CHAPTER FIVE

PHYTOGEOGRAPHY

GEOGRAPHIC DISTRIBUTION

Like many other genera of the Labiatae, Salvia is well represented in the Mediterranean basin, though found virtually throughout the world, including southern Africa and North America, and the Neotropical highlands and southwestern Asia are major centers of diversity. The range of variation expressed by these species is marked, as Hedge has made apparent in his treatments of the 86 Anatolian species (1982b), 50 percent of which are endemic, and the 59 African species (1974), most of which are confined to that continent. Many of the Near East species groups described by Hedge (1982b) are monotypic, and this is true for the African species as well. The nearly 500 species of subg. Calosphace are centered in the highlands of Mexico, Brazil, and Peru (Epling, 1939a,b), and represent the only significant extension of the genus into tropical latitudes. This group also has a high proportion of endemics and small species groups, though these have apparently originated from a common Old World ancestor.

The derivations of the Eurasian species are much less clear. Of 45 species described from the U.S.S.R. (Pobedimova, 1954), 35 are endemic, with the greatest concentration of species in the Causasus region between the Black and Caspian seas. Secondary centers of concentration in the U.S.S.R. are the European region north and east of the Black Sea, and Soviet Central Asia, east of the Caspian Sea and north of Iran. Eastern Siberia harbors no species, and only the widespread, mesophytic S. plebeia is recorded from the Soviet Far East. This annual, tropical weed of fallow land has spread throughout Asia and to Australia, and is the lone, native representative of the genus in such humid, tropical regions as Malesia (Keng, 1978). Xerophytic phylads have spread throughout Central Asia and inhabit dry, stony places in Iran and Afghanistan. Possibly 20 or more species can be found in China, of which 10 to 15 are apparently native (Steward, 1958; Noda, 1955; Iconographia Comophytorum Sinicorum, 1980). The related Japanese flora includes nine species of Salvia (Ohwi, 1965), of which only two are also found in mainland Asia, one of these the widespread S. plebeia. The genus is well represented in Mediterranean regions characterized by summer drought, including the Balkan, Italian, and Iberian peninsulas, and especially northwest Africa (about 25 spp.)

and Palestine (22 spp.). Areas with similar climates in southern Africa (22 spp.) and California (19 spp.) have also been colonized (Hedge, 1974; Zohary, 1962; Epling, 1938), but not the Mediterranean type vegetation of soutwestern Australia. Several Mexican species also extend into Texas, but only two (three) of these have spread into the deciduous forests of eastern United States, and one additional species (S. lyrata) of Old World affinities is native to the eastern states.

Species of Salvia are found within several, broad phytogeographic regions, as outlined by Zohary (1962). They are best represented in the floristically diverse Irano-Turanian region which extends from Bulgaria, southward to Palestine and eastward to Mongolia. This region consists largely of a series of steppes and deserts which are considered, by Zohary, the center of origin for numerous genera and species. The large plateau between western Anatolia and Afghanistan, in particular, is suggested as a primary center of speciation for a xerophytic flora consisting largely of steppe plants. Many Salvia species of Anatolia are considered Irano-Turanian elements (Hedge, 1982b), often inhabiting the originally forested deciduous scrub or inner areas of treeless steppe.

These species are common on rocky, limestone or igneous slopes, or in <u>Pinus</u> or <u>Quercus</u> woodlands, but also in meadows and different types of steppe. Habitats within the U.S.S.R. are also typically dry, stoney, or gravelly, often calcareous mountain slopes, sometimes upland steppes, meadows, or arid woods.

Irano-Turanian stock is also considered by Zohary (1962) to have supplied many derivitives to the younger Mediterranean region, a secondary center of speciation which developed fully perhaps only in the Pleistocene (Axelrod, 1975). The typical Mediterranean climate consists of cool, moist winters, and hot, dry summers, though a continuum exists from severe summer drought (e.g., in Spain) to a condition with no significant drought (e.g., in northern Turkey). All areas surrounding the Mediterranean fall somewhere along this continuum, except perhaps some arid parts of northern Africa. The Mediterranean native vegetation is dominated by evergreen, sclerophyllous shrubs, and similar life forms are found in distant regions with Mediterranean-type climates, such as southernmost Africa and southern California (Mooney & Dunn, 1969). These dense scrublands, known as machie, machia, or maquis in the Middle East, are roughly analogous to the chaparral of California. The

Mediterranean batha or garigue are more xeric, dwarf-shrub communities which have expanded in range since primeval times at the expense of the maquis and sclerophyllous oak forests (Zohary, 1962). In California, similar xeric communities are known as soft chaparral, sage or coastal scrub (Brown, 1982). In every area there are transitions from batha or machia-covered slopes to scattered woodland trees in sclerophyllous shrublands, to sclerophyllous forests with a rich understory of shrubs and trees (Axelrod, 1975; Davis, 1965). Salvia are found in all these types of communities and are often dominant elements in the sclerophyllous forests and maquis climaxes. They are mostly herbaceous perennials which die back to the ground surface during the period of drought, or may be woody with drought-deciduous leaves, or rarely they are drought-evading annuals. Apparently, Salvia, of Irano-Turanian origin and centered in southwest and central Asia, differentiated when colonizing the Mediterranean communities in the Near East, Europe, and northwest Africa. The genus has also radiated in the more distant sclerophyllous communities of southern Africa and California. In southern Africa, Salvia species are found in habitats which include coastal sand dunes, coastal bush, flats, rocky banks, hillsides and watercourses, shales, burnt grassland and wasteground, sclerophyllous forests and clearings, grassy valleys and steppes (Hedge, 1974). In California, Salvia species are mostly confined to either the Larrea-Franseria shrub formation of the Colorado desert or the related Artemesia californica-Salvia shrub formation of the coastal plain (Epling, 1938).

Like the Mediterranean region, the relatively young, species-depauperate Saharo-Sindian region has expanded because of increasing aridity, and is characterized by many derivitives of Irano-Turanian stock. Today, this region extends from arid northern Africa across the Sahara and Sinai deserts, through Arabia, southern Iraq and Iran, to Pakistan. Several Salvia extend into this region, most notably sect. Eremosphace sensu Briquet (Notiosphace sensu Bentham) which currently consists of about 11 xerophytic species. Salvia also extend into the various mesophytic forests of the Euro-Siberian region, especially in the European portion of the U.S.S.R., north of the Black Sea.

In Africa, the species of Salvia treated by Hedge (1974) are concentrated in the northwest and the southern Cape area, with most of the species endemic to one or the other of these regions. The few species which extend into tropical East Africa are not considered to be links between these regions. There are six endemic species in Madagascar, only one of which is considered by Hedge to have affinities with an African species. The Canary Islands harbor an endemic with no obvious allies, two widespread species, and another with some links to species from southwestern Africa. Of 59 species described, 43 are endemic to Africa, and these exhibit much of the variability that exists within the genus. Many of Hedge's species groups are monotypic, a considerable number of which exhibit little variability and can be considered relicts. Some of these distinct taxa show no obvious affinities with any others, while some display character states intermediate between those of traditional infrageneric categories.

Section Heterosphace consists of 10 species from the eastern Cape region of Africa, as well as several disjunct species in North America. While these form a distinct group in southern Africa, they are also extremely polymorphic, have many synonyms, and are the source of innumerable problems for the taxonomist. The two south African representatives of sect. Plethiosphace are also very variable and apparently evolutionarily unstable.

Salvia namaensis and S. granitica, on the other hand, are each oligomorphic, south African species considered by Hedge (1974) to be very distinct and isolated taxonomically within the genus. There are no south African members of sections Eusphace or Drymosphace, but sect. Hymenosphace is represented by a cluster of five species. Another south African species group is characterized by the Hymenosphace-type inflated calyx, but shows affinities with an Irano-Turanian species of sect. Aethiopis.

Sections Notiosphace (Eremosphace sensu Briquet) and subg. Sclarea are both well represented in northwestern Africa, while sections Hymenosphace, Drymosphace, and Heterosphace are absent. Though northwestern Africa has more distinct, oligomorphic species than southern Africa, there are also more links with south European and southwest Asian taxa. Floristic links between Spain and Morocco are great and several Mediterranean-Irano-Turanian vicariads have been identified by Davis and Hedge (1971). Unlike the east-west Mediterranean vicariads reported by the authors, eastern links for northwest African Salvia are with Irano-Turanian taxa. Variations of this pattern, where species of northern and southern Africa are independantly linked to species of the Irano-Anatolian plateau but not to each other, are repeated throughout the Old World, supporting the view of the Irano-Turanian region as a center for the genus.

Section Eusphace has its main center of development in Anatolia, and those species with pinnately compound leaves are especially concentrated in the central and eastern Irano-Turanian portion of the peninsula. Section Drymosphace is primarily an east Asian group, with species in the Himalayan region and China. Two species extend westward into Turkey: the widespread *S. glutinosa*, common in the forests along the Black Sea, and the Bulgarian *S. forskohlei*. These mesophytic herbs are considered by Hedge (1982b) to be Euro-Siberian elements. In contrast with other *Salvia* which are associated with stoney, semi-arrid habitats in the Near East, species of sect. Drymosphace are found in the more humid, broad-leaved and coniferous forests. Problems concerning the status and limits of sect. Hymenosphace, the group with large, expanded fruiting calyces, have been discussed above. Most of these are scattered through Soviet Central Asia, Turkey, Iran, and Afghanistan, and disjunct in the Canary Islands and southern Africa. Transitional species between those with and without expanded calyces are found in Turkey and southern Africa.

Section Aethiopis is a large Irano-Turanian group which has spread throughout the Mediterranean region and also extends into northwestern Africa and eastward across Iran and into Afghanistan and the Himalayas. The related sect. Plethiosphace is best known of all Salvia taxa because of its concentration in Europe, though also represented in northwestern and southern Africa. The northernmost extensions of the genus are mostly species of Plethiosphace, which may be found in much of Soviet Europe, including the Baltic states and the upper Volga area, and also western Siberia and Soviet Central Asia (Pobedimova, 1954). Salvia viridis and the possibly conspecific S. horminum (sect. Horminum) are Mediterranean elements distributed throughout that region and extending to Crimea, Causasia, Iran, and northern Iraq. These entities are some of the few annuals in the region, and the only annuals in Turkey (Hedge, 1982b).

Subgenus Leonia, as suggested above, is probably an artificial group of offshoots from primitive Salvia stock. These morphologically anomolous taxa have no clear affinities within the genus and at least one group (subg.

Allagospadonopsis sensu Briquet, 1897) should probably be excluded from Salvia. The segregation by Briquet (1897) of Leonia into four subgenera reflects the apparent great taxonomic distances between the various phylads. Geographic distribution, like the floral structures, are anomolous and suggest no clear relations with any other taxa. For instance, several species from China and Japan, including the widespread S. plebeia, were grouped by Briquet (1897) into sect. Notiosphace. [Neisess (1983) suggested that sect. Notiosphace exhibits a pre-Gondwanaland breakup origin, with species in China, Japan, tropical Asia, and Australia, but aside from the facts that southeastern Asia and the Far East were never part of Gondwanaland, and the age of the genus is not likely to be nearly that old, the group's extension into tropical Asia and Australia is due only to the distribution of the widespread, weedy annual, S. plebeia. The nutlets of this mesophyte are less than 1 mm long, and as proposed by Ridley (1930), may be transported on muddy potatoes in Sumatra. This easily dispersed weed of fallow land can evidently not be used as evidence for any ancient, continuous distribution.] Most of the other species since described from China and Japan are presumably allied to this group.

Section Heterosphace has not been studied as a group in this century, but if the taxonomic framework created by Bentham (1832) and Briquet (1897) is accurate (and chromosomal evidence obtained since then suggests that it is), these species exhibit an interesting disjunction. The 10 species in southern Africa mostly grow in the eastern Cape region under subhumid conditions and cannot be considered Mediterranean climate disjuncts. As mentioned above, this is a distinct, yet taxonomically problematic group which appears to be evolutionarily unstable and probably quite young. Aside from an extension into tropical East Africa (Hedge, 1974) recognized by Briquet as the monotypic sect. Neosphace, the only affinities exhibited by this species complex are apparently with several North American species. Two (three) of the New World Heterosphace are centered in the Edwards Plateau area of Texas and neighboring states, while _S_. _lyrata_ is widespread in eastern United States.

The California section Audibertia, though never formally assigned to subg. Leonia, should probably also be included in this artificial assemblage of sections, especially because Neisess (1983) has presented evidence linking

Audibertia with Heterosphace. The affinities of sect. Echinosphace are much less clear, and these four species are considered by Neisess (1983) as the fragmented remains of a once highly diverse taxon. Both Audibertia and Echinosphace are centered in the summer drought region of California among a largely sclerophyllous flora. Three additional Texan species have traditionally been segregated from _Salvia_ as _Salviastrum_, on the basis of a ring of hairs in the calyx and three-angled nutlets. These species have stunted, non-cohering secondary thecae and should rightfully stand alongside the other distant offshoots grouped together in Bentham's (1832) subgenus Leonia.

Another very distinct species group is the xerophytic sect. Eremosphace which currently consists of 11 Saharo-Sindian species in Iran, Arabia, Palestine, and Egypt (Hedge, 1974). The monotypic sections Allagospadon from China and Gymnosphace from India have been traditionally included in _Salvia_, though today this view must be questioned. Finally, sect. Hemisphace is yet another taxon which is morphologically anomolous within _Salvia_, though its center of distribution, in the Near East and Mediterranean regions, is the same as that of the genus. _Salvia verticillata_ is particularly widespread in Europe and western U.S.S.R., extending northward almost to the Arctic circle in the Karelia-Lapland region (Pobedimova, 1954).

The enormous subgenus Calosphace is the only Salvia taxon which has significantly radiated into tropical latitudes, accomplishing this, in fact, with such success that Salvia probably represents the most speciose genus in Mexico. The centers of its diversity are the highlands of Mexico, Brazil, and the northern Andes, with the highlands of British Guiana, Cuba, and Haiti representing subsidiary areas of endemism (Epling, 1939b). Thirty percent of the genus occurs in Mexico alone (275 species) and most of these are endemic to that country (Ramamoorthy, 1984). Epling (1935-37) recognized 182 species from South America (50 from Peru, 48 from Brasil, 44 from Columbia, 27 from Argentina, and 21 from Bolivia). In Mexico, Salvia are conspicuous elements of the various mosaics of oak and pine forests which comprise much of the mountainous terrain between elevations of 1200 and 3000 meters. It is interesting that although the climate of the Old World (Anatolian) center of diversity for the genus is more arid and cold than that of the Neotropical center, the most important associates, oaks and pines, are the same. Like oaks and pines, salvias have been particularly evolutionarily successfull in drier sites with seasonal rainfall and often poor, thin, stony substrates. In Mexico, other common associates of Salvia include Juniperus, Abies, and many Compositae, especially species of Eupatorium (sensu lato) and Stevia. The Sierra Madre Occidental is particularly rich in species, as is the Sierra Madre del Sur and the Sierra Madre de Oaxaca. The transverse neovolcanic axis also harbors many species and Ramamoorthy (1985) described 34 species from the valley of Mexico alone. Though the total range of Salvia in the New World is large (from the Great Lakes to the plains of Argentina), it is the speciose nature of the group, with almost 500 species, which is most impressive from the standpoint of biogeography.

