middle.
- Leaves acute at base, mostly petioled..... (d) *cuneata* (p. 324).
- Leaves obtuse at base, sessile..... (e) *buzifolia* (p. 325).
- Fruiting bracts fusiform with attenuate beak 2 mm. or more long. (Leaves linear-spatulate.) (f) *falcata* (p. 325).

38a. *ATRIPEX NUTTALLI TYPICA*.—Stems erect from a decumbent woody very freely and intricately branched base; leaves oblong or spatulate or narrowly obovate, obtuse, 3 to 5 cm. long, 0.5 to 1 cm. wide, tapering to a short petiole; fruiting bracts ovate or orbicular-ovate in outline, sessile or an occasional one short-stalked, 4 to 6 mm. long, sharply few-toothed at summit, the terminal pair of teeth commonly forming a flat lanceolate beak, the sides covered with numerous conspicuous sharp appendages, some of which commonly are more or less flattened. (*A. nuttalli* Watson, Proc. Am. Acad. 9:116, 1874.) Alkaline plains and hillsides, Saskatchewan to eastern Wyoming, central Colorado, northern Utah, Idaho, and Alberta; also in western Nebraska (where introduced in stock-cars, according to Bates, Asa Gray Bull. 6:35-37, 1898) and a doubtful collection from northwestern Arizona. Type locality, not definitely stated. Collections: Round Valley Lake, Saskatchewan, *Macoun* and *Herriot 76722* (NY); Leeds, North Dakota, 1900, *Lunell* (Gr); Owl Butte, South Dakota, *Griffiths 339* (US); Centennial, Albany County, Wyoming, *Goodding 2114* (NY, UC, US); Delta, Colorado, *Cowen 4071* (Gr, R, US, type collection of *A. oblanceolata* Rydberg, minor variation 14); Price, Utah, June 20, 1898, *Stokes* (UC); Salt Lake City, Utah, July 24, 1879, *Jones* (NY); Fort Mojave, Arizona, April, 1884, *Lemmon* (UC, data doubtful); Blackfoot County, Montana, *Griffiths* and *Lange 282* (US); Helena, Montana, July 29, 1898, *Brandegee* (UC). Additional stations where either this or one of the two next

following subspecies occurs, all represented by specimens in the Rocky Mountain Herbarium of the University of Wyoming, are Waihalla, in North Dakota; northwestern and eastern Harding County, in South Dakota; Laramie, Point of Rocks, Sweetwater River, Big and Little Laramie Rivers, Granger, Poison Spider Creek, Buffalo, Howell Lakes, Seven-mile Lakes, Red Desert, Steamboat Lake, Wamsutter, Leucite Hills, North Fork Vermillion Creek, and Carter (Uinta County) in Wyoming; Montrose in Colorado; Mendon (Cache County) and Cannonville in Utah; and Clyde (Blaine County) and Falks (Cañon County) in Idaho.

38b. *ATRIPLEX NUTTALLI TRIDENTATA* (Kuntze). Stems strictly erect from a compact base, the decumbent portion short and the plants therefore narrow; leaves oblong or linear-oblong, obtuse, 2.5 to 5 cm. long, 0.3 to 0.8 cm. wide, narrowed to a subsessile base; fruiting bracts orbicular-ovate, with a shortly cuneate base, broadest below the middle, sessile, 4 to 5 mm. long, broad-margined, with usually 3 prominent and several smaller teeth at summit, the middle tooth often the largest, the sides smooth or rarely with a few small tubercles. (*A. tridentata* Kuntze, Rev. Gen. Pl., 546, 1891.) Wyoming, northern Colorado, and Utah. Type locality, near Corinne, Utah. Collections: Sweetwater County, Wyoming, *Nelson 3667* (Gr); Point of Rocks, Wyoming, *Nelson 4429* (Gr, R, type collection¹ of *A. pabularis* Nelson, minor variation 15); Granger, Hams Fork, Wyoming, *Nelson 3893* (NY, US); Uinta County, Wyoming, *Gooding 1179* (Gr, form approaching minor variation 4, *A. eremicola* Osterhout).

38c. *ATRIPLEX NUTTALLI GARDNERI* (Moquin).—Stems erect from a woody branching base; leaves narrowly oblong or oblanceolate, obtuse, 1.5 to 4 cm. long, 0.3 to 1 cm. wide, tapering to a short petiole; fruiting bracts oblong with a cuneate base or narrowly obovate, broadest above the middle, sessile, 4 to 6 mm. long, with several prominent teeth across the summit, the middle tooth usually the largest, the sides smooth or with a few tubercles. (*Obione gardneri* Moquin, in DeCandolle, Prodr. 13²:114, 1849.) Alkaline plains and slopes of southern Wyoming, northern Colorado, and southern Idaho. Type locality, along the Platte River. Collections: Type collection, La Platte River, *Gordon* (Gr); Laramie River, Wyoming, *Nelson 8174* (Gr); Big Laramie River, Wyoming, *E. Nelson 736* (Gr); 8 km. east of Medicine Bow, Wyoming, September 10, 1919, *Hall* (CI, a broad-leaved form); Steamboat Lake, southern Wyoming, July 21, 1898, *Osterhout* (Gr); southern Wyoming, July, 1896, *Osterhout* (Herb. Osterhout, type of *A. eremicola* Osterhout, minor variation 4); Howell Lakes, Albany County, Wyoming, *E. Nelson 4463* (NY, same variation); Howell Lakes, Wyoming, *A. and E. Nelson 6910* (Gr, bracts partly typical, see fig. 46); Point of Rocks, Wyoming, *Hall 10935* (UC, see note under minor variation 15); between Strevell and Albion, Idaho, September 17, 1919, *Hall* (UC).

38d. *ATRIPLEX NUTTALLI CUNEATA* (Nelson).—Stems erect from a decumbent, decidedly woody, much branched base; leaves broadly elliptic, very obtuse, 2 to 6 cm. long including the petiole or rarely only 1.2 cm. long and sessile, 0.6 to 2.5 cm. wide, cuneately narrowed to a short petiole or base; fruiting bracts globose in outline or slightly elongated, sessile or short-stalked, 5 to 7 mm. long, irregularly toothed at summit, the sides with numerous conspicuous crest-like appendages, these commonly more or less flattened (fig. 45, *a, b*). (*A. cuneata* Nelson, Bot. Gaz. 34:357, 1902.) Southwestern Colorado, northern New Mexico, northern Arizona, and southern Utah. Type locality, Emery, Utah. Collections: Alkaline plains at Mesa Grande, along the Gunnison River, Colorado, *Purpus 82, 209* (UC); Grand Junction, Colorado, common on alkaline plateaus, *Hall 11048* (UC); San Juan Plains, southwestern Colorado, *Brandegge 1086*, in part

¹ Nelson's 4429 is labeled as the type in the Rocky Mountain Herbarium and his 3712, from the same locality, is there indicated as a cotype. The latter number is cited first in connection with the original description. Both collections are of the *pabularis* form.

(UC); Mancos, southern Colorado, *Baker, Earle, and Tracy 420* (Gr, UC); near Farmington, San Juan County, New Mexico, *Standley 7066* (US, type of *A. neo-mexicana* Standley, minor variation 10); 5 and 8 km. south of Shiprock Station, San Juan County, New Mexico, *Hall 11143, 11144* (CI, UC); dry hills near Shiprock, New Mexico, *Standley 7278* (US); type collection, 2,140 m. altitude, June 16, 1894, *Jones 5443* (R, NY, UC); same locality and date, *Jones 5445r* (US); just south of Green River Station, Utah, abundant, *Hall 11036* (UC).

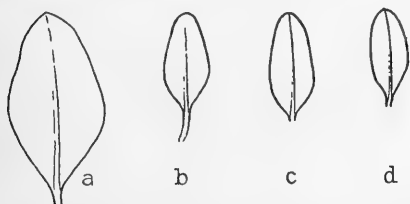


FIG. 45.

Leaves of *Atriplex nuttalli*: a, b, subspecies *cuneata* from Shiprock, New Mexico (686245 US); c, d, subspecies *buxifolia* from Sheep Creek, Wyoming (393362 US). All $\times 1$.

38e. *ATRIPLEX NUTTALLI BUXIFOLIA* (Rydberg).—Stems erect or ascending from a decumbent, very woody base; leaves elliptic, obtuse, 2 cm. or less long, 0.5 to 0.8 cm. wide, abruptly narrowed to an obtuse sessile base; fruiting bracts ovate or globoid in outline, sessile or nearly so, 4 to 5 mm. long, irregularly toothed at summit, the sides with conspicuous crest-like appendages which are more or less flattened or these appendages wanting (fig. 45, c, d). (*A. buxifolia* Rydberg, Bull. Torr. Club 39: 311, 1912.) Dry plains of eastern Wyoming. Type locality, Dayton, Sheridan County, Wyoming. Collections: Type collection, 1,220 m. altitude, September, 1899, *Tweedy 2456* (NY); Sheep Creek, Wyoming, August 21, 1899, *Schuchert* (US).

38f. *ATRIPLEX NUTTALLI FALCATA* (Jones).—Stems erect or ascending from a decumbent base, the woody portion very short; leaves linear-spatulate or rarely oblong-spatulate, commonly more or less falcate, 2 to 4 cm. long, 0.2 to 0.7 cm. wide, tapering to a short petiole; fruiting bracts lanceolate or narrowly ovate in vertical section, forming an approximately fusiform fruit, sometimes long-stalked but often sessile (even in the type specimen), 4 to 6 mm. long exclusive of stalk (only 3 or 4 mm. broad), the free tips conspicuously elongated and beak-like (2 or 3 mm. long), the sides with few to numerous conspicuous sharp appendages, these slightly or not at all flattened, or the sides sometimes smooth (in *A. n. anomala* Jones, minor variation 11). (*A. nuttalli* var. *falcata* Jones, Contr. West. Bot. 11:19, 1903.) Northern part of the Great Basin; western Montana to northern Utah (according to Jones), Nevada, northeastern California, eastern Washington, and Idaho. Type locality, Weiser, Idaho. Collections: Horse Valley, southwestern Montana, *Hall 11503, 11561* (UC); Dolly Varden Smelter, eastern Nevada, July 24, 1891, *Jones* (Herb. Jones, type of *A. nuttalli anomala* Jones, minor variation 11); Battle Mountain, Elko County, Nevada, *Kennedy 3074* (US); Winnemucca Lake, Nevada, *Kennedy 1974* (US, young and doubtful); 16 to 24 km. west of Amedee, Lassen County, California, June 24, 1897, *Jones* (Herb. Jones); dry hillsides near Willow Creek Valley, Lassen County, California, *Davy 3402* (UC); near Beattys, Butte County, Oregon, *Leiberg 2611* (US); dry ground at the Narrows, Harney County, Oregon, *Peck 1677* (Gr); Powder River Valley, eastern Oregon, *Cusick 1928* (Gr, US); near Egbert Springs, Douglas County, Washington, *Sandberg and Leiberg 349* (Gr, NY, UC, US); type collection, July 7, 1899, *Jones* (Herb. Jones); Antelope Valley, Idaho, *Henderson 3635* (US); Twin Falls and Shoshone Falls, Idaho, *Nelson and Macbride 1351* (NY, UC, US); Pocatello, Idaho, *Palmer 407* (Gr, US); Leadore, Lemhi Valley, eastern Idaho, *Hall 11506* (UC).

MINOR VARIATIONS AND SYNONYMS.

1. *ATRIPLEX ACANTHOCARPA* var. *CUNEATA* Jones, Contr. West. Bot. 11:20, 1903.—Based upon *A. cuneata* Nelson, which is here treated as a subspecies of *A. nuttalli*. No reasons were given for the reduction to *acanthocarpa*. If this arrangement were accepted, then all of the forms of *nuttalli* should go with it. This seems unnecessary, for although the two are closely related, the heavy and strictly entire leaves of *cuneata* and its allies are very unlike those of *acanthocarpa*. Even when the fruiting bracts are heavily appendaged, as in *cuneata*, and therefore exceptionally large in total expanse, the body itself is never so thick nor turgid as in *acanthocarpa*.

2. *A. BUXIFOLIA* Rydberg, Bull. Torr. Club 39:311, 1912.—*A. nuttalli buxifolia*.

3. *A. CUNEATA* Nelson, Bot. Gaz. 34:357, 1902.—*A. nuttalli cuneata*, with the exception of two of the cited specimens, i. e., *Wright 573*, which is *A. acanthocarpa*, and the plant from Holbrook, Arizona, which is *A. obovata*.

4. *A. EREMICOLA* Osterhout, Bull. Torr. Club 25:284, 1898.—*A. nuttalli gardneri*. The type, which came from southern Wyoming, is a plant in which the fruiting bracts are very smooth, the edges nearly parallel, but cuneately narrowed at base and slightly enlarged at summit through the development of herbaceous teeth. (Fig. 46, *w* to *z*.)

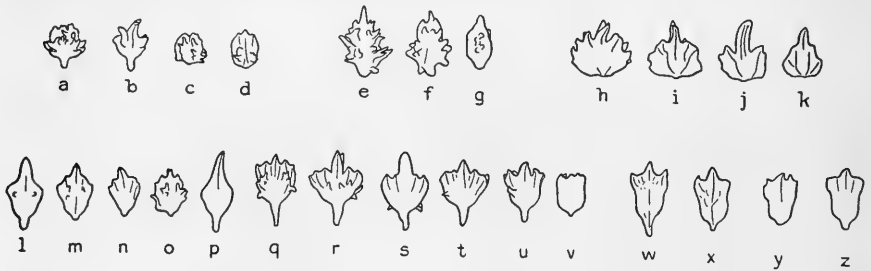


FIG. 46.—Variation in fruiting bracts of *Atriplex nuttalli*: *a* to *d*, from one plant of subspecies *typica* (Centennial, Wyoming, 128609 UC); *e* to *g*, from another plant of *typica* (Price, Utah, 110313 UC); *h* to *k*, from one plant of subspecies *tridentata* (west of Rock Springs, Wyoming, 205252 UC); *l* to *p*, from one plant of subspecies *gardneri* (Little Laramie River, Wyoming, 35325 R); *q* to *v*, from another collection of *gardneri*, all probably from a single plant (Laramie, Wyoming, 205354 UC); *w* to *z*, from another collection of *gardneri* (southern Wyoming, type of *A. eremicola*, minor variation 4). All $\times 2$.

5. *A. FALCATA* Standley, N. Am. Fl. 21:68, 1916.—*A. nuttalli falcata*.

6. *A. FRUTICULOSA* Osterhout, Bull. Torr. Club 25:207, 1898.—Changed by Osterhout to *A. eremicola* because of the earlier *A. fruticulosa* Jepson. (See under No. 4.)

7. *A. GARDNERI* Standley, l. c., 66, 1916.—Based upon *Obione gardneri*, which see.

8. *A. GARDNERI* var. *TRIDENTATA* Macbride, Contr. Gray Herb. N. S. 53:11, 1918.—Based upon *A. tridentata*, which see.

9. *A. GORDONI* Hooker, Jour. Bot. and Kew Misc. 5:261, 1853.—Based upon *Obione gardneri*, which see. The specific name was changed by Hooker, since it was Gordon (not Gardner) who collected the type specimen.

10. *A. NEOMEXICANA* Standley, l. c., 67, 1916.—A form of *A. nuttalli* differing from subspecies *cuneata*, with which it was collected in northwestern New Mexico, only in the remarkable foliaceous development of the free tips of the bracts. These are orbicular-rhombic and as wide as or wider than the body. The relation of this to the usual form requires further field study.

11. *A. NUTTALLI* var. *ANOMALA* Jones, Contr. West. Bot. 11:19, 1903.—The same as *A. nuttalli falcata*, except that the fruiting bracts are smooth on the faces and margins, or only occasionally with a few teeth or mucronations. According to Jones, intermediates occur in the Green River Basin, Wyoming, and in western Utah. Most of the specimens cited under subspecies *falcata*, including the type, exhibit both appendaged and smooth bracts. Type locality of *anomala*, Dolly Varden Smelter, eastern Nevada.

12. *A. NUTTALLI* var. *FALCATA* Jones, l. c.—*A. nuttalli* subspecies *falcata*.

13. *A. NUTTALLI* var. *UTAHENSIS* Jones, l. c.—A narrow-leaved form of *A. nuttalli typica*. The description applies better to subspecies *tridentata*, but the leaves in the type specimen are spatulate rather than linear, and very obtuse. Representative leaves measure 2 to 2.5 cm. long by 3 to 5 mm. wide at the broadest part, i. e., above the middle. The type is from Salt Lake City, Utah (*Jones 1760*).

14. *A. OBLANCEOLATA* Rydberg, Bull. Torr. Club 31:403, 1904.—A low form of *A. nuttalli typica* and common with it. Described as differing also in having short-petioled leaves, brown staminate flowers, and a

whiter tomentum, but none of these features are sufficiently well-marked to be of service in distinguishing this from true *nuttalli*. Type locality, Delta, Colorado.

15. *A. PABULARIS* Nelson, Bull. Torr. Club 25: 203, 1898.—*A. nuttalli tridentata*. This is a form with crowded strictly erect leafy stems clustered on a very short woody base, the branches of which are slightly spreading. Thus the plants come to form close rounded tufts. The bracts are about as in typical *tridentata* but some of them tend to be broadest toward the summit, thus approaching subspecies *gardneri* (fig. 46). At the type locality, namely, Point of Rocks, Wyoming, some plants with the habit of *pabularis* have bracts so broad above that they are referred to subspecies *gardneri* (Hall 10935). As far as known the *pabularis* form is confined to highly alkaline clays of low flats immediately adjacent to saline streams.

16. *A. PABULARIS EREMICOLA* Nelson, in Coulter and Nelson, Man. Rocky Mt. Botany, 168, 1909.—Based upon *A. eremicola* Osterhout, which see.

17. *A. TRIDENTATA* Kuntze, Rev. Gen. Pl. 546, 1891.—*A. nuttalli tridentata*.

18. *OBIONE GARDNERI* Moquin, in De Candolle, Prodr. 13: 114, 1849.—*A. nuttalli gardneri*. According to both the International and American Codes this form should be taken as the type of the collective species, the name of which would then become *Atriplex gardneri* (Moquin) Standley. Under this arrangement all of the subspecies here assembled would be transferred to *A. gardneri*. The reasons for retaining *A. nuttalli* as the inclusive name are that it has become well established in the literature, that its typical form is abundant and well-known to botanists, and that if the other name were adopted there would still remain a difference of opinion as to whether or not it should be corrected to *gordoni*, as proposed by Hooker (Jour. Bot. and Kew Misc. 5: 261, 1853).

RELATIONSHIPS.

Atriplex nuttalli belongs to a small group of dioecious species which stand intermediate between the herbaceous and the truly shrubby forms. Its derivation doubtless was from a Mexican stock, which yielded also such semi-shrubby species as *A. barclayana*, *A. acanthocarpa*, and *A. obovata*. In the process of its northward migration it left these forms behind, both geographically and phylogenetically, so that it has now come to inhabit the alkaline plains and slopes from the southern Rocky Mountains and Great Basin northward and has developed a combination of essential characters not found in any of the others. The only related species which grows well within its area is *A. corrugata*, a still less shrubby form with its own peculiar characters, as will be later indicated.

In the process of establishing itself in the extensive area now occupied, the original *nuttalli* stock diverged into several subspecies and a large number of minor variations. All of these are so closely held together by intermediate forms that the separation into district species is impracticable. Standley's 8 species, diagnosed in the North American Flora, are based upon features which field study and the abundance of recent collections have demonstrated to be unstable. The only one which stands out distinctly over most of its area is *falcata*. This is based upon its narrow fruiting bracts, and, although exact intermediate forms have not as yet been found, the character is of such a nature that it may be expected to vary. Jones, the original sponsor of *falcata*, gave it varietal rank under *nuttalli*.

The first three subspecies form a very close group, and since they occupy the same region, it is questionable if all should not be treated as one. But the peculiar bracts of subspecies *gardneri* are quite distinctive in the extreme form, being decidedly broadest above and with margins uniformly narrowed toward the base. The bracts are thus cuneate-oblong with a truncate summit. However, the sides are sometimes so nearly parallel that it is difficult to say whether the bracts belong to this or to subspecies *tridentata* (e. g., in Nelson 3667 from Sweetwater County, Wyoming, and in Hall 10935 and Nelson 4429, both from Point of Rocks, Wyoming, the latter the type of *A. pabularis* Nelson, minor variation 15). A few of the shapes are shown in figure 46. The two subspecies of this group with bracts broadest below, i. e., *typica* and *tridentata*, differ from each other in habit as well as in the characters used in the chart. The latter is the less woody at base and the strictly erect stems form a close, almost columnar plant. The tendency toward the absence of appendages on the bracts is tentatively employed

as a distinguishing feature, since it seems to run parallel with habital and foliage characters. But its variability in other species and the absence of entire constancy even here, as shown in plate 51, also figure 46, suggest that further field studies may nullify its criterial value. The lack of constancy is mentioned in the original descriptions of *nuttalli* and *gardneri*.

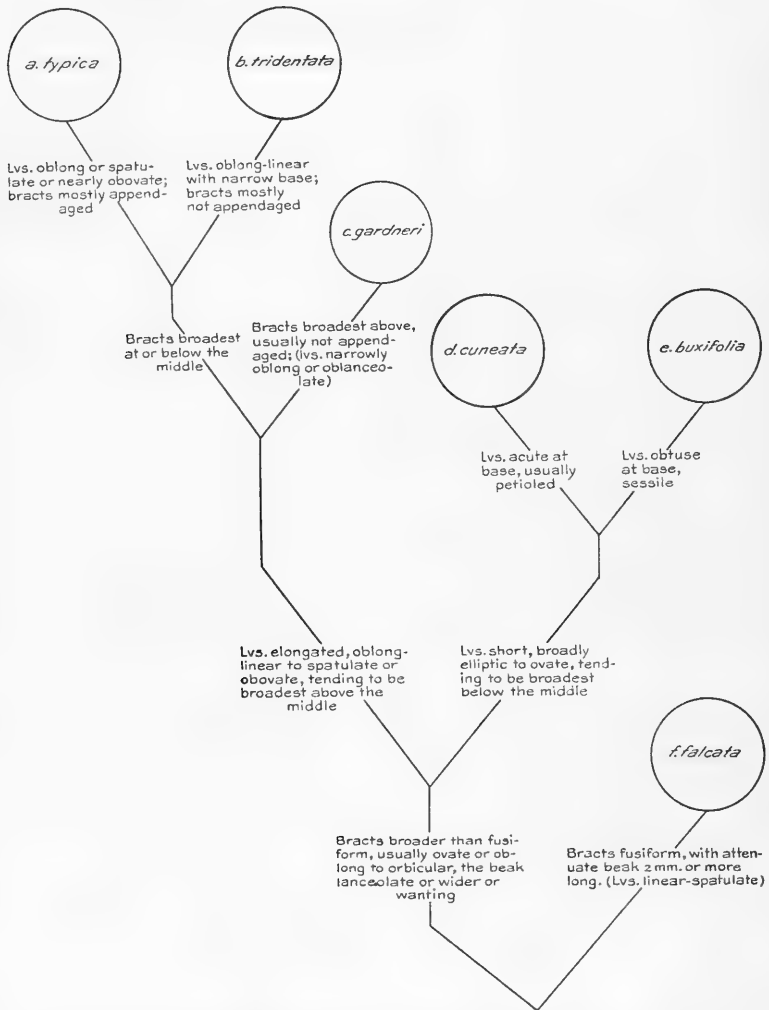


FIG. 47.—Phylogenetic chart of the subspecies of *Atriplex nuttalli*.

