THE ROLE OF INTROGRESSIVE HYBRIDIZATION IN THE DEVELOPMENT OF SALVIA: SECTION AUDIBERTIA (LABIATAE)

By WILLIAM A. EMBODEN, JR.[1]

ABSTRACT: The nineteen western North American species of *Salvia* (section Audibertia), while occupying distinct niches, are frequently sympatric throughout a part of their range. Hybridization within the section is not uncommon and blocks of characters found in closely related species suggest hybrid origins. Prior to this paper only one instance of introgression has been reported, and the documentation of one more pair of introgressed species suggests that introgression is of greater importance than was previously realized, and may have played an even more significant role in the formation of the plexus as it is known today. Degrees of genetic exchange within the section are diagrammed.

The integrity of subsection Echinosphace is vindicated by a corrected chromosome count for one of the species which was miscounted and another member which was imperfectly known cytologically. Further chromosome counts of subsection Pycnosphace substantiate thirteen as the gametic chromosome number; previous reports had varied considerably.

INTRODUCTION

The role which hybridization has played in the development of the North American species of *Salvia*: section Audibertia, will never be fully comprehended, for we have almost no fossil record for this derivative of the Madro-Tertiary geoflora. Studies by Epling (1938), Munz (1927), Epling, Lewis, and Raven (1962), and Emboden (1964 and 1967) all point to hybridization as one of the most important factors in the evolution of *Salvia* as it occurs in the western United States and Baja California. The arguments rest largely upon morphological and palynological data. Beyond simple hybridization, there is introgression, defined by Anderson in 1953 as, "the concept of infiltration of germplasm of one species into that of another as a consequence of hybridization and repeated backcrossing." This definition is refined from the less eloquent enunciation by Anderson and Hubricht who originated the concept in 1938.

In his 1938 monograph of section Audibertia, Epling pointed out that this section of the genus *Salvia* is confined primarily to arid portions of the southwest. Most members are components of either the *Larrea-Franseria* shrub formation of the Colorado desert or the related *Artemesia californica-Salvia* shrub formation of the coastal plain. Since distributions were well

[1]Research Associate, Los Angeles County Museum of Natural History; Professor of Biology, San Fernando Valley State College, Los Angeles, California 91324.

1

mapped by Epling, one need only note the addition of *S. chionopeplica* and its range to this section of the monograph. *Salvia chionopeplica* was discovered by Wiggins in 1931, thirty-six miles east of Rasario (Stanford University type specimen 5300). Epling (1940) agreed to its inclusion in subsection Jepsonia of Audibertia. This subsectional disposition was later vindicated by chromosome counts made by Epling, Lewis, and Raven (1962). Of the nineteen species of *Salvia* in this section, seven are conspicuous localized elements of the *Larrea-Franseria* association, five are important elements of the *Artemisia californica-Salvia* formation, and the remaining seven are ubiquitous, or are disjunct elements of one of the previously mentioned groups; all, presumably, are derivatives of the Madro-Tertiary geoflora. This section makes its greatest impression as an element of the coastal sage formation.

It was Epling (1938) who first suggested that most members of section Audibertia have arisen through hybridization. This he based upon the frequency with which natural hybrids occur, especially in instances of sympatric distributions of species of subsections Jepsonia and Munzia. Communication with Dr. Philip Munz has established that the report of a hybrid between *Salvia carduacea* and *S. mellifera* (1959): was a misreading of Epling's monograph (1938) and that he knows of no such hybrid. This eliminates the inexplicable link between subsections Echinosphace and Parishiella.

Floral morphology in section Audibertia, comprised of nineteen species is more variable than that of section Calosphace (circa five hundred species) and one sees a progressive change from one extreme to the other, especially in the morphology of the androecium. A careful study of the overall morphology of Audibertia suggests a series of interchanges of blocks of characters that could only have arisen through hybridization and subsequent introgression. Epling would relate section Audibertia to subgenus Calosphace, but the examples which he uses, *S. clinopodioides* and *S. axillaris*, are most unlikely progenitors for this western plexus. Recent evidence for the antiquity of the genus in north temperate regions perhaps as early as the Miocene (Emboden, 1964) argues against making comparisons between two species of more southern distribution and an entire assemblage of nineteen species which could be assigned subgeneric status. This coupled with the Pleistocene glaciation and progressive aridity of the southwest might in itself be argument against making such contemporary species comparisons. However, recent evidence from Crowell (1962 and 1968) on paleogeographical coordinations suggests that the coastal block west of the San Andreas fault has been transported northward along the coast since the Early Miocene by a distance of perhaps 175 miles. Such geographical, climatic, and paleogeographical coordinations make speculation on specific ancestors of section Audibertia seem quite inconsequential. The significance of this sort of data is that it helps explain some of the opportunities which occurred in the past for hybridization

of now disjunct entities, some of which still retain the capacity to exchange genes.