COLONIZATION ABILITY

With extensions into the cold midwestern United States and Baltic region of Europe, the hot tropics of eastern Africa and southeastern Asia, the mild summer-drought regions of northern Turkey and southern Africa, the severe summer-drought regions of Spain, northwestern Africa, and southern California, the xeric belt across northern Africa and

Arabia, the humid-temperate regions in eastern Asia and eastern North America, the semi-arid regions in southwestern Asia and southwestern United States, and the montane Neotropics, Salvia boasts an ability to adapt to a range of stressfull environments. What is more, several of these regions have been independantly colonized by different phylads within the genus. The south African species, for example, represent a composite of three disjunctions, those of sections Heterosphace, Hymenosphace, and Plethiosphace. Three very distinct phylads also represent the genus in southwestern United States, excluding the extension of subg. Calosphace from the south. The wide range of habitats has been mentioned above, and the range in elevation is similarly large. Hedge (1974) has found that in Africa there are few habitat types in which Salvia is absent.

Although few species are widespread (S. aegyptiaca and S. plebeia are exceptions), the ability of Salvia to colonize and diversify in response to available niches is evident. While the high degree of speciation is at least partly due to breeding systems and selection for animal pollinators, the evolutionary success of the genus owes much to an opportunistic capability to adapt to new environments. The climate and habitat types of southern Africa, southern California, the Mediterranean region, and most importantly, the montane Neotropics, are all relatively young (Axelrod, 1975; Raven & Axelrod, 1975; Axelrod, 1976; Berry, 1982). Early development of Salvia in the Near East apparently did not lead to the fine tuning of structural adaptations to stressfull conditions of seasonal drought or temperature extremes. Instead, members of the developing genus developed a "generalist" ability to cope with various environmental stresses, mainly by dying back to the ground surface during a period unfavorable for growth. Although a few drought-evading annuals exist, most species are true drought-resistant perennials with highly effecient hormonal mechanisms that regulate the rhythms of initiation and recovery from dormancy. Although little is known about the genetics of Salvia, many species apparently have the requisite gene pool to quickly adapt to new environments. Selection may be for more or less vigorous growth, an increase or decrease in the size of the plant and its parts (notably the leaves), development or loss of protective mechanisms, increase or decrease in the activity of secretory glands, and so on, but especially involves the timing of the periods of growth and dormancy. In this way, plants are pre-adapted to new microhabitats and more distant regions which may differ somewhat in climate.

DISPERSAL

A few Labiatae have specialized mechanisms for dispersal such as hooked bristles on the calyx, or corky nutlets which are able to float in water for an extended period. In cases where the calyx acts as the diaspore, the calyx teeth generally point inward, preventing the nutlets from falling out. In *Salvia*, the calyx is often vertically compressed as the nutlets are developing (e.g., *S. gracilis*, *S. fulgens*), opening when they are mature. Often, the lower calyx lip is curved slightly upward so that nutlets do not drop out of the calyx until the event of a wind or rainstorm. Hedge (1974) reports that upon soaking the axis of *S. taraxicifolia* in water, the pendant pedicels and calyces are brought up into a horizontal position and the throats of the closed calyces are opened. *Salvia viridis* is also described as similarly hygrochastic. The calyx of *S. glutinosa* is very sticky, as is the whole plant, and Ridley (1930) suggests that it will readily attach to a passing animal while the nutlets remain enclosed. Zohary (1962) has reported that plants of some

Salvia species in Palestine are tumbleweeds, in which the stem breaks near its base and the entire seed-bearing shoot is rolled around by the wind. Experiments have shown (Ridley, 1930) that some nutlets of *S. pratensis* will float for six days before sinking. The nutlets of the widespread *S. plebeia* are less than 1 mm. long and can certainly be transported in mud on animals such as birds. It has been suggested (Murbeck, 1919; Ridley, 1930) that the mucilage produced by the nutlets may be an aid to dispersal. This would explain why the nutlets of *S. glutinosa* produce no mucilage (Hedge, 1970), since it is the calyx, in this case, which acts as the diaspore. Still, the mucilage is produced only when the nutlets become wet, remaining until the seeds germinate days later, and is not likely to be related to dispersal. In most *Salvia*, the nutlets simply fall out of the calyx and are dispersed over relatively short distances by gravity, ground surface water, or wind, and dispersal over a significant distance must be considered an improbable, though possible, isolated event. *Salvia* is not known to have reached Hawaii or any other distant oceanic Islands, (save for several species apparently from the Galapagos; see sect. Micranthae). The only Labiatae, in fact, which are native to Hawaii are three genera, derived from one Indo-Malayan introduction, all with thick-fleshed drupelets rather than the dry nutlets typical for the family (Degener, 1946; Keng, 1978).

In the case of a long distance introduction, the stresses posed by the new environment become the critical factors which dictate whether the new arrival can become established. Self-incompatability in the genus does not appear to be strong, for one can always find some viable seeds produced by single plantings in cultivation. Other factors such as the capacity to adapt to new pollinators and the threat of inbreeding depression have not been studied for Salvia, but evidence exists that long distance dispersal has occured in the history of the genus.

PHYTOGEOGRAPHIC HISTORY

It is clear, from examining relationships between extant taxa within Salvia, that some disjunctions are much older than others. To attribute some disjunctions to separation upon drifting continental plates, as some authors have done (Hedge, 1974; Neisess, 1978), is questionable considering the probable age of the taxa involved. The earliest fossil pollen was reported by Emboden (1964) from the upper

Miocene of Alaska. This report, based on one pollen grain, represents the earliest pollen known for the family as well. According to Muller (1970, 1981), the earliest macrofossils known for the Lamiales are from the Pliocene, and the author suggests a Neogene differentiation for the order. Within the Lamiales, Salvia is relatively young, as evidenced by pollen morphology (Emboden, 1964), floral anatomy (Hillson, 1959), and androecium conformation (discussed above), and so one would not expect the group to be much older than the Pliocene or Miocene.

Yet Neisess (1983) suggested that the North American Salvia split from the southern group, now known as subg. Calosphace, with the breakup of Gondwanaland in the mid-Cretaceous. The northern elements are proposed to have spread through Laurasia in the late Cretaceous, while Calosphace remained isolated in South America throughout most of the Tertiary. This scheme cannot even be reconciled with the views of Raven and Axelrod (1974), who differ with Muller (1970) and suggest a Paleogene differentiation for the Lamiales. It is true that subg. Calosphace stands apart from the rest of the genus, but its species are never found in tropical lowlands and not likely to have diversified in West Gondwanaland before significant

Neogene volcanism and tectonism created the high cordilleras, where extant taxa are found. What is more, the nature of relationships among the Calosphace suggest that this group is young, active, and evolutionarily unstable. Many narrow endemics are known, species are often highly variable, and sections are often composed of barely distinguishable entities. Epling (1939b) described these constellations as closely related groups of species, these probably "coenospecies" in the sense of Turreson. Cytological data (discussed below) suggests, as does morphological data, that the Calosphace are rapidly evolving species and species clusters, differentiating in response to pollinators and the relatively young diversity of terrain of Neotropical highlands (see Chapter Seven).

Also, if subg. Calosphace was isolated in South America for so long, only later spreading through Mexico, relationships within and among the sections in North and South America should reflect their contrasting histories. Yet South American taxa do not appear relictual; in fact, most species from the Andes are related to species in Mexico but not Brazil, and species from Brazil are allied to ones in Mexico but not the Andes (Epling, 1939b). Only the large complex, sect. Angulatae, is common to all three areas.

This pattern suggests an intitial introduction into Mexico, where almost all species groups within subg. Calosphace are represented. The source of the introduction is not clear, but likely to be the Old World center in the Near East, where other derived taxa (sects. Aethiopis and Plethiosphace) have apparently originated. The time of introduction is probably during a late stage of development of the genus, perhaps during late Neogene or even later.

The disjunctions created by the taxa in the western United States are not so easily explained by long distance dispersal. Sections Audibertia, Echinosphace, Heterosphace, and the segregate genus Salviastrum, each comprise a distinct offshoot from primitive Salvia stock. Of these, only sect. Heterosphace is believed to have close counterparts in the Old World, these being the taxonomically difficult species cluster in southern Africa. Although Neisess (1983) has proposed that Old World Heterosphace are progenitors of sect. Audibertia, relationships of these North American taxa are obscure, perhaps due to extinctions. These species may be derived from four, seperate Old World introductions, occuring when the genus was in its earliest stages of diversification, but this is not clear.

The endemics found in Japan (sect. Notiosphace) are similar to those in California, in that they also suggest a distant offshoot from primitive Salvia. All these offshoots, originally grouped together by Bentham (1832) in the artificial subg. Leonia, form a pattern of widely scattered relicts. These distributions contrast with those of the more specialized sects. Aethiopis, Plethiosphace, and subg. Calosphace, each group with a large number of clearly related species which have radiated in a distinct region of the globe. Most of the distant disjunctions seem to be older, involving the most primitive forms of the genus, several of which have sometimes been recognized as distinct genera. These distributions suggest that conditions for the spread of Salvia may have been more favorable in the past.

There are no specific, long-range disjunctions known for the genus, though several species groups are widely separated. Species in Japan, southern Africa, and California, are almost exclusively endemic to these regions. Excluding sect. Heterosphace, no sections are common to both the New and Old World. The numerous sectional disjunctions between North and South America are especially meaningful because the separated species are often very closely related. Dispersal of Salvia from one of these continents to another in recent geological history has apparently not been an unlikely event. Salvia, though, is essentially adapted for short-distance dispersal, and the likelihood of successful, long-distance dispersal is a question of probabilities. These probabilities are not constant since factors of ecological equivilance, bird migration and wind patterns, configuration of continents, and presence of "stepping stone" islands, all change in geologic time. Distribution patterns of extant Salvia suggest that long-range, east-west dispersal, including that betwen the Old and New World, was more probable in the past, when Salvia was in its earliest stages of diversification.

As outlined above, Salvia are common elements in the sclerophyllous forests and maquis-type vegetation of several, distant regions. Although arguments have been put forth (e.g., Stebbins & Day, 1967) which suggest certain, interrupted migration routes to explain the floristic similarities between these regions, most authors (Mooney & Dunn, 1969; Thorne, 1972; Raven, 1972; Wolfe, 1975; Axelrod, 1975, 1976) reject the notion of any continuity of arid habitats to explain these floristic links. Although no dry belt ever extended from western United States to the Mediterranean region, there is evidence that in the mid-Tertiary, a semihumid belt of sclerophyllous vegetation covered each continent at low to middle latitudes, forming an ecotone between the tropical and temperate forests (Axelrod, 1975, 1976). In North America, dryer climates of the late Tertiary and Quaternary caused this "Madro-Tertiary" geoflora to undergo selection and segregation, resulting in derivitive floras such as the California coastal sage community where Salvia are extant. The flora of the Mediterranean region was derived in a similar way from the preceeding "Tethyan-Tertiary" geoflora. In the Miocene, decreased rainfall and colder temperatures restricted, to some degree, interchange between Eurasia and North America to elements of the humid-temperate Arcto-Tertiary geoflora (Axelrod, 1975,1976). But before its breakup, the sclerophyllous pathway between the continents offered greater probabilities of dispersal for many taxa, as the Atlantic was narrower, probably dotted with Islands, and the climate was warmer than at present (Raven, 1972; Raven & Axelrod, 1974). Neither the age of Salvia nor the time when colder climates developed in eastern North America is known with certainty, but both probably date back to sometime in the late Tertiary. Considering the several, long-distance, east-west disjunctions of relictual _Salvia_ taxa, it seems likely that progenitors of extant _Salvia_ were elements of the belt of Madro and Tethyan-Tertiary geofloras. A possible scenario would have the earliest forms of _Salvia_ diversifying during the later stages in the history of these geofloras, and significant expansion of the genus during the breakup of the geofloras.

CHAPTER SIX

CYTOTAXONOMY

LITERATURE REVIEW

The first detailed study of the cytology of Salvia was by Scheel (1931), who counted 31 taxa and suggested the base numbers for the genus to be 8 and 11, though these perhaps secondary and of polyploid origin, with 6 as the original base number. Phylogenetic development within subg. Calosphace is viewed as having coincided with a reduction in chromosome number from 11, while 8 is probably the base number for the Old World groups. Scheel commented on the irregularity of meioses in the genus and attributed this mostly to climatic influences.

Carlson and Stuart (1936) examined the spores and gametophytes in several North American sages and recognized two basic types of megagametophyte. Their distinction was pertinent at the time, for it supported the view that the species of the Californian segregate genus Ramona should be transferred back into Salvia, since these species are more similar to Old World taxa than those of Calosphace. Their division based on type of embryo development also supports Neisess' later (1983) view that sects. Audibertia and Echinosphace find their origins in Old World taxa. Meiotic irregularities were discussed and attributed to hybridism. Several chromosome counts were obtained, with n=16 recorded for two species of subg. Calosphace, both later listed as x=11 by other authors. Subsequent reports of meiotic irregularities and conflicting chromosome counts would later prove to characterize the cytological literature for Salvia.

Delestaing (1954) studied the chromosomes of 32 species of Salvia and established the following series of base numbers for the genus: x=6, 7, 8, 9, 10, 11, 13, 14, 15, 17, and 19. He also reported on meiotic irregularities and attributed these to a hybrid origin of material studied.

Epling, et al. (1962) counted the chromosomes of the 19 Californian species of sect. Audibertia, correcting in some cases previously published data. While they do not exclude the possibilty of a species with more than one cytotype, they cite known mistaken chromosome counts and question the validity of others. Their report of n=13 for S. columbariae, for example, contradicts the previous report of n=16 (Carlson and Stuart, 1936). Three subsections of sect. Audibertia with n=15 were viewed as young, closely related taxa derived from the older, fragmented subsect. Echinosphace, with n=16. The monotypic, annual subsect. Pycnosphace (S. columbariae), with n=13, was similarly thought to be derived from a shrubby n=15 ancestor. Thus, n=16 was viewed as the base number for the section, this probably of polyploid origin, and certainly the authors were aware that x=8 is most frequent in the genus.