Subspecies *cuneata* and *buzifolia* are more southerly in their distribution. This, together with their shorter and relatively broader leaves and bracts, the latter with prominent flattened appendages, suggests a former connection with such related species as *obovata* and *acanthocarpa*. The compression of the appendages occurs at times also in *typica* and is too variable to be depended upon for purposes of identification.

Although almost always dioecious, *A. nuttalli* is occasionally monoecious. For example, on the plains south of Grand Junction, Colorado, where the plants are mostly unisexual, a few specimens with the usual naked terminal spikes of staminate flowers have also an abundance of well-formed and apparently fertile pistillate flowers in the upper leaf-axils (*Hall 11048*, UC).

ECOLOGY.

Atriplex nuttalli is the most characteristic dominant of strongly alkaline clay soils throughout the larger portion of the sagebrush association of the Great Basin, and in the northwestern portion of the mixed prairie. It is especially abundant in western Wyoming and Colorado, Utah, and southern Idaho, where it covers thousands of square miles of saline plains and bad-land slopes. Owing to the resistance it affords to wind and water erosion, the plants on plains occur almost universally on low mounds 6 inches to a foot high and a foot or two across, simulating dunelets. It shares this habit with its constant associate in the heart of its region, namely, *A. corrugata*. On the strongly alkaline slopes of Mancos shale and other bad-land formations, *nuttalli*, usually with *corrugata*, forms the first perennial associates of the xerosere, following immediately the pioneer annual communities, such as *A. saccaria*, *A. graciliflora*, and *Eriogonum inflatum*. On the extensive plains at the base of such ranges it lies in contact with *Sarcobatus* and *Chrysothamnus nauseosus consimilis* in the valleys, and *A. confertifolia* on less alkaline slopes or on rocky ridges. The spaces between the mounds are often covered with annuals, of which *A. powelli*, *A. argentea*, *A. rosea*, and *Eriogonum inflatum* are the most important. The most adaptable of the subspecies appears to be *falcata*, which ranges from saline valleys with *Sarcobatus* and *Suaeda* to uplands, where it occurs with *Artemisia tridentata* and *frigida*. According to Kearney and his associates, the salt-content of the first foot in the *Sarcobatus-Atriplex* community of the Tooele Valley in which *nuttalli* was found, ranges from 0.08 to 0.61 per cent, while for the fourth and fifth feet the averages were 1.15 and 1.58 per cent respectively. At Tucson the salt-content ran much higher, as it undoubtedly does on many bad-land slopes, namely, as high as 3.5 per cent in the first foot, 3.3 per cent in the second foot, and 2.5 per cent in the third.

USES.

This is an important browse plant in the alkaline districts where it grows. Stockmen in eastern Utah report it as very good for cattle and sheep after the snow leaves in the spring. In Wyoming, also, where it makes dense stands in low moist places along alkaline streams, it is said to furnish large amounts of fodder relished by sheep. Like other saltbushes, however, it is seldom if ever eaten by choice to the exclusion of other foods. Doubtless an extensive diet of this plant alone would lead to injurious effects similar to those of the related *A. corrugata*, which is pretty well known to be poisonous. Knight, Hepner, and Nelson report on *A. nuttalli* as follows:

"This is the most important of the native salt-bushes (in Wyoming) It is readily eaten by stock and endures close grazing. Where it is cropped continuously, it becomes matted and sends up numerous leafy shoots. It is very common in many parts of Wyoming and in the Red Desert furnishes a large part of the winter forage. It readily reseeds and maintains itself where once established. Occasionally it spreads into fallow fields and here makes a thrifty growth." (Wyo. Exp. Sta. Bull. 65:46, 1905.)

A chemical analysis is given in connection with this report. An earlier analysis given as for this plant by Forbes and Skinner (Ariz. Exp. Sta. Rep. 13:269, 1902) applies to *A. canescens*, there having been an error in the determination of the material examined.

39. ATRIPLEX CORRUGATA Watson, Bot. Gaz. 16:345, 1891. Plate 51. MATSCALE.

Spreading subshrub, woody at the base, forming dense leafy mats, 1 to 2 dm. high; branches decumbent at base but the flowering stems strictly erect, slender, not angled, densely furfuraceous, the bark breaking in age into fibrous sheaths on the old parts; leaves mostly opposite, the upper alternate, sessile, broadly linear or linear-spatulate, narrow at base, rounded to the obtuse summit, 0.5 to 2.0 cm. long, 0.2 to 0.5 cm. wide, strictly entire, densely and permanently white-furfuraceous; flowers dioecious or sometimes monoecious, the staminate in large glomerules along nearly naked terminal spikes, the pistillate in elongated terminal spikes which far overtop the leafy stems; perianth 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile or subsessile, thick, scarcely spongy, united nearly to summit, narrowly fan-shaped, the terminal free portion very broad and obtuse, 4 to 6 mm. long, 3 to 4 mm. wide, the sides with thick wart-like or somewhat flattened appendages; seed about 2 mm. long, reddish-brown; radicle superior.

Alkaline plains of western Colorado, southern Utah, and northern New Mexico. Type locality, Grand Junction, Colorado. Collections: Type collection, May, 1891, *Eastwood* (Gr, UC, US); Colorado: mesa southeast of Grand Junction, *Hall 11049* (UC); Whitewater, *Hall 11050* (UC); San Juan Plains, *Brandegee 1086*, in part (UC); between Hotchkiss and Crawford, *Cowen 1118* (Gr); Mesa Grande, on the Gunnison River, *Purpus 334* (UC); Solitude, Utah, *Coville and Kearney 2603* (US); Desert Station, Utah, *Rydberg and Garrett 8314* (NY, US); Emery, Utah, *Jones 5444* (NY, UC, US); south of Green River, Utah, *Hall 11038* (UC); mesas south of San Juan River, 5 km. south of Shiprock Station, New Mexico, September 22, 1920, *Hall* (CI).

SYNONYM.

ATRIPLEX NUTTALLI CORRUGATA Nelson, in Coulter and Nelson, Man. Rocky Mt. Bot. 163, 1909.—No reasons were given for this reduction to a species which differs in several fundamental features, as will be indicated beyond.

RELATIONSHIPS.

Atriplex corrugata does not closely approach any other species in its characters. It is commonly placed next to *A. nuttalli* in taxonomic treatments, perhaps because the two are somewhat similar in superficial appearance and occupy the same habitat. Where they grow together, *corrugata* may be recognized at a glance, for its lower, more compact, and mat-like habit and the small crowded leaves give to the plant a more delicate aspect. Its technical characters indicate a considerable phylogenetic divergence. Especially notable are the opposite position of the leaves and the shape of the fruiting bracts, which are relatively much broader above and have the free terminal portion developed into a broad, smooth, essentially entire, lip-like appendage. The opposite leaves suggest a possible connection with some group more primitive than the *Nuttalliana*, for example, the opposite-leaved *A. decumbens* or *A. matamorensis*. The flowers are occasionally monoecious at the type locality. Miss Eastwood has here collected specimens, some of which are purely staminate, some purely pistillate, and others with several of the lower clusters in each spike pistillate, the remainder of the spike staminate (Grand Junction, May, 1892, *Eastwood*, UC).

ECOLOGY AND USES.

Atriplex corrugata resembles *A. nuttalli* closely in its ecological behavior, evidently having sprung from it as an adaptation to greater drought arising from increased salt-content. They occur together throughout the range of the former, sometimes mixing on apparently equal terms, but with *corrugata* regularly taking the more halophytic depressions and ridges. It is especially typical of the most saline bad-land ridges,

and sometimes pushes as far into white-alkali flats as does *Suaeda*. It forms low mounds in the manner of *nuttalli*, but these are smaller, owing to its more appressed habit.

This species is looked upon with disfavor by the stockmen of Utah, who call it "poison clover." It is browsed to a considerable extent by sheep, especially after other forage has been used up, with the result that many of the animals are fatally poisoned. While this has not been corroborated by carefully controlled feeding experiments, the range evidence comes from trustworthy sources. It is probable that the poisoning is due to saponin, as seems to be the case with *A. canescens*. The only other browse on the range at the time of greatest injury is *A. nuttalli*, which is much less if at all injurious.

40. ATRIPLEX POLYCARPA (Torrey) Watson, Proc. Am. Acad. 9:117, 1874. Plate 52.
ALLSCALE.

Erect shrub, woody throughout, intricately much branched to form twiggy and usually rounded plants 8 to 20 dm. high (seedlings sometimes fruit abundantly when only 3 dm. high); branches not angled, at first gray-scurfy, later smooth and light or yellowish brown, the old bark dark and breaking longitudinally; leaves crowded on the young twigs, early deciduous, alternate, usually sessile, elliptic-oblong or spatulate, narrowed at base, acutish or obtuse at apex, usually 0.3 to 1.5 cm. long and 0.2 to 0.4 cm. wide, but up to 2.5 cm. long on sterile twigs, often with very small leaves fascicled in the axils, entire, thickish, gray with a dense permanent scurf, 1-nerved; flowers dioecious, the staminate glomerules in axillary and terminal spikes, the pistillate crowded along the numerous divergent branches of profuse terminal panicles; perianth 5-cleft in staminate flowers, wanting in the pistillate; fruiting bracts sessile, moderately or scarcely compressed (the margins sometimes broad and flat), united to well above the middle or rarely distinct nearly to the base, cuneate-orbicular, 2 to 4 mm. long or up to 6 mm. when the teeth are well developed, as broad or broader, the thin margins shallowly to deeply and laciniately dentate above the base, the faces copiously cristate-appendaged to tuberculate or smooth; seed 1 to 1.5 mm. long, pale brown; radicle superior. (*Obione polycarpa* Torrey, Pacif. R. R. Rep. 4:130, 1857.)

Desert areas from southern Nevada, southern Utah, Arizona, and Sonora west across Lower California, north to the San Joaquin and Owens Valleys, California; abundant on the Colorado Desert of western Arizona and eastern California, also in the south and west portions of the San Joaquin Valley, California. Type locality, Valley of the Gila River, Arizona. Collections: 13 km. above Rioville, Nevada, April 11, 12, and 13, 1894, *Jones* (US); St. George, Utah, *Jones* (Herb. Jones); type collection, October 28, 1846, *Emory* (NY); Arizona: Tempe, *Kearney 89, 119* (US); Maricopa, September 3, 1901, *Thorner* (UC); Mellen, along the Colorado River, February 25, 1910, *Grinnell* (UC); Yuma, *Hall 11209* (UC); near Tucson, *Thorner 109a* (NY, UC, US); Sonoyta, Sonora, *Mearns 2732* (US); San Francisquito Bay, Gulf of California, *Rose 16754* (NY, US); Puerto Refugio, Angel de la Guardia Island, Gulf of California, *Johnston 3368* (SF, UC); Lower California: Comondu, April 24, 1889, *Brandege* (UC, type of *A. curvidens* Brandege, minor variation 3); Point Abrejos, *Rose 16254* (US); San Bartolome Bay, April 12, 1897, *Brandege* (UC); Rosalia Bay, *Anthony 130* (UC, US); California: Borregos Springs, Colorado Desert, April 18, 1895, *Brandege* (UC); Palm Springs and southward, *Schellenger 34* (UC); Indio, *Kearney 8* (US); Mecca, *Parish 8262* (Gr); Dry Lake near Rosamond, western end of Mojave Desert, *Hall 10969*; west side of Tehachapi Pass, *Hall 10966, 10967, 10968* (UC); Bakersfield, September 28, 1894, *Eastwood* (UC); near Kern Lake, *Davy 2137* (UC); near Lost Hills, western Kern County, *Hall 11774, 11775* (UC); Shandon, San Luis Obispo County, *Severin* (CI); between Mendota and Coalinga, Fresno County, *Hall 11763* (UC); Wildcat Cañon, western Merced County, *Severin* (CI); sandy plains of Owens Valley, *Purpus 3043*

(UC); near Bennett Wells, Death Valley, *Coville* and *Funston 196* (US); additional localities mentioned by Merriam (N. Am. Fauna 7:325, 1893) include Lone Pine to Haway Meadows in Owens Valley, California, and the following, all in Nevada: Grapevine Cañon, Oasis Valley, south of Pahranaagat Lake, Virgin and Lower Muddy Valleys, and east of Pahrump Valley.

MINOR VARIATIONS AND SYNONYMS.

1.—Variation in the sculpturing and dentation of the bracts, to be expected in most species of *Atriplex*, is here very marked. These variations often occur in varying degrees on neighboring plants. But at one locality in the Tehachapi Pass, California, certain individual plants have only smooth or nearly smooth bracts; other plants close by have only bracts in which the faces are covered with tubercles and cristate appendages; still others have the two kinds of bracts in about equal proportions. This last-mentioned form appears to be a hybrid between the other two, which, if this is the case, should be considered as genetic races. Samples of the plants are filed at the Herbarium of the University of California (Nos. 205322, 205323, 205331, respectively).

2.—A form with exceptionally small, ovate leaves has been collected at Maricopa, Arizona (September 3, 1901, *Thornber*, UC, Nos. 7195, 7196). In many other collections there occur similar leaves but only fasciated in the axils of longer normal ones. In the Maricopa plants even a portion of the primary leaves are ovate, closely sessile by a subcordate base, and only about 4 mm. long. They suggest the sagittate-sessile leaves of *A. julacea*. (See plate 52.)

3. *ATRIPLEX CURVIDENS* Brandegee, Proc. Calif. Acad. Sci. II, 2: 201, 1889.—An extreme form as to the fruiting bracts, which are broadly obovate with a cuneate base, broader than long, mostly not appendaged, and with remarkably broad, thin margins which are cleft into numerous linear often curved segments. Type, Comodu, Lower California, April 24, 1889, *Brandegee* (UC); known also from San Esteban Island, Gulf of California, *Johnston 3193* (SF, UC). Intermediate forms in which the bracts are of the same shape and size but with shorter and thicker marginal teeth have been collected near Tucson, Arizona (October 16, 1901, *Thornber*, UC). It has been suggested by Standley (Bull. Torr. Club 44: 424, 1917) that the type specimen may be abnormal as the result of a fungus which grew upon it.

4. *OBIONE POLYCARPA* Torrey, Pacif. R. R. Rep. 4:130, 1857.—The original publication of the species, although the same name appeared earlier without a description (Torrey in Emory, Notes Mil. Rec. 150, 1848).

RELATIONSHIPS.

The relationships of this species are with *A. julacea* and *A. barclayana*, as has been more fully indicated under the former. The fruiting bracts tend to the obovate rather than to the ovate shape characteristic of *julacea* and the leaves are never truly sagittate-clasping as in that. But on occasional plants some of the leaves are ovate-cordate and closely sessile, as described under minor variation 2. Such specimens suggest a former connection between the two.

ECOLOGY.

Atriplex polycarpa forms characteristic consocieties in alkaline basins in the Southwest. In the region of *lentiformis* it lies above the latter on better-drained soil, making the next stage in the succession, the two mingling through a considerable ecotone. Beyond the range of this it is the chief dominant of strongly alkaline valleys, often associated with *Suaeda* and sometimes zoned about it. In the Santa Cruz and Gila Valleys of southern Arizona it may form the center within a zone of *A. canescens*, or the two may mix over considerable areas. It is often associated with *Prosopis* and *Larrea*, and may extend up rocky slopes to mix with *Parkinsonia*, *Fouquieria*, and *Cereus*. In the Antelope Valley of California it grows with *A. confertifolia* in the *Larrea* community. It is nearly as tolerant of alkali as *lentiformis*, Kearney finding a salt-content of 3.12 per cent for the first foot, 2.18 for the second foot, and 0.69 for the third.

USES.

The allscale, also called cattle spinach, probably equals *A. canescens* in its value as a browse plant, practically always assuming a low compact form wherever cattle and sheep are present. Its value is high, owing to its usual association with a number of unpalatable species. In some districts, such as the westerly slopes of the San Joaquin

Valley, California, where it occupies extensive areas too hot and arid for other shrubs, it serves as browse for large numbers of sheep while these are being moved from one range to another. In such places, where all feed is at a premium, the shrubs are often stripped of their scant foliage and many plants finally die as a result of repeated browsing. In some portions of the Lost Hills district over 50 per cent of the plants have been killed, presumably because of this. *Atriplex polycarpa* is regarded by Severin as the most important of the shrubby food-plants of *Eutettix*. Like most species of the genus, it may be an occasional cause of hay-fever.

41. ATRIPLEX JULACEA Watson, Proc. Am. Acad. 20:370, 1885. Plate 52.

Procumbent subshrub with ascending or erect crowded slender twigs, these only slightly woody; branches (2 to 6 dm. long) slender, not angled, gray-scurfy or glabrate, the bark thick brown and corky on old basal portions; leaves crowded and sometimes imbricate on the branchlets, alternate, closely sessile by a sagittate-clasping base, ovate-triangular, usually sulcate by the folding back of the margins, obtuse at apex, 0.2 to 0.4 cm. long, 0.1 to 0.2 cm. wide, entire, thick, gray with a dense permanent scurf, 1-nerved; flowers dioecious, solitary or in few-flowered axillary glomerules; perianth cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile, not compressed, united to above the middle, ovate, 4 to 6 mm. long, about as broad, the surface covered with irregular corky appendages; seed about 1 mm. long, reddish-brown; radicle superior.

Pacific Coast of Lower California from near the northern boundary to San Gregorio. Type locality, Todos Santos Bay. Collections, all from Lower California: Type collection, September 30, 1884, *Orcutt* (Gr); Todos Santos Island, March 9, 1897, *Brandegee* (UC); Enseñada, *Jones 3737* (NY, US); Sauzal, April 11, 1885, *Orcutt* (Gr, US); Cape San Quentin, May 10, 1885, *Greene* (DS, US); San Quentin Bay, *Palmer 726* (Gr, NY, US); San Telmo, May 31, 1893, *Brandegee* (UC); Socorro, May, 1889, *Brandegee* (UC); Natividad Island, *Anthony 365* (DS, UC); San Bartolome Bay, April 12, 1897, *Brandegee* (UC); Point Abrejos, *Rose 16252* (US); San Gregorio, April 6, 1889, *Brandegee* (UC).

RELATIONSHIPS.

Watson's statement following the original description that this species is related to *A. polycarpa* is borne out by all of the evidence assembled from more recent collections. It is less woody than that and therefore seems to stand between it and the subshrubby *Atriplexes* like *A. barclayana*. But it is more woody than descriptions lead one to believe. Sometimes the hard stems are 3 mm. thick and some herbarium specimens indicate that the principal stems are sometimes erect from a very short spreading base (*Anthony 365*). Such specimens look very much like young plants of *A. polycarpa*. *A. julacea* is well set off from all other species by the minute and sagittate-clasping leaves.

ECOLOGY AND USES.

Nothing is known regarding the ecology of this plant, aside from the fact that it forms low, tangled masses in the proximity of the sea. It has no uses as far as known.

42. ATRIPLEX HYMENELYTRA (Torrey) Watson, Proc. Am. Acad. 9:119, 1874.
Plate 53. HOLLYSCALE; DESERT HOLLY.

Erect compactly branched shrub, woody throughout, of rounded outline when normally developed, 3 to 10 dm. high and broad; branches not striate, white with a dense and long-persisting scurf; the bark rough and gray on old basal portions; leaves numerous, persistent, alternate, on petioles 5 to 10 mm. long, orbicular or round-ovate, truncate subcordate or short-cuneate at the base, obtuse at apex, the blade 1.5 to 3 cm. long and about as wide, deeply and irregularly dentate with salient sharp teeth, thick, silvery-

white with a dense, smooth, persistent scurf, 1-nerved from the base; flowers dioecious, in short dense leafy panicles and short axillary spikes, or the pistillate inflorescence sometimes more open and less leafy; perianth 5-parted in the staminate flowers, wanting in the pistillate; fruiting bracts borne on a short fusiform or turbinate stalk, strongly compressed, except for the small convex body, distinct or nearly so, orbicular or round-reniform, 6 to 12 mm. long and about as broad, the margins entire, the faces smooth but reticulate-veiny; seed about 2 mm. long, brown; radicle superior. (*Obione hymenelytra* Torrey, Pacif. R. Rep. 4:129, plate 20, 1857.)

Alkaline deserts of southeastern California, southern Nevada, and southwestern Utah, south across western Arizona to Sonora and Lower California. Type locality, hills and gravelly places on Williams River, Arizona. Collections: California: West from Bennett Wells, Death Valley, *Coville* and *Funston 195* (Gr, US); near Fremonts Peak, Mojave Desert, *Hall* and *Chandler 6855* (UC); near Barstow, Mojave Desert, *Rose 12060* (US); Borregos Springs, Carisso Creek, and Split Mountain, all on the Colorado Desert, *Brandegee* (UC); Coachella, Colorado Desert, April, 1905, *Greata* (UC); Signal Mountain, Colorado Desert, December 29, 1907, *Abrams* (Gr); west of Logan, Clark County, Nevada, *Heller 10452* (DS, Gr, NY, US); southern Utah, *Palmer*, 1870, acc. Bot. King; gravelly mesa near Mellen, Arizona, February 25, 1910, *Grinnell* (UC); Bill Williams Fork, Arizona, *Bigelow* (Gr); Mohawk Station, lower Gila River, Arizona, *Greene 1089* (Gr); Gila, Sonora, *Thurber* (Gr); Cucupa Mountains, Lower California, *MacDougal 143* (NY); Los Angeles Bay, Lower California, *Johnston 3441* (SF, UC). Additional localities in California and Nevada are listed by Coville (Contr. U. S. Nat. Herb. 4:180, 1893).

RELATIONSHIPS.

This is one of the most distinct of the American species of *Atriplex*. It is unlike any other in its roundish, deeply dentate leaves and in its large, orbicular, thin-winged bracts. The development of a wing from the upper portion of the bract, the position of the seed, and the short stipe-like base to the bracts, all suggest *A. confertifolia*, but the body of the bract is not indurated as in that, and otherwise these two species are quite unlike.

ECOLOGY AND USES.