CONTEMPORARY ASPECTS OF HYBRIDIZATION

A summary of known hybridization within section Audibertia is presented in Figure 1 and is fairly representative of the extent of hybridization which may be realized. All but *S. mohavensis*, *S. pachyphylla*, and *S. clinopodioides* have been grown in the gardens and greenhouses of San Fernando Valley State College at Northridge, California, and repeated reciprocal crosses have been attempted between all of these species. It is possible to make crosses between plants which are seasonally isolated by altering amounts of water and temperatures, both being important factors in floral initiation. Most of the crosses obtained had previously been reported to occur in nature or had been found growing in botanical gardens when allopatric species were grown in proximity to each other. It is obvious, both in morphology and breeding behavior, that subsections Greenostachys and Echinosphace are isolated from the other subsections, and the only connection between *S. columbariae* of subsection Pycnosphace and the other subsections is the infrequent hybrid with *S. mellifera* of subsection Parishiella. As a generalization, it may be said that whenever members of subsections Jepsonia and Parishiella have sympatric distribution patterns, it is likely that hybrids will be found, especially in instances of a disturbed environment. Prior to this paper, only one documented instance of introgressive hybridization has been found in this section and that is between *S. apiana* and *S. mellifera*. So important is this latter instance of introgression that it drew the attention of Epling (1947), Anderson and Anderson (1954), Webb and Carlquist (1964), and Emboden (1964, 1967, and 1969). Since the 1949 publication by Anderson of *Introgressive Hybridization*, this phenomenon has continued to be one of the most controversial aspects of evolution among higher plants, and to a lesser extent among the cryptogams and lower animals. It is especially noteworthy, therefore, that an unpublished instance of introgression in this section of one of the largest genera of flowering plants be documented.

CHROMOSOMES, CYTOLOGY, AND SUBSECTIONAL DISPOSITION

Before discussing the particulars of introgression in section Audibertia, it is necessary to clarify some cytological phenomena that are in error or imperfectly known. Epling, Lewis, and Raven (1962) did a great deal to clarify the unfortunate miscounts published by Carlson and Stuart (1936), Stewart (1939), and Delestaing (1954), and added seven unpublished counts. Most counts were made from somatic material, especially roottips, because of the difficulties attendant with fixation of the oily buds. Of the nine species from which meiotic counts were taken by Epling et al., none showed meiotic irregularities. All members of section Jepsonia and Parishiella, of which there are fourteen species, have a gametic number equal to fifteen. Of the collections of *S. columbariae*, the only member of subsection Pycno-

sphace, the gametic number was thirteen. Since this species hybridizes with *S. mellifera*, having a gametic number of fifteen, it seemed probable that more than one number might occur in this species. Earlier reports of gametic numbers of sixteen, fourteen, and eight were questioned by Epling et al. with the following comment, ". . . the possibility of more than one chromosome number in this species cannot be excluded. However, the known errors in determining chromosome numbers for other species leads us to question the validity of reports other than *n* equals thirteen for this species." Subsequently, I have sampled four widely disjunct populations of *S. columbariae* and have obtained meiotic counts of thirteen in all cases (vouchers L.A. 7678-76881).

Whereas subsection Echinosphace has been characterized by Epling et al. as being "chromosomally and morphologically the most variable within Audibertia," it seems likely that the variable morphology is due to contemporary selective pressure, for when grown under uniform greenhouse conditions, all of these members show a striking degree of morphological similarity except for the annual habit of *S. carduacea*. As for chromosomal dissimilarity, I must take exception. The material of *S. greatae* collected by Lewis was not amenable to meiotic preparations and consequently the examination of three premeiotic divisions in another tissue of a bud too immature for meiotic divisions led to a report of circa 30 as a somatic count. Subsequently, I have had the opportunity to observe a prepared slide of root-tips of *S. greatae* (L.A. 77004) from a plant growing in a canyon north of Hidden Springs in the Orocopia Mountains of Riverside County, California, and this material revealed several cells with a somatic number of 32; this then is consistent with other members of subsection Echinosphace which have chromosome numbers built upon a gametic number of 16. Epling et al. report a gametic count of circa 32 from a single plant of *S. funerea* from Hole in the Rock Spring, Inyo County, California. The authors state, ". . . the probability exists that it was an autotetraploid but aberrant for the species as a whole." Since there were frequent quadrivalents in the chromosomal configurations of this plant (L.A. 76882), it was thought to be an autotetraploid. Although, as these authors note, "genomes of *Salvia* species of section Audibertia are structurally similar, and quadrivalents might be expected in an allotetraploid." In order to clarify this enigmatic count, I collected flowering material from several plants of *S. funerea* growing in Titus Canyon of Death Valley, one mile west of Klare Spring. Meiotic preparations of this material revealed a maximum configuration of 22 pairs and five alternate disjunctive rings of four chromosomes, substantiating the earlier count of 64 as a somatic count and 32 as a meiotic number. Anaphase was normal in every way, and the pollen was 97.5 per cent viable as stained with lactophenol blue. The question of allopolyploidy versus autopolyploidy remains unresolved. Further cytological work as well as an attempt to reconstruct the putative allopolyploid from extant species might provide a

solution. It does not seem likely that such crosses can be made, as they have already been attempted, and the possibility of reconstructing an autopolyploid from colchicine treatment of any member of this subsection does not seem promising. These additional counts do argue strongly for the unity of sub-section Echinosphace as established by Epling in 1938, in contrast to the later statement (as quoted previously) concerning chromosomal dissimilarity. The only apparent chromosomal dissimilarity is the size relationships; *S. carduacea*, an annual of semiarid regions, has much larger chromosomes than the other species in this subsection.