Fujita (1970) summarized Labiatae cytotaxonomy and proposed a model of chromosome number evolution for Salvia. Most of the family's genera have a base number between 5 and 11, and, except for x=5, this series characterizes Salvia as well. Fujita suggested that these primary base numbers reflect a stepwise reduction in chromosome number from 11 to 5, with n=11 considered primitive in both family and genus. Based on this reasoning, Salvia was proposed as the most primitive genus in the family, and S. sclarea (2n=22) was recognized as primitive within the genus. This hypothesis is apparently (all but the paper's abstract is in Japanese) supported by the occurence in, S. sclarea, of l-linalool, a "primitive" essential oil. Secondary base numbers (13, 15, 17, 19) are derived from secondary polyploidy (the primary base numbers are ultimately derived from an initial "protopolyploidy"), after which secondary reductions occured in the manner of 2x-1. Unfortunately, Fujita did not attempt to correlate his limited cytological and biochemical data with other evidence. The floral morphology of S. sclarea is relatively specialized within the genus, and Salvia, with its specialized reproductive character states (see Chapter Four), can in no way be considered the primitive genus within the family.

Gill (1971) counted the chromosomes of 14 taxa from his own Himalayan collections, apparently unaware that seven of these were cultivated or adventive members of the New World subg. Calosphace, and at least two others cultivated as well. Almost all taxa were counted as either n=8 or n=11, one exception being S. involucrata (counted as n=7), notable because my own count of a Mexican collection (Reisfield 1213) was n=11. Also unusual was the report of n=8 for S. splendens, for which there have been several different counts reported, though 2n=44 (x=11) is by far the most common.

Afzal-Rafii (1971,1976) reported several more chromosome numbers which conflict with earlier counts, making more plausible the idea of numerous cytotypes within a species. *Salvia pratensis*, for example, a widely cultivated polymorphic entity with several recognized subspecies, has been reported to have 2n=16, 18, 20, and 32. 2n=16 and 2n=18 have each been counted by several workers and Afzal-Rafii (1971) suggested that the species is polybasic, with x=8, 9, and 10. *Salvia virgata*, an ally of *S. pratensis*, which twice has been previously counted as 2n=32, is here reported as 2n=16. A particularly interesting case is *S. tomentosa* (=*S. grandiflora*), which has been previously counted as 2n=14 and 2n=16; Afzal-Rafii (1976) maintained both these counts, describing the two as cytotypes allopatric in eastern and western Turkey, but overlapping in a small region where 2n=14, 15 (sic), and 16 were counted. This region of overlap, characterized by variable cytological and morphological forms and apparent evolutionary instability, also harbors two narrow endemics derived from *S. tomentosa*, each with 2n=16. All these entities exhibit meiotic abnormalities except the western populations with n=7, these most resembling the European *S. officinalis* (n=7) from which they were probably derived. This data suggests ascending aneuploidy in the eastern populations of *S. tomentosa*, where trisomy for one of the seven chromosomes or some other mechanism for chromosome gain has become stabilized to various degrees.

Vij and Kashyap (1976) report n=11 for S. leucantha, contradicted by Battacharya (1978) who counted n=16 (as did Carlson & Stuart, 1936), but later supported by Haque and Goshal (1980a), who again reported n=11. It is difficult to imagine that these discrepancies reflect cytotypes which differ in five pairs of chromosomes, though this is known for polybasic species which form aneuploid complexes (e.g., Claytonia virginica, Cardamine pratensis). In Salvia , S. verbenaca has six separate numbers: 2n=16, 32, 42, 48, 54, 64, and other uncounted forms would likely augment this total. These dysploid series, though, invariably involve substantial chromosome duplication, and the loss or gain of individual chromosome pairs could occur with fewer deleterious effects because the genomes are represented by duplicate copies. It is also unusual that in S. leucantha, the two proposed base numbers are those most common for the genus, suggesting that the chromosomes of Salvia somehow "want" to be in groups of 8 or 11. A similar situation exists for S. splendens, though this exhibits a more extensive dysploid series, with 2n=16, 20, 32, 36, and 40, though 2n=44 (x=11) is most commonly reported.

The possibility of mistaken counts is significant as the chromosomes of Salvia are tiny and often exhibit clumping or "sticking" during meiosis (Peterson, 1978). The division is very rapid and meiotic figures are not easily found, the figures often exhibiting various abnormalities. Battacharya (1978) reported pollen mother cells with varying numbers of chromosomes, laggard chromosomes during meiotic anaphase, and secondary association of bivalents. Haque and Goshal (1980b) also reported variations in bivalent numbers along with univalent and tetravalent formation, unequal anaphase separations, laggards and bridges, chromosome stickiness, ring chromosomes, and tripolar separation, and found these abnormalities to be directly correlated with increased pollen sterility. Many of these irregularities are likely the result of heterozygosity for inversions or translocations, suggesting that the nuclei are of heterogeneous origin.

Relevant to the reports of aberrant meioses is the fact that the plants studied are almost exclusively cultivated forms, with seed banks, breeding stations, and botanical gardens as the sources of material. It is reasonable that introgressive hybridization is more frequent under such artificial growth conditions as naturally operating isolating mechanisms are removed and desirable hybrid forms are nurtured. In addition, plants with reduced fertility due to meiotic abnormalities would not be selected against; in fact, such semi-sterility might be selected for if it is correlated with desirable morphological traits. It is apparent that the many discrepancies in chromosome number reports, though due sometimes to multiple cytotypes for a given species, are also occasionally artifacts of the research methods employed, or of unrepresentative source material. The real danger of misdetermined plants must also be considered. Voucher specimens, for many of these studies, if made at all, are deposited in Indian herbaria and thus unavailable for inspection. Misidentification is certainly suggested by the conflicting reports of $x=8$ and $x=11$, since these are the two most common base numbers for the genus.

Another possible, though unlikely, cause for chromosome number discrepancies is the secondary association of partly homologous (homeologous) chromosomes to form multivalents which may be mistaken for bivalents. If $n=11$ is derived from $n=8$ by the stabilization of the trisomic condition for three of the eight chromosomes, or from $n=16$ by the loss of five chromosomes, then a scenario can be constructed whereby a cell with n=11 might be miscounted as n=8 (9,10) due to three (or fewer) unrecognized multivalents. It is even possible that certain environmental influences or workers' research methods (e.g., fixation of material) may influence this behavior.

Finally, another possible source of error might be called "cytotaxonomic suggestion," whereby a worker faced with a difficult chromosome count is influenced by previous reports in the literature, in this case resulting in a bias towards x=8. When Carlson and Stuart (1936) counted n=16 for both S. leucantha and S. splendens, they had, at the time, no idea that these species were part of a group generally characterized by n=11. Although most wide disparities in the literature aren't likely to be caused by this type of error, the chance of such a mistake is increased when one considers the variation in number of bivalents in a mother cell encountered by some workers. Battacharya (1978) reported n=11 for S. nubicola but also noted cells with n=8, 9, 10, and 12. For S. splendens she reported n=22, but counted also n=15, 21, 23, and 30, and for S. leucantha she observed mother cells with n=11, 13, 16, and 17, reporting n=16. Could Battacharya, unaware of both the affinities of S. leucantha and previous reports of n=11, simply have "chosen" the wrong number to report?

It would seem to me that these explanations can not satisfactoraly be applied to the series of numbers reported for _S_. _splendens_ which is probably polybasic and represented by several chromosomal races. The species is distinct and many cultivated varietes are known. Although most workers report 2n=44 (x=11), others reported 2n=16 (x=8), 2n=20 (x=10?), 2n=36 ([8+10]x2 or [9+9]x2?), and 2n=40 (x=10?). While hypothetical origins for this heteroploid series with base numbers of 8, (9), 10, and 11 are here noted, one is reminded of the warnings of Davis and Heywood (1973), that "...the temptation to play chromosome arithmetic...must be resisted unless there is strong supporting evidence from other sources." Nevertheless, crosses between different cytotypes and chromosome duplication could yield new chromosome numbers, possibly stabilizing to form new cytotypes. The new races would have nuclei of heterogeneous origin, explaining the many irregularities noted. Battacharya observed that the chromosomal irregularities did not greatly reduce the percent seed set and, in fact, irregular gametes may remain viable and enter into fertilization, contributing to the origin of polyploids.

ORIGINAL CHROMOSOME COUNTS

MATERIALS AND METHODS

Flower buds were collected from wild populations and immediately fixed in Jackson's solution (4 ethanol: 2 methanol: 2 chloroform: 1 propionic acid: 1 acetone). After about 12 hours the buds were transferred to 70% ethanol and stored. Meiocytes were removed from the young anthers in 45% acetic acid and, before squashing, 1% carmine in 45% acetic acid and Hoyer's medium (Beeks, 1955) were added. These were viewed with a Zeiss phase-contrast microscope.

RESULTS

Few unquestionable chromosome counts were obtained due to several problems, some already mentioned by other workers. Chromosomes in Salvia are small and the meiocytes were full of tiny chromatin-like granules of no fixed number. These bodies were not confined to the nuclei but did, for the

Figure 26: Meiocyte of _Salvia_ _divinorum_ (subg. Calosphace sect. Dusenostachys)

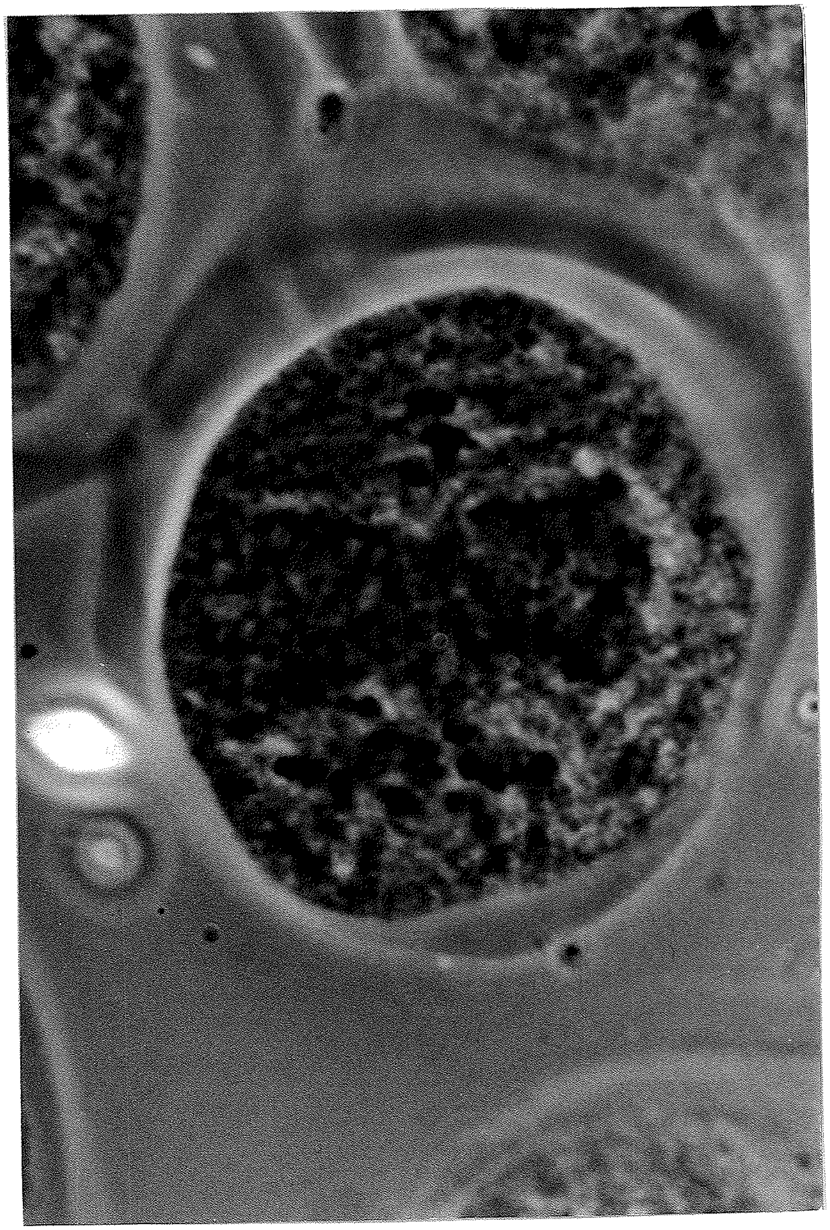


Figure 27: Meiocyte of _Salvia madrensis_ (subg. Calosphace sect. Longipes)