Atriplex hymenelytra practically never forms a dominant community, but grows sparsely or copiously in association with the dominants of dry rocky slopes about valleys in which *polycarpa* or *lentiformis* is usually found. Its usual associates are *Encelia*, *Franseria*, *Larrea*, *Fouquieria*, *Opuntia*, etc. The flowering period is earlier than that of any other species, the staminate flowers opening from February to April.

The plants are normal and symmetrical, and show no evidence of being browsed. Their silvery, spiny leaves and symmetry make them in demand for decoration, and carloads are shipped East, especially at Christmas time.

43. ATRIPLEX LENTIFORMIS (Torrey) Watson, Proc. Am. Acad. 9:118, 1874.
Plates 54 and 55. LENSACLE.

Erect shrub, woody throughout, either rigidly or flexuously much branched, globose or dome-shaped in outline when well developed, 10 to 30 dm. high and with a spread of 1 to 50 dm; branches either terete or sharply angled, gray-scurfy at first, soon smooth and pale, the bark rough and gray on old trunks; leaves numerous, deciduous in desert forms and the branchlets then spiny, alternate, petioled or the upper ones sessile, deltoid or rhombic to ovate or oblong (nearly orbicular in minor variation 4), truncate to cuneate at base, obtuse and short-mucronate at apex, 1 to 5 cm. long, 0.5 to 5 cm. wide, entire or subhastate, rather thin, gray or bluish with a fine, close permanent scurf, 1-nerved from the base; flowers dioecious or monoecious, both staminate and pistillate crowded along

the branches of profuse terminal panicles, the fruiting branches sometimes curved downward by the weight of their load; perianth 4- or 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile, moderately compressed, united only near the base or up to the middle, orbicular or slightly broader than long or rarely broad-elliptic, 2 to 5 or 7 mm. long and broad, the free margins entire or crenulate, the faces smooth; seed 1.2 to 1.5 mm. long, brown; radicle superior. (*Obione lentiformis* Torrey in Sitgreaves Rep. Exp. 169, 1853.)

Southern half of California, both on the coast and inland, to Nevada, southwestern Utah, New Mexico, Sonora, and the border of Lower California.

SUBSPECIES.

The forms of *Atriplex lentiformis* may be assembled into four subspecies. Each inhabits a different geographic area although *typica* and *torreyi* closely approach each other in eastern California. Subspecies *typica* is central, both geographically and phylogenetically, but since the others probably were derived from it, this form is given first place in the sequence.

Key to the Subspecies of Atriplex lentiformis.

- Twigs not sharply angled.
 Mature bracts mostly crenulate on the margins, 2.5 to 4 or rarely 5 mm. broad; leaves mostly 1 to 2.5 cm. wide. Interior..... (a) *typica* (p. 335).
 Mature bracts mostly entire, 3.5 to 5 or rarely 7 mm. broad; leaves mostly 1.5 to 5 cm. wide. Coastal..... (b) *breweri* (p. 335).
 Twigs sharply angled by several raised rib-like longitudinal striae.
 Mature bracts orbicular; leaves deltoid to ovate, rarely oblong..... (c) *torreyi* (p. 336).
 Mature bracts broader than long; leaves narrowly ovate to narrowly oblong..... (d) *griffithsi* (p. 336).

43a. *ATRIPLEX LENTIFORMIS TYPICA*.—Branches and twigs terete or with only obtuse and irregular angles, often rigid, rarely becoming spiny; leaf-blades usually 2 to 4 cm. long, 1 to 2.5 cm. wide; flowers mostly dioecious but some plants with both sexes; mature bracts flattish or only slightly convex, mostly 2.5 to 4 mm. in diameter, or up to 5 mm. and spongy-thickened when borne with staminate flowers, the margins minutely crenulate or rarely entire. (*Obione lentiformis* Torrey in Sitgreaves, Rep. Exp. 169, 1853.) Salinas and San Joaquin Valleys, California, to southwestern Utah; southward in the interior to Lower California and Sonora. Type locality, "on the Colorado of California." Collections: California: Firebaugh, northwestern Fresno County, *Hall 11760* (UC); 2.5 km. west of Coalinga, Fresno County, *Hall 11765* (UC); 8 km. south of King City, Salinas Valley, October 11, 1918, *Severin* (UC, pocket), Bakersfield, September 24, 1894, *Eastwood* (Gr, UC); Kern Lake, *Davy 2911* (UC); Resting Springs Valley, Inyo County, *Coville* and *Funston 264* (US); near Saratoga Springs, Death Valley, *Coville* and *Funston 303* (US); type collection, Sitgreaves Expedition, November, 1851 (Gr); southwestern part of Colorado Desert, *Orcutt 2083, 2084* (US); between Coachella and Wolters, Colorado Desert, *Schellenger 54* (UC); Salton Crossing, Colorado Desert, April 3, 1901, *Brandege* (UC); St. Joe, Nevada, *Jones 5030k* (US); Colorado River, Arizona, opposite Needles, March 3, 1910, *Grinnell* (UC); Chemehuevis Valley, Arizona, *Jepson 5197* (DS); Yuma, Arizona, *Hall 11208* (UC); Tempe, Arizona, September 1, 1901, *Thornber* (UC, US); Gardners Lagoon, Lower California, *Schoenfeldt 2913* (US); 20 km. north of Lerdo, Sonora, December 2, 1898, *Price* (DS); Altar River, Sonora, August 25, 1884, *Pringle* (Gr, NY, US). Additional stations, some of which may be for subspecies *torreyi*, include the following, according to Merriam (N. Am. Fauna 7: 327, 1893): Oasis, Pahrnagat, Virgin, and Lower Muddy Valleys, all in Nevada; Amargosa Cañon and North of Willow Spring, Antelope Valley, California; and Santa Clara Valley, Utah.

43b. *ATRIPLEX LENTIFORMIS BREWERI* (Watson). Branches and twigs terete or with only obtuse and irregular angles, not becoming spiny; leaf-blades usually 3 to 5 cm.

long, 1.5 to 5 cm. wide; flowers either dioecious or monoecious; mature bracts flattish or convex, mostly 3.5 to 5 mm. in diameter or up to 7 mm. when borne in staminate inflorescences, commonly thicker than in other forms, the margins usually entire or only obscurely undulate. (*A. breweri* Watson, Proc. Am. Acad. 9:119, 1874.) Coast of California from Suisun, San Francisco Bay, to Orange County. Type locality, Santa Monica, California. Collections, all from California: Railroad embankment near Teal, Suisun Marshes, October 15, 1905, *Dudley* (DS); sandy creek bottoms south of Hollister, San Benito County, October 15, 1919, *Hall* (UC); ocean bluffs, near Santa Barbara, *Eastwood 209* (NY, UC, US, monoecious in part, therefore minor variation 5, *A. orbicularis* Watson); Santa Cruz Island, *Francheschi* (UC); river-bottoms, Santa Maria, October 17, 1919, *Hall* (CI); Ventura, October 18, 1919, *Hall* (UC, most of the plants monoecious, therefore minor variation 5, *A. orbicularis* Watson); type collection, "on banks of seashore, Santa Monica," *Brewer 75* (Gr, UC, US); base of bluffs, seashore, Santa Monica, *Parish 1126* (Gr, type of *A. orbicularis* Watson, minor variation 5); Ballona, Los Angeles County, *Braunton 710* (UC, US); Avalon, Santa Catalina Island, only one plant seen, June, 1898, *Trask* (US); San Clemente Island, *Trask 19* (US); San Juan Capistrano, Orange County, June, 1896, *McClatchie* (UC).

43c. *ATRIPLEX LENTIFORMIS TORREYI* (Watson).—Branches and twigs acutely angled by prominent striae, becoming somewhat spiny as the leaves and bracts are lost; leaf-blades mostly 1.5 to 3 cm. long, 0.5 to 2 cm. wide; flowers dioecious; mature bracts flattish or somewhat convex, 2 to 4 mm. in diameter, the margins minutely crenulate. (*Obione torreyi* Watson, Bot. King's Expl. 290, 1871.) Principally in Nevada, extending southwest to the Mojave Desert, California, and east into southwestern Utah. Type locality, dry valleys bordering the Truckee and Carson Rivers, Nevada. Collections, all from Nevada, except as otherwise indicated: Gerlach, northern Washoe County, *Hall 11792* (UC); Reese River Valley, *Warren* (DS); type collection, Humboldt County, 1865, *Torrey 463* (Gr, NY); Carson Desert, *Watson 984* (Gr, NY); Truckee Cañon, below Vista, *Hall 11230* (UC); Smoke Creek, *Griffiths* and *Hunter 511* (NY); Las Vegas, *Hall 10801* (UC); alkaline plain near Dry Lake, Antelope Valley, California, *Davy 2945*; Barstow, California, *Jepson 5174* (DS); Lone Pine, California (according to Jepson, Fl. Calif. 440, 1914); St. George, Utah, *Jones 6094* (NY, UC).

43d. *ATRIPLEX LENTIFORMIS GRIFFITHSI* (Standley).—Branches and twigs acutely angled by prominent striae, perhaps becoming spiny in age; leaf-blades (as far as known) 1 to 2.5 cm. long, 0.3 to 1 cm. wide (elliptic-ovate to narrowly oblong); flowers dioecious; mature bracts nearly flat but slightly convex, 4 to 6 mm. broad (4 to 5 mm. long, thus broader than long), the margins minutely crenulate or some entire. (*A. griffithsi* Standley, N. Am. Fl. 21:63, 1916.) Known only from the vicinity of the type locality, Willcox, southeastern Arizona. Collections: Type collection, *Griffiths 1895* (NY); Willcox Flat, Arizona, *Shreve 4239* (UC).

MINOR VARIATIONS AND SYNONYMS.

1. *ATRIPLEX BREWERI* Watson, Proc. Am. Acad. 9: 119, 1874.—*A. lentiformis breweri*.
2. *A. GRIFFITHSI* Standley, N. Am. Fl. 21: 63, 1916.—*A. lentiformis griffithsi*.
3. *A. LENTIFORMIS* Watson, l. c., 118, 1874.—Based upon *Obione lentiformis*, which see.
4. *A. LENTIFORMIS BREWERI* (Watson).—A form with spatulate-orbicular entire to dentate leaves 1.5 to 3 cm. broad and bracts 9 to 10 mm. broad has been collected on the seacoast bluffs at Playa del Rey, Los Angeles County, California (*Parish 11871*, UC). With only an occasional exception, the ovaries fail to develop and the whole appearance of the plant is that of a monstrosity. There is no evidence of injury due to insects. Staminate plants from the same locality (*Johnston 1900*, UC) have similarly broad suborbicular leaves, some of which are truncate at base, the remainder tapering to the petiole. The leaf-shape is approached in specimens of subspecies *typica* from the Colorado River bottoms near Needles (March 3, 1910, *Grinnell*, UC). According to Johnston, there is a considerable area at Playa del Rey where the peculiar form grows to the exclusion of normal *breweri*. The latter, however, grows along near-by lagoons.

5. *A. ORBICULARIS* Watson, l. c., 17:377, 1882.—The monoecious state of *A. lentiformis breweri*, "the small dense staminate clusters with the pistillate flowers and in slender terminal moniliform spikes." Watson did not compare his proposed species with any member of the *lentiformis* group, but Parish, the collector of the type specimen, has reduced it to *breweri*, and has given ample reason for so doing (*Erythea* 7:91, 1899). Still later studies along the coast of southern California, especially in Ventura County, confirm Parish's conclusion. Nearly all stages in the separation of the sexes are found. Some plants are about equally male and female, others in the same environment and not distinguishable by other characters vary to purely pistillate and to purely staminate. Very few plants of either sex fail to reveal at least a few flowers of the other sort on careful examination. Santa Monica is the type locality for both *breweri* and *orbicularis*.

6. *A. TORREYI* Watson, l. c., 9:119, 1874.—*A. lentiformis torreyi*.

7. *OBIONE LENTIFORMIS* Torrey, in Sitgreaves, Rep. Exp. 169, 1853.—*A. lentiformis typica*.

8. *O. TORREYI* Watson, Bot. King's Expl. 290, 1871.—*A. lentiformis torreyi*.

RELATIONSHIPS.

When taken in the extended sense here adopted, *Atriplex lentiformis* is well set off from all other species. The compressed orbicular fruiting bracts suggest a relationship with *A. hymenelytra*, while the very woody and subspinose habit suggests connections with *A. confertifolia*. It is more primitive than either of these in the retention of a strong tendency toward monoecism in subspecies *breweri* and *typica*.

The four subspecies are geographic as well as morphologic, as has been mentioned in the paragraph introductory to the key, but only subspecies *griffithsi* is truly isolated, the ranges of the others meeting along their borders. Subspecies *typica* and *breweri* are the most difficult to distinguish. The best mark of the former is the crenulation of its fruiting bracts. But plants with entire bracts are sometimes found well within the area of *typica* and with the other features of this form (Bakersfield, California, September 24, 1894, *Eastwood*, Gr, UC; Kern Lake, *Davy 2911*, UC). The crenulations are never very pronounced in *typica*, which was originally described by Torrey as "bracteis orbicularis integris vel remote repando denticulatis," and the bracts of *breweri* commonly are at least undulate. The degree of compression of the bracts also has been used as a distinguishing character, but without much success. The impressions made upon different botanists is indicated by the fact that, although Standley (*N. Am. Fl.* 21: 63-64, 1916) describes the bracts of *breweri* as strongly convex and those of typical *lentiformis* as strongly compressed, Parish (*Erythea* 7:91, 1899) and Jepson (*Fl. Calif.* 440, 1914) could see no difference between *breweri* and *orbicularis*, the bracts of the latter also described by Standley as strongly compressed. Field studies indicate that the bracts of *breweri* have a tendency to be thicker than those of *typica*. This is perhaps the effect of the maritime habitat of the former. The leaves and bracts average larger in *breweri*, as would be expected in a seacoast form, and this may in turn account for the smoothing out of the margins. Monoecism is common in *breweri*, but not wanting in *typica*, for in the San Joaquin Valley, California, where this subspecies abounds and where dioecism is the rule, entire branches loaded with fruiting bracts may be found on plants otherwise staminate, while on other plants the sexes are about equally represented, the two kinds mixing in the inflorescences. Specimens illustrating these intergradations in various characters are on file in the herbarium of the University of California.

Subspecies *typica* is met along the easterly part of its range by subspecies *torreyi*. It is not known that they actually intermingle, although they have been reported from the same locality. The latter form is more inclined to be spinescent, in keeping with its more arid habitat, but its distinguishing feature is the development of sharp longitudinal ridges on the twigs. No exact intermediates in this respect are known, but in a specimen of *typica* from Tempe, Arizona (September 4, 1901, *Thorner*, UC) the branches of the staminate inflorescence are decidedly angular, approaching in appearance those of *torreyi*. Subspecies *griffithsi* is a little-known form of southeastern Arizona, remarkable for its narrow leaves and relatively broad fruiting bracts.

ECOLOGY.

Atriplex lentiformis is essentially uniform in its ecological behavior, in spite of the differences that mark the subspecies. It is typically an intense halophyte, as shown by the determinations of Kearney. The salt-content of the first foot ranged from 2.5 to 4 per cent, for the second foot from 0.72 to 1.38 per cent, and for the third from 0.30 to 0.57 per cent. In chemical composition the alkali contained one-half NaCl, one-fifth NaHCO₃, and considerable Na₂CO₃ and CaSO₄. Its tolerance of alkali is greater than that of any other plant investigated, and this is in accord with its dominance in the most alkaline habitats of the Southwest. The subspecies agree in constituting initial consocieties that are often pure and of considerable size. In the case of *typica* these may be almost impenetrable jungles acres in extent and 10 to 15 feet high, especially about the Salton Sea and on the flood-plain of the Colorado River. *Breweri* behaves similarly in salt-basins and on shores along the coast, though regularly lower and less dense. Both forms resemble *A. canescens* in growing frequently on dunes. Their regular associates are naturally either intense halophytes, such as *Suaeda*, *Spirostachys*, *Sarcobatus*, *Salicornia*, *A. polycarpa*, etc., or species capable of enduring strong alkali, such as *Distichlis*, *Sporobolus*, *Prosopis*, etc.

USES.

The lenscale, or quailbrush, as this saltbush is sometimes called, is of some value for browse, especially by cattle in the desert area and in Nevada. An analysis by Forbes and Skinner (Ariz. Agr. Exp. Sta. Rep. 13:269, 1902) indicates that it contains less protein and more fiber than most species of *Atriplex*. The dense shrubs provide a shelter for rabbits, quail, and other animals, a list of which has been prepared for the Lower Colorado Valley by Grinnell (Univ. Calif. Publ. Zool. 12:74, 1914). The subspecies *breweri* is cultivated to a considerable extent on the coastal slope of southern California as an ornamental foliage plant. Its greatest use is for clipped hedges in wind-swept places near the ocean.

The Coahuilla Indians of southern California utilize the seeds of this species for food by grinding them up and cooking with salt and water (D. P. Barrows, Ethnobotany of the Coahuilla Indians of Southern California 65, 1900). Notes on the Indian uses of various species of *Atriplex* are given by Standley (Contr. U. S. Nat. Herb. 23:252, 1922).

44. ATRIPLEX CONFERTIFOLIA (Torrey and Fremont) Watson, Proc. Am. Acad. 9:119, 1874. Plate 56. SHADSCALE; SPINY SALTBUSH.

Erect shrub, very woody throughout, rigidly branched, spiny, of rounded outline when normally developed, 2 to 8 dm. high; branches not angled, stout, erect or ascending, sparsely scurfy at first, soon smooth and straw-colored, the bark gray and exfoliating on old basal stems; leaves at first crowded, deciduous from the twigs which then change into spines, alternate, short-petioled, orbicular-ovate, orbicular-obovate, or elliptic, rounded or cuneate at base, obtuse at apex, 1 to 2 cm. long, 0.5 to 1.2 cm. wide, entire, firm but not especially thick, gray with a close permanent scurf, 1- or 3-nerved from the base; flowers dioecious, the staminate glomerules in the axils of reduced upper leaves and thus forming short leafy-bracted spikes, the pistillate solitary or several in each of the upper leaf-axils, perianth 5-cleft in the staminate flowers, wanting in the pistillate; fruiting bracts sessile, convex and united over the seed, otherwise flat and free, nearly orbicular or broadly elliptic, 6 to 12 mm. long, 5 to 10 mm. broad, entire (except in minor variation 1), the faces smooth; seed 1.5 to 2 mm. long, reddish brown; radicle superior. (*Obione confertifolia* Torrey and Fremont, in Fremont's Rep. Rocky Mts. Ore. Calif. 318, 1845.)

Dry alkaline plains and slopes; Montana, North Dakota, Wyoming, and Colorado to Chihuahua (according to Torrey, Bot. Mex. Bound. 183, 1859), northern Arizona, eastern California (except on the Colorado Desert), eastern Oregon, and southern Idaho. The most abundant species on stony plains and hillsides in the Great Basin. Type locality, borders of Great Salt Lake. Collections: Colgate, eastern Montana, *Sandberg 8947* (UC); Medora, North Dakota, *Lee 606* (NY); Powder River, Wyoming, *Nelson 9420* (Gr); Carter, Wyoming, *Nelson 4619* (UC); near Pueblo, Colorado, *Greene* (Gr, UC); Grand Junction, Colorado, May, 1892, *Eastwood* (UC); Naturita, southwestern Colorado, *Payson 2325* (SF, UC); Holbrook, Arizona, 1883, *Rusby* (NY, UC); Navajo Reservation, Arizona, *Standley 7481* (US, type of *A. collina* Wooton and Standley, minor variation 1); Granite Wells, San Bernardino County, California, *Parish 10186* (DS, UC); south of Lone Pine, Owens Valley, California, *Hall and Chandler 7315* (UC); Honey Lake Valley, California, *Davy 3274* (UC); Las Vegas, Nevada, *Goodding 2314* (Gr, NY, UC); Palisade, Nevada, August 1885, *Brandegee* (UC); St. George, Utah, *Goodding 795* (DS, UC); type collection, Utah, *Fremont* (NY); near Christmas Lake, eastern Oregon, *Leiberg 775* (Gr, NY); Twin Falls and Shoshone Falls, Idaho, *Nelson* and *Macbride 1379* (Gr, NY, UC, type collection of *A. subconferta* Rydberg, minor variation 4); south of Albion, southern Idaho, September 17, 1819, *Hall* (UC). Additional localities within the area represented by the above citations may be obtained in abundance from herbaria. Merriam (N. Am. Fauna 7:323, 1893) gives details of distribution in southern Nevada and California. Western McKinley and San Juan Counties, New Mexico, are stations mentioned by Wooton and Standley (Contr. U. S. Nat. Herb. 19:205, 1915).

MINOR VARIATIONS AND SYNONYMS.

1. *ATRIPLEX COLLINA* Wooton and Standley, Contr. U. S. Nat. Herb. 16: 119, 1913.—Distinguished from typical *confertifolia* by the elliptic-obovate or rarely suborbicular small leaves and especially by the fruiting bracts, which are dentate at least near the bases of the wings. Plants are sometimes found with the leaves of the shape and size characteristic of *collina*, but with bracts as in typical *confertifolia* (Mineral County, Nevada, *Brandegee*, UC; near Albion, Idaho, *Hall*, UC). The only specimens seen with regularly dentate bracts are the types of *collina*. In a specimen from Thompson's Spring, southeastern Utah (*Rydberg and Garrett 8331*, NY) the leaves are as in typical *confertifolia*, while the bracts vary from entire through undulate to obtusely 2-toothed on each margin. This indicates so much variation in the characters used for the separation of *collina* that its acceptance as a distinct species may be deferred at least until better known. The type locality is the north end of the Carrizo Mountains, Arizona, but the distribution is extended in the North American Flora to include southwestern Colorado, southeastern Utah, and northeastern Arizona.

2. *A. CONFERTIFOLIA* × *CANESCENS*.—An undoubted hybrid between these species was found at Winslow, Arizona (*Loftfield and Hall 11176*, UC). The habit is that of *confertifolia*; the leaves are intermediate, being elliptic-oblong and elliptic-spatulate, 1 to 2 cm. long, 0.4 to 1 cm. wide; the fruiting bracts vary all the way from those of *confertifolia* to equally 4-winged, as in *canescens*, many of them with a pair of flat terminal wings and one or two divergent basal lobes. Some of the seeds are shriveled and infertile, others appear to be normal, and these probably are viable. Both of the supposed parents grew on the hillside where the specimen was collected.

3. *A. SPINOSA* Dietrich, Syn. Pl. 5: 536, 1852.—Based upon *Obione spinosa*, which see.