The most questionable subsectional disposition is that of Jepsonia and Parishiella, the members of which show no chromosomal dissimilarity in size or number, and freely exchange genes when found in sympatric dis-tributions. The morphology is quite similar among these species with the exception of the conspicuous and highly colored bracts of *S. pachyphylla* and a few of the subspecies of *S. dorii* (formerly *S. carnosa*). It is interesting to note that palynological size relationships do not as readily distinguish subsections Jepsonia and Parishiella as the others (Emboden, 1964).

INTROGRESSION

The observation of introgression dates back to the early eighteenth century, for Lawson (1714) hints at introgression in describing the natural history of Carolina. Subsequently papers have appeared which suggest that this phenomenon is common to most families of flowering plants, and in-cludes such woody members as the pines, spruces, oaks, junipers, birches, etc. Some of this data has paleohistorical import as well. Both fossil leaves and pollen suggest paleohistorical introgression of the oaks, *Quercus macro-carpa* and *Q. gambelii* in the Early and Late Pleistocene (Maze, 1968). Since the 1949 publication of Anderson, hundreds of papers have appeared in which introgression figures as a major feature of evolution and speciation. It is not the purpose of this paper to present a bibliography of such studies, but since this plethora of information has accrued, a synoptical bibliography on introgression would be in order. This aspect of hybridization, once thought to be restricted to a few plant species, has now been found in animal genera as well. It includes such genera as: *Drosophila* (Van Valen, 1969; Pipkin, 1968); Rotaria (Pefler, 1956); *Hyla* (Mechan, 1966); *Bufo* (Guttman, 1968); *Cyanocitta* (Brown, 1963), to mention but a few. It is to be anticipated that greater numbers of animal genera, including the vertebrates, will soon figure in introgression studies. Like polyploidy, the occurrence of this phenomena, has been neglected by zoologists until recently. A lesser frequency among animals is to be expected due to behavioral factors, ease of migration, frequently shorter life spans, and generally less physiological plasticity. It has not been emphasized by botanists that introgression is probably much more frequent among perennials than among annuals, for the conditions which permit the establishment of introgressants are often ephemeral, but

once established, the effect upon gene flow is considerable and is operative for several successive years.

The role of introgression in evolution is multifaceted and certainly controversial. It is not of equal import in all taxa in which it is known to occur, but it is of some consequence to authenticate those instances in which it does occur or has occurred with some frequency. Hulten (1956) has presented an impressive body of evidence substantiating introgression to be the *primary* agent responsible for the variation encountered in the *Cerastium alpinum* complex, and this would seem to obtain for the genus *Elymus* (Brown and Pratt, 1960), Tucker's (1970) study of the *Quercus undulata* complex is the synopsis of a long-term study and indicates that introgression and transgressive segregation account for the variation patterns in this group. These are but a few examples of studies in which introgression is a major feature of evolution.

With respect to the genus *Salvia* in western North America, the interchange of blocks of characters among the species, noted by Epling (1938) were attributed to hybridization. It would be more appropriate to say that this variation could come about only through hybridization followed by subsequent backcrossing, or in a word—introgression! Much of the variation in Audibertia may be accounted for historically by post Pleistocene disruption resulting in the creation of new habitats (in Anderson's terms, the "hybrid habitat") which could be exploited by hybrid entities or introgressants. Such a postulate would help to account for the extant gene flow between contemporary Audibertias (Figure 1). Reproductive isolation has rarely been achieved in this section of the genus except in instances where distribution patterns indicate relictual populations which have doubtless had long histories of isolation, or where populations are geographically disjunct. While Figure I indicates known gene flow in Audibertia to date, further studies may indicate that this hybridization is more extensive than it is now assumed to be. To date the only introgression recorded for this section has been that of *Salvia apiana* x *S. mellifera*. This paper presents one more example of contemporary introgression, that of *S. apiana* x *S. leucophylla*.