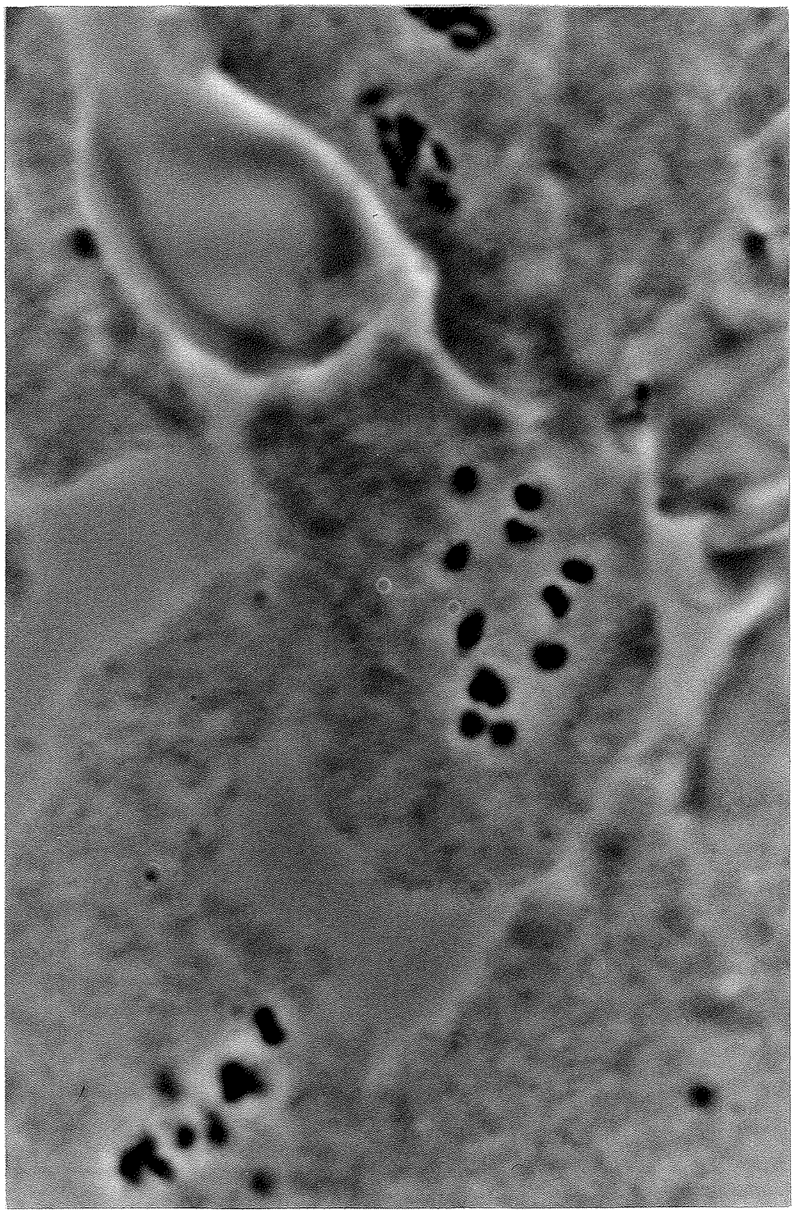
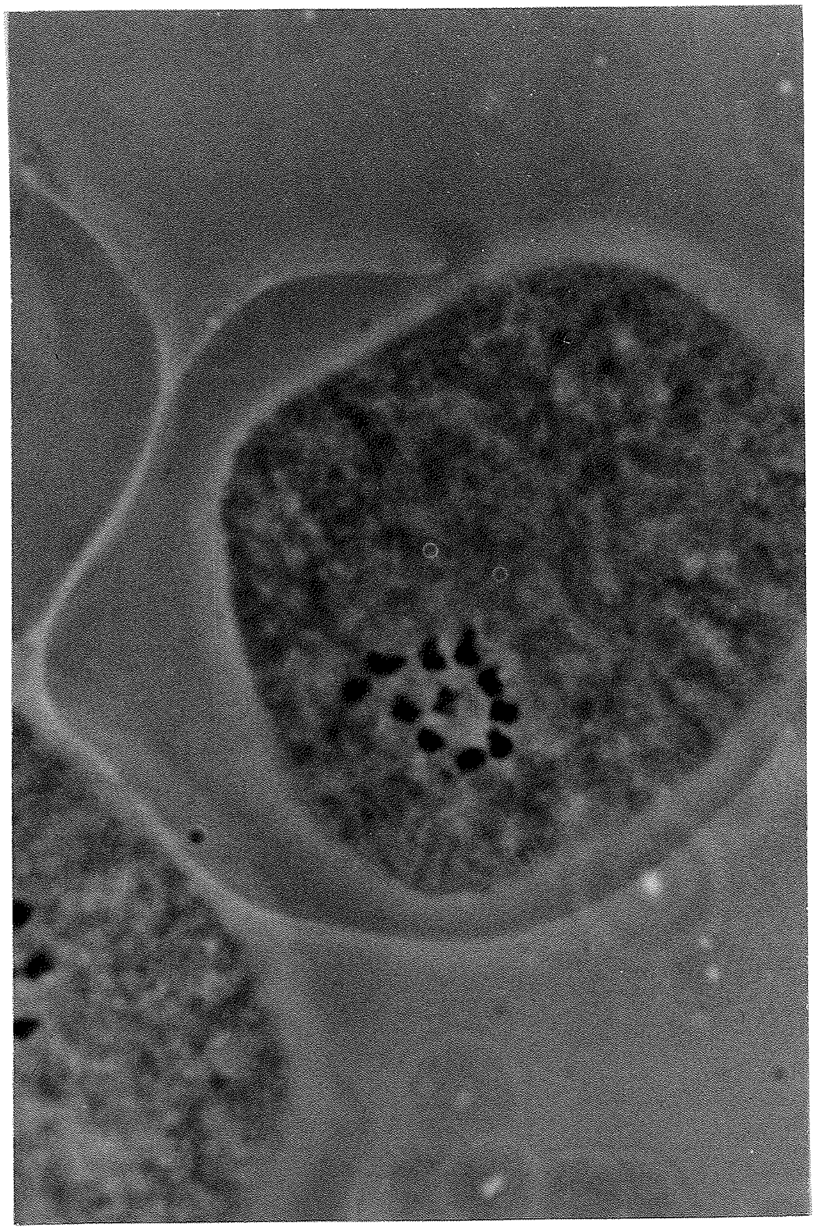


Figure 28: Meiocyte of _Salvia_ _involucrata_ (subg. Calosphace sect. Cardinales)



most part, disappear during the meiotic division. Meiosis is rapid and many anthers contained both immature meiocytes and tetrads of microspores. Occasionally chromosomes exhibited clumping or sticking, and it is assumed that the penetration of fixative into the anthers may have, at times, been too slow.

Chromosome numbers reported here with confidence are for S. madrensis [Reisfield #1302] (n=11; fig. 27), S. involucrata [Reisfield #1213] (n=11; fig. 28), and S. divinorum [Reisfield #1242] (n=11; fig. 26). Metaphase I and II were most useful for counting as the prophase chromatin was less condensed and not as discreet. The count of n=11 for S. involucrata conflicts with the earlier report of n=7 (Gill, 1971), while the other numbers are reported here for the first time.

DISCUSSION

A summary of all known chromosome counts suggests that Salvia species are highly polybasic as a group, with x=6 (1-3% of species sampled), x=7 (12-16%), x=8 (22-30%), x=9 (7-12%), x=10 (6-8%), and x=11 (17-19%). Percentages can not be known with precision because of conflictiong reports and questions involving synonomy. Furthermore, the species counted comprise less than 15% of the genus and the sample is biased toward cultivated entities. Secondary base numbers of probable polyploid origin, x=13, 15, and 17, have also been reported. These are not common, though n=15 is significant in characterizing 14 species of sect. Audibertia. Still more rare, though reported, are euploid series and dibasic polyploid sterile hybrids.

Trends with regard to chromosome number in the genus are not easily interpreted. The series of primary basic numbers for the family, in fact, are found repeated within the genus, within most subgenera and some sections, and possibly even within some species (e.g., S. splendens). The higher subgeneric categories of Bentham and Briquet which are based on calyx, corolla, and stamen morphology have been questioned (Hedge, 1974), and chromosome number reports have not generally supported the recognition of these higher taxa. At this point in time, there are few correlations between chromosome numbers and other characters, yet this can not be interpreted as negative evidence with regard to the higher categories. For subg. Calosphace, recognized as a natural assemblage by virtually all workers, reports exist representing every primary base number for the genus. There is reason to believe that within the range of x=6 to x=11, chromosome gains and losses have become independently stabilized several times.

There are several instances where chromosome numbers correlate with morphological variation, these patterns illustrating the potential value of cytology to taxonomy. Section Aethiopis (subg. Sclarea) is apparently characterized by x=11, an uncommon base number for Old World Salvia. Its species were distinguished by Bentham (1832) on the basis of cochleariform rudders and a calyx whose middle, upper-lip tooth is shorter than the laterals. Within subg. Calosphace, sects. Blakea and Hastatae of series Dilatae comprise a distinct group held together by their spade-shaped leaves and solitary blue flowers with characteristic short rudders. Three species of this alliance have been counted as x=9, a base number rare within subg. Calosphace.

Previous extrapolations on chromosome evolution in Salvia have not only been based on limited data, but have largely failed to take into account the alpha-taxonomic classifications devised for the genus. Haque and Goshal

(1980a) suggested a primitive or advanced status for various taxa on the basis of certain features of their karyotype. _Salvia farinacea_, for example, was proposed as primitive within the genus because the authors believe that its base number and uniquely large chromosome size indicate primitiveness. Since _S. farinacea_ is characterized by an asymmetrical karyotype, the authors conclude that the evolutionary trend within the genus is from an asymmetrical to a symmetrical karyotype. However, _S. farinacea_ belongs to the New World subg. Calosphace, which is almost certainly derived from an Old World taxon, and probably developed in prairie-like habitats in the south-western United States and northern Mexico, north of the subgeneric center of differentiation. Peterson (1978) studied sect. Farinaceae and was unable to comment with confidence on their degree of advancement. Haque and Goshal (1980a), whose report of 2n=18 for _S. farinacea_ conflicts with that of Peterson (2n=20), also elsewhere (1980b) described many meiotic abnormalities and suggested a hybrid origin for this species. As a group, sect. Farinaceae is polybasic and, in general, gives the impression of being evolutionary unstable. If indeed these are derived from other Calosphace species, karyotype evolution in _Salvia_ might entail an increase in the amount of chromatin per genome (in contrast with the views of Haque and Goshal), since the greatest amount has been reported for *S. farinacea*.

Salvia grahamii (=*S. microphylla*), *S. coccinea*, *S. tiliaefolia*, and *S. leucantha*, of various affinities within subg. Calsophace, are reported by Haque and Goshal (1980a) to be very similar in chromosome number (2n=22) and karyotype morphology. The karyotype of *S. reflexa*, also in subg. Calosphace but with 2n=20, is similar, as is that of *S. splendens* with 2n=44. Interestingly, *S. aethiopis* (sect. Aethiopis, subg. Sclarea) is said to fall into this group, perhaps identifying this taxon as an Old World ally of the derived, Neotropical subg. Calosphace.

While all the species with x=11 are described by Haque and Goshal (1980a) as having similar karyotype morphology, those with x=8 (*S. pratensis*, *S. horminum*) contrast strongly with each other, as do those with x=7 (*S. officinalis*, *S. nemorosa*). In general, species with x=8, the base number most common for the genus, form a more or less heterogeneous and fragmented group with distinct and sometimes relictual entities. *Salvia horminum* (2n=16), for example, has been placed in its own section alongside Aethiopis and Plethiosphace (subg. Sclarea). *Salvia* verticillata (2n=16; sect. Hemisphace, subg. Leonia) is also recognized as distinct; in fact, Bentham was tempted to describe a separate genus for this and two other species based on stamen structure. Neisess (1983) suggested that sect. Echinosphace (2n=32, x=8) is a distinct and possibly very ancient offshoot of Salvia, and these four species are highly relictual fragments of a very old taxon. Also distinct is sect. Notiosphace (subg. Leonia), in part comprised of S. plebeia (2n=16) and S. aegyptiaca (2n=28, x=7), these suggested by Neisess (1983) to have a pre-Gondwanaland breakup origin (quite unlikely, see Chapter Five). The base numbers x=7 and 8 are also associated with each other in sect. Eusphace (subg. Salvia) for which only these numbers have been counted (of 15 reports). In terms of floral morphology, the subgenera Salvia and Leonia have fertile secondary anther thecae and are probably primitive in the genus.

Conversely, the base number x=11, though second most frequent in the genus, is reported almost exclusively for two groups, sect. Aethiopis (subg. Sclarea) and subg. Calosphace. Though there are no obvious affinities between these taxa, a possible link with respect to karyotype has been mentioned above and a common ancestor is possible. A complete loss of secondary anther thecae characterizes both groups, each developing a different modification of the lower connective arm. Whether these links are actual or not, the data suggests an aneuploid progression within Salvia from 8 to 11, and perhaps from 7 or even 6 to 11.

Though aneuploid series more commomly entail reductions in chromosome number, there is evidence that increases are not uncommon in Salvia and the Labiatae. In fact, S. canariensis (x=11) is endemic to the Canary Islands and allied to the S. aurea group (x=8; sect. Hymenosphace, subg. Salvia) of South Africa (Hedge, 1974). It seems to me that S. canariensis, with completely sterile lower anther thecae, is derived from the continental entities with rudimentary secondary anther thecae. The probable progression from the European entities, S. officinalis and S. tomentosa (n=7), to the eastern populations of S. tomentosa (n=8) has been discussed above. In addition, Scora (1966) believes that within Monarda, x=11 is derived from x=9.

As mentioned above, Fujita (1970) proposed x=11 as the primitive number for the Labiatae and Salvia, and Salvia as primitive within the family. This claim is supposedly supported by the distribution of essential oils in the genus, but conflicts with data from floral morphology which suggests a derived status for Salvia. On the other hand, the closely allied Rosmarinus apparently has a gametic number of 12 (as does the somewhat more distant Horminum) which may strengthen Fujita's claim. This would imply aneuploid reductions from 11 to 6 occuring independently in different genera of the family, and in different subgenera and sections of Salvia. In some ways this mode of evolution is most plausible as aneuploid chromosome losses would be viewed as a consistent trend within the Labiatae. A duplication of a primitive genome with n=6 to give n=12 for Rosmarinus would be consistent with the view of x=8 as primitive within Salvia, but this would imply an early aneuploid progression within the genus followed by losses of chromosomes within subg. Calosphace. On the other hand, claims which consider taxa with x=11 as hypoploids, derived from a higher polyploid number, are not consistent with the extant variations of the basic series between n=7 and n=11 in different groups of different ranks.

While information is clearly insufficient to offer a conclusion with confidence, I feel that the existing body of data supports the view that the early evolutionary expansion of Salvia was associated with an aneuploid gain in chromosome number, with x=8 being most primitive. It is clear that the numerous meiotic irregularities reported and a lack of a satisfactory infra-generic system are due to a complex evolutionary history where the origin of phylads has sometimes involved introgressive hybridization. Though many groups within Salvia are today in an active state of evolutionary flux, some species and sections appear static and relictual. Evidently, The history of Salvia has been characterized by cytological changes which have occured during widely separated periods of speciation.

Battacharya (1978) emphasized the importance of structural alterations of chromosomes in the evolution of various phenotypes. Haque and Goshal (1980b) elaborated on this, saying that "...polyploidy and alteration of chromosome morphology are the two principle factors associated with speciation in Salvia." Yet in the same publication they discussed the close similarity between the karyotypes of four Calosphace species which are widely different in almost every other way. Epling, et al. (1962) stressed the much studied morphological and ecological differences between S. apiana and S. mellifera, these not associated with structural change or repatterning of the chromosomes as indicated by the nearly complete meiotic pairing in hybrids between the two. It is possible that the importance of karyotypic rearrangement in Salvia speciation varies between different phyletic lines. For subg. Calosphace, selection for pollinators seems to be most important in the various evolutionary diversifications, though cytological factors may certainly be involved in post-zygotic isolating mechanisms. Within the genus as a whole, there is little correlation between morphological change and variation in chromosome number, and this cytological character, like other characters often studied, is not necessarily connected with the heredity of forms.

CHAPTER SEVEN

FLORAL ISOLATION WITHIN SALVIA SUBGENUS CALOSPHACE

With approximately 275 species in Mexico and nearly 200 species in South America, the New World subg. Calosphace accounts for over half the species of Salvia. The success of the genus in general, and of subg. Calosphace in particular, has been discussed above, and credited, in part, to an opportunistic capability to adapt to new environments. Many of the the numerous local endemics in the Neotropics are apparently derived from populations of more widespread species which have been isolated on mountain tops, gorges, and otherwise isolated woodlands, or in geologically differentiated areas such as calcareous plateaus. Various mechanisms for allopatric, sympatric, gradual, and quantum ("catastrophic") speciation in flowering plants have been proposed (Stebbins, 1950; Baker, 1963; Lewis, 1966; Grant, 1949, 1971; Levin, 1978), but the theory of gradual divergence of spatially isolated populations (Mayr, 1942) continues to be widely favored. In this model of speciation, populations would become reproductively isolated as a by-product of divergent evolution, since changes caused by mutation, recombination, and selection are occuring independently in the separated populations. Derived isolating mechanisms would tend to reinforce or augment the effeciency of the primary speciation which is allopatric. Mayr (1942) has since stressed the distinction between the older "dumbbell" model of speciation and the more recently favored founder population or "peripatric" model, in which a gene pool of a small population is rapidly and drastically reorganized, resulting in the quick acquisition of isolating mechanisms along with drastic morphological modifications and ecological shifts. Given the highly fragmented nature of the montane Neotropical landscape, the effects of founder populations evolving in isolation are no doubt important. Still, there is certainly more than one speciation model which characterizes Calosphace evolution, though our knowledge in this area is limited, as is our understanding of isolating mechanisms in Salvia.