4. *A. SUBCONFERTA* Rydberg, Fl. Rocky Mts. 248, 1917.—Separated from *A. confertifolia* on the basis of its oblanceolate, acute or acutish leaves and its lance-oblong usually acute bracts. The type specimen, which came from "Twin Falls and Shoshone Falls," Idaho (*Nelson and Macbride 1379*) appears to be abnormally developed. In one of the duplicates of the type at the University of California some of the bracts have a very small body and narrow, lanceolate wings, while other bracts on the same stem have well-formed bodies and ovate, obtuse wings. Bracts of the latter type are 8 mm. long by 6 mm. broad. The foliage is not exactly like that of any specimen seen of genuine *confertifolia*, the leaves being exceptionally narrow in proportion to their length.

5. *OBIONE CONFERTIFOLIA* Torrey and Fremont, in Fremont, Rep. Calif. 318, 1845.—The original name of *Atriplex confertifolia*.

6. *O. SPINOSA* Moquin, in DeCandolle, Prodr. 13: 108, 1849.—Universally regarded as a synonym of the earlier *O. confertifolia*, which, from the description, it appears to be. Based upon plants gathered somewhere on the drainage basin of the Columbia River by Nuttall.

RELATIONSHIPS.

Atriplex confertifolia is the central and by far the most abundant and widespread member of a close group of three species, the other two being *spinifera* and *parryi*. All of these have developed a decidedly spinose habit, which, however, is found also in certain forms of *A. lentiformis*, a species otherwise very different. In addition to the spinose habit, the *confertifolia* group is marked by characters of the fruiting bracts not found elsewhere in the genus. The bracts of each pair are firmly united at the base into a small indurated thickened body from the upper portion of which the free margins are developed into a pair of thin, flat wings standing face to face and much broader than the body itself. Differences in the shape of the body and in the size and shape of the wings constitute the principal characters used to differentiate the species of the group.

ECOLOGY.

Atriplex confertifolia ranks next to *Artemisia tridentata* in importance as a consociation of the Basin sagebrush association. In Nevada it is often more abundant than sagebrush, owing to the prevalence of hard, stony, alkaline soils on benches and slopes. Over much of its range it regularly mixes or alternates with *Artemisia* and its associates, such as *Grayia*, *Chrysothamnus*, and *Tetradymia*. It endures alkaline soils better than most of these and its most typical position, both as to topography and succession, is in a zone between such strongly halophytic dominants as *Sarcobatus* or *Atriplex nuttalli* and *corrugata* on the one hand and sagebrush on the other. It may even occur on alkali flats with such marked halophytes as *Salicornia*, and is frequently associated with *Kochia vestita*, and in Nevada with *Artemisia spinescens*. It is a characteristic dominant of the bad lands of the Great Basin, especially the Cretaceous ones of the Mancos, Fort Steele, and Lewis formations, covering the less alkaline slopes between *Atriplex nuttalli* at the base and the sagebrush climax above.

Kearney, Briggs, Shantz, McLane, and Piemeisel have found the salt-content to range from 0.06 per cent in the first foot to 0.09 per cent in the fourth foot where the plants were exceptionally large and healthy, while the average range was from 0.07 in the first foot to 0.93 per cent in the fourth foot (Indicator significance of vegetation in Tooele Valley, Utah. Jour. Agr. Res. 1:396, 1914).

USES.

Chiefly because of its great abundance over large areas where other browse and forage plants are scarce, the shadscale is of much value to the stock interests in western North America. It is used especially as a winter browse for sheep in Nevada and adjacent States and to some extent also for cattle, the spines, however, interfering with its use by the latter. Otherwise the species is of economic interest only as a cause of hay-fever. It is almost certain that the pollen extracts could be advantageously used for purposes of desensitization against this malady in the case of some patients, as explained under *A. rosea* (p. 260).

45. ATRIPLEX SPINIFERA Macbride, Contr. Gray Herb. n. s. 53:11, 1918. Plate 57.

SPINESCALE.

Erect shrub, very woody throughout, rigidly branched and spiny, normally much taller than broad, 3 to 15 dm. high; branches not angled, but sometimes striate, stout, mostly erect, white-scurfy at first, glabrate but still very pale, the old bark gray, splitting longitudinally on the surface and exfoliating; leaves either crowded or rather sparse, deciduous from the twigs which then become modified into rigid horizontal or widely divergent spines, alternate, mostly short-petioled, the upper sessile, deltoid-ovate or elliptic, cuneate at the base or the sessile ones truncate, obtuse at apex, 1 to 2 cm. long, 0.5 to 1.5 cm. wide (undeveloped leaves of the ultimate twigs often much smaller, as in the type specimen), entire or especially those on sterile shoots subhastate, thinnish,

gray or nearly white with a close permanent scurf, 1-nerved from the base; flowers dioecious, the staminate not known, the pistillate solitary or in small glomerules in the upper leaf-axils; perianth wanting in the pistillate flowers; fruiting bracts closely sessile and adjacent pairs often fused at base, the body globoid or slightly longer than broad (4 to 6 mm. thick), the free margins developed above the body into orbicular or oblong wings, the whole bract 7 to 15 mm. long, 3.5 to 10 mm. broad, entire or the wings irregularly dentate, the faces either smooth or with a few cristate appendages; seed 2 to 2.8 mm. long, reddish-brown; radicle superior.

California, from the westerly side of the San Joaquin Valley to the western part of the Mojave Desert. Type locality, Maricopa Hills, Kern County, California. Collections, all in California: 1.5 km. north of Volta, Merced County, *Severin* and *Hall 11018* (UC); western Fresno County, 5 km. south of South Dos Palos, *Severin* and *Hall 11021, 11754* (UC); Mendota, western Fresno County, *Severin* and *Hall 11761* (UC); 5 km. south of Shafter, Kern County, *Severin* and *Hall 11779* (UC); type collection, May 15, 1913, *Eastwood 3269* (Gr); Buena Vista Hills, Kern County, April 9, 1893, *Eastwood* (UC, pocket); base of Fremonts Peak, Inyo County, *Hall* and *Chandler 6866* (UC); Dry Lake, near Rosamond, Antelope Valley, *Hall 10581* (UC); Kramer, Mojave Desert, *Brandegee* (UC); Daggett, Mojave Desert, *Brandegee* (UC).

RELATIONSHIPS.

Atriplex spinifera is a far-western development from *A. confertifolia*, which it resembles in the spiny habit and in the general features of the inflorescence and fruiting bracts. The branches are more nearly erect than in *confertifolia* and the plants therefore less rounded and spreading. The hastate tendency evident in the summer foliage is not known in the other species and the thick-bodied bracts, contracted just beneath the wing-like free terminal margins, are distinctive. During the late summer the broader subhastate leaves drop off, leaving only the small entire ones of the twigs, but the fruiting bracts persist into the late autumn. The type specimens consist only of twigs and bracts gathered in May, and do not show the larger, hastate leaves which may not have been present on the plants at that period. The bracts, too, are undersized and look as though they came from a plant flowering out of season. This accounts for certain discrepancies between the original description and the one given above.

ECOLOGY AND USES.

Atriplex spinifera attains its best development, both in size and abundance, on the moderately alkaline plains of western San Joaquin Valley in California. It forms open stands, often pure, but sometimes mixed with *A. polycarpa*, or in Antelope Valley with the closely related *confertifolia*. It may also grow on low alkaline mounds, with the intervening flats occupied by *Gastridium*, *Trichostema*, *Eremocarpus*, *Frankenia*, and *Salsola*. It is a marked halophyte, apparently intermediate between *polycarpa* and *confertifolia* in its tolerance of alkali.

There is no evidence that this species has any economic value, though it may be occasionally browsed by sheep. The beet leaf-hopper (*Eutettix tenella*) has been bred from it, and Severin believes that it is an important winter food-plant of this insect. (See further under *A. bracteosa*, p. 307.)

46. ATRIPLEX PARRYI Watson, Proc. Am. Acad. 17:378, 1882. Plate 57.

Erect shrub, woody throughout, rigidly branched, spiny, of rounded outline, 2 to 4 dm. high; branches not angled, slender, erect or ascending, white-scurfy, glabrate and then straw-colored, the old bark becoming dark and longitudinally broken; leaves at first crowded, deciduous from the twigs which are then transformed into spines, alternate, sessile, orbicular-ovate or subreniform, cordate or subcordate at base, obtuse at apex or those of the inflorescence acute, 0.5 to 1.2 cm. long, 0.7 to 1.5 cm. wide, entire, thin,

gray or whitish with a close permanent scurf, 1- or 3-nerved from the base; flowers dioecious, the staminate glomerules in the upper axils, forming dense leafy-bracted panicles, the pistillate 1 to several in each of the upper axils, thus forming small panicles; perianth of staminate flowers 5-cleft (as far as known), wanting in the pistillate; fruiting bracts sessile or very shortly stalked, compressed but thick and rigid, united to above the middle and sometimes to the broad summit, forming a compressed-campanulate sac bordered above by the thick margins, truncate-flabelliform when pressed, 3 to 4 mm. long, 3.5 to 4.5 mm. broad, entire, the face smooth; seed 1 to 1.5 mm. long, brown or amber; radicle superior.

From the Mojave Desert, California, to western Nevada. Type locality, Lancaster, Mojave Desert, California (according to Parish, *Zoe* 5:113, 1901). Collections, all in California except the last: Type collection, 1881, *Parry 282* (Gr); near Lancaster, *Brandege* (UC); near Rosamond and Dry Lake, Antelope Valley, *Davy 2190, 2195, 2227, 2232, 2946, 2947* (UC); near Troy, Mojave Desert, *Johnston 4092* (Pomona); Rabbit Springs, Mojave Desert, *Parish 1350* in part (US); near Keeler, Inyo County, *Coville* and *Funston 843* (DS, Gr, NY, US); Resting Springs Valley, Inyo County, *Coville* and *Funston 274* (US); Beattie, Nevada, *Heller 10421* (DS, Gr, NY, US). Additional localities recorded by Coville (*Contr. U. S. Nat. Herb.* 4:181, 1893) are the following: California: Rabbit Springs, Mojave Desert, Death Valley, west shore of Owens Lake, north of Searles, between Lone Pine and Big Pine; Nevada: Ash Meadows, Oasis Valley, Grapevine Cañon, Sarcobatus Flat.

RELATIONSHIPS.

This species is of the *confertifolia* group, but does not closely approach the others. It is much more slender-twigged than either *confertifolia* or *spinifera* and is readily distinguished from either of these by the closely sessile subcordate leaves. The fruiting bracts differ from those of related species in the absence of free, thin, terminal, wing-like margins, the summit consisting instead of a truncate thick border around the orifice formed by the united bracts. Although probably derived from *A. confertifolia*, it is not isolated from this, for the two grow near each other at many places within the limited area of *A. parryi*.

ECOLOGY AND USES.

Atriplex parryi is an intense halophyte of the desert area of eastern California and southern Nevada, apparently with a tolerance close to that of *lentiformis* and *polycarpa*. It is abundant or even dominant in alkaline flats, and also invades the edge of the desert scrub about the margin, where it mingles with *Arrea*. It is not known to be of use.

47. ATRIPLEX CANESCENS (Pursh) Nuttall, Gen. Pl. 1:197, 1818. Plate 58.

WINGSCALE.¹

Erect shrub, woody throughout, loosely to densely branched and exceedingly variable in outline, 2 to 25 dm. high; branches terete, stout, gray-scurfy, glabrate and then pale, the old bark gray and splitting on the surface, after which it exfoliates; leaves numerous, alternate, sessile or subsessile, linear to spatulate-oblong or broadly elliptic, narrowed at the base, usually obtuse at apex (except in subspecies *garretti*), 1 to 5 cm. long, 0.1 to 1 cm. wide (up to 1.8 cm. wide in *garretti*), entire, thick, gray with a dense permanent scurf, 1-nerved; flowers dioecious (or rarely monoecious, according to Standley), the staminate glomerules in dense spikes of long terminal panicles, these leafy below, the pistillate in dense leafy-bracted spikes and panicles; perianth 4- or 5-cleft in staminate flowers, wanting in the pistillate; fruiting bracts sessile or stalked, the body not compressed, firmly united to the summit of the body, above which the free tips project as flat wings, the whole bract 4 to 12 or rarely 20 mm. long, above as broad, the margins developed into a pair of flat, broad wings, a second pair of wings developed also from the medial line of each

¹ *Atriplex canescens* is sometimes called "shadscale," a wholly inappropriate name for this species. The term shadscale is here restricted to *A. confertifolia*, to which also it has been applied in the literature and the fruiting bracts of which it aptly describes.

exposed face, the four wings thus formed entire to lacinate, the faces smooth or with small appendages between the wings; seed 1.5 to 2.5 mm. long, brown; radicle superior. (*Calligonum canescens* Pursh Fl. Am. Sept. 370, 1814.)

Widely distributed in western North America; Alberta to Kansas, western Texas, Zacatecas, Lower California, eastern Washington, and Montana.

SUBSPECIES.

Key to the Subspecies of Atriplex canescens.

- Leaves linear to oblong or wider, 2 mm. or more wide; fruiting bracts 6 to 15 mm. or more long, or if shorter the leaves then 4 mm. or more wide.
- Blade of leaf usually widest above middle, linear-spatulate to oblong-spatulate, 0.2 to 1.2 cm. wide.
- Shrub normally 4 to 15 dm. high; leaves linear-spatulate or narrowly oblong. . . . (a) *typica* (p. 343).
- Shrub 2 to 4 dm. high; leaves oblong or oblong-spatulate. . . . (b) *aptera* (p. 343).
- Blade of leaf widest at middle, broadly elliptic, 0.8 to 1.8 cm. wide. Shrub under 4 dm. high. . . . (c) *garretti* (p. 344).
- Leaves linear, mostly 2 mm. or less wide; fruiting bracts 4 to 8 or rarely 10 mm. long.
- Fruiting bracts sessile or nearly so, the stalks 2 mm. or less long. . . . (d) *linearis* (p. 344).
- Fruiting bracts on stalks 4 to 10 mm. long. . . . (e) *macropoda* (p. 344).

47a. *ATRIPLEX CANESCENS TYPICA*.—Shrub 4 to 15 dm. high; leaves linear-spatulate or narrowly oblong, mostly widest above the middle, obtuse or barely acute at apex, 1.5 to 4 or rarely 5 cm. long, 0.2 to 0.8 cm. wide; fruiting bracts (including wings) 6 to 15 or rarely 20 mm. long, on straight or recurved stalks 2 to 15 mm. long; wings 4 to 8 or rarely 12 mm. wide (reduced to 2 to 4 mm. wide in variety *macilentia* Jepson, minor variation 6; broad, thin, and deeply lacinate in variety *laciniata* Parish, minor variation 5), usually much exceeding the triangular free terminal portion of the bracts. (*Calligonum canescens* Pursh, Fl. Am. Sept. 370, 1814.) South Dakota to Kansas, western Texas, Zacatecas, Lower California, eastern Washington, and Idaho; by far the most common form almost throughout western North America. Type locality, plains of the Missouri River, near the Big Bend, South Dakota. Collections: Natrona County, Wyoming, *Goodding 246* (NY); Uva, Laramie County, Wyoming, *Nelson 8584* (UC); near Denver, Colorado, *Eastwood 112* (UC); Grove County, Kansas, *Hitchcock 440* (Gr, NY); Redford, western Texas, *Hanson 812* (Gr); Animas Creek, Sierra County, New Mexico, *Metcalfe 1124* (Gr, SF, NY); 6 km. northwest of Tucson, Arizona, *Thorner 111* (NY, UC); Casas Grandes, Chihuahua, *Goldman 423* (Gr); near Saltillo, Coahuila, *Palmer 298* (Gr, UC, US); San Luis Potosi, *Schaffner 35* (Gr); Cedros, Zacatecas, *Lloyd 36* (US); San Gregorio, Lower California, February 6, 1889, *Brandege* (UC); South Coronado Island, Lower California, *Parish 8836, 8837* (UC); Caleb, Colorado Desert, California, *Parish 8256* (Gr, type collection of *A. canescens laciniata* Parish, minor variation 5); Salton Creek, Colorado Desert, California, April 3, 1901, *Brandege* (UC); Glendale to Burbank, Los Angeles County, California, *Braunton 906* (UC); Clark County, Nevada, *Heller 10980* (UC); Reno, Nevada, June, 1890, *Sonne* (UC); Alvord Desert, eastern Oregon, *Cusick 2595* (UC); near Spokane, Washington (R); Pocatello, Idaho, *Nelson* and *Macbride 1397* (UC). Numerous additional localities may be secured by consulting herbaria. Detailed distribution in eastern California and southern Nevada is given by Merriam (N. Am. Fauna 7:326, 1893).

47b. *ATRIPLEX CANESCENS APTERA* (Nelson).—Shrub 2 to 4 dm. high; leaves oblong to oblong-spatulate, mostly widest above the middle, obtuse at apex, 2 to 4 cm. long, 0.4 to 1.2 cm. wide; fruiting bracts 4 to 8 mm. long, on stout erect or spreading stalks 1 to 5 mm. long or some sessile; wings 1 to 5 mm. wide, sometimes 1 or more of them wanting (in the type material), about equaling or slightly exceeding the free terminal portion of the bracts. (*A. aptera* Nelson, Bot. Gaz. 34:356, 1902.) Southern Alberta to northern Colorado. Type locality, Laramie, Wyoming. Collections: Rosedale Trail, Alberta, *Moodie 986* (DS, Gr, NY, SF, US); Deer Lodge, Montana, October, 1888, *Anderson* (US); type collection, September, 1901, *E. Nelson 738* (Wyo.); type locality, on saline flats, *A.*

Nelson 8653 (Gr, NY, US) and *8675* (UC); type locality, along border of an alkaline draw just west of Laramie, *Johnston 2331* (UC).

47c. *ATRIPLEX CANESCENS GARRETTI* (Rydberg).—Shrub about 3 dm. high; leaves broadly elliptic, widest across the middle, acute or slightly rounded at apex, 1 to 3.5 cm. long, 0.8 to 1.8 cm. wide; fruiting bracts 6 to 12 mm. long, sessile or subsessile; wings 2 to 3 mm. wide, usually but not always exceeded by the free terminal portion of the bracts. (*A. garretti* Rydberg, Bull. Torr. Club 39:312, 1912.) Eastern Utah and western Colorado. Type locality, vicinity of Moab, Utah. Collections: Type collection, 1,200 to 1,500 m. altitude, *Rydberg and Garrett 8465* (NY); above Palisade, Colorado, *Crandall 112* (Gr).

47d. *ATRIPLEX CANESCENS LINEARIS* (Watson).—Shrub 4 to 20 or 25 dm. high; leaves nearly linear, tending to widest above the middle, acute or obtuse at apex, 1 to 3 or rarely 5 cm. long, 0.1 to 0.25 cm. wide; fruiting bracts 4 to 8 mm. long, on short stalks less than 2 mm. long, or sessile; wings 1 to 4 mm. wide, usually exceeded by the lanceolate free terminal portion of the bracts but this feature variable. (*A. linearis* Watson, Proc. Am. Acad. 24:72, 1889.) Arizona to Sonora, Lower California, and the Colorado Desert of Alta California. Type locality, alkaline soil about Guaymas, Sonora. Collections: Phoenix, Arizona, *Griffiths 5895, 6179, 6181* (US); Tempe, Arizona, *Kearney 118, 133* (US); Maricopa, Arizona, September 3, 1901, *Thorner* (NY, US); 6 km. northwest of Tucson, Arizona, *Thorner 110* (DS, UC); Guaymas, Sonora, *Palmer 120, 121, 235* (Gr, NY, US, all cited with the original description, only *235* in mature fruit at the Gray Herbarium); Las Animas Bay, Lower California, *Johnston 3490* (SF, UC); La Paz, Lower California, *Johnston 3041* (SF, UC); Agua de San Esteban, north of San Ignacio, Lower California, *Nelson and Goldman 7207* (US); Durmid, Salton Sea, California, *Parish 8073* (DS, Gr). See further under minor variations 1 and 17.

47e. *ATRIPLEX CANESCENS MACROPODA* (Rose and Standley).—Shrub, the size not known; leaves nearly linear, tending to widest above the middle, obtuse at apex, 1 to 2 cm. long, 0.1 to 0.15 cm. wide; fruiting bracts (including wings) 6 to 10 mm. long, on slender stalks 4 to 10 mm. long; wings 2 to 4 mm. wide, much exceeded by the oblong to triangular free portion of the bracts. (*A. macropoda* Rose and Standley, N. Am. Fl. 21: 72, 1916.) Known only from the type collection, Pinchilique Island, Gulf of California, *Rose 16518* (NY, US).

MINOR VARIATIONS AND SYNONYMS.

1. *ATRIPLEX ANGSTIOR* Cockerell, Proc. Davenport Acad. 9: 7, 1902.—Based upon *Obione occidentalis angustifolia*, which see in this list. In New Mexico the *angustior* form produces flowers and fruits a month or six weeks earlier than *typica*, according to Wootton and Standley (Contr. U. S. Nat. Herb. 19: 204, 1915).

2. *A. APTERA* Nelson, Bot. Gaz. 34: 356, 1902.—*A. canescens aptera*.

3. *A.?* BERLANDIERI Moquin, Chenop. Enum. 65, 1840.—From the description this appears to be *A. canescens typica* with undeveloped fruiting bracts. It is reduced to this species by most writers on the genus. The type came from Mexico.

4. *A. CANESCENS* VAR. *ANGUSTIFOLIA* Watson, Proc. Am. Acad. 9: 121, 1874.—Based upon *Obione occidentalis angustifolia*, which see.

5. *A. CANESCENS* VAR. *LACINIATA* Parish in Jepson, Fl. Calif. 442, 1914.—A form of *A. canescens typica* in which the wings of the fruiting bracts are 6 to 8 mm. broad, thin, and saliently laciniate. Variation in the wings from entire through deeply toothed to cut into narrow lobes has been noted by Torrey (Bot. Mex. Bound. 184, 1859, under *Obione occidentalis*). A form with similarly laciniate, but narrow and thick wings, has been described as *A. odontoptera* Rydberg (No. 11 of this list). Such variations are too numerous to render feasible their taxonomic recognition when the species as a whole is taken into account. Type locality, Caleb, Colorado Desert, California. Collections: type collection, *Parish 8256* (Gr); Dos Palmas, in the same district, January 21, 1921, *Childs* (UC); near Newberry, Mojave Desert, 1907, *Morefort* (Pomona).

6. *A. CANESCENS* VAR. *MACILENTA* Jepson, Fl. Calif. 442, 1914.—As to fruiting bracts, this is the opposite extreme from variety *laciniata*, the wings being much reduced, 1.5 to 3 mm. broad, and only dentate. According to Jepson, *macilenta* is not uncommon in the southern part of the Colorado Desert and has an aspect very different from typical *canescens*. Type locality, Holtville, California. Not seen.