Introgression between *Salvia apiana* and *Salvia leucophylla*

In Los Angeles County, Topanga Canyon Boulevard winds through a canyon of coastal chaparral vegetation which includes *S. apiana*, *S. leucophylla*, *S. mellifera*, *S. spathacea*, and *S. columbariae* as well as all of the other elements which typify this association. In several areas *S. apiana* and *S. mellifera* are sympatric and F1 hybrids are relatively frequent. Hybrids between *S. mellifera* x *S. leucophylla* and *S. apiana* x *leucophylla* are less often encountered, both for reason of less frequent appearance, and less frequent populational contact. One site along the boulevard, just 3.7 miles north of the town of Topanga is of especial interest, for here *S. apiana* and
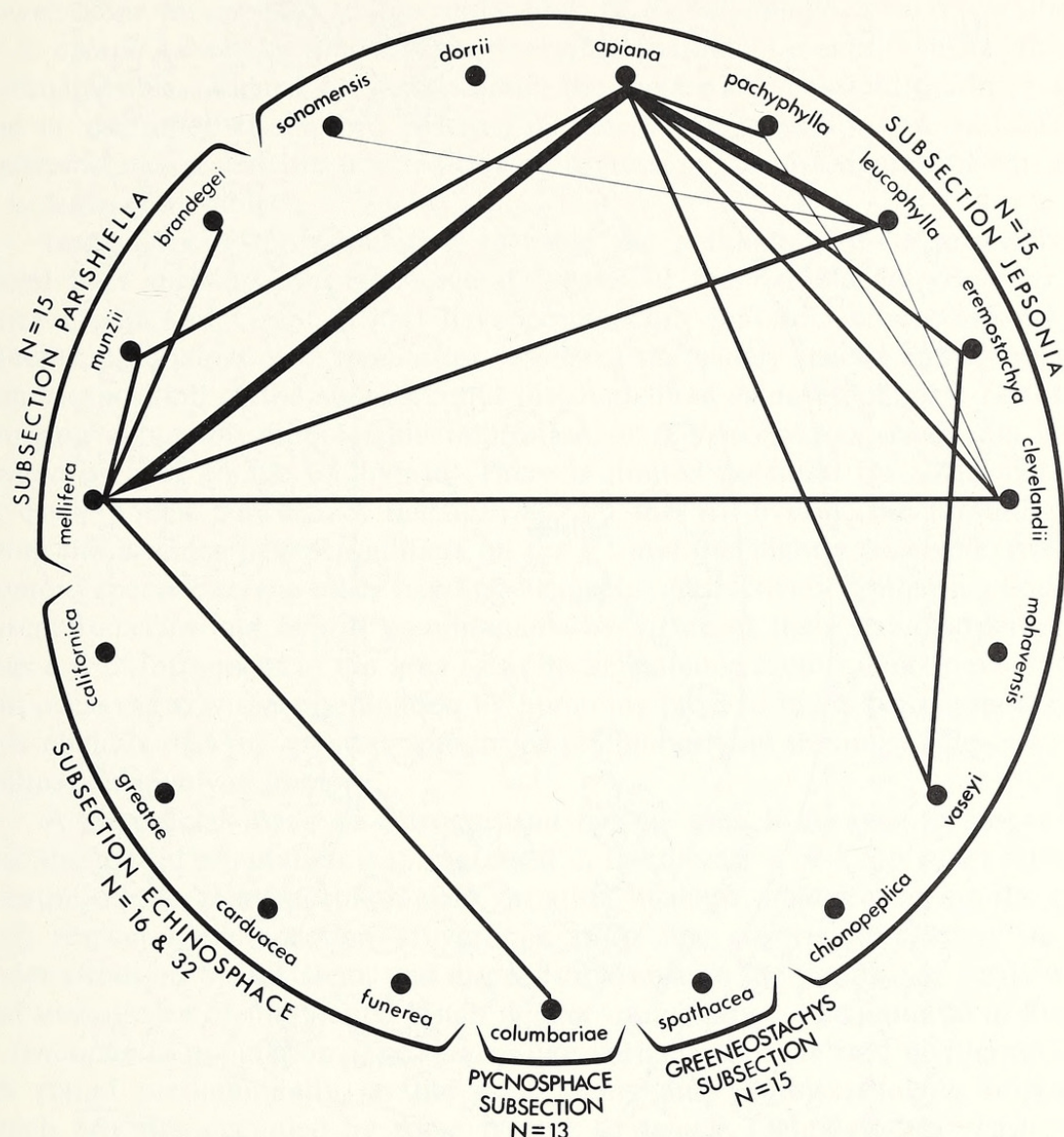
SALVIA : SECTION AUDIBERTIA

FIGURE 1. Breeding behavior in *Salvia*: section Audibertia. Known crosses between species in this section are indicated as follows: Hybrids which have been found in nature————Hybrids which have been made by deliberate pollination————Introgression which has been found in nature ▬▬