Nevertheless, it is certain, judging from the exceptional variation in flower structure and color, that pollinating mechanisms play a significant role in the speciation process. The adaptation to different pollinators would, indeed, augment geographic speciation, but my observations of flower types and their pollinators in Mexico suggest that the role of pollinators in Salvia speciation is complex, and perhaps of primary importance. It is generally accepted that the origins of reproductive isolating mechanisms are not only incidental but may be the object of selection (Grant, 1949, 1971; Levin, 1978), but the question of whether adaptation to two different pollinators may initiate strictly sympatric speciation is somewhat more open. I will not address this question here, nor review the various debates over proposed models of speciation, but will try to show that in Salvia speciation, at least, the role of pollinators is of the highest significance, and may be of far greater importance than that of a gradual, incidental reinforcement of barriers set up by spatial isolation, or perhaps even more significant than the augmenting of drastic speciation in founder populations. The focus of the following discussion then, will be floral isolation, and its significance in speciation of subg. Calosphace.

FLORAL SYNDROMES

Flowers of subg. Calosphace are here divided into three basic types. The first is the classical melittophilous (bee) blossom, occuring in a great number of species which are often distinguished with difficulty because of the great redundancy of this flower type. The corollas are always a shade of blue, the tube short and ventricose, the lower lip large in proportion to the blossom, and the lever mechanism operative. The large and taxonomically difficult sects. Angulatae and Polystachyae serve as good examples of such bee flowers. Generally, these are light or sky-blue and the corolla tubes are only a few mm. long, but variations in shade of blue are common, and a subset of this group has slightly larger, dark blue flowers (e.g., _S. flaccidifolia_).

The second flower type is the classical ornithophilous blossom, cited in various pollination ecology treatises (e.g., Faegri & Van der Pijl, 1979) to illustrate the hummingbird pollination syndrome. The slender corolla tube is greatly elongated, the landing platform much reduced in size, the stamens exserted and the lever mechanism inoperative, and the flower brilliant red. Species clusters such as Cylindriflorae and Incarnatae are examples, these sections with significantly fewer species than the large, melittophilous complexes. The pollination mechanisms for both of these basic types have been discussed in Chapter Four.

The third category of flower type within subg. Calosphace must be much more broadly defined. In short, these are flowers which do not fit neatly into either of the classical floral syndromes. They may be, for example, large (6 cm.), fiery red flowers which gape wide open and have movable stamens (S. fulgens); violet-purple flowers with slightly exserted, movable stamens and a slender, cylindrical corolla tube (S. purpurea); large (4.5 cm.), gaping, blue flowers with a wide throat and falcate galea (S. patens); purple flowers with a long (2.5 cm.), sigmoid corolla tube, a reddish galea and blue lower lip (S. pichinchensis). Many flowers belong in this intermediate category, some of which deviate only slightly from one of the classical syndromes, while others seem anomolous from the standpoint of pollination ecology.

Entities within subg. Calosphace are largely distinguished by corolla characters subject to strong selection for pollinators, but which pollinator is favored by a given corolla conformation is often unclear. The great diversity of corolla character states suggests adaptive radiation for pollinators, but the large number of flowers which seem not to be specialized for a particular pollinator suggest that they are in a transition phase. Within the evolutionarily active subg. Calosphace, there are many local neo-endemics, as there are closely related clusters of species and polymorphic entities. The young age of many species of subg. Calosphace, though, is also reflected by the many intermediate pollination syndromes.

Bees which pollinate *Salvia* flowers are large and strong enough to activate the lever mechanism. Butterflies, lacking such strength, rarely feed on *Salvia* flowers, although I have seen them on an individual of *S. elegans*, where the lever mechanism has degenerated and there is an open pathway to the deeply contained nectar. Lepidoptera may presumably visit other similar, cylindrical *Salvia* flowers but apparently do so rarely. Likewise, smaller insects are not strong enough to push past the stamen rudders, and should they do so, would not be in the position to be dusted with pollen. Mexican salvias, then, are not promiscuous, yet both bees and birds can potentially transfer pollen between flowers of many species.

The pollinators which visit the flowers of a given population of plants most frequently and effectively in a given region will co-evolve with the flowers. Floral characteristics such as corolla color and architecture are molded by these pollinators (Stebbins, 1974; Grant, 1949). But species which restrict their flowers to a single pollinator are probably infrequent, and it is generally believed (Baker, 1963; Stebbins, 1974) that changes in plant-pollinator relationships usually occur gradually, by a process of "bridging." Specialization for bee pollination may give way to adaptations for bird pollination if a plant population receives a greater number of pollinating visits by birds, but there will be an intermediate stage during which both vectors will be capable pollinating the flower.

In terms of numbers of _Salvia_ species, bee flowers predominate. Floral isolation and divergence in relation to the constancy of bees has been documented for _Salvia_ species and other flowering plants (Grant, 1949, 1950; Grant & Grant, 1964). Whatever the precise mode of speciation, the ability of bees to perceive likenesses and differences in flower color, form, and odor, has certainly been important in the radiation of bee-pollinated salvias throughout the New World. The diversity of melittophilous species in the genus is such that it may promote the development of mechanisms which would invite visitation by birds. Competition among the plant species for flower-visiting bees would be lessened by adaptations to hummingbirds (Grant & Grant, 1968; Levin, 1978). Many Old World and northern bee-pollinated taxa of flowering plants have come into contact with the family of hummingbirds centered in the Neotropics, initiated by the migration of plant taxa or sometimes by that of the birds. Entities within many of these melittophilous families and genera have changed over in their mode of pollination to exploit the new potential pollinators. Grant and Grant (1968) cited numerous examples of bee-pollinated genera with species that have changed over to bird pollination. For example, several different sections of Penstemon in California have independently undergone this transition. The Old World progenitors of subg. Calosphace are also certainly melittophilous species, as are the most primitive representatives of Calosphace in the New World.

The taxonomic difficulty within subg. Calosphace is, in part, due to the repeated shift from melittophily to ornithophily in many different phylads, transitions which are still occuring and can be observed in various stages today. The consequent convergent adaptations have tended to obscure phylogenetic relationships, and so while hybridization is apparently not common, patterns of relationships often appear web-like and character states occur in various combinations. The result, then, of the repeated, independent, adaptive radiations for both bee and bird pollination has been a great diversification of species, but also, to the student of the genus it has caused a great deal of taxonomic confusion. Observations supporting some of these ideas are presented below.

Of 91 sections erected by Epling (1939a), 43 are comprised exclusively of red-flowered species, accounting for about one third of the species in subg. Calosphace. About half of these sections are South American, the remainder either Mexican or on both continents. The greater number of South American ornithophilous species correlates with the greater hummingbird diversity there, especially in the Andes. Many characters which distinguish these species relate to the dimensions of the floral tube, and this can be viewed in light of the diversity of bill proportions of South American Hummingbirds (Grant, 1949). There are, to be sure, cylindrical blue flowers which are pollinated primarily by birds, though the opposite case of bees pollinating red flowers does not occur. Since bees can not see red wavelengths of light, there is seldom a question concerning the co-evolved pollinator of a red flower, and the various floral architectures indicate only the degree of specialization.

CASE STUDIES

Salvia fulgens has brilliant, scarlet corollas which are as long as 6 cm., but have not been structurally modified in any other way for pollination by birds. There is a large, landing platform, included stamens, and, while the lever mechanism shows some sign of degeneration (the rudders do not completely occlude the tube), it is still operative. The slightly smaller flowers of *S. mexicana* var. *major* are similar, except that they are dark blue. I observed hummingbirds pollinate the flowers of both these species, and at Mil Cumbres (Michoacan), a bird ignored the red flowers of *S. fulgens* and *S. iodantha* while pollinating all open, blue flowers of *S. mexicana*. Wagner (1946) reported that the white-eared hummingbird (*Cynanthus leucotis*) visits *S. cinnabarina* (with red flowers) and *S. cacaliaefolia* (with blue flowers) in Guatemala, while feeding almost exclusively on *S. mexicana* (with blue flowers) in Mexico. This bird avoids flowers of *S. cardinalis* [=*S. fulgens*] which is pollinated by the larger, blue-throated hummingbird. The Mexican violet ear (*Colibri thalassinus*) is also reported by Wagner to favor the montane flowers of *S. cinnabarina* and *S. cacaliaefolia*. *Salvia mexicana* var. *minor* has smaller flowers, is sympatric in range, but is never found with var. *major* at a given site. There are apparently some intermediate forms, but the extent of divergence of the two subspecific entities is not clear. Birds can also be found visiting the flowers of *S. mexicana* var. *minor*. A digger bee (*Anthophora* sp.) visiting *S. mexicana* var. *major* (*Reisfield 1273*) and a bumblebee (*Bombus nigrodorsalis*) systematically piercing the calyx and corolla from the side and robbing nectar from flowers of *S. mexicana* var. *minor* (*Reisfield 1281*) were observed. Although the flowers of var. *minor* do not have a very long corolla tube, the bumblebee, which I also observed on *S. lavanduloides* which has smaller flowers, may be incapable of legitimately pollinating flowers of this taxon.

The corolla architectures of *S. divinorum* and *S. madrensis* somewhat resemble each other, both species with the lower lip reduced and the throat constricted, but with a sigmoid tube in the former. The flowers of S. madrensis are yellow, a rarity in subg. Calosphace (there are only four other known yellow-flowered species in Mexico), and the structure of the corolla seems intermediate with regard to specialization. The corolla of S. divinorum is white, while the calyx and rachis are violet. Older flowers develop a blush of blue distally, suggesting that the white color may be due to an inhibitor blocking pigment synthesis rather than the loss of an essential enzyme (Harborne, 1967). The shift in corolla color from blue may be associated with an evolutionary shift in pollen vector. I observed a hummingbird systematically visit the flowers of one population (Reisfield 1242) at dawn, returning several times and effectively transferring pollen. Apparently attracted by my orange poncho which was worn with some local hunters in mind, it hovered in front of my face for some time. Because of the well known tendency of hummingbirds to investigate brightly colored objects, I was able to inspect its conspicuously decurved bill, significant because of the sigmoid shape of the corolla tube of S. divinorum. Two bumblebees were also active but ignored the white-flowered Salvia, and I have never seen any bee legitimately pollinate its flowers. [See Chapter

Eight for a detailed discussion of the botany of this species].

Salvia purpurea and S. iodantha are placed in different sections by Epling (1939a), distinguished by the exserted stamens of the former, but the distinction is minor. The two species, which can sometimes be found growing together, are very similar, but can be separated by details of the corolla: the style of S. purpurea is sometimes pubescent below the stigma, but glabrous in S. iodantha; the length of the connectives and degree of stamen exsertion may be one to several mm. longer in S. iodantha; the calyx of S. purpurea is usually more pubescent with attenuate teeth, while that of S. iodantha has a somewhat truncate mouth; the corolla of S. purpurea is violet-purple, while that of S. iodantha is slightly redder, often recorded as wine-red. Salvia purpurea is a widespread, variable, and conspicuous element of southern Mexico's landscape, and is often teeming with bees. Salvia iodantha, concentrated in western Mexico, is apparently pollinated only by birds. At Mil Cumbres (Michoacan), S. iodantha is a locally common shrub on a steep slope in a Pinus forest. Among these plants, I observed one individual of S. purpurea (Reisfield 1271) being pollinated by a bee which ignored all individuals of S. iodantha (Reisfield 1270). The two entities at Mil Cumbres are virtually identical in floral architecture, and the main observable difference, though subtle, is that of color. I suspect that these species (and others in sects. Purpureae and Iodanthae) are very closely related, and that S. iodantha has become inconspicuous to bees, guaranteeing a supply of nectar for a hummingbird pollinator.

Salvia recurva has large (ca. 5 cm.), deep blue flowers, of the same general conformation as those of S. fulgens and S. mexicana, with minor differences. The throat is wide enough so that bees are not denied entrance to the tube, and I observed bees inserting their heads into the tube and activating the lever in that way. While no birds have been reported visiting these plants, the flowers suggest that they may be subject to selection for increased corolla size. The corolla color of one Vera Cruz population (Reisfield 1220, in part), a purplish, wine-red or burgundy, is similar to that of the bird-pollinated S. iodantha. This color polymorphism might potentially act to isolate populations, and thus might be viewed as an early stage in their divergence. Color morphs are also regularly found in populations of sect. Carneae, a taxonomically troublesome complex of entities which grade into one another. Bumblebees (Bombus formosus) were observed on small, purple-flowered plants in the Estado de Mexico, while large bees (Deltoptila sp.) pollinated larger, blue and purple-flowered forms in Guerrero (but also smaller-flowered forms in Guerrero). This species group illustrates, to some degree, the dynamics of evolution within subg. Calosphace, and so a detailed account follows.

The Salvia gracilis complex

Epling's (1939a) sect. Carneae consists of perennial herbs characterized by included stamens, a three-veined upper calyx lip, and purple (blue) flowers with papillate, ventricose corolla tubes and a lower lip usually longer than the upper. These have been distinguished from sect. Angulatae with small, epapillate blue or white flowers, and from sect. Polystachyae with shorter petioles and denser inflorescences of blue or white flowers. The species of sect. Carneae are widely distributed in mountainous regions, especially those of volcanic origin, from the Mexican state of Hidalgo south to Colombia. While Epling assigned nine species to this group, he was well aware that several of these were vaguely delimited and apparently in the throes of evolution. The Mexican and Central American forms had been named variously by Bentham, Fernald, and Epling, the latter author starting a list of synonyms which grew as collections accumulated.

Following Epling's (1939a) treatment, most of the entities have been recognized either as the small flowered *S. gracilis* Benth. or the larger flowered *S. membranacea* Benth. Many of the Costa Rican collections are substantially more pubescent, with leaves dark purple beneath, and large, purple flowers (corolla tubes 15 to 19 mm long), these segregated as *S. iodochroa* Briq. Two collections from Hidalgo and Puebla have similarly large purplish flowers, with narrow corolla tubes (14 to 17 mm long) which are sigmoid, curving upward from the calyx, these plants named *S. simulans* by Fernald (1907). Collections with even larger flowers (corolla tubes over 20 mm long) from Guerrero were later named *S. punicans* by Epling (1940). Recent collections from Panama (e.g., *Stevens #18153*) are very similar.