7. *A. GARRETTI* Rydberg, Bull. Torr. Club 39: 312, 1912.—*A. canescens garretti*.
8. *A. LINEARIS* Watson, Proc. Am. Acad. 24: 72, 1889.—*A. canescens linearis*.
9. *A. MACROPODA* Rose and Standley, N. Am. Fl. 21: 72, 1916.—*A. canescens macropoda*.
10. *A. OCCIDENTALIS* Dietrich, Syn. Pl. 5: 537, 1852.—The same as *Pterochiton occidentale*, which see.
11. *A. ODONTOPTERA* Rydberg, Bull. Torr. Club 31: 404, 1904.—A form in which the thick wings of the fruiting bracts are irregularly lacinate-dentate. Perhaps best referred to *A. aptera* (*A. canescens aptera* of this treatment), as proposed by Rydberg (Fl. Rocky Mts. 249, 1917). Variation in the wings is noted under No. 5 of this list.
12. *A. TETRAPTERA* Rydberg, Bull. Torr. Club 39: 311, 1912.—Based upon *Obione tetraptera*, which see.
13. *CALLIGONUM CANESCENS* Pursh, Fl. Am. Sept. 370, 1814.—The original description of *A. canescens typica*.
14. *OBIONE BERLANDIERI* Moquin, in DeCandolle, Prodr. 13^o: 114, 1849.—Based upon *Atriplex berlandieri*, which see.
15. *O. CANESCENS* Moquin, Chenop. Enum. 74, 1840.—The same as *Calligonum canescens*.
16. *O. OCCIDENTALIS* Moquin, in DeCandolle, Prodr. 13^o: 112, 1849.—Based upon *Pterochiton occidentale*, which see.
17. *O. OCCIDENTALIS* var. *ANGUSTIFOLIA* Torrey, Bot. Mex. Bound. 184, 1859.—Leaves narrowly linear or lanceolate-linear, otherwise as in *A. canescens typica*. Perhaps referable to subspecies *linearis*. The types came from the Valley of the Rio Grande.
18. *O. TETRAPTERA* Bentham, Bot. Voy. Sulph. 48, 1844.—A form of *A. canescens*, differing from the type form "in its narrow, linear leaves, only 2 to 5 mm. wide, in its more strongly reticulate fruit wings, which have a broad sinus at the apex, and in that the free portion of the bracts is less than half as long as the width of the wing" (Rydberg, Bull. Torr. Club. 39: 311, 1912). It is now known that no one of these characters is sufficiently constant, nor do any two of them vary in unison to such an extent as to render of any value the recognition of *tetraptera* as a species or as a subspecies. The type came from the coast of California and probably from San Diego, where plants answering the description can now be found (e. g., *Hall 11216*, UC), but plants with the same combination of characters grow as far inland as Utah (cf. Rydberg, Rocky Mt. Fl., 249, 1917). Bentham made no reference to the earlier *Calligonum canescens* in connection with his description.
19. *PTEROCHITON CANESCENS* Nuttall, Jour. Acad. Phila. II, 1: 184, 1847.—The same as *A. canescens*.
20. *P. OCCIDENTALE* Torrey and Fremont, in Fremont, Rep. Rocky Mts. Ore. Calif. 318, 1845.—The form of *A. canescens typica* in which the leaves are linear-oblanccolate and the strongly veined wings of the fruiting bracts 4 to 6 mm. or more wide, the margins only sinuate or dentate. Described without reference to *Calligonum canescens*, the original name for the species, which apparently was overlooked.

RELATIONSHIPS.

Although one of the most widely distributed of American *Atriplexes*, this species exhibits almost no tendency to intergrade with any other. Its most distinctive feature is the development of dorsal as well as lateral wings from the fruiting bracts so that the whole body comes to be 4-winged. In subspecies *aptera* there is sometimes a decided reduction in these wings, and they are even wanting in a few bracts of this form. Since *aptera* has also the merely shrubby habit and the broad leaves of *A. nuttalli*, it may be that it represents an intermediate stage in the evolution of *canescens*, but it is also possible that it is a hybrid, notwithstanding its apparently fertile seeds. The infrequent occurrence and the widely separated localities where it has been gathered, all within the general range of the supposed parents, suggest a hybrid origin. A series of bracts from the type of *aptera* are shown in plate 58. Some of these are not very unlike bracts frequently found in *A. nuttalli* (cf. plate 51 and fig. 46, p. 326). Whatever the origin of subspecies *aptera* may be, the evidence as far as available points toward *A. nuttalli* as the nearest relative of *A. canescens*.

The five subspecies here accepted fall into two natural groups. One of these includes *typica*, which is by far the most common and widely distributed of all, *aptera*, already discussed, and *garretti*. This last is too little known to permit of definite placing in the phylogenetic scheme. Its exceptionally broad and veiny leaves are unlike anything known in genuine *canescens*, although the bracts are exactly as in the common typical form. The leaf characters suggest a connection with *A. obovata*, but there is no evidence that these two intergrade or hybridize. Further field studies and collections are much needed in the southern part of the Great Basin, whence this form comes.

The second group of subspecies consists of *linearis* and *macropoda*, both inhabitants of the arid Southwest. They are characterized by narrower leaves and mostly smaller fruiting bracts than are found in *typica*, but it will be noted from the descriptions that there is a considerable overlapping in these features. Forms intermediate between *linearis* and *typica* are too numerous to justify the retention of the former in specific rank. The collections of *macropoda* are too meager to permit of definite statements, but its principal character, the elongated stalks to the fruiting bracts, is almost certain to vary to a considerable extent and not in unison with other features.

ECOLOGY.

Atriplex canescens is by far the most widely distributed of all the shrubby species of the genus. While its original rôle was evidently as a consociation of the Basin sagebrush association, it occurs in the mixed prairie of the western Dakotas and Nebraska, the desert plains and desert scrub of the Southwest, and in the Coastal sagebrush of California. Though it has a wide range of adaptability, growing from *Sarcobatus* flats to grassland valleys with practically no alkali, it is usually found in soils with a salt-content ranging from 0.03 to 0.10 per cent. In the Basin sagebrush association, *A. canescens* typically occupies well-drained valleys, while in the Coastal sagebrush it runs from the edge of alkaline depressions well into the mixture of *Artemisia*, *Salvia*, *Eriogonum*, and *Pentstemon*, or occurs in peculiar forms along the seashore back of the strand. It is frequent in alkaline flats in desert plains and scrub from western Texas to the Mojave Desert, often associated with *A. polycarpa*, and less often with *lentiformis*. It is a regular associate with *Prosopis* on the dunes formed by the latter, from the White Sands of New Mexico to the dunes of the Imperial Valley, though in itself it is a poor dune-former. This universal tendency to form a subclimax that is post-climax in nature is further seen in the Oligocene bad-lands of the Black Hills region, where it is frequent in ravines and on more stable slopes.

USES.

This species is exceptional in the genus for its economic value. Its vigorous growth and masses of wing-fruits give it considerable worth as an ornamental in somewhat alkaline soils, where it also may be grown into a serviceable hedge. Its chief importance, however, is for grazing. It is the most palatable of the shrubby species, at least, and possesses unique value during drought periods when the grass crop is short. It has been successfully introduced into the desert plains at Tucson, Arizona, and can probably be grown with even greater success in the other associations of the grassland formation. Its value in the Southwest has been discussed by Griffiths (U. S. Dept. Agr. Bur. Plant Ind. Bull. 4:17, 1901). As a form of insurance against recurrent drought periods it deserves a permanent place in grazing economy.

Reports that the herbage is poisonous to stock have led to a detailed chemical and experimental investigation by the Nevada Experiment Station, the complete results of which are not yet ready for publication. Analyses made by Miller, the chemist at this station, reveal the presence of saponin in large amounts, of pectins, and of glucosides. It is believed by Miller that the glucosides are not injurious, but that poisoning, if it occurs, is due to the saponins. Experiments on sheep indicate that the plants are sometimes harmless, while in other cases death results. It is probable that the high value of *Atriplex canescens* when browsed under normal conditions and when mixed with other feed much more than offsets its possibly injurious effects in certain cases.

The seeds of this and other shrubby species are ground into meal by the Indians and mixed with other flours in the preparation of food. The pollen has been found to be a cause of hay-fever in a few cases and therefore is used in the preparation of immunization extracts.

EXPLANATIONS OF PLATES 36 TO 58, GENUS ATRIPLEX.

PLATE 36.

Atriplex hortensis. (Drawn from fresh material from Logan, Utah, except figures 4 and 5, these from a specimen from Austria, 7174 UC.)

- (1) Leaf and part of pistillate inflorescence, $\times 1$.
- (2) Fruiting bracts, $\times 2$.
- (3) Vertical section of the seed, showing the inferior position of the radicle, $\times 16$.
- (4) Summit of stem with staminate inflorescence, $\times 1$.
- (5) Staminate flower, $\times 16$.

PLATE 37.

Atriplex patula hastata.

- (1) Inflorescence and upper leaves, $\times 1$. (Drawn from fresh material from Logan, Utah.)
- (2) Portion of stem with an average leaf, $\times 1$. (From the same plant as 1.)
- (3) Staminate flower, $\times 16$. (From San Francisco Bay, California.)
- (4) Fruiting bracts, $\times 2$. (From San Francisco Bay, California.)
- (5) Vertical section of the seed showing the inferior position of the radicle, $\times 16$. (From the same material as 1.)
- (6) Inflorescence and upper leaves of a minor variation (*carnosa*), $\times 1$. (Drawn from fresh material from Solano County, California.)
- (7) Portion of stem with leaves, $\times 1$. (From the same plant as 6.)

Atriplex patula typica. (Material from San Francisco Bay, California.)

- (8) Part of inflorescence, with typical leaves, $\times 1$.
- (9) A pair of fruiting bracts as seen from above, the seed visible in the opening; $\times 2$.
- (10) Fruiting bracts, showing gradation in size, dentations, and sculpturing; $\times 2$.

PLATE 38.

Atriplex rosea. (Drawn from fresh material and photographs from Logan, Utah, and from Byron, California.)

- (1) Upper portion of plant showing leaves and inflorescence, $\times 1$.
- (2) Portion of stem with lower leaf, $\times 1$.
- (3) Sketches to show variation in habit; all gradations from simple-stemmed to bushy plants are common; small sketches, $\times 0.1$, bushy plant $\times 0.02$.
- (4) Staminate flower, $\times 16$.
- (5) Fruiting bracts showing variation on a single plant, $\times 2$.
- (6) Vertical section of seed showing the ascending position of the radicle, $\times 16$.

Atriplex maritima. (Material from New Brunswick, Blake 5692, Gr.)

- (7) Upper portion of stem with leaves, $\times 1$.
- (8) A series of three fruiting bracts, $\times 2$.

Atriplex tatarica. (Material from Pensacola, Florida, 110231 UC, the bracts from Camden, New Jersey, US.)

- (9) Branch showing the characteristic pinnatifid leaves and the inflorescence, $\times 1$.
- (10) Fruiting bract, $\times 2$.
- (11) Fruiting bract with cristate appendages, $\times 2$.

PLATE 39.

Atriplex semibaccata. (Drawn from fresh material of plants growing in California.)

- (1) Branches showing leaves and fruiting bracts and the short staminate clusters; stems trailing; $\times 1$.

PLATE 39—continued.

- (2) Staminate flower, $\times 16$.
- (3) Fruiting bract, fleshy and reddish; $\times 2$.
- (4) Vertical section of the seed showing the inferior but lateral position of the radicle, $\times 16$.

Atriplex halimoides. (Material from introduced plants collected in San Diego County, California, 110273 UC.)

- (5) Twig with leaves and small staminate clusters, $\times 1$.
- (6) Two leaves from farther down the stem, $\times 1$.
- (7) Fruiting bract, thick and spongy, $\times 2$.
- (8) Vertical section of seed showing the inferior position of the radicle, $\times 16$.

Atriplex californica. (Drawn from fresh material from Ventura County, California.)

- (9) Spray showing the numerous fruiting bracts in the axils of the crowded leaves, prostrate from a fusiform taproot, $\times 1$.
- (10) Staminate flower, $\times 16$.
- (11) Fruiting bracts, united only at very base; $\times 2$.
- (12) Vertical section of seed showing the inferior position of the radicle, $\times 16$.

PLATE 40.

Atriplex phyllostegia. (Drawn from fresh material from north of Reno, Nevada.)

- (1) Upper portion of plant showing characteristic leaves, fruiting bracts, and staminate clusters; $\times 1$. The plants are strictly erect.
- (2) Staminate flower, $\times 16$.
- (3) Fruiting bracts, $\times 2$.
- (4) Vertical section of seed showing the superior position of the radicle, $\times 16$.
- (5) Fruiting bracts with unusual appendages, $\times 2$. (From the type of *A. draconis*, minor variation 2.)

Atriplex dioeca. (Material from Johnson County, Wyoming, 51442 UC.)

- (6) Branch showing the very smooth leaves and the staminate inflorescence, the minute fruiting bracts hidden in the axils of the leaves; $\times 1$.
- (7) Staminate flower, $\times 16$.
- (8) Fruiting bracts, $\times 2$.
- (9) Vertical section of the seed showing the superior position of the radicle, $\times 16$.

Atriplex monilifera. (Drawn from type material, Gr.)

- (10) Leafy branch, probably prostrate; $\times 1$.
- (11) Staminate inflorescence, $\times 1$.
- (12) Staminate flower, $\times 16$.
(The pistillate flowers of this species are unknown.)

PLATE 41.

Atriplex tularensis. (Drawn from fresh material from the type locality.)

- (1) Upper portion of a large plant showing the leaves and the virgate inflorescence, $\times 1$.
- (2) An entire smaller plant, $\times 1$.
- (3) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
- (4) A series of four fruiting bracts, all from the same plant as illustrated in fig. 1; $\times 2$.
- (5) A series of three fruiting bracts taken from plants growing near the ones shown in figs. 1 and 2, $\times 2$.
- (6) Staminate flower, $\times 16$.

Atriplex tenuissima. (Drawn from specimens of the type collection, 206831 UC, except fig. 11.)

- (7) Branch with leaves from type collection, $\times 1$.
- (8) A series of four bracts from a single plant, $\times 2$.

EXPLANATIONS OF PLATES 36 TO 58, GENUS *ATRIPLEX*.

PLATE 41—continued.

- (9) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
- (10) Staminate flower, $\times 16$.
- (11) Branch with leaves from the type of a minor variation, $\times 1$. (*A. greenii*, from Rock Springs, Wyoming, 78605 R. For a comparison between the bracts of this form and typical *tenuissima* see fig. 34, p. 274.)

Atriplex pusilla. (Drawn from fresh material from Wells, Nevada.)

- (12) Entire plant of slightly less than the average size, $\times 1$.
- (13) Staminate flower, $\times 16$.
- (14) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
- (15) Fruiting bract, $\times 2$. As far as known the bracts are always of this shape and devoid of dentations and appendages.

Atriplex parishi.

- (16) Branch with mostly opposite but a few alternate leaves, $\times 1$. (Material from Orange County, California, 111236 UC.)
- (17) Two bracts from the same plant as 16, $\times 2$.
- (18) Branch with alternate leaves, $\times 1$. (Drawn from fresh material from Chowchilla, California.)
- (19) Three fruiting bracts from the same plant, $\times 2$.
- (20) Vertical section of the seed showing the superior position of the radicle, $\times 16$. (Drawn from one of the bracts shown in 19.)
- (21) Staminate flower from the same plant, $\times 16$.
- (22) Two bracts of a single pair, $\times 16$. (Drawn from the type of minor variation 1, *A. depressa*.)
- (23) Habit sketch of a plant growing in heavy, alkaline, cracked clay soil in Glenn County, California.

PLATE 42.

Atriplex graciliflora. (Drawn from fresh material from Book Cliffs, eastern Utah, 205346 UC, except fig. 4.)

- (1) One of the ascending branches, terminated by a staminate inflorescence; $\times 1$.
- (2) Twig showing more clearly the fruiting bracts, these distinguished from the leaves by the heavier shading in the center; $\times 1$.
- (3) A series of three immature bracts showing a gradation towards the *truncata* type of bract, $\times 2$.
- (4) A series of three bracts with the characteristic suborbicular outline, $\times 1$. (Material from Price, Utah, Hb. Jones.)
- (5) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
- (6) Staminate flower, $\times 16$.

Atriplex wolfei. (Drawn from fresh material from Grand Junction, Colorado, the bracts and seed from the type specimen.)

- (7) Branch showing the numerous twigs and the leaves, $\times 1$.
- (8) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
- (9) Two fruiting bracts, $\times 2$.

Atriplex truncata. (Drawn from fresh material from Longmont, Colorado.)

- (10) Entire plant of a moderately strict form, $\times 1$.
- (11) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
- (12) Two fruiting bracts, $\times 2$.

PLATE 43.

Atriplex saccaria.

- (1) Branch showing leaves, appendaged bracts, and staminate inflorescence; $\times 1$. (Drawn from fresh material from Green River, Utah.)
- (2) Twig with nearly flat leaves, $\times 1$. (Material from Marysvale, Utah, 159008 UC.)
- (3) Portion of branch with only moderately appendaged bracts, $\times 2$. (Material from Chalcedony Park, Arizona, 205283 UC.)
- (4) Fruiting bract from the same collection as fig. 3; most bracts on some plants are of this form, suggestive of *A. truncata*; $\times 2$.
- (5) Fruiting bract from same plant as fig. 1, $\times 2$.
- (6) Staminate flower from the same, $\times 16$.
- (7) Vertical section of a seed from the same showing superior position of radicle, $\times 16$.

Atriplex argentea typica. (Drawn from material from Longmont, Colorado, except as indicated.)

- (8) Branch showing the short-petioled upper leaves and the fruiting bracts, $\times 1$.
- (9) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
- (10) A series of four fruiting bracts, all from the same plant showing variation in margins, appendages, and length of stalk; $\times 2$.
- (11) Staminate flower, $\times 16$.

Atriplex coronata.

- (12) Branch of a garden plant grown at Berkeley California; $\times 1$.
- (13) Portion of twig and leaf of the type specimen (Gr), $\times 1$.
- (14) Series of three fruiting bracts, $\times 2$. (Material from south of Dos Palos, California, 205345 UC.)
- (15) Staminate flower from the same plant as fig. 12, $\times 16$.
- (16) Vertical section of one of the bracts showing the superior position of the radicle, $\times 16$.
- (17) Two fruiting bracts with strongly cristate appendages, $\times 2$. (From the type of var. *notator*, minor variation 1, Hb. Jepson.)

Atriplex cordulata.

- (18) A virgate branch showing the closely sessile, cordate leaves; $\times 1$. (Drawn from fresh material from Chowchilla, California.)
- (19) A small, unbranched plant; $\times 1$. (Material from Volta, California, 204515 UC.)
- (20) Staminate flower from the same collection as fig. 19, $\times 16$.
- (21) Vertical section of a bract from the same collection showing the superior position of the radicle, $\times 16$.
- (22) Series of three fruiting bracts from the same collection, $\times 2$.
- (23) Series of three fruiting bracts from the type specimen (Hb. Jepson), $\times 2$.

PLATE 44.

Atriplex argentea expansa. (All drawings are from a single plant collected in the Livermore Valley, middle western California, except fig. 19.)

- (1) A leafy fruiting branch showing the closely sessile upper leaves, $\times 1$.
- (2) Habit of the mature plant growing in a fallow field, $\times 0.1$.
- (3) to (8) A series of leaves selected to show the range of variation from the lower to the upper on a single plant, $\times 1$.
- (9) Vertical section of the seed showing the superior position of the radicle, $\times 16$.

EXPLANATIONS OF PLATES 36 TO 58, GENUS ATRIPLEX.

PLATE 44—continued.

- (10) Twig showing fruiting bracts mixing with a few staminate flowers, $\times 2$.
- (11) Inflorescence of staminate flowers only, $\times 2$.
- (12) Staminate flower taken from the inflorescence shown in fig. 11, $\times 16$.
- (13) to (18) A series of fruiting bracts selected to show range of variation on one plant, $\times 2$.
- (19) Seedling grown from seed collected with the plant from which the other drawings were made, to show the opposite lower leaves.

PLATE 45.

Atriplex powelli. (Drawn from fresh material and photographs from Green River, Utah, the bracts from near Grand Junction, Colorado.)

- (1) Upper portion of a plant almost entirely pistillate, showing the three-ribbed leaves; $\times 1$.
- (2) Branch of the inflorescence from a mostly staminate plant, $\times 1$.
- (3) Leaf from a pistillate plant showing large size and characteristic venation, bottom view; $\times 1$.
- (4) Sketch of habit of a staminate plant, $\times 0.08$.
- (5) Sketch of habit of a pistillate plant, $\times 0.08$.
- (6) Staminate flower, $\times 16$.
- (7) A series of three fruiting bracts showing the characteristic transverse terminal lobe, $\times 2$.
- (8) Vertical section of the seed showing the superior position of the radicle, $\times 16$.

Atriplex leucophylla. (Drawn from fresh material and photograph from Ventura, California.)

- (9) An ascending branch, $\times 1$.
- (10) Tip of a leafy shoot showing the staminate clusters and upper bracts, $\times 1$.
- (11) Habit sketch of a plant, the base covered by blown sand, $\times 0.8$.
- (12) Staminate flower, $\times 16$.
- (13) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
- (14) A series of six bracts, all from the plant shown in fig. 11, showing variation in shape and sculpturing; $\times 2$.

PLATE 46.

Atriplex pentandra arenaria. (Drawn from material from Westport, Massachusetts, 7151 UC, except the habit sketch.)

- (1) Portion of branch showing leaves, bracts, and a short terminal staminate inflorescence; $\times 1$.
- (2) Habit sketch of plant, the base covered with blown sand; $\times 0.08$. (From a photograph taken at Nahant, Massachusetts.)
- (3) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
- (4) Fruiting bract with a pair of crested appendages, $\times 2$.
- (5) Fruiting bract from the same plant, the faces smooth; $\times 2$.
- (6) Staminate flower, $\times 16$.

Atriplex pentandra muricata. (Material from Coahuila, 110219 UC.)

- (7) Portion of branch with leaves and bracts, $\times 1$.
- (8) Two fruiting bracts from the same branch, $\times 2$.

Atriplex pentandra typica.

- (9) Portion of branch showing leaves and bracts from a plant collected in Cuba, $\times 1$. (*Britton and Wilson 53*, N.Y.)
- (10) Fruiting bract from the same branch, $\times 2$.
- (11) Fruiting bract from plant collected in Curaçao, $\times 2$. (*Britton and Shafer 2926* N.Y.)
- (12) Two leaves from the type of *A. texana* (= *A. pentandra* minor variation 16), $\times 1$.

PLATE 46—continued.