S. leucophylla are sympatric in an area which still bears the scars of a previous roadcut, the disturbances resulting from the laying of underground telephone cables at some earlier date, and constant erosion of the decomposing granite-shale hillside resulting from construction of the present boulevard. The site has so many edaphic disturbances coupled with light differences in the form of a northwest slope and a southwest slope that it presents an ideal environment for introgression (Figure 2). In this area, it
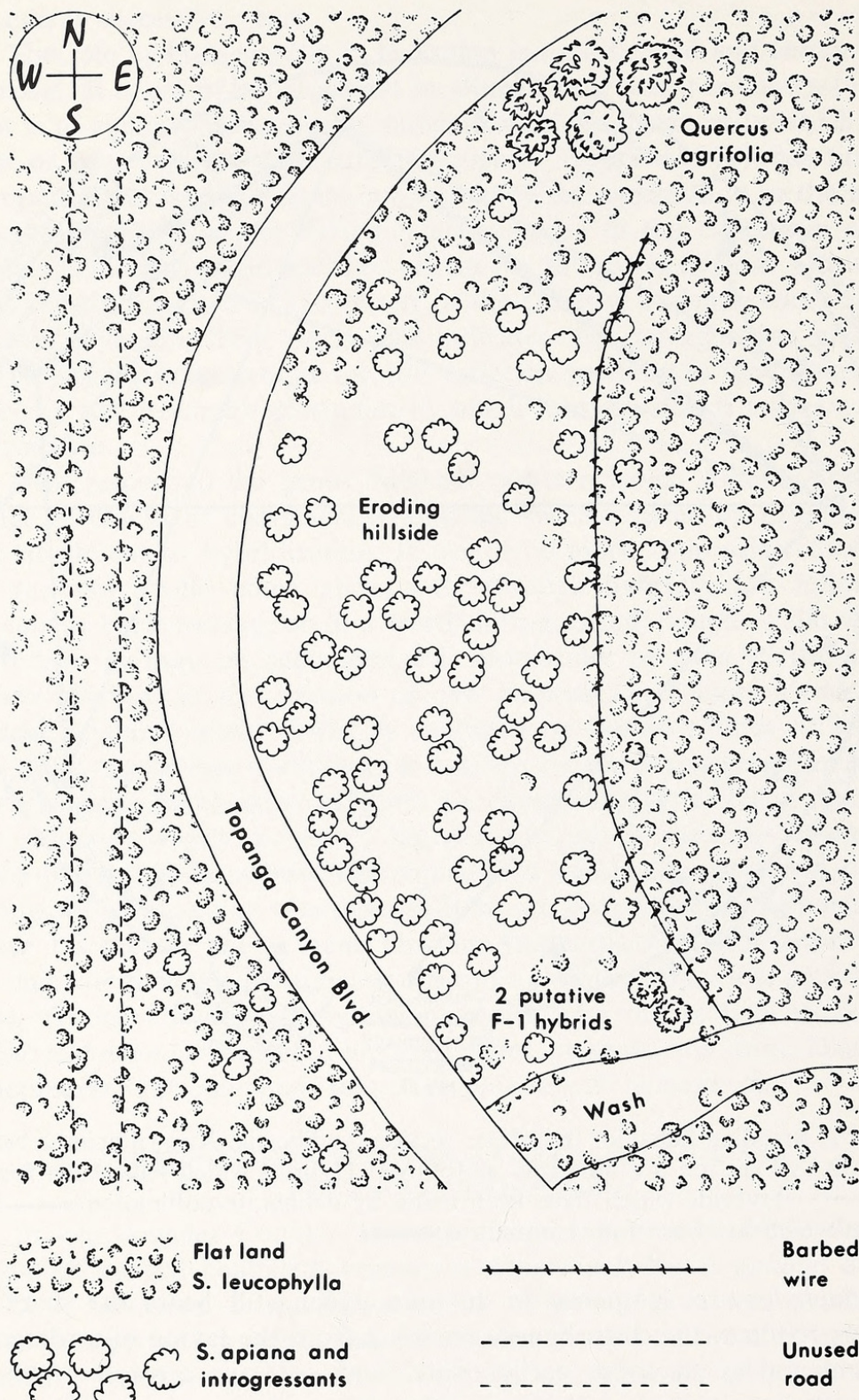
FIGURE 2. Site of introgression between *S. apiana* x *S. leucophylla* 3.7 miles north of Topanga.

is easy to see occasional F1 hybrids which show such a degree of heterosis that they appear monstrous in overall appearance; this coupled with the pink flower color as opposed to the violet-pink of *S. leucophylla* and the white of *S. apiana* as well as a host of more cryptic characters makes them readily distinguishable (Figure 3). Ascertaining the degree of gene infiltration into one or the other of the two parental species is not so easily observed. As Anderson has repeatedly pointed out, introgression is most significant when it is least observable.

Inspection of the population revealed the pollinators to be primarily social bees such as *Apis* and several species of the bumblebees, *Bombus*. Since Grant and Grant (1964) have pointed out that social bees are not effective pollinators of *S. apiana* for reason of the widely spaced anthers and acentric position of the style, I could discount these as an ethological factor bringing about any appreciable infiltration of *S. leucophylla* genes into *S. apiana* or back to the F1 hybrid. There is limited potential for social bees to carry pollen between *S. leucophylla* and the F1 hybrid, the limitation being the distance between anthers on the F1 and the slightly recurved style. *Bombus* species, on the other hand, are capable of effectively pollinating both parental species and hybrid recombinants by virtue of their size. Carpenter bees are so infrequent in the area as to be a negligible factor, and I have not had occasion to witness pollination by humming-birds or night-visiting moths. It is obvious that the greatest amount of pollination and the most efficacious pollination involves *Bombus*.

A superficial assay of introgression in this area leads one to suspect that the hybrid population is introgressed in the direction of *S. apiana*, partly because of the great morphological variation in the *S. apiana* growing there with respect to compaction of verticils, pink dots covering the lower lip, violet striations on the stem, and a great difference in the number of verticils and overall size of the plants. Much greater uniformity is encountered in the *S. leucophylla* population. The *apiana*-like variants, as indicated in Figure 3 are found predominantly on the west facing and southwest-facing slopes which are also occupied by some typical *S. apiana*. Gentle slopes, washes and flatlands are more favorable to the growth of *S. leucophylla*, although they do invade the northwest-facing slopes in this area. *Salvia apiana* and *S. apiana*-like individuals, can occupy steep, eroding, sun-baked hillsides with little competition from any other plants.