While the slender, sigmoid corolla tubes of *S. simulans* do seem somewhat distinct, the corollas of the other large flowered forms are virtually identical to their smaller flowered allies, save a slightly longer galea and tube more gently ventricose. Plants with slightly shorter corolla tubes (about 15 mm long) but otherwise identical have been found in Guerrero, Oaxaca, and Panama, and these are usually annotated as *S. membranacea*. Following Epling (1939a), entities of this species complex are called *S. gracilis* if the corolla tubes are shorter than 10 mm. Specimens from Chiapas with epapillate corolla tubes but otherwise like *S. gracilis* were named by Epling (1939a) *S. pseudogracilis*.

As material of this conglomeration of species has accumulated, it has become apparent that the lines between the different types are indeed blurred and most of the Mexican and Central American entities are probably flower size races of one variable "swarm." There can be little doubt that *S. gracilis* and *S. membranacea* are conspecific, though the status of *S. simulans*, *S. punicans*, and *S. iodochroa* is less obvious. Though both *S. iodochroa* and *S. punicans* apparently also grade into smaller-flowered and glabrate forms, the extremes of these series are quite distinct.

Most of the entities now known as *S. gracilis* and *S. membranacea* should be recognized by the former name as this was described first in Bentham's *Labiatarum* (1832). But the upper limit of corolla size on a plant going by this name must here remain an open question. Certainly mass collections, careful observations of whole populations in the wild, experimental crosses, uniform environment growth experiments and other biosystematic techniques would shed light on the problem. The species cluster will here be referred to as the *S. gracilis* complex.

Synonyms of *S. gracilis* considered by Standley and Williams (1973) were *S. membranacea*, *S. pseudogracilis*, *S. myriantha*, and *S. natalis*. *Salvia myriantha* is certainly very similar. As described by Epling, this entity from Guatemala and Chiapas (and Mt. Orizaba?) is distinguished from the *S. gracilis* complex by its white flowers with epapillate corolla tubes, and, in fact, is placed in a different section, Angulatae. The many collections of Standley and Williams from Guatemala indicate that the distinction between *S. myriantha* (Angulatae) and *S. gracilis* (Carneae) is problematic. Although the Guatemalan populations (mostly referred to as *S. myriantha*) have somewhat denser inflorescences and more pubescent leaves, the taxonomic significance of corolla color is questionable, especially since flowers of sects. Angulatae and Polystachyae vary from blue to white on different individuals. The significance of corolla tube papillae must also be questioned since *S. pseudogracilis* represents an entity with epapillate corollas but otherwise identical to *S. gracilis*. Whether conspecific or not, *S. myriantha* certainly represents a link between the small, blue and white-flowered sect. Angulatae with epapillate corollas, and the pink and purple (red, blue, white) flowered *S. gracilis* complex with papillate corollas.

The inclusion of *S. natalis* in Standley and Williams' (1973) list of *S. gracilis* synonyms is significant because it too is placed by Epling in a different section, Maxonia. Members of Maxonia have blue, papillate corollas with a lower lip subequal or shorter than the upper, and a usually five-veined upper calyx lip. The series of flower sizes in the *S. gracilis* complex illustrates that the lips of the larger flowers tend to be subequal while the lower lip of small flowers is generally longer. Yet the corolla tube of *S. natalis* is not long (10 mm), and it is not clear whether the entity is misplaced in sect. Maxonia, misinterpreted by Standley and Williams, or represents an actual link between sects. Maxonia and Carneae.

A Hinton collection (14798) from Guerrero, apparently representing a large-flowered entity within the S. gracilis complex, was named S. sapinae by Epling (1941) and placed in sect. Uricae. Apparently, individuals of this entity may have an upper calyx lip with 3, 5, or 7 veins. Also, an extremely large-flowered form from Chiapas, named by Epling (1939a) S. matudae, was placed in sect. Purpureae, but may be identical with that which he named (1940) S. punicans.

Section Polystachyae is another large complex with blue or white corollas, these distinguished from sect. Carneae by the shorter petioles and more crowded inflorescences, and from sect. Angulatae by the papillate corolla tubes. Epling (unpubl.) eventually felt that sect. Polystachyae was hardly to be separated from sect. Angulatae. It is clear that with more and better material at hand, the lines between the groups discussed here are increasingly blurred, and the web-like pattern of relationships between the entities defies classification by orthodox, taxonomic methods.

From Volcan Orizaba, there are a group of collections of somewhat pubescent plants with biserrate leaves and epapillate blue flowers resembling those of the S. gracilis complex, referred to by Epling as S. biserrata. The calyces relative to the corolla are shorter and stouter than those of S. gracilis, much like those of the allied S. flaccidifolia, both originally placed by Epling in sect. Dusenostachys. While Epling (1941) transferred S. flaccidifolia into sect. Angulatae near S. myriantha, S. biserrata was viewed by him (Epling, unpubl.) as part of the S. gracilis complex, here recognized as S. membranacea. It is apparent that Epling had decided at this point to disassemble sect. Dusenostachys and the transferrals were made somewhat randomly. Salvia flaccidifolia, at least, is quite distinct from the many members of sect. Angulatae.

The difficulty in delimiting taxa within sect. Carneae is understandable considering the apparent state of active evolution in this group, but the reticulate pattern of relationships may yet be more significant. Not only are lines between allied species unclear, but even the major series within subg. Calosphace blend together. Thus the large, red or purple-flowered type which suggests ornithophily (S. punicans) is at one end of a continuum of entities, while the small, blue-flowered melittophilous type (S. gracilis) is at the other, the two extreme types almost identical in all other aspects. Of the various flower size morphs, I have found only a single form growing at any one site, and it is likely that most populations would intergrade upon contact. On the other hand, were the extreme forms of this floral continuum to become sympatric, they would probably be reproductively isolated by their different pollinating mechanisms, suggesting a "ring of races" like that described by Grant (1971) for Diplacus puniceus (Scrophulariaceae).

That these species of Salvia (and others) thus seem to be undergoing divergence in relation to pollinators can hardly be questioned. Most of the flower size and color morphs are pollinated by various bees, but the large-flowered forms, if not actively subject to selection by hummingbirds, are certainly pre-adapted to such bird pollination. If birds are or newly become the exclusive pollinators, it is conceivable that the plants would diverge relatively rapidly from their allies. In this way, the affinities of many natural groups are obscured, and delimitation of sections based on convergences of corolla size and color, both subject to strong selection by pollinators, is often artificial and confusing. Unfortunately, other characters such as habit, indumentum, corolla tube papillae, and even calyx venation, do not express variation in a way that can help the taxonomist to easily solve these problems.

THE TRANSITION FROM MELITTOPHILY TO ORNITHOPHILY

While the detailed mechanisms of speciation in Salvia are beyond the scope of this discussion, certain important aspects of this process can be mentioned. If the range of a taxon is extended beyond the boundaries of its primary pollinator or into an area where this pollen vector is scarce or unreliable, adaptations may give way to those favoring a new, more effective vector (Stebbins, 1974). Since many entities of subg. Calosphace are apparently transitional with respect to pollinator, we can assume that they have come into contact with new potential pollinators, and the relationships with these animals are dynamic. The diversity of terrain in the Neotropical highlands can be correlated with a diversity of insect fauna, and the colonization of a new area is likely to bring a population of Salvia into contact with a new, potential pollen vector.

Thus the role of genetic drift in speciation within the rapidly evolving subg. Calosphace is probably minor compared to that of selection for new pollinators. Such selection would likely be rapid in many cases, due to the drastic effects experienced by founder populations.

As Cruden (1972) has pointed out, hummingbirds are active throughout the day regardless of clouds or rain, while bees are relatively poor pollinators under such conditions. High elevations in Mexico are often characterized by such poor flight conditions, and for this reason have more bird-pollinated species than middle elevations. The transition from blue-flowered salvias to red flowered ones is evident when one drives up a steep mountainside. A plant population at lower elevations, adapted for pollination by long-tongued bees or transitional in specialization, can be considered pre-adapted to hummingbirds. If such plants colonize a new montane habitat where the sun rarely shines, chances are that birds will replace bees as the primary pollinators, and characteristics of the flower will be selected by the new pollinators.

The pre-adaptedness of many melittophilous populations to hummingbirds seems to be a key element in the transition.

The pre-adaptations include both those of floral architecture and color. Birds have been observed to regularly feed on bee flowers (Grant & Grant, 1968), returning again and again, and it is possible that such "illegitimate" visits may influence the direction of evolution. Some populations transitional in pollinator specialization may, at a given time or place, be pollinated by bees and birds with equal effectiveness. The evidence for floral constancy in birds is mixed, but they can apparently be very constant to a single flower in a given area over a given period of time (Grant, 1949). Adaptations for long-tongued bees may also prepare a flower for the transition to hummingbirds. In addition, the nectar preferred by birds, in that it is sucrose-rich, is similar to that enjoyed by long-tongued bees (Baker & Baker, 1983).

Flower Color

The importance of flower color is not so much in attracting hummingbirds, but, by excluding insects, nectar is reserved for the bird vector. A survey of the many corolla types within subg. Calosphace reveals that the modification of the gene pool necessary to effect a shift in color from blue to red is a relatively simple one. Occasional purple flowers on blue-flowered plants is the result of a recessive red factor being expressed in the homozygous state (see below) and indicates that color polymorphism is not uncommon. Grant (1949) has detailed the steps whereby a recessive factor might spread through a population in the heterozygous condition, segregating out upon reaching a critical frequency. The appearance in one generation of many red-flowered mutants, if fixated upon by birds, may lead to a divergence of populations. The significance, though, of a gene pool polymorphic for color factors is not in supporting the notion of sympatric speciation, but in explaining the apparent ease of transition from blue to red flowers. Among the many corolla types of subg. Calosphace, there are no tiny flowers with large landing platforms which are red, but there are many flowers which, except for their brilliant red color, do not fit the ornithophilous syndrome. Presumably, the stage is set for these flowers to increasingly develop more specialized adaptations for hummingbirds.

The biochemical basis for color in higher plants is fairly well understood (for pertinent literature, see Scott-

Montcrieff, 1936; Beale, 1941; Harborne, 1967; Scogin, 1983). There are three, major pigments which, either singly or in mixtures, impart color to flowers. These anthocyanins, based on a single aromatic structure ,differ in the number of hydroxyl groups attached to the phenyl "B"-ring. Pelargonidin, cyanidin, and delphinidin are the skeletal forms of the glycosidic anthocyanins (called anthocyanidins) with one, two, and three hydroxyl groups respectively. Most flower color variation is due to mutations at genetic loci controlling anthocyanidin hydroxylation. A single mutant gene may result in a plant's inability to produce an enzyme necessary for hydroxylation of an anthocyanidin. This is apparently what often occurs in nature, as delphinidin, which is present in blue flowers, is the most complex of the three anthocyanidins, requiring the greatest number of steps in its synthesis. Pelargonidin, present in pink and red flowers, is a simpler substance requiring fewer stages for its synthesis, and derived from cyanidin or delphinidin by a "loss" mutation. The enzyme needed to attach an hydroxyl group to the "B"-ring is absent, and pelargonidin is considered recessive. Mutants in nature are usually loss mutations, and pelargonidin-containing red flowers are derived from cyanidin or delphinidin-containing blue or purple flowers.

The correlation between anthocyanidin and pollinator is quite regular, as bird flowers usually contain pelargonidin and bee flowers contain delphinidin, while cyanidin may be found in either type (Harborne & Smith, 1978). The dominance relationships of the pigments can thus be correlated with evolutionary shifts in pollen vectors within subg. Calosphace and other groups of flowering plants. All three types of anthocyanidin have been extracted from Salvia flowers, in fact seven kinds of anthocyanins were isolated from petals of S. splendens (Shibata, et al., 1966). These variants of the three main anthocyanidins differ from each other in the number and nature of sugar substitutions, and additional fine-tuning of flower color is due to variations in the amount of pigment, the ph of the cell sap, co-pigmentation, metal complexing, and other factors. The large range in color expressed by Salvia flowers is due to the presence of variants of the three anthocyanidins in different combinations along with modifying factors, and evolutionary change is almost always from blue to red.

Sympatry and Hybridization

Of almost 1000 species in the genus, only a few Californian species have been studied with respect to reproductive biology (see Epling, 1947b; Anderson & Anderson, 1954; Grant & Grant, 1964). Hybridization between *S. apiana* and *S. mellifera* was found to be restricted by ecological, seasonal, ethological, and especially mechanical isolating mechanisms, as well as partial sterility and lack of pollinators for the hybrid. Hruby (1935) found few genetic barriers to hybridization between species within sect. Plethiosphace, but far crosses attempted were not successful.

The degree and patterns of sympatry exhibited by salvias in Mexico highlight the significance of floral isolation. It is not uncommon to find as many as six species growing at a given locality, usually characterized by diverse flower types. For example, between a *Pinus*-*Quercus* forest and a disturbed streamside at Yalichin (Chiapas), *S. polystachya* (*Reisfield 1226*), *S. cinnabarina* (*1227*), *S. lavanduloides* (*1228*), *S. purpurea* (*1229*), *S. karwinskii* (*1230*), and *S. recurva* (*1237*) all grow within several dozen meters of each other. The only real overlap in flower type is between the small, blue flowers of *S. polystachya* and *S. lavanduloides*, and these differ in the larger corolla of the former species. The taller stature of *S. polystachya* may also act as an ethological isolating mechanism (Levin, 1978). Yet plants of *S. polystachya* can be found growing beside other salvias with very similar corollas. Near Patzcuaro (Michoacan), *S. polystachya* (*Reisfield 1284*), *S. fluviatilis* (*1283*), *and S. thyrsiflora* (*1285*) grow side by side. A variant form of the first species with smaller, lilac corollas suggests that there may be some breakdown occuring, but this is not clear. In general, *Salvia* hybrids are difficult to recognize as such because of the great number of species and the large range of variation.

Throughout Mexico, I observed many bees on *Salvia* flowers, including species of *Bombus*, *Xylocopa*, *Anthophora*, *Deltoptila*, and *Apis mellifera*. Some bee species were found to visit more than one species of *Salvia*, but the significance of this is unclear since the overlap was not at one site, but the different salvias were in widely separated areas. The complexities of population ecology have been pointed out by Davis and Heywood (1973) who recognized that various factors causing reproductive isolation occur at different intensities, evolve at different rates, and operate in different parts of populations in different ways, and with various degrees of effectiveness.

Summary

I have attempted, in this discussion, to stress the significant role played by pollinators in the adaptive radiation of subg. Calosphace. The numerous, independent shifts from melittophily to ornithophily in different phylads, and the transitional nature of many flowers has been emphasized. Some aspects of the speciation process have been touched upon, but it is stressed that isolating mechanisms in Salvia are very little understood. The focus of this discussion has been floral isolation, both ethological and mechanical, which may either actively augment an isolation originally set up by geographical or ecological factors, or possibly initiate a divergence of populations. The role played by the various post-mating reproductive barriers such as cross-incompatability and hybrid sterility is not known. Nevertheless, it is the co-evolution between plant and pollinator which is, without doubt, of the highest significance in speciation of

Neotropical _Salvia_ species.