- (13) Two bracts from the same plant as 12, $\times 2$.
- Atriplex elegans typica*. (Drawn from fresh material from Yuma, Arizona, except as otherwise indicated.)
- (14) Branches heavily laden with fruiting bracts, $\times 1$.
 - (15) Habit sketch of a normally developed plant, $\times 0.07$.
 - (16) Staminate flower, $\times 16$.
 - (17) Fruiting bracts, $\times 2$.
 - (18) Cluster of fruiting bracts and an exceptionally dentate leaf, $\times 1$. (Material from Durango, 110218 UC.)
 - (19) Two bracts from the cluster shown in 18, $\times 2$.
 - (20) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
 - (21) Branch of a plant with crested bracts, $\times 1$. (Minor variation 1, var. *thronberi*. Material from Santa Cruz Valley, Arizona, 7216 UC.)
 - (22) Fruiting bracts from branch shown in 21, $\times 2$.
- Atriplex elegans fasciculata*. (Material from Borregos Springs, California, 110270 UC.)
- (23) Tip of leafy fruiting shoot, $\times 1$.
 - (24) Fruiting bract showing the minutely dentate margins, $\times 2$.

PLATE 47.

Atriplex bracteosa. (Drawn from fresh material from Manteca, California, except as otherwise noted.)

- (1) Branches showing leaves, fruiting bracts, and staminate inflorescence; $\times 1$.
- (2) Typical leaf showing the characteristic shape and dentation, $\times 1$. (Material from Tulare, California, 14100 UC.)
- (3) Staminate flower, $\times 16$.
- (4) A series of three fruiting bracts, $\times 2$.
- (5) Vertical section of the seed showing the superior position of the radicle, $\times 16$.

Atriplex wrightii. (Drawn from material from Tucson, Arizona, 128543 UC.)

- (6) Portion of inflorescence showing fruiting bracts on a lower branch and long staminate branches above, $\times 1$.
- (7) Leaf from lower down, $\times 1$.
- (8) Staminate flower, $\times 16$.
- (9) Series of three bracts, $\times 2$.
- (10) Vertical section of the seed showing the superior position of the radicle, $\times 16$.

Atriplex linifolia. (Drawn from material from Durango, 110220 and 110228 UC.)

- (11) Upper portion of staminate inflorescence with upper leaves, $\times 1$.
- (12) Upper portion of a chiefly pistillate inflorescence but with some staminate glomerules above; from another plant; $\times 1$.
- (13) Staminate flower, $\times 16$.
- (14) A series of three fruiting bracts, $\times 2$.
- (15) Vertical section of the seed showing the superior position of the radicle, $\times 16$.

PLATE 48.

Atriplex microcarpa. (Drawn from material from Laguna, Orange County, California.)

- (1) Branch showing leaves, fruiting bracts, and staminate clusters; $\times 1$.
- (2) Fruiting bract, $\times 2$.
- (3) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
- (4) Staminate flower, $\times 16$.

EXPLANATIONS OF PLATES 36 TO 58, GENUS ATRIPLEX.

PLATE 48—continued.

- Atriplex fruticulosa.* (Drawn from a living specimen grown at Berkeley, California, the original seed from the San Joaquin Valley, except 9.)
- (5) An ascending branch showing leaves, fruiting bracts, and staminate clusters, $\times 1$.
 - (6) Staminate flower, $\times 16$.
 - (7) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
 - (8) A series of three fruiting bracts, $\times 2$.
 - (9) A series of three fruiting bracts from the type specimen, $\times 2$. (Herb. Jepson.)
- Atriplex coulteri.* (Drawn from material from La Jolla, San Diego County, California.)
- (10) A branch showing the leaves, fruiting bracts, and staminate clusters, $\times 1$.
 - (11) Staminate flower, $\times 16$.
 - (12) Two fruiting bracts, $\times 2$.
 - (13) Vertical section of the seed showing the superior position of the radicle, $\times 16$.

PLATE 49.

- Atriplex decumbens.* (Drawn from fresh material from San Diego County, California.)
- (1) Branch of a prostrate pistillate plant, $\times 1$.
 - (2) A series of three fruiting bracts, $\times 2$.
 - (3) Vertical section of the ovary showing the superior position of the radicle, $\times 16$.
 - (4) Branch of a staminate plant, $\times 1$.
 - (5) Staminate flower, $\times 16$.
- Atriplex matamorenensis.* (Material from southwestern Texas, Palmer 11601 US.)
- (6) Tip of a branch from a pistillate plant, $\times 1$.
 - (7) Fruiting bracts, $\times 2$.
- Atriplex barclayana typica.*
- (8) Branch and inflorescence of a staminate plant, $\times 1$. (Material from Estaban Island, Gulf of California, Johnston 5190 UC.)
 - (9) Staminate flower from 8, $\times 16$.
 - (10) Branch of a pistillate plant with bracts, $\times 1$. (Material from Isla Partida, Gulf of California, Johnston 3228, UC.)
 - (11) Three thick fruiting bracts of typical *barclayana*, $\times 2$. (From the same plant as 10.)
 - (12) Two fruiting bracts, compressed as in subsp. *palmeri*; $\times 2$. (From the same plant as 10 and 11.)
 - (13) Vertical section of a typical thick bract, $\times 16$.
- Atriplex barclayana lurida.* (From type, 110251 UC.)
- (14) Leaves showing characteristic dentation, $\times 1$.
 - (15) A series of three fruiting bracts, $\times 2$.
- Atriplex barclayana sonorae.* (Drawn from the type material, 635444 US.)
- (16) A series of three fruiting bracts, $\times 2$.
- Atriplex barclayana dilatata.* (Material from San Benito Island, Anthony 269 UC.)
- (17) A series of four fruiting bracts, $\times 2$.

PLATE 50.

- Atriplex obovata.* (Drawn from fresh material from northwestern New Mexico.)
- (1) Branch of staminate plant, $\times 1$.
 - (2) Staminate flower, $\times 16$.
 - (3) Branch of pistillate plant, $\times 1$.
 - (4) A leafy sterile shoot, $\times 1$.
 - (5) Fruiting bract, $\times 2$.
 - (6) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
 - (7) Habit sketch of a staminate plant, $\times 0.12$.

PLATE 50—continued.

- (8) Habit sketch of a pistillate plant, $\times 0.12$.
- Atriplex acanthocarpa.* (Staminate material from San Luis Potosi, 110337 UC; pistillate material from Torreón, Coahuila, 110223 UC.)
- (9) Staminate inflorescence, $\times 1$.
 - (10) Staminate flower, $\times 16$.
 - (11) Branch of a pistillate plant, $\times 1$.
 - (12) Fruiting bract, $\times 2$.
 - (13) Another fruiting bract from the same plant but showing more lacinate margins and appendages, $\times 2$.
 - (14) Vertical section of the seed showing the superior position of the radicle, $\times 16$.

PLATE 51.

Atriplex nuttalli gardneri. (Drawn from fresh material from Point of Rocks, Wyoming.)

- (1) Erect leafy stem with fruiting bracts, $\times 1$.
- (2) Tip of a branch from a staminate plant, $\times 1$.
- (3) Staminate flower, $\times 16$.
- (4) Vertical section of the seed showing the superior position of the radicle, $\times 16$.

Atriplex nuttalli typica. (Drawn from fresh material from Green River, Utah, and Grand Junction, Colorado.)

- (5) Leaf and fruiting stem of pistillate plant, $\times 1$.
- (6) Branch of another plant showing a staminate inflorescence, $\times 1$.
- (7) Habit sketch, $\times 0.1$.
- (8) An unusual type of fruiting bract, representing a primitive form; $\times 2$.
- (9) A common type of bract with numerous cristate appendages, $\times 2$.
- (10) Staminate flower, $\times 16$.

Atriplex corrugata. (Drawn from material and photographs from Green River, Utah, the staminate inflorescence from Gunnison River, Colorado.)

- (11) Leafy branches and spikes of fruiting bracts, $\times 1$.
- (12) Inflorescence of a staminate plant, $\times 1$.
- (13) Staminate flower, $\times 16$.
- (14) Fruiting bracts showing the flat-appendaged faces and the broad terminal lobe, $\times 2$.
- (15) Vertical section of the seed showing the superior position of the radicle, $\times 16$.
- (16) Habit sketch, $\times 0.1$.

PLATE 52.

Atriplex polycarpa. (Drawn from fresh material from Tehachapi Pass, Calif., except 3, 6, and 7.)

- (1) Branch of a pistillate shrub, the leaves still adhering; $\times 1$.
- (2) End of a branch showing the pistillate inflorescence, $\times 1$.
- (3) Staminate flower, $\times 16$. (Material from Bakersfield, California, 7097 UC.)
- (4) Vertical section of the seed showing the unusual basal position of the plumule, the three embryos examined all exhibited this peculiarity; $\times 16$.
- (5) A series of five fruiting bracts, the lower row smooth, from one plant, the other two from another plant; $\times 2$.
- (6) A series of three fruiting bracts from the type specimen of *A. curvidens* (minor variation 3), $\times 2$.
- (7) A series of three fruiting bracts from Tucson, Arizona, (128246 UC) of a form resembling *curvidens*; $\times 2$.

EXPLANATIONS OF PLATES 36 TO 58, GENUS *ATRIPLEX*.

PLATE 52—continued.

Atriplex julacea. (Drawn from material from San Bartolome Bay, Lower California, 110297 UC.)

- (8) Twig of pistillate plant, $\times 1$.
- (9) Leaf showing the sessile hastate base, $\times 8$.
- (10) Two fruiting bracts, $\times 2$.
- (11) Vertical section of the seed showing the superior position of the radicle, $\times 16$.

PLATE 53.

Atriplex hymenelytra.

- (1) Branch of a pistillate shrub showing the characteristic foliage, the leaves silvery white with a dense scurf, $\times 1$. (Drawn from fresh material from Yuma, Arizona.)
- (2) Habit sketch of normal mature plant as it grows in alkaline desert gravel at Yuma, $\times 0.066$.
- (3) Inflorescence of a staminate plant, $\times 1$. (Material from Inyo County, Calif., 110265 UC.)
- (4) Staminate flower, $\times 16$. (Drawn from the same material as 3.)
- (5) A series of four fruiting bracts, $\times 2$. (Drawn from the same material as 6.)
- (6) Portion of a pistillate inflorescence showing the fruiting bracts, $\times 1$. (Material from Split Mountain, California, 110314 UC.)
- (7) Vertical section of the seed showing the superior position of the radicle, $\times 16$. (From the same material.)

PLATE 54.

Atriplex lentiformis breweri.

- (1) Leafy fruiting inflorescence of a plant chiefly pistillate but with a few staminate glomerules, $\times 1$. (Drawn from fresh material from south of Hollister, California.)
- (2) Habit sketch of a shrub growing near Ventura, California, just back of the beach; $\times 0.02$. Many of the plants are more symmetrical and round-topped.
- (3) Three types of leaves common in coast plants, $\times 1$.
- (4) Vertical section of the seed with inside view of the bract, $\times 16$.
- (5) Fruiting bract from plant shown in fig. 1, $\times 2$.
- (6) Two fruiting bracts from a single plant, the margins crenulate as in *typica*; $\times 2$. (Material from Ventura County, California.)
- (7) Two fruiting bracts from another plant, $\times 2$. (Material from Ventura County.)
- (8) Staminate flower, $\times 16$. (From the inflorescence shown in fig. 10.)
- (9) Portions of inflorescence showing a mixing of the staminate and pistillate flowers, $\times 1$. (Drawn from fresh material from Ventura County.)
- (10) Staminate inflorescence of a plant growing near the one shown in fig. 1, $\times 1$.

Atriplex lentiformis typica.

- (11) Leaf, $\times 1$. The shape is often similar to that of fig. 3.
- (12) Two bracts from the same plant showing the small size and characteristic margins of *typica*, $\times 2$. (Material from south of Bakersfield, California.)
- (13) A bract from a plant in the area of *typica* but with the smooth margins of *breweri*, $\times 2$. (Material from south of Bakersfield, Calif.)

PLATE 55.

Atriplex lentiformis griffithsi. (Drawn from the type specimen, NY.)

- (1) Twig with fruiting bracts, $\times 1$. The stems are angled as in subspecies *torreyi*.
 - (2) Two fruiting bracts, $\times 2$.
- Atriplex lentiformis torreyi*. (Drawn from fresh material from the Truckee River Valley, near Vista, Nevada.)
- (3) A leafy inflorescence from a staminate plant at the height of the flowering season, $\times 1$.
 - (4) A naked inflorescence from a pistillate plant taken late in the season, $\times 1$.
 - (5) Cross-section of stem showing the raised angles, $\times 4$.
 - (6) Habit sketch of a pistillate shrub, $\times 0.02$.
 - (7) Staminate flower, $\times 16$.
 - (8) Vertical section of the seed showing the superior radicle, $\times 16$.
 - (9) Fruiting bracts, $\times 2$.

PLATE 56.

Atriplex confertifolia.

- (1) A nearly leafless spiny branch in winter condition, $\times 1$. (Material from Antelope Valley, California.)
- (2) An exceptionally leafy branch of a pistillate plant in early summer condition, growing in fairly good soil, $\times 1$. (Material from western Idaho.)
- (3) A less foliaceous branch from a plant in dry soil, $\times 1$. (Material from southern Idaho.)
- (4) Branch of a staminate plant showing the glomerules, $\times 1$. (Drawn from fresh material from Antelope Valley, California.)
- (5) Habit sketch of a normal plant, $\times 0.07$.
- (6) Fruiting bract, $\times 2$. (Material from Antelope Valley, California.)
- (7) Fruiting bract, $\times 2$. (Material from Naturita, Colorado, 205353 UC.)
- (8) Vertical section from bract shown in 7, $\times 16$.
- (9) Staminate flower from branch shown in 4, $\times 16$.
- (10) Leaf from the type of *A. collina* (i. e., minor variation 1, p. 339), $\times 1$.
- (11) Two fruiting bracts from the same type as 10, $\times 2$.

PLATE 57.

Atriplex parryi. (Drawn from material from Antelope Valley, California, the type locality, 7064 and 7113 UC.)

- (1) Twig showing the spiny habit and cordate leaves, $\times 1$. The shape of the shrub is similar to that shown of *confertifolia* in plate 56, fig. 5.
- (2) Bracts showing variation in the shape of the base, $\times 2$.
- (3) Vertical section of a seed showing the superior position of the radicle, $\times 16$.
- (4) Staminate flower, $\times 16$.

Atriplex spinifera. (Drawn from fresh material from western Fresno County, California, except figs. 8 and 9.)

- (5) Branch showing the autumn condition, the leaves mostly fallen but some of the fruiting bracts still persisting; $\times 1$.
- (6) Branch showing the more leafy summer condition, $\times 1$.
- (7) A fruiting bract, $\times 2$.

EXPLANATIONS OF PLATES 36 TO 58, GENUS *ATRIPLEX*.

PLATE 57—continued.

- (8) A fruiting bract from Antelope Valley, California, showing the marked constriction at base of terminal lobe; $\times 2$.
- (9) Vertical section of the same showing the superior position of the radicle, $\times 16$.

PLATE 58.

Atriplex canescens typica.

- (1) Fruiting twig from a shrub growing at Piru, Ventura County, California; $\times 1$.
- (2) Portion of an inflorescence of a staminate plant from the Argus Mountains, California (128981 UC); $\times 1$.
- (3) Staminate flower from the same, $\times 16$.
- (4) Fruiting bracts of a plant from the Coronados Islands, Lower California; $\times 2$. (195317 UC, see minor variation 20, p. 345.)
- (5) Fruiting bracts from Clark County, Nevada (176399 UC), similar to those from the islands; $\times 2$.

PLATE 58—continued.

- (6) A fruiting bract from southern California (7060 UC), $\times 2$.
 - (7) A fruiting bract from plant shown in fig. 1, $\times 2$.
 - (8) End view of the same, $\times 2$.
 - (9) Vertical section of the same showing the superior position of the radicle, $\times 2$.
 - (10) Habit sketch of a shrub at Winslow, Arizona; $\times 0.032$.
 - (11) A fruiting bract of var. *laciniata*, $\times 2$. (From the type collection, Gr. See minor variation 5, p. 344.)
- Atriplex canescens aptera*.
- (12) Three fruiting bracts from the type specimen, $\times 2$. (64938 R.)
- Atriplex canescens linearis*. (Drawn from the type specimen, Gr.)
- (13) Fruiting bracts, $\times 2$.
 - (14) Leaves showing the narrow shape, $\times 1$.



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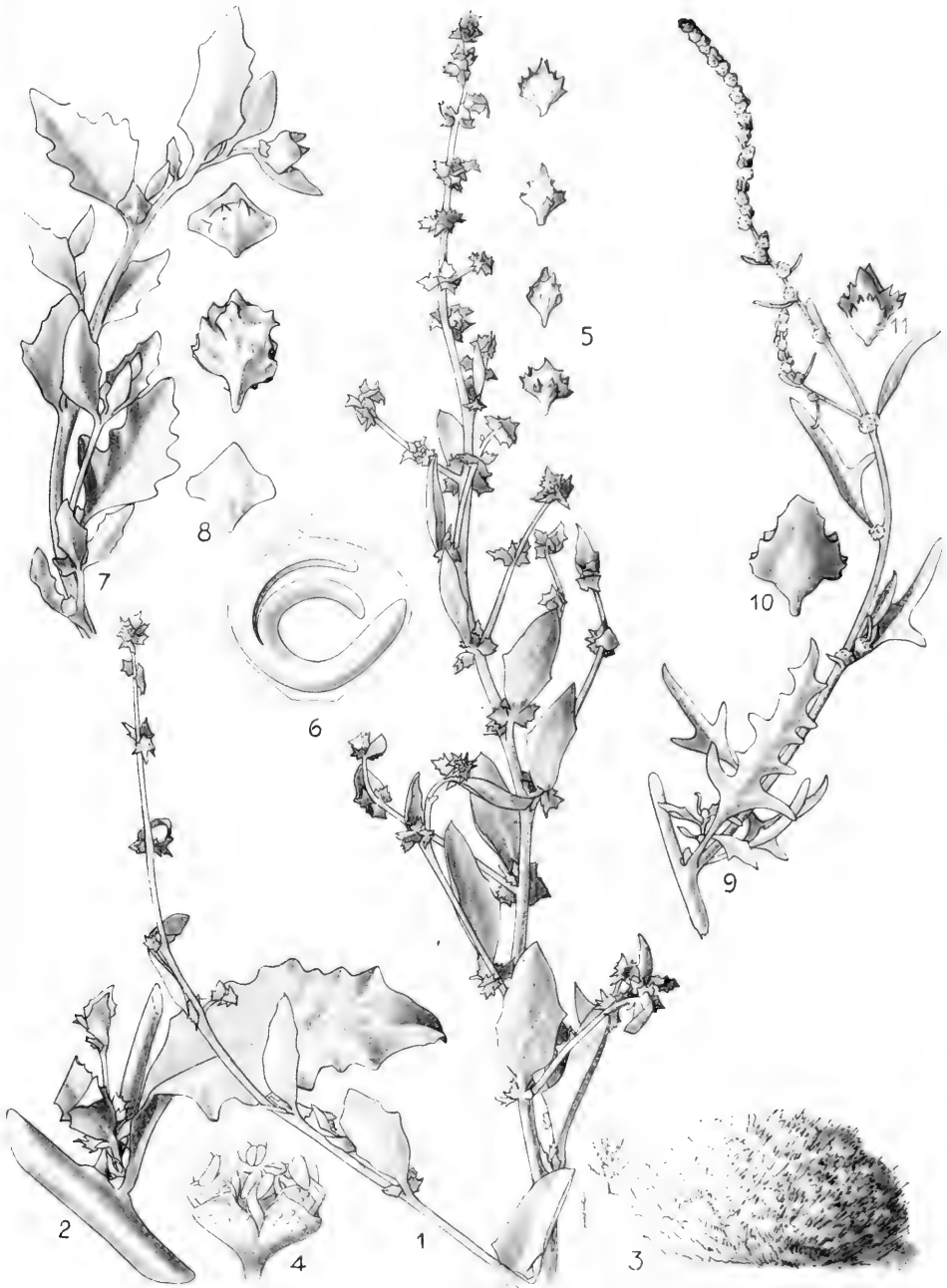
Atriplex hortensis.



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Atriplex patula hastata, figs. 1 to 7.

Atriplex patula typica, figs. 8 to 10.



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Atriplex rosea, figs. 1 to 6.

Atriplex maritima, figs. 7 and 8.

Atriplex tatarica, figs. 9 to 11.



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Atriplex semibaccata, figs. 1 to 4.

Atriplex halimoides, figs. 5 to 8.

Atriplex californica, figs. 9 to 12.

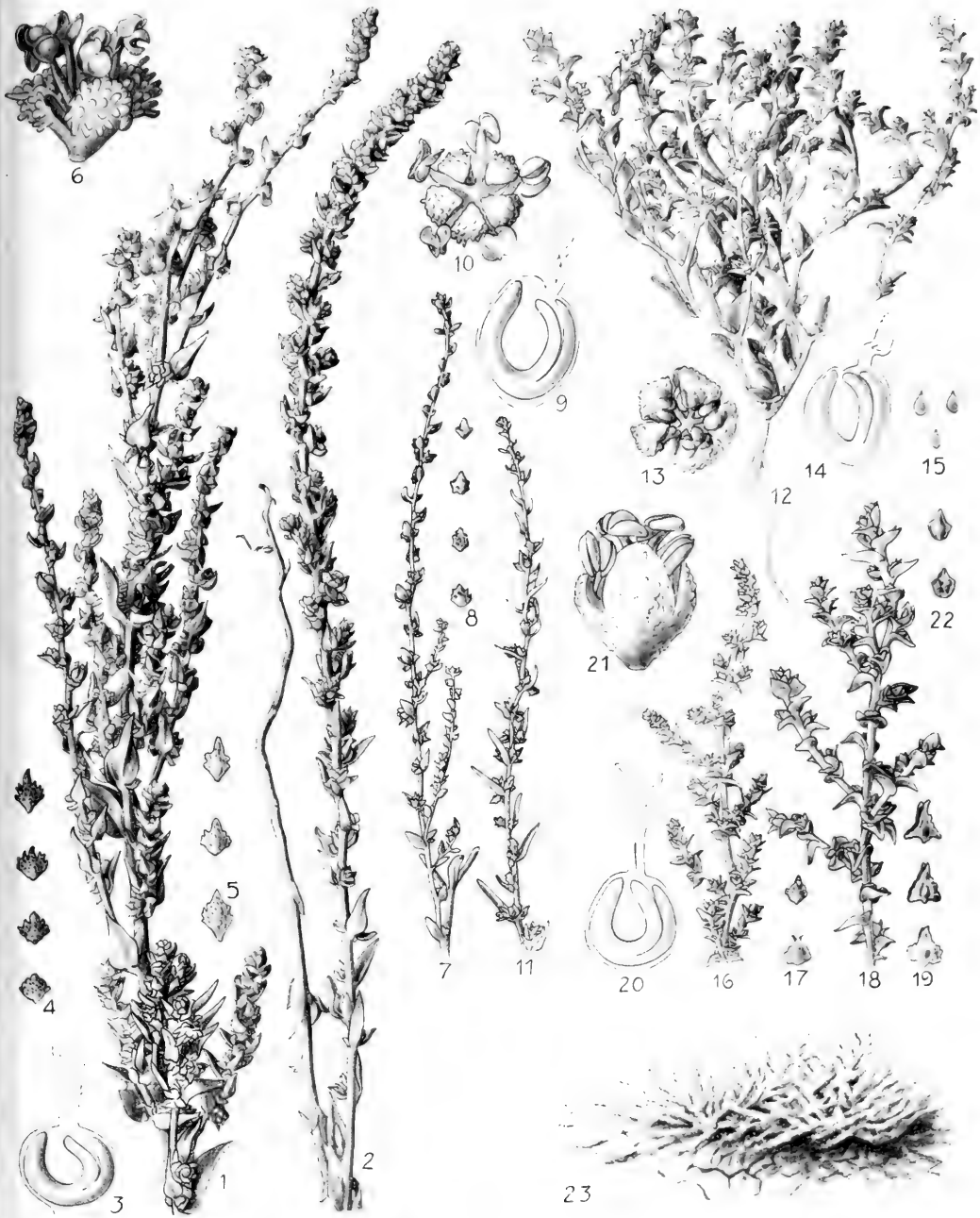


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Atriplex phyllostegia, figs. 1 to 5.