In analyzing the population it was desirable to collect representative specimens (LACM Herbarium 70578-70622) and to prepare a scatter diagram (Figure 4) to clarify the occurrence of introgression. Two characters which exhibited measurable extremes in character states were the distance between verticils and the breadth of the lower lip; these were selected as ordinate and abscissa. Other characters could have been used to portray the same phenomenon, although perhaps not as effectively. Having positioned the metroglyphs utilizing these two characters, the other five characters chosen
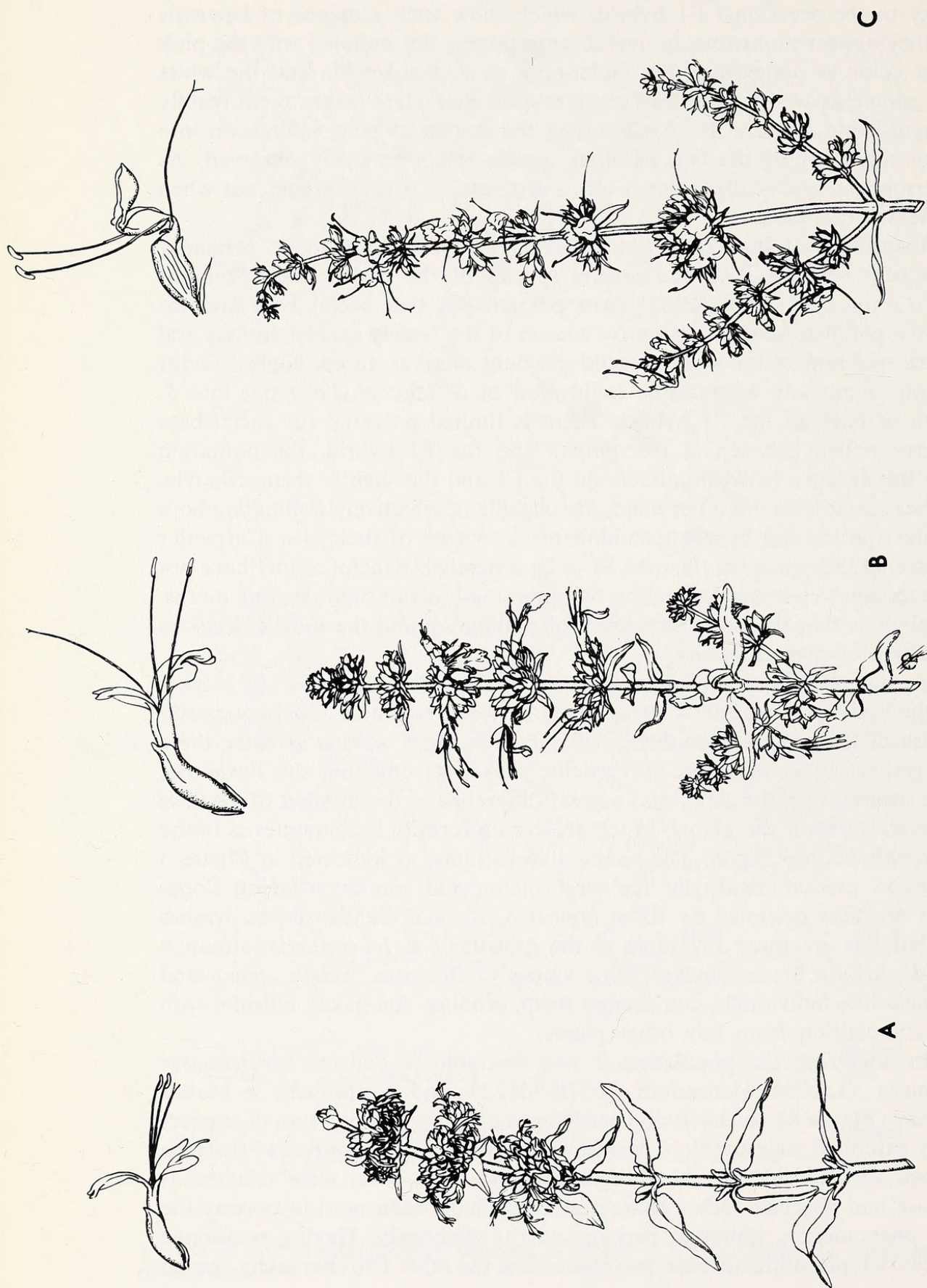
FIGURE 3. Hybridization between *Salvia apiana* x *Salvia leucophylla* showing the upper portion of the inflorescences and examples of each flower. A. *S. leucophylla*; B. F1 hybrid between *S. leucophylla* x *S. Apiana*; C. *S. apiana* found in nature.

were reduced to three states and were indicated as whiskers on the metro-glyphs. The resultant scatter diagram (Figure 4) shows the introgressants to be *apiana*-like in most instances, as was anticipated by a casual perusal of the population. Parental types are easily distinguished in this diagram and show a distributional cohesion which further vindicates this mode of presentation. Variation in the hybrids is considerable and conspicuous which suggests that introgression at this site is not of great antiquity. Another interesting feature of the area is the lack of real intermediacy of the habitat. Studies which I made previously (1964 and 1967) are indicative that the "hybrid habitat" of Anderson consists primarily of a disturbed area in proximity to the parent which is experiencing introgression. Unpublished data which I have on soil types in instances of introgression between *S. apiana* and *S. mellifera* indicate that introgressants are supported by a soil type which is similar to that of *S. mellifera* in humus, mineral and moisture content, and light exposure which is also similar to *S. mellifera*. A thorough study of the nature of the "hybrid habitat" in instances of introgression is in order. The ability of an introgressant to compete satisfactorily with a parental species which has presumably reached an adaptive peak for that area is difficult to explain, except in instances where the "hybrid habitat" is an area which is reconstituted edaphically and climatically. Observations on the effects of heterosis would seem to indicate that the hybrid vigor conferred through this process of massive gene flow might be the key to the establishment and perseverance of recombinants. It should also be stressed that in most instances involving introgression the plants in question are perennials; the critical period in their development is the seedling stage of growth, and once established it is not difficult for the plant to persist and compete. Frequently the introgressants and apparently "good" parental types are found growing adjacent to one another in what would seem to be an identical habitat; more frequently, however, the introgressants occupy a niche, or a series of micro-niches, which is not totally characteristic of either of the parental species.