CHAPTER EIGHT

THE BOTANY OF SALVIA DIVINORUM EPLING & JATIVA-M

Of all the almost 1000 species of Salvia in the world, none have fired the imagination as much as S. divinorum, the enigmatic species ceremoniously employed by the Mazatec Indians of Oaxaca, Mexico. The western world first learned of this salvia in 1962, when Epling and Jativa described the entity from material given to them by Hofmann and Wasson (Wasson, 1962; Hofmann, 1980), naming it S. divinorum after its reported use in divination and curing by the Mazatec. A self-styled ethnomycologist, Gordon Wasson, visited the Sierra Mazateca in northern Oaxaca every year between 1955 and 1962, exploring these highlands to study the role of hallucinogenic mushrooms in the religous life of the indians. As a result of Wasson's studies and many contributions to the ethnopharmacological literature (Wasson, 1962, 1963, 1980; Wasson & Wasson, 1957; Wasson, et al., 1957), the Mazatec Indians and their use of several psychotropic plants have become well known.

Soon after establishing local contacts, Wasson learned of the psychotropic plant in the mint family employed by the

Mazatecs. In 1962, Hofmann and Wasson criss-crossed the Sierra Mazateca on horseback searching for it but never once were able to locate it. The material that eventually reached Epling was brought to Hofmann and Wasson by Indians in the village of San Jose Tenango, though no one was willing to take them to a living plant. Wasson (1962), therefore, concluded that *S. divinorum* is a cultigen which may not exist in the wild state.

Because of this aura of secrecy surrouding *S. divinorum*, western science has not known of this species until recently, although the uses of mushrooms (mostly *Psilocybe* spp.) and morning glories (*Turbina corymbosa* (L.) Raf. and *Ipomoea violacea* L.) have been known since they were described by the Spanish chroniclers in the Sixteenth Century (Wasson, 1963; Valdes, *et al*., 1983). A botanist making general collections is not likely to collect *S. divinorum* because its distribution is restricted and it flowers infrequently, thus the few collections of this species have all been made in conjuntion with ethnological investigations.

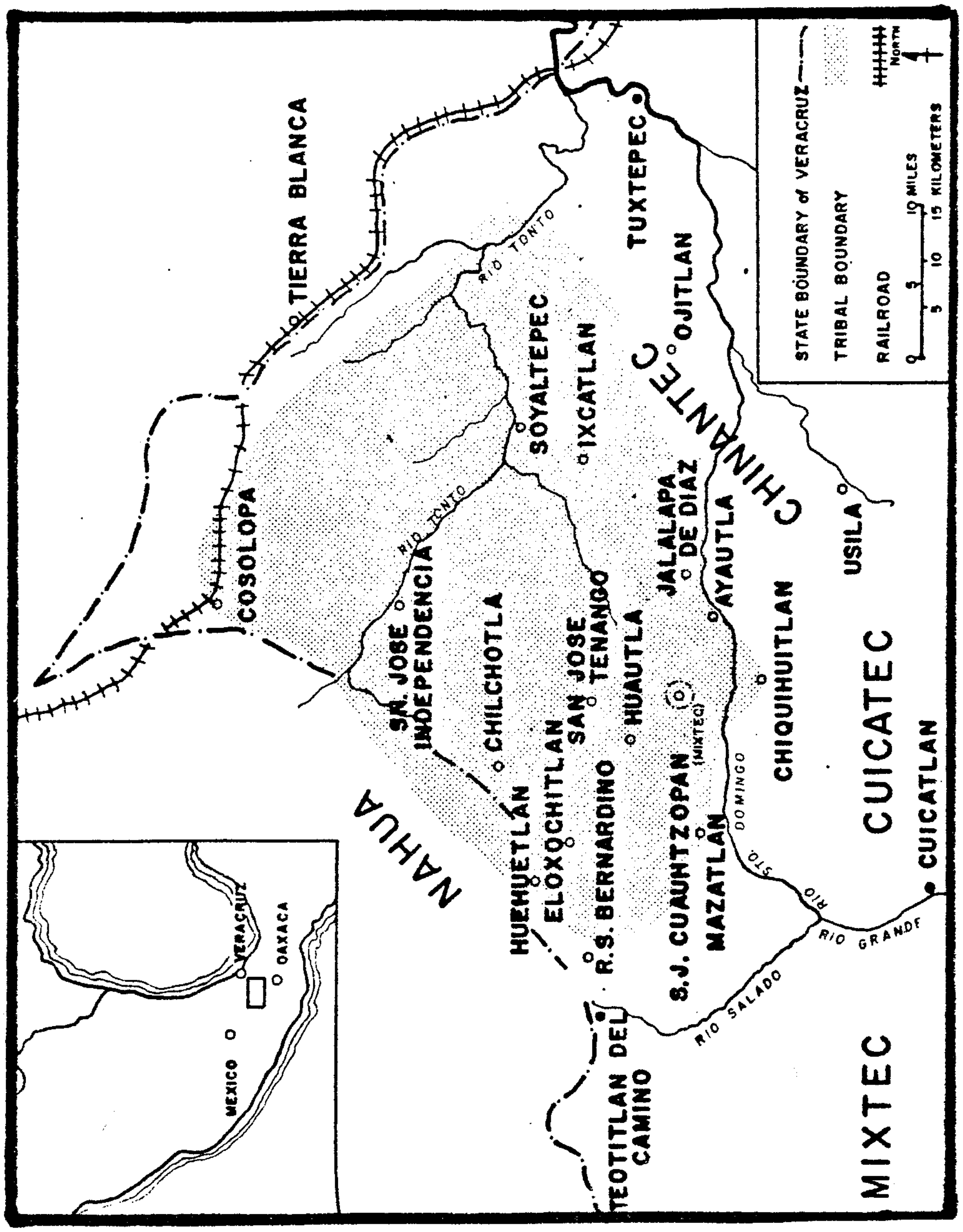
To the Mazatecs, *S. divinorum* is a sacred plant, and while local people know where populations may be found, it is not ingested without a valid purpose and the guidance of a curandero, as the local shaman or healer is called. For his part, the curandero is not quick to divulge localities or share other information with an outsider, and only with the greatest persistance have botanists or ethnologists been able to wrest the secrets of S. divinorum from the reluctant Mazatecs. Valdes (Valdes, et al., 1983) cited the jealous and secretive nature of the native shaman as the reason why his Ph.D. dissertation was based on information from a single source. In my own case, it was only after several long and exhausting trips during the winter of 1983-84 in search of wild populations did our Mazatec guide finally decide to show me several stands growing only within a ten minute walk from my bed. There have now been several students who have gained the trust of local people and learned about the role of S. divinorum in divination, curing, and shamanic training. [For literature concerning these ethnopharmacological studies and related ones concerning the Mazatec Indians, the reader is referred to Diaz, 1975, 1979; Hofmann, 1980; Incháustegui, 1977; Johnson, 1939; McMahon, 1973; Schultes & Hofmann, 1980; Valdes, 1983; Valdes, et al., 1983; Valdes, et al., 1987; Wasson, 1962, 1963, 1980; Wasson, et al., 1974; Wasson & Wasson, 1957; Weitlaner, 1952; Weitlaner & Hoppe, 1969].

To this day, S. divinorum is still a plant of mystery. It has been found growing only in the region inhabited by the Mazatec Indians; no plants have ever been observed to set seed in the wild; and though plants may be found flowering at any time from September until the following May, they apparently rarely do so. The corolla conformation suggests no clear pollination syndrome and the flowers do not point to any obvious taxonomic affinities. These and other questions regarding the biological status of S. divinorum cannot be understood without consideration of the magico-divinatory aspects of the species. Although information regarding the Mazatecs is limited, recent interest in these people and their medico-religious approach to healing has shed light on certain facts which may be relevant to the natural history of the species.

THE MAZATEC PEOPLE AND LANDSCAPE

The Mazatec Indians have lived in a relatively isolated area in northernmost Oaxaca, wedged in between the states of Puebla and Veracruz, since well before the arrival of the Spanish in the Sixteenth Century. This region lies

Figure 29: Stippled region represents the area inhabited by the Mazatec. Note that the Aleman Dam, created with waters from the Tonto River, is not shown (see fig. 30). (Map taken from Weitlaner & Hoppe, 1969.)


TIERRA BLANCA
TUXTEPEC
COSOLOPA
SOYALTEPEC
IXCATLAN
OJITLAN
CHINANTEC
RIO TONTO
RIO TONTO
SR. JOSE INDEPENDENCIA
CHILCHOTLA
SAN JOSE TENANGO
HUAUTLA
JALALAPA DE DIAZ
AYAUTLA
USILA
CHIQUIHUITLAN
CUICATEC
NAHUA
HUEHUETLAN
ELOXOCHITLAN
R.S. BERNARDINO
S.J. CUAUNTZOPAN
(MIXTEC)
MAZATLAN
RIO STO. DOMINGO
CUICATLAN
RIO GRANDE
RIO SALADO
TEOTITLAN DEL CAMINO
MIXTEC
MEXICO
VERACRUZ
OAXACA
STATE BOUNDARY of VERACRUZ
TRIBAL BOUNDARY
RAILROAD
0 5 10 MILES
0 5 10 15 KILOMETERS
NORTH

between 18° and 18°30' north latitude and 96° and 97°45' west longitude (fig. 29). The topography of the region is diverse and can be correlated with Mazatec subgroups. The rugged highland areas are virtually without level ground, there are few roads, and transportation is difficult. The fragmentation of this region is reflected by the many dialects of the Mazatecan language spoken. In the course of my fieldwork, I was often surprised to hear my Mazatec guide speak Spanish to Mazatecs from other communities, as the dialects of "Mazateco" differed so much between virtual neighbors as to be mutually unintelligible. Another outcome of the dissected terrain is the unique "lenguage silbado," or whistle language, by which the Mazatecs can carry on a conversation with whistle sounds only. Like the yodeling of the Alps, communication from one peak to another is made easier using a vocabulary of sounds especially tailored for that purpose.

The rugged highlands of the Sierra Mazateca, roughly 1200 to 2500 m. in elevation, grade into lowland areas which comprise somewhere near 40 percent of the total area inhabited by the Mazatec (McMahon, 1973; Vasquez, 1981). These areas are south and east of the highland region and are part of the extensive Papaloapan river basin. While the various lowland communities are much less isolated from each other, they are, as a group, distinct from those inhabited by the highland natives. While the highlanders speak the Mazateco-Huautla dialect, the lowland natives speak the distinctly different Mazateco-Popoloca dialect (Vasquez, 1981). About half of the roughly 1000 square kilometers of lowland terrain once inhabited by the Mazatecs was inundated with water in 1955 to form the Miguel Aleman Dam. This huge hydro-electric project forced over 20,000 Mazatecs to abandon their homes, although the electricity produced is exported to other parts of Mexico. Some of the displaced were relocated by the Mexican government and some moved to the cities on the coastal plain of Veracruz, but many now live on the banks of the dam, including the eastern shores (where _S_. _divinorum_ does not grow, see below). San Pedro Ixcatlan, for example, is a village on a peninsula formed by the inundation where 1600 Mazatec now reside (McMahon, 1973; Vasquez, 1981).

The climates of highland and lowland Mazatec country are quite unlike each other. At an elevation of 1700 m., the large and central community of Huautla de Jimenez is cool and wet. Relief from the unrelenting fog comes only during the short dry season between late March and early May, though the fog is often replaced by torrential downpours in the summer. The annual precipitation ranges from 256 cm. to over 400 cm. in very wet years, and the average annual temperature is 61°F. To the east, the village of Ayautla (733 m. above sea level) receives a similar amount of precipitation annually, but is warmer, with an average temperature of 68°. Further east is San Pedro Ixcatlan (675 m.) on the peninsula, and the adjacent low-lying "tierra caliente" on the eastern side of the dam. These areas also receive a similar yearly amount of rainfall, but they are still warmer, with annual average temperatures over 78° (Garcia, 1973; Vasquez, 1981). The low-lying areas which surround the dam are much more uniform in temperature and moisture regime than the dissected highlands, and are therefore more easily characterized. The rainy seasons (June-August; September-October) and the dry seasons (August, in part; March-May) are less variable than in the highlands, where different faces of a mountain may have widely different microclimates.

One significant climatic feature of the highlands is the constant fog, reflected by the patches of native cloud forest vegetation which are found in the few areas not planted to coffee or otherwise disturbed. For example, within a coffee plantation near Huautla where *S. divinorum* (*Reisfield & Solheim 1077*) was collected, cloud forest remnants included *Liquidambar*, *Alnus*, *Hedyosmum*, *Clethra*, *Oreopanax*, and many epiphytes, including ferns and orchids. At a somewhat lower elevation (1200 m.), near the village of Chilchotla, a large, flourishing population of *S. divinorum* (*Reisfield & Solheim 1093*) was found. This area, while slightly warmer (annual average of 65°) than Huautla, is considerably more humid, with 472 cm. of rain annually (Garcia, 1973). Remnants of native vegetation found here suggest a transiton between cloud forest (e.g. *Hedyosmum*, *Liquidambar*) and tropical evergreen forest (e.g. *Chamaedorea*, *Syngonium*, and other Araceae). Still lower in elevation (300 m.), *S. divinorum* (*Reisfield & Solheim 1102*) was collected from among tropical evergreen forest elements including the genera *Brosimum*, *Dendropanax*, *Urera*, and *Cedrella*. This site, located in the lower, eastern portion of the Mazatec country, and on the western bank of the Aleman Dam, is warmer than both the Huautla and Chilchotla sites and has fewer days covered with dense fog. San Pedro Ixcatlan and the low-lying villages which clothe the southern and eastern banks of the dam are warmer yet, and *S. divinorum* is apparently not cultivated in these areas. Diaz (pers. com.) has explained to me that some displaced

Mazatecs have tried unsuccessfully to transplant _S. divinorum_ to the eastern side of the dam, and these people now occasionally travel across the dam by boat to gather fresh leaves when needed.

SALVIA DIVINORUM: HISTORY OF USE

Exactly how long _S. divinorum_ has played a role in the medico-religious rites of the Mazatecs is unknown. The plant is known as _ska_ (pronounced shka) _Maria_ or _ska pastora_, referring to its patroness, the Virgin Mary. The Spanish common names, _hoja de Maria_, _hojas de la pastora_, _yerba de Maria_, and _la Maria_, are translations of the Mazatec names which mean "leaves of the sheperdess," or "leaves of Mary." Many aspects of divination and healing with _S. divinorum_ refer to the association between the Virgin Mary and her incarnation in the form of this plant. Shamans often compare her to Santa Ana and San Venanzio, the saints associated with the potent mushrooms, who are not as good at healing as the _Virgen María._ While eating too many mushrooms can "leave one crazy," with visions that are often "tricky," "the Maria, on the other hand, accepts you." The Mazatecs also say that "the Maria speaks with a quiet voice," and the "pastora's voice is timid and becomes frightened if it hears other voices" (Valdes, 1983), alluding to the comparatively weak psychotropic effects of the plant. Thus ceremonial divinations with S. divinorum are performed in absolute quiet and darkness.