Atriplex dioeca, figs. 6 to 9.

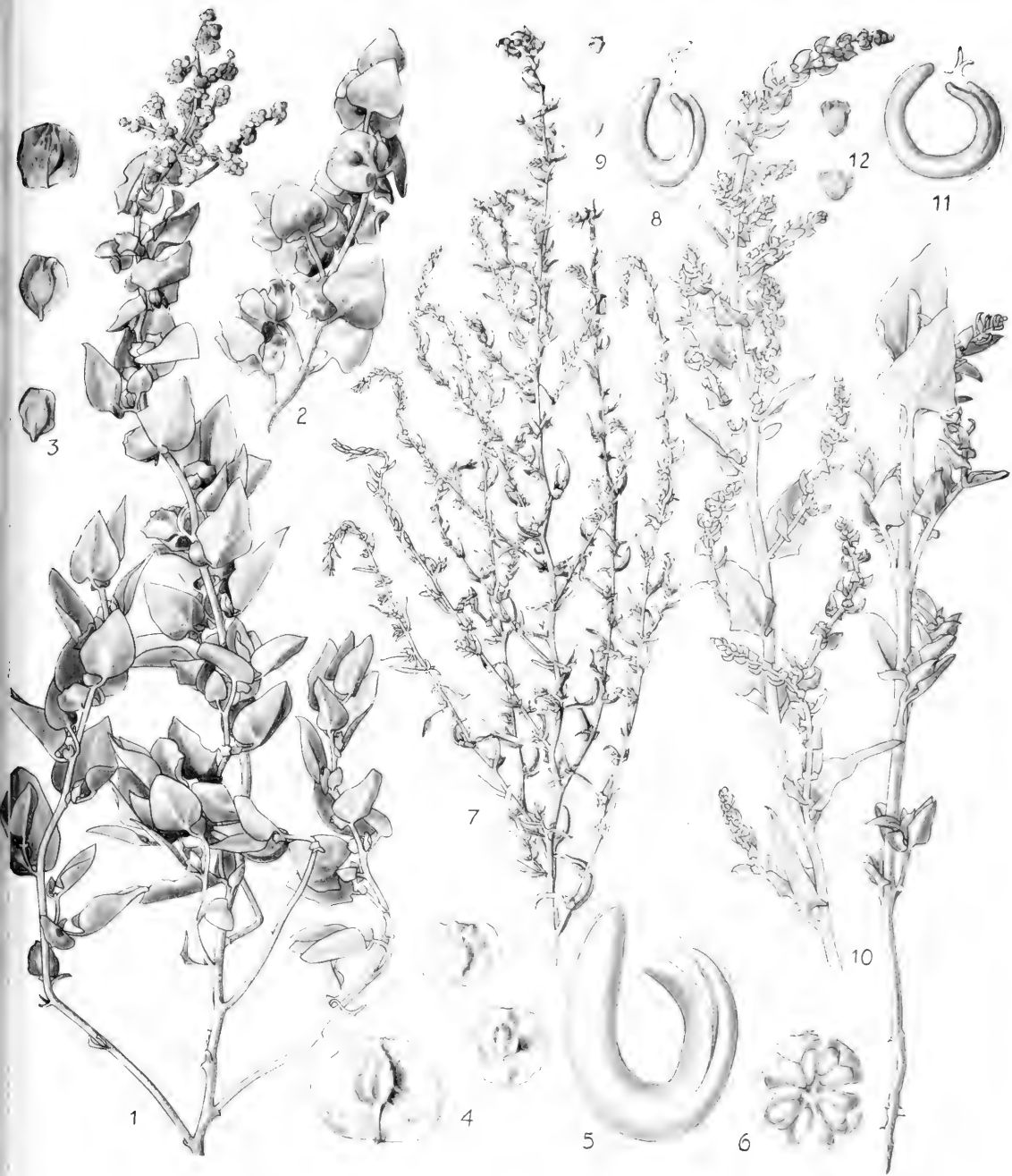
Atriplex monilifera, figs. 10 and 12.



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Atriplex tularensis, figs. 1 to 6.
Atriplex tenuissima, figs. 7 to 11.

Atriplex pusilla, figs. 12 to 15.
Atriplex parishii, figs. 16 to 23.



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Atriplex graciliflora, figs. 1 to 6.

Atriplex wolfei, figs. 7 to 9.

Atriplex truncata, figs. 10 to 12.



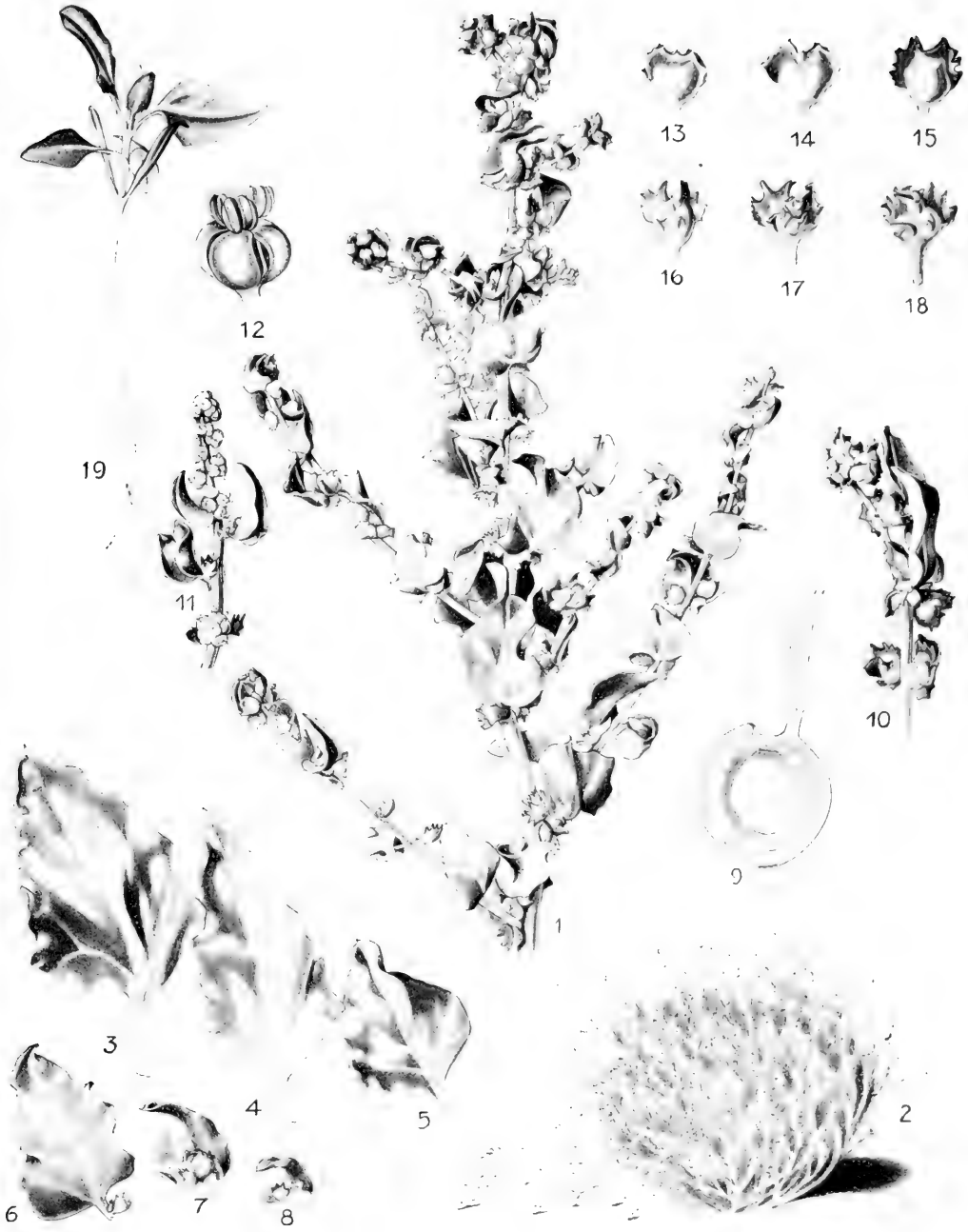
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Atriplex saccaria, figs. 1 to 7.

Atriplex argentea typica, figs. 8 to 11.

Atriplex coronata, figs. 12 to 17.

Atriplex cordulata, figs. 18 to 23.



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Atriplex argentea expansa.



Atriplex powelli, figs. 1 to 8.



Atriplex leucophylla, figs. 9 to 14.



Atriplex pentandra arenaria, figs. 1 to 6.
Atriplex pentandra muricata, figs. 7 and 8.

Atriplex pentandra typica, figs. 9 to 13.
Atriplex elegans typica, figs. 11 to 22.

Atriplex elegans fasciculata, figs. 23 and 24.

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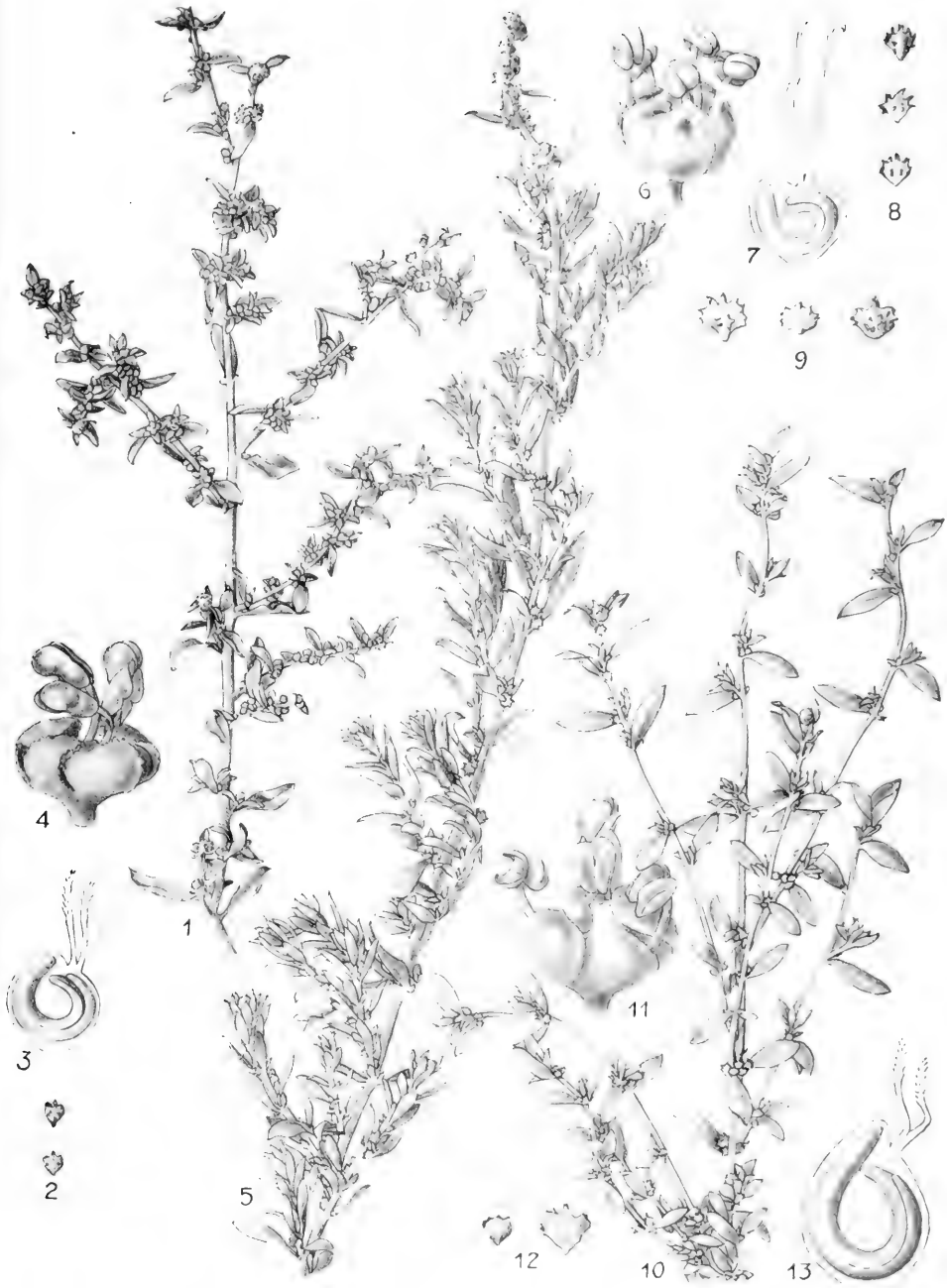


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Atriplex bracteosa, figs. 1 to 5.

Atriplex wrightii, figs. 6 to 10.

Atriplex linifolia, figs. 11 to 15.



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Atriplex microcarpa, figs. 1 to 4.

Atriplex fruticulosa, figs. 5 to 9.

Atriplex coulteri, figs. 10 to 13.



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Atriplex decumbens, figs. 1 to 5.

Atriplex barclayana typicala, figs. 8 to 13.

Atriplex barclayana sonoreae, fig. 16.

Atriplex matamorensis, figs. 6 and 7.

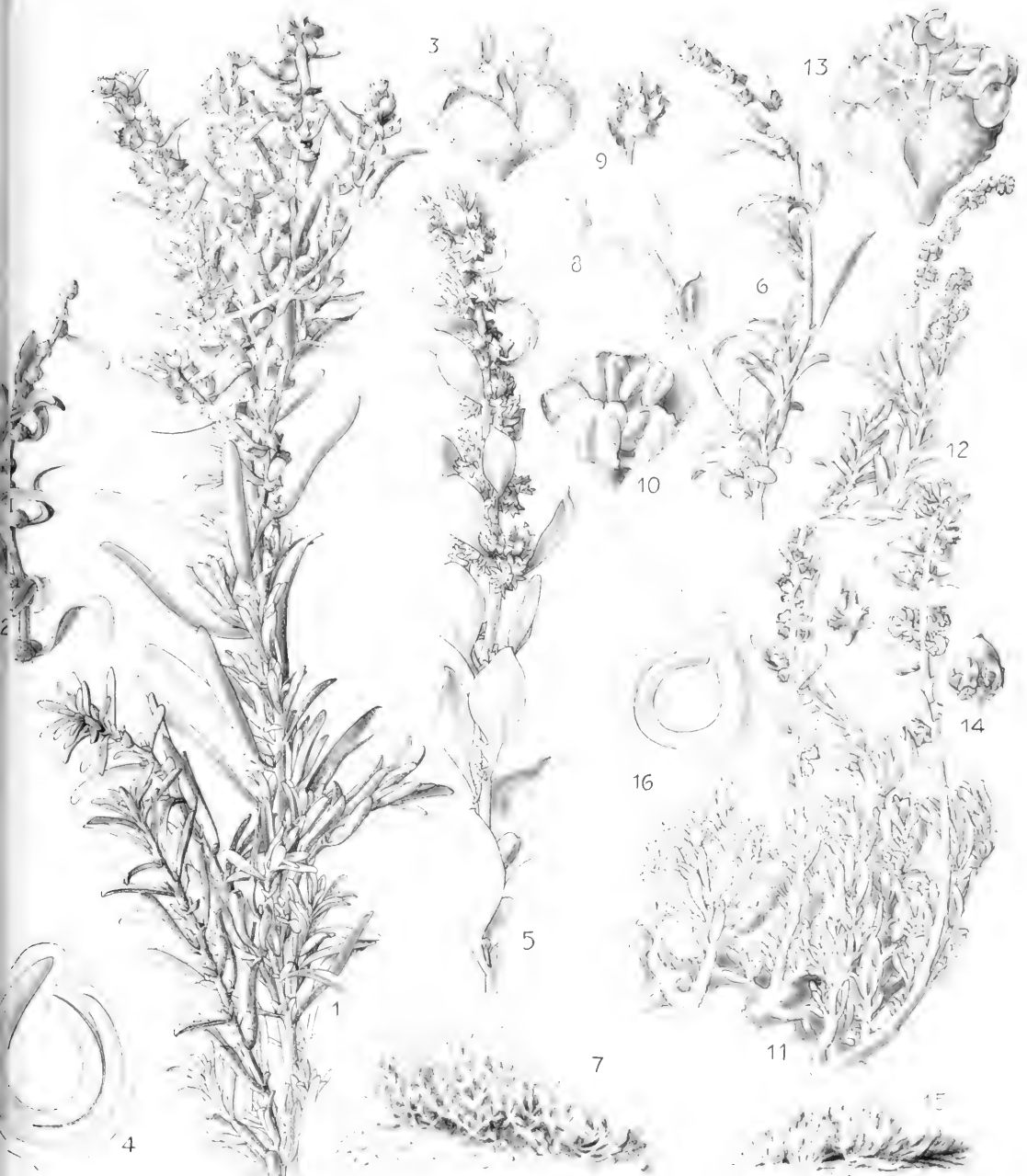
Atriplex barclayana lurida, figs. 14 and 15.

Atriplex barclayana dilatata, fig. 17.



Atriplex obovata, figs. 1 to 8.

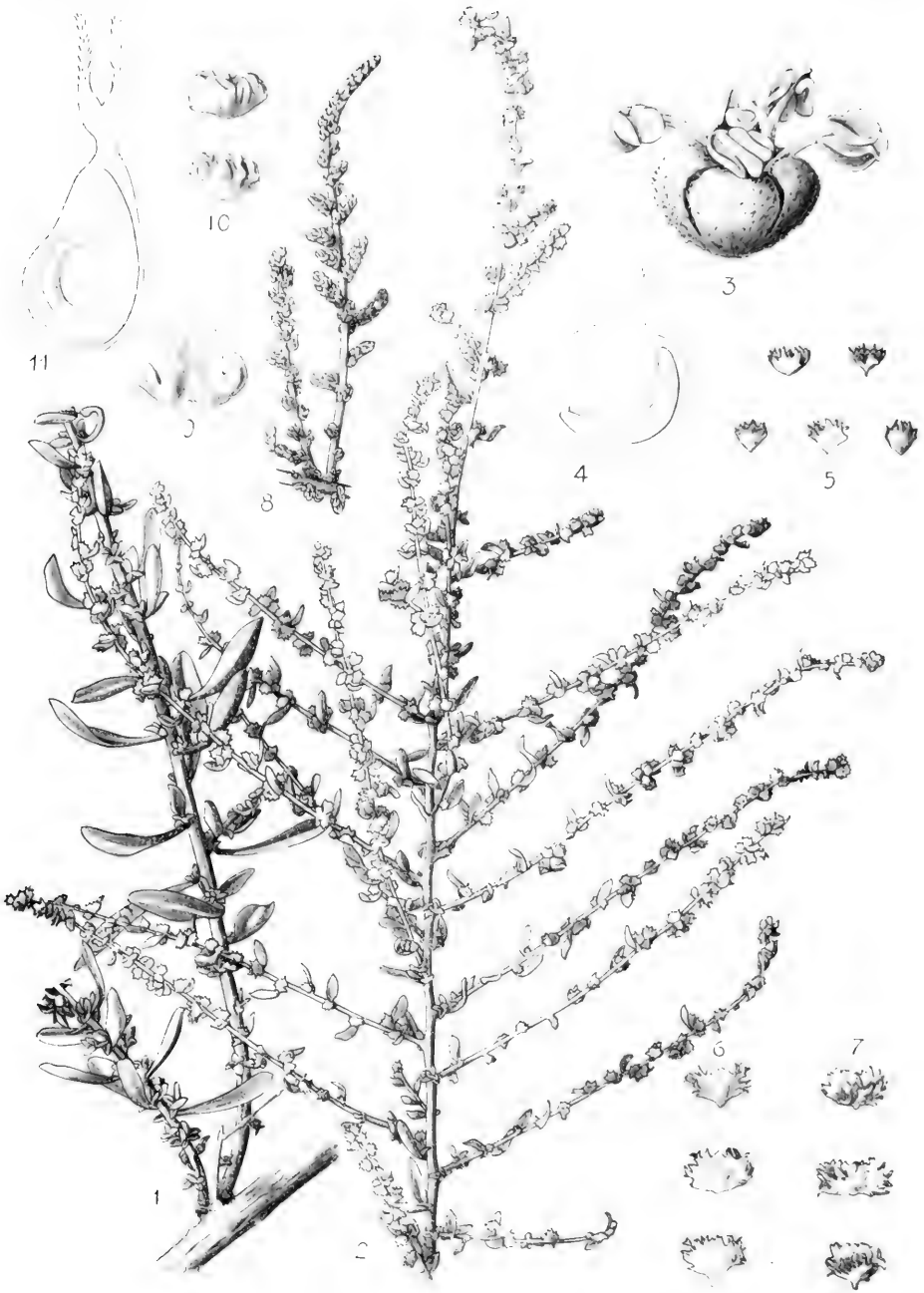
Atriplex acanthocarpa, figs. 9 to 14.



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Atriplex nuttalli gardneri, figs. 1 to 4.

Atriplex nuttalli typica, figs. 5 to 10.