TAXONOMIC ASPECTS OF INTRODUCTION IN AUDIBERTIA

An outstanding feature of the two aforementioned populations which involve introgression with *S. apiana* is the apparent compaction of the loose paniculate inflorescence of *S. apiana* into symmetrical compressed cymes which approximate those of the species from which genetic infiltration is taking place. This compacted inflorescence of *S. apiana* has been recognized as a variety of *S. apiana* by Munz (1927) on the basis of a collection made at Morongo Wash in the Colorado Desert in Riverside County, California. He characterizes this variety as having, "Panicles condensed, spicate, branches being reduced, and appressed; otherwise much as in (*S. apiana*) typica." His diagnosis of this compact form is correct, and I believe that his implication that *S. vaseyi* is in some way involved is also correct. However, I have noted that when *S. apiana* is found hybridizing with *S. mellifera* or
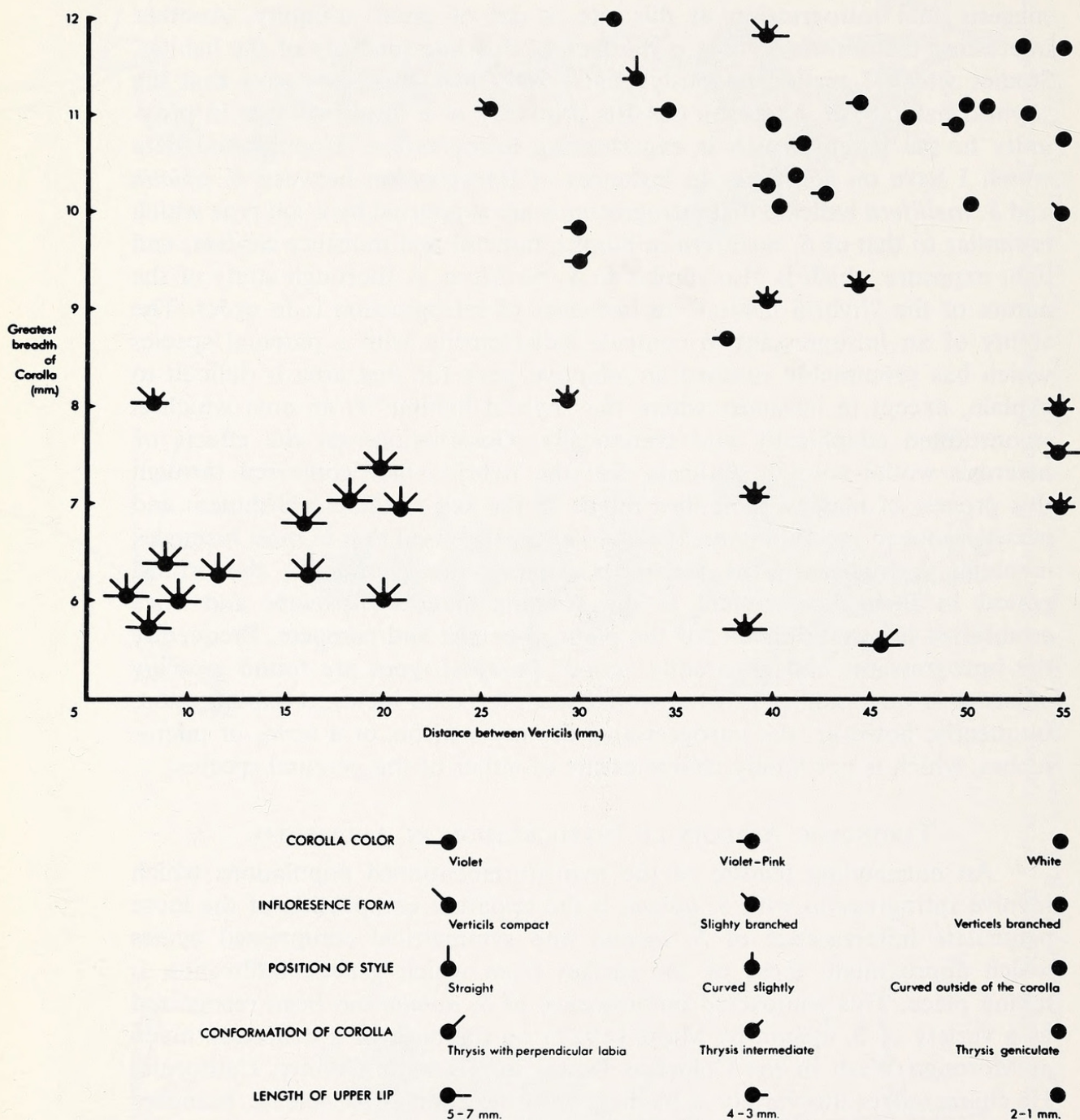
FIGURE 4. Scatter diagram indicating an introgressed population of *S. apiana* x *S. leucophylla.*

S. leucophylla, numerous members of the *S. apiana* population exhibit compact verticils. I suggest that this is due to historical or contemporaneous introgression with these other species. Further support of such a hypothesis comes from a careful analysis of other features of the compact variety. For example, when introgression with *S. mellifera* or *S. leucophylla* is involved the degree of verticilate compaction in *S. apiana* is likely to be greater and the cymose condition is less prominent. When the introgression is with *S. mellifera*, the compact form of *S. apiana* usually exhibits blue-violet dots over the labia; when the compaction is due to gene infiltration from *S. leucophylla*, the dots on the labia of the compact variety are violet-pink. An extension of this study will be to seek out contemporary instances of introgression between *S. apiana* and *S. vaseyi* and present further evidence in support of this contention.

I question the taxonomic status of a variety whose characteristic aspects are derived independently from three different species of a section in disjunct areas. The compact form is by no means localized. It has been collected from various extensions of the range of *S. apiana* and is, I believe, but one aspect of introgression, either historically based or through present gene flow.

The importance of introgression in general has been well summarized by Anderson; its impact on evolution has yet to be clearly understood. Massive short term gene flow between two sympatric species certainly has the advantage of increasing the range of the introgressant by the exploitation of newly opened habitats. It is a source of variability which is of a magnitude considerably greater than that of mutation, and whereas the variability involved in mutation is fortuitous, the variability introduced via introgression is far from chance, but represents recombinations, or blocks of characters, which have a history of being at a selective advantage in a habitat not altogether dissimilar to that occupied by the introgressant. This has doubtless led to the preservation of taxa during periods of disruption. In section Audibertia, introgression may be the primary source of species which constitute the section at this time. Whereas most flowering plants and animals produce sterile or partially sterile F1 hybrids, in section Audibertia the hybrids encountered are quite fertile, averaging around 75 per cent good pollen in the F1 (as determined by staining with lactophenol blue). Epling (1947) records 50 per cent of the nutlets developing in hybrids between *S. apiana* and *S. mellifera*, and 2.0 per cent of these being viable. He refers to the degree of fertility as, "sufficient to permit frequent localized hybrid swarms." If the effect of introgression is sufficient to preserve *frequent* hybrid swarms, while not swamping parental species, it permits rapid exploitation of new environments by new recombinants as such niches become available. This would indicate that the effect of introgression approximates that of *allopolyploidy*, and in short terms, exceeds that of mutation. Its importance can only be minimized by the limited instances in which we can cite this feature of

evolution as an active force; these examples are growing, and a new perspective will soon be in order.

With reference to the *S. apiana* x *S. leucophylla* introgressants discussed in this paper, it is one more piece in a complex jigsaw that will lead to an understanding of one of the most important elements of the vegetation of western North America, as well as contributing to a clearer understanding of the magnitude of role of introgression in the process of evolution.

LITERATURE CITED

ANDERSON, E. 1949. Introgressive Hybridization. John Wiley and Sons, London.
––––––––. 1953. Introgressive Hybridization. Cambridge Phil. Soc. Bull. Rev. 28:280-307.
––––––––, and B. ANDERSON. 1954. Introgression of *Salvia apiana* and *Salvia mellifera*. Ann. Mo. Bot. Gard. 41:329-338.

BROWN, J. 1963. Ecogeographical variation and introgression in an avian visual signal. Evolution 17:23-29.

BROWN, W., and G. PRATT. 1960. Hybridization and introgression in the grass genus Elymus. Amer. Jour. Bot. 47:669-767.

CARLSON, E. M., and B. C. STUART. 1936. Development of spores and gametophytes in certain New World species of *Salvia*. New Phytol. 35:1-49.

CROWELL, J. 1962. Displacement along the San Andreas Fault. Calif. Geol. Soc. Am. Spec. Paper. 61 p.
––––––––. 1968. The California coast ranges. U. M. R. Jour. No. 1 (April):133-155.

DELESTAING, N. 1954. Contribution à l'étude cytologique du genre *Salvia*. Rev. Cytol. et Biol. Veg. 15:195-236.

EMBODEN, W. A., JR. 1964. Pollen morphology of the genus *Salvia*, section Audibertia. Pollen et Spores 6:527-536.
––––––––. 1969. Detection of palynological introgression in *Salvia* (Labiatae). Los Angeles Co. Mus. Contrib. Sci. 156:1-10.
––––––––, and H. LEWIS. 1967. Terpenes as taxonomic characters in *Salvia*: section Audibertia. Brittonia 19:152-160.

EPLING, C. 1938. The California Salvias. A review of *Salvia*, section Audibertia. Ann. Mo. Bot. Gard. 25:95-188.
––––––––. 1940. Supplementary notes on *Salvia*: Audibertia. Ann. Mo. Bot. Gard. 27:259-262.
––––––––. 1947. Natural hybridization of *Salvia apiana* and *S. mellifera*. Evolution 1:69-78.
––––––––, H. LEWIS, and P. RAVEN. 1962. Chromosomes of *Salvia*: section Audibertia. Aliso 5:217-221.

GRANT, K., and V. GRANT. 1964. Mechanical isolation of *Salvia apiana* and *Salvia mellifera*. Evolution 18:196-212.