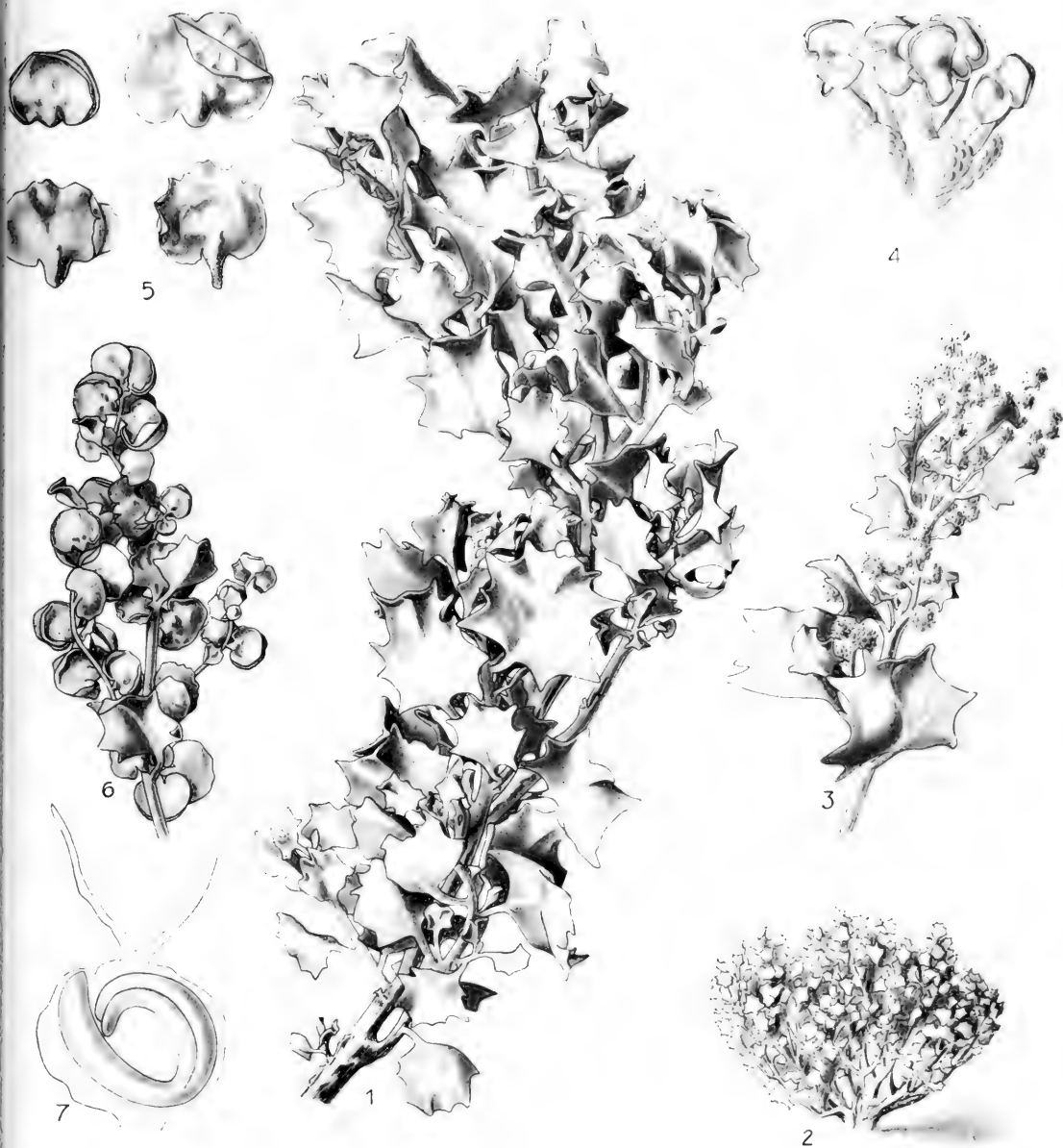
Atriplex corrugata, figs. 11 to 16.



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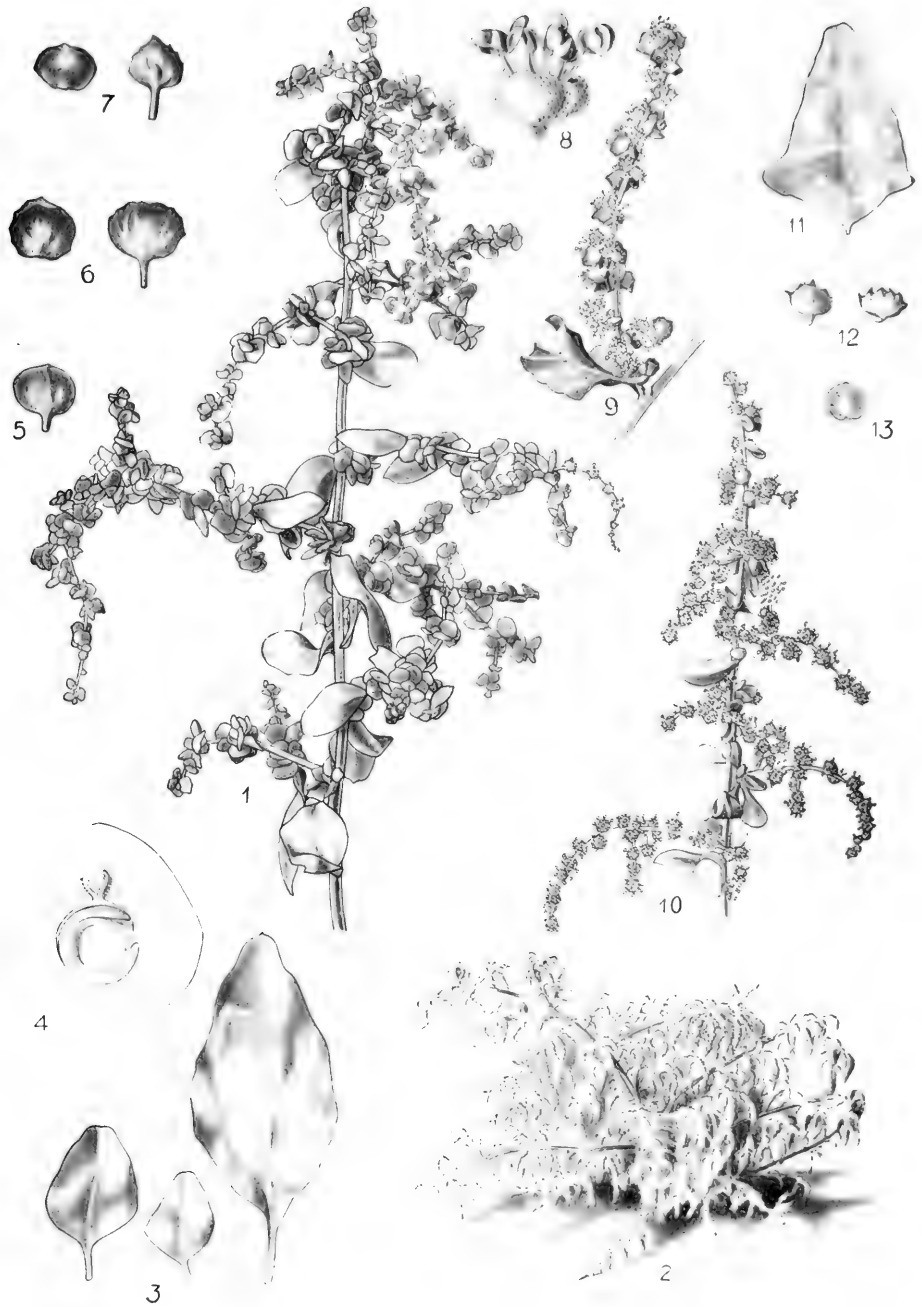
Atriplex polycarpa, figs. 1 to 7.

Atriplex julacea, figs. 8 to 11.



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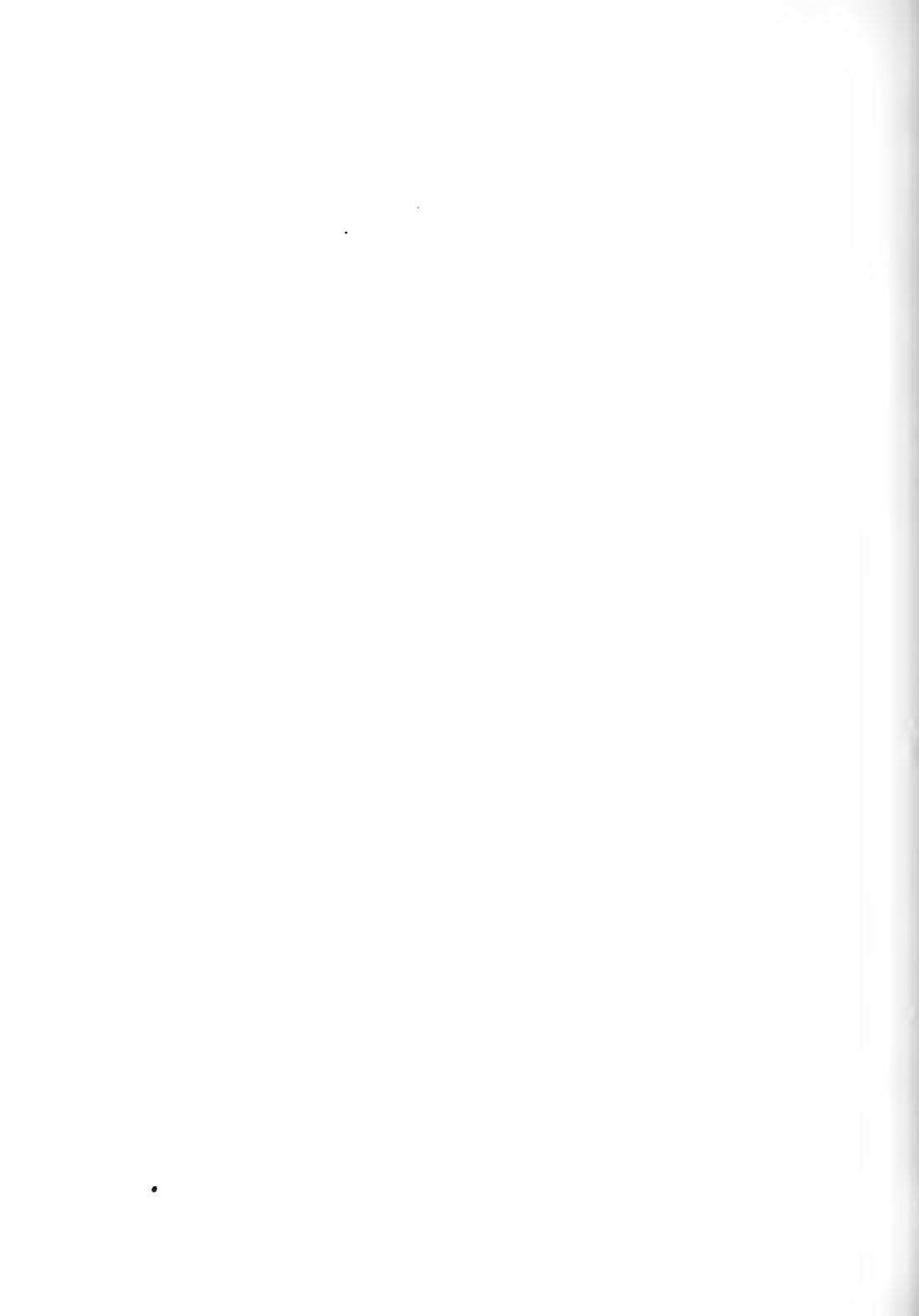
Atriplex hymenelytra.



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Atriplex lentiformis breweri, figs. 1 to 10.

Atriplex lentiformis typica, figs. 11 to 13.





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Atriplex lentiformis griffithsi, figs. 1 and 2.

Atriplex lentiformis torreyi, figs. 3 to 9.



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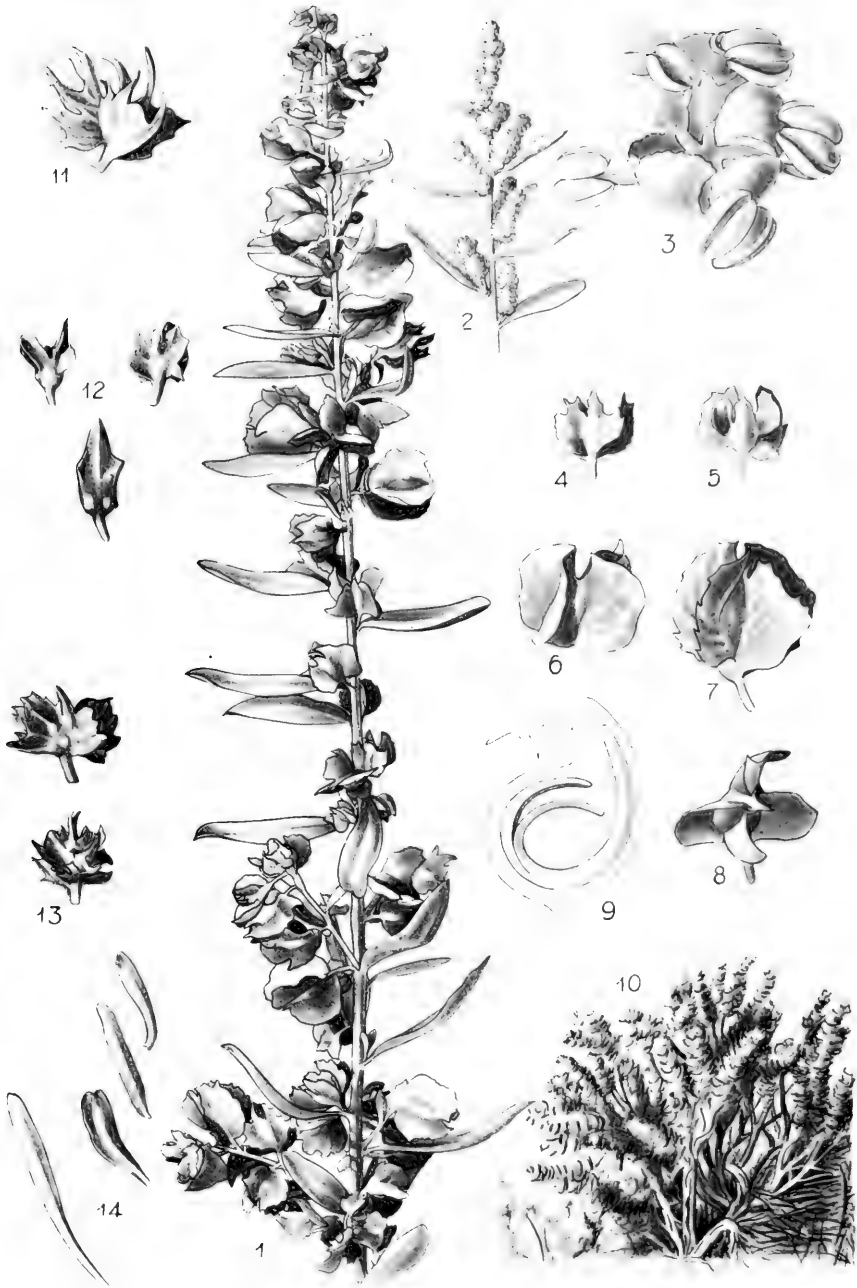
Atriplex confertifolia.



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Atriplex parryi, figs. 1 to 4.

Atriplex spinifera, figs. 5 to 9.



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Atriplex canescens typica, figs. 1 to 11. *Atriplex canescens* aptera, fig. 12.
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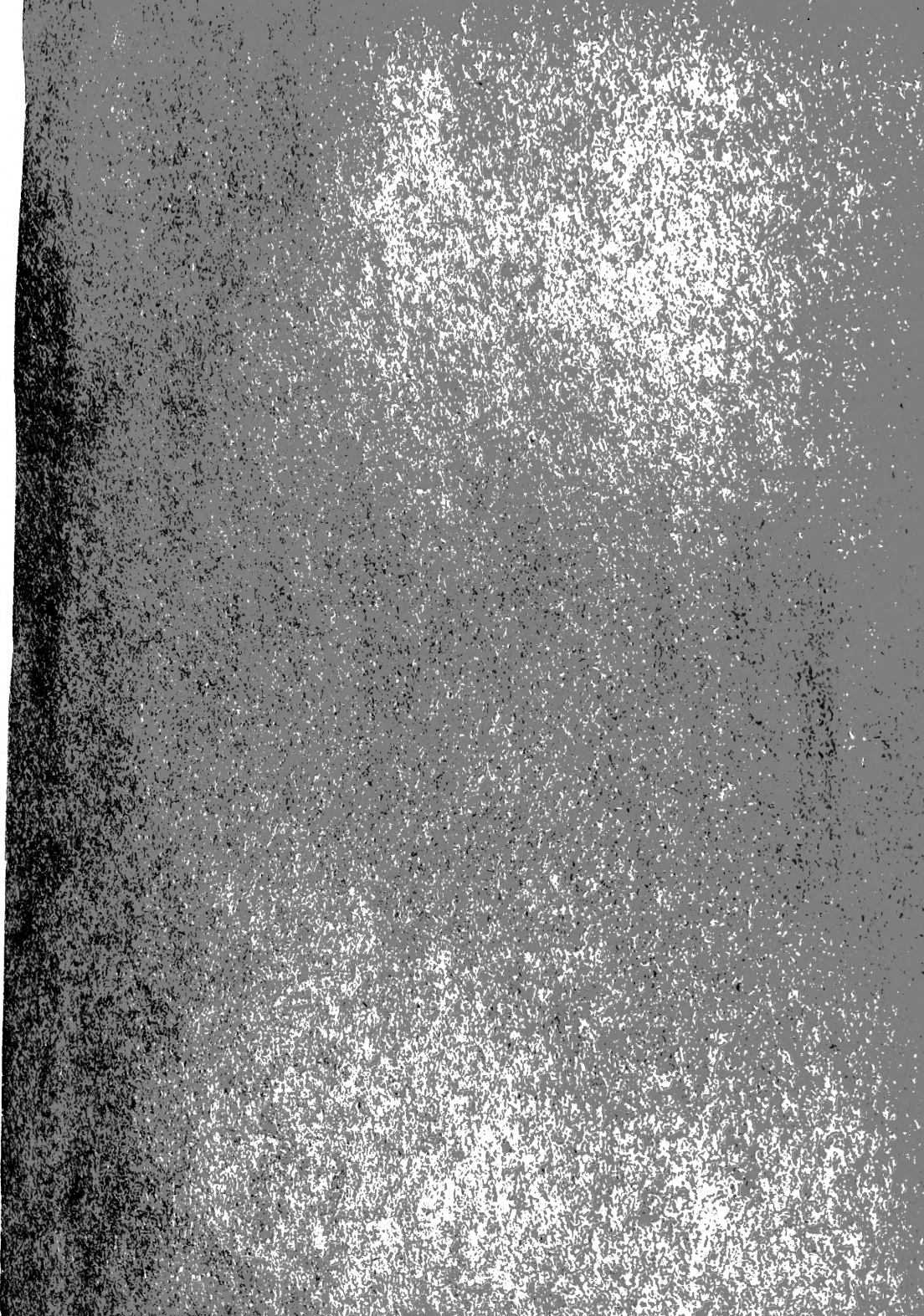
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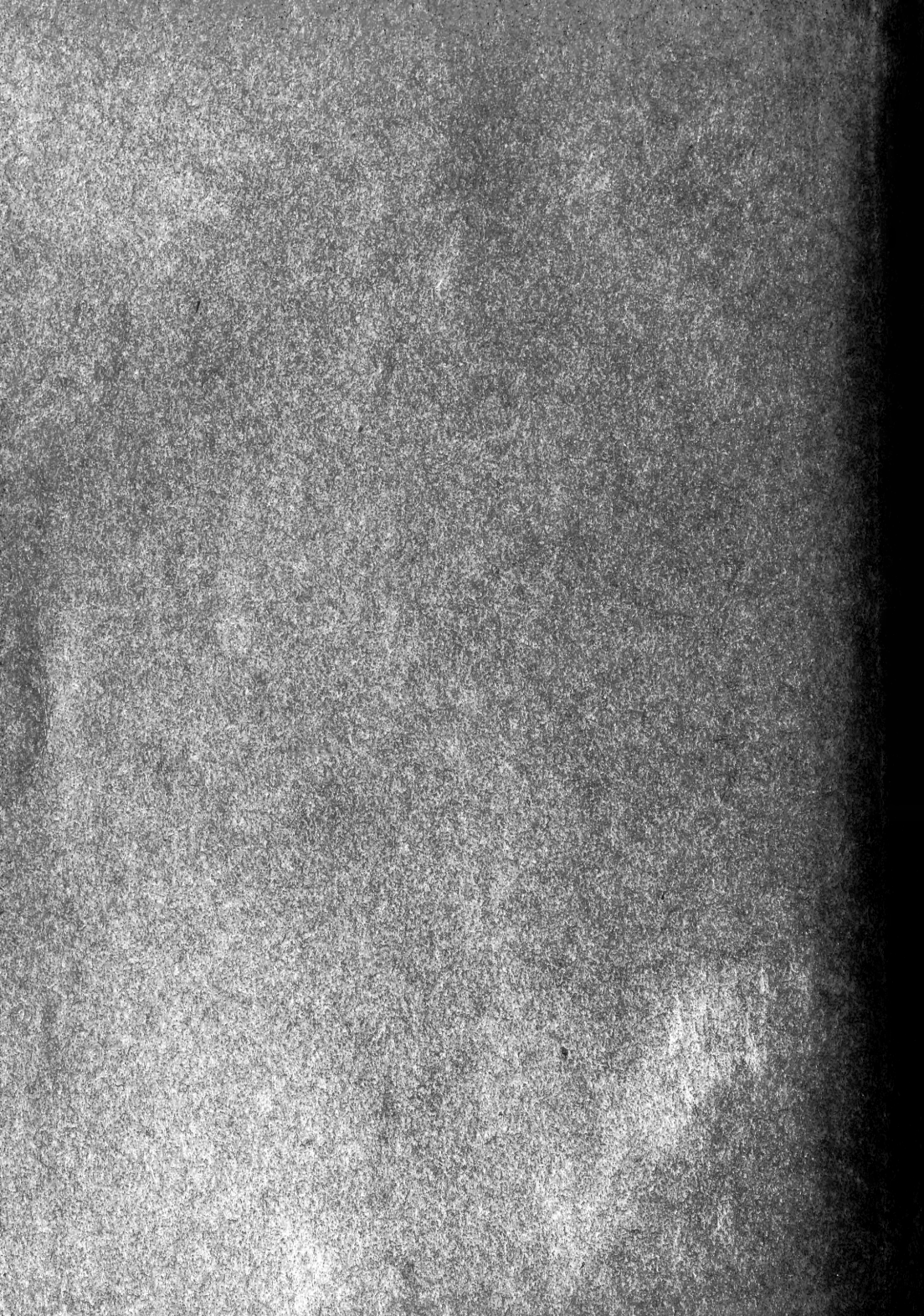
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