As in many other regions of Mexico, the but incomplete catechization of the Mazatecs by Spanish missionaries has resulted in a hybrid belief system, one in which traditional pre-Columbian beliefs are incorporated into the Roman Catholic conceptions of God and the Saints. The Saints are, in fact, considered to have been the first healers, and S. divinorum and the morning glories are siblings, under the protection of the Virgen Mary and Saint Peter (Valdes, 1983). Although the Mazatec are believed to have the lowest percentage of Spanish speakers of any native group in Mexico (Beals, 1969), no name for S. divinorum which predates the Spanish conquest is known. In fact, the name "Mazatec," after a local village named Mazatlan, was imposed on the natives of the area by the Spanish (Valdes, 1983).

Wasson (1963) suggested that the plant Pipiltzintzintli of the Aztecs is S. divinorum, and Emboden (1979) subscribes to this view, calling attention to figures resembling bilabiate flowers in the Dresden Codex. The identity of *Pipiltzintzintli*, though, continues to be debated, and proposals include *Cannabis sativa* L. and *Turbina corymbosa* (L.) Raf. (Diaz, 1979; Valdes, 1987). The Nahua trade arteries along the Papaloapan drainage basin probably passed through Mazatec country, and a positive identification of *S. divinorum* as Pipiltzintzintli may be relevant to our understanding of the origin of the species.

Wasson (1962) and Emboden (1979) also suggest that *S. divinorum* is used by the neighboring Cuicatec and Chinantec Indians, and Weitlaner (1952) reported that the Otomi people in Hidalgo use a plant called "*yerba de la virgen*," which may be identical to "*yerba de Maria*" of the Mazatecs. To date, no reports of the plant's occurance or ritual use outside Mazatec territory have been substantiated, and the few collections of the plant so far made are all from the Sierra Mazateca.

ETHNOPHARMACOLOGICAL INVESTIGATIONS

In general, *S. divinorum* has proved perplexing to practitioners of various disciplines within western science, including pharmacologists. Despite recent pharmacological investigations, questions regarding psychoactive components and the manner in which one's perception is affected after ingesting the plant have yet to be answered conclusively. Though Valdes (1983; Valdes, et al., 1983; Valdes, et al., 1987), in particular, has provided the scientific community with a thorough pharmacological account (to which I refer below), S. divinorum still seems to resist categorization in many ways.

As discussed above, local people are secretive about all aspects regarding S. divinorum. They use it for a wide range of purposes, including shamanic training, divination of robbery or loss, regulation of eliminatory functions, induction of visions and foretelling the future, finding causes and cures of illnesses, and obtaining answers to questions regarding friends, relatives, and enemies.

The effects of the plant are elusive, subtle, and difficult to codify. Reports have stressed the importance of "set" and "setting" (see Valdes, et al., 1983), and the skillful manipulation by shamans of the conditions under which the plant is ingested. The subject's mind is evidently left in a receptive state by both La Maria and the ceremonial setting, and the subject's visions are strongly influenced by the shaman's orations. Reports of the plant's effects by Wasson (1963), Diaz (1975, 1979), Hofmann (1980), and Valdes (1983; Valdes, et al., 1983) emphasize the inconsistency of the experience, but several interesting points emerge. Hofmann (1980) recalls that he was "in a state of mental sensitivity and intense experience," while Diaz noticed a progressive increase in his awareness of the plant's effects each of the six separate times he ingested the plant.

It was explained to Valdes, et al. (1983) that there is a tree in heaven with all the medicinal herbs on it, and the future healer ingests La Maria as a kind of heavenly teacher, to learn the ways of healing and the identification and use of medicinal plants. The ceremonies performed by a Mazatec shaman for Valdes and Diaz, both from "the University," were oriented for such an instructional purpose, and the Virgen Mary and other Saints were called upon by the shaman to teach the visitors the ways of curing [The following quotes are excerpts from Valdes, et al., 1983]:

<u>Shaman</u>: Maria, show Leandros, that he may see what there is in the world...<u>in nomine spiritu santo</u>...Lord Saint Anthony, Lord Saint Peter, Jesus Christ. You are the only three who know about <u>La Maria</u>. You must show him all that is medicinal...All that is your history.

After the lengthy orations of the shaman, Valdes, and especially Diaz, a Mexican biochemist and ethnopharmacologist, began to see visions involving plants:

<u>Diaz</u>: ...And I have had, in the past minutes, many images of plants and flowers...some of them unknown to me...of many colors...I saw something like the flower of the...of the seed of the Virgen. Quite clearly with its purplish color. I...<u>Ipomoea violacea</u>, no?...like flowers again, very luminous, no? As if they had an interior light...like very illuminated in the middle. Now it has changed into a light...there are like fields planted with...and full of plants. Planted with all plants that produce...produce grain that is used for food...

<u>Valdes</u>: ...I see things that look like fruits. Very strange, I can see the seeds, I can see the oranges and yellows and colors, strange, like giant fruit.

During an earlier unrecorded ceremony, Valdes described seeing a mountain made of ice, which slowly changed into Cerro Rabon, a 2100 m. tall mountain considered in Mazatec legends to be a semidormant volcano with a magical lake at its summit, and populated by gods, demons, and magical beings (Inchaustegui, 1977; Valdes, et al., 1987). Interestingly, Valdes, et al. (1987) suggested that S. divinorum is native to Cerro Rabon (but see below).

My own experience, after ingesting over 60 leaves during a divinatory ceremony, is not only difficult to describe to the reader, but equally difficult to categorize in my own mind. While the effects of any "hallucinogen" are not amenable to intellectual dissection and analysis, in the case of La Maria, there is no particular sensation which I am unable to describe. Instead, it was the general experience under the influence of the plant that was somehow "different," but I am unsure to what extent that experience was due to a psychoactive substance in the plant's leaves. In Wisconsin, the ingestion of an infusion made from roughly the same amount of leaves had no effect on me. I am tempted, then, to suggest that not only is the geographic distribution of La Maria confined to the small region in Mexico inhabited by the Mazatec, but in addition, its ability to produce visions can only be realized in the context of this region. Finally, the significance of the role played by the shaman in evoking the plant's powers cannot be overemphasized.

CHEMICAL STUDIES

Diaz (1979) cited the great variability and instability of the constituents in *S. divinorum* as the reason why his attempts to isolate the active ingredient were unfruitful. He tested fractions in a cat-based bioassay (1975) and concluded that the active fractions were likely to contain terpenes, pointing out that psychoactive terpenes were already known from other Labiatae such as *Nepeta cataria* and *Lagochilus inebrians*. Hofmann, the chemist famous for discovering LSD and isolating psilocybin and lysergic acid amides from the mushrooms and morning glories used by the Mazatecs, also attempted to isolate the active compound in *S. divinorum*. On the now famous 1962 expedition with Wasson during which the type material of *S. divinorum* was collected, Hofmann had also preserved juice from the leaves in alcohol. Back home in Switzerland, his phytochemical investigations based on this material failed, and he concluded (1980), after self-experimentation, that the psychoactive principle was unstable. Ortega, et al. (1982) isolated a diterpene from S. divinorum and named it salvinorin, without knowledge of the compound's biological activity. Valdes, on the other hand, undertook a bioassay-directed approach to isolate the active component. His trials are chronicled in his Ph.D. dissertation (1983), where he describes the various bioassays attempted before he successfully identified one of two diterpenes, named by him divinorins, as biologically active (Valdes, et al., 1984). Upon learning that his compound had already been isolated by Ortega, et al. (1982), divinorins A and B were renamed by Valdes as salvinorins A and B (Valdes, et al., 1987). Since then, Valdes, et al. have noticed that salvinorin A does not account for the full range of biological activity attributed to S. divinorum, thus chemical and pharmacological investigations continue.

BOTANICAL INVESTIGATIONS

Previous Research

In the course of his pharmacological research, Valdes (1983; Valdes, et al., 1987) performed several experiments designed to help answer questions regarding the reproductive biology of S. divinorum. Plants collected by him in the Sierra Mazateca were propogated in Michigan alongside plants derived from the original type material given to Epling by Hofmann and Wasson. In 1963, Epling had placed cuttings of these plants in the UCLA Botanical Gardens, which later provided clonotypic material to UC Berkeley, which in turn provided living specimens to Valdes. Valdes also purchased living plants from the firm of J.L. Hudson, Seedsman, this material also descended from the clonotypic material propogated at UCLA. In fact, the various botanists and rare plant or drug plant enthusiasts growing S. divinorum around the country are likely to all be growing plants derived from the type material acquired by Hofmann and Wasson at San Jose Tenango in 1962.

Carl Epling never saw these plants flower in the gardens at UCLA, and he mistakenly described them as having blue corollas. The source of this error is made apparent by Hofmann (1980), who recalls the time that he and Wasson received the plant material: "From an old Curandera, a venerable woman in a strikingly magnificent Mazatec garment, with the lovely name Natividad Rosa, we received a whole bundle of flowering specimens of the sought-after plant,... [she would not] tell us where she had gathered the leaves. They grew in a very, very distant forest valley. Wherever she dug up the plant, she put a coffee bean in the earth as thanks to the gods... We now possessed ample plants with flowers and roots, which were suitable for botanical identification... The plants had blue flowers crowned with a white dome..." In fact, the "white dome" referred to by Hofmann was the corolla, which, in the specimen described, had apparently not yet opened. Likewise, the illustration of _S_. _divinorum_ in Schultes and Hofmann (1980) includes only flowers in bud, and the artist's rendition of the individual flower parts emphasizes the mistake: the stamen, style, and corolla are each drawn as they appear before the flower opens. Hofmann and Wasson, neither of whom had any idea what the flowers of _Salvia_ look like, did not realize that what they described as "blue flowers, crowned with a white dome" were actually blue calyces with unopened white corollas. The mistake survived in Epling and Jativa's (1962) original description of the species because they never themselves saw living flowers, and the white corollas turn brown upon drying. Diaz (1975), Emboden (1979), and Valdes (1983; Valdes, et al., 1987) have all correctly reported that the corollas of S. divinorum are pure white, while the calyx and flowering stem are violet blue.

Valdes (1983; Valdes, et al., 1987) questioned the blooming requirements of S. divinorum and its failure to set seed. Flowering plants collected by him in the Mazatecan village of Cerro Quemado were cross-pollinated by hand with pollen from Hofmann's original clonotypic plants. Of 14 flowers pollinated, four set seed, though the number of nutlets which reached maturity is unclear (the ovary of each flower consists of four mericarps). Attempts to grow the seeds in a growth chamber failed when the chamber overheated, drying the medium and killing the seeds. He concluded that the species was self-sterile, though no attempt was made to self-pollinate any flowers. No explanation was offered as to why only four (or 16?) of a possible 56 nutlets reached maturity.

Valdes also carried out daylength experiments in order to explain the blooming requirements of S. divinorum. Previous reports (Wasson, 1962; Emboden, 1979) referred to the difficulty of finding flowering populations in the wild. Blooming was reported to be sporadic, the flowers supposedly borne on stems at least seven feet long. Noting that flowers had only been collected during the "short-day" period between August and the following March, Valdes subjected plants in growth chambers to gradually decreasing daylengths (from 16 to 11 hours over a period of four weeks). All plants flowered at heights of less than one meter, and increasing the daylength to over 12 hours caused the plants to revert to vegetative growth and abort flowers. Valdes concluded that S. divinorum is an obligate short-day plant, with plant height a minor factor in flower initiation.

Again, these experiments posed as many questions as they answered. The sporadic flowering of wild populations, the conditions which promote flower initiation, and the failure of the flowers to lead to fruit formation are aspects which remained unclear. These and other questions regarding co-evolved pollinators and biological status are addressed in the following pages. Investigations described below have involved visiting and collecting material from many populations in the field, a "stakeout" at a flowering population to observe visitors, chromosome number determination, greenhouse flower induction experiments, artificial self and cross-pollinations, pollen stainability studies, fluorescence microscopy for looking at pollen tube growth through styles, and nectar analyses.

MATERIALS AND METHODS

Fieldwork was carried out during the winter of 1983-84, and consisted mainly of searching the Sierra Mazateca for populations of *S. divinorum*. Although ravines were regularly searched for wild populations, this work mostly involved establishing contacts with native people who were willing to lead myself and an assistant, Stephen Solheim, to wild or naturalized populations. A guide, Bolmaro Garcia, was employed for the entire period and served as translator, also providing invaluable assistance with virtually every aspect of getting around in the Sierra Mazateca. Thorough collections and site descriptions were made whereever *S. divinorum* was found, unless the population was obviously "en casa," that is intentionally planted near someone's home.

Flowering populations of S. divinorum near Cerro Quemado, a village on the western side of the Aleman Dam, were visited in October, 1985. I watched the population for two days and one night, waiting to note any visitors to the flowers. Observations regarding corolla color (white) and shape, the daily pattern of nectar secretion, and nectar sugar ratios, raised the possibility that the co-evolved pollinator was a nocturnally active hawkmoth. Plants were thus observed during the night by periodically shining a red-filtered incandescent lamp on the flowers. After being visited (as it will be discussed, by a hummingbird), flowers were inspected to see whether pollen had been deposited on the stigma, and whether the store of nectar had been depleted.

Plants from several sources were propogated at the University of Wisconsin Botany Department (UW) greenhouses. Valdes, whose work is described above, provided me with potted plants derived from three sources: a collection from Cerro Rabon, near the Mazatec village of Ayautla, a collection from near the village of Cerro Quemado, and clonotypic material obtained from Berkeley. Later, plants collected by myself, near Cerro Quemado (Reisfield & Solheim #1102) and Ayautla (Reisfield & Solheim #1111), were added to the living collections. The plants were easily propagated in the frost-free greenhouse, though whitefly infestation became a particular problem. Systemic chemical control was combined with regular hosings with water to keep down these pest populations. The flowers, however, proved to be sensitive to various chemical insecticides, aborting or developing abnormally upon exposure to the chemicals.

While the results of Valdes' growth chamber experiments strongly suggest that flowering in _S_. _divinorum_ is initiated by the onset of shorter days, the critical period of daylight is not clear. Valdes learned from Robert Ornduff (pers. com.) that plants grown in the gardens at both UC Berkeley and UCLA formed flower buds which subsequently reverted to vegetative growth. (This, in fact, also occured on plants growing in the UW greenhouses during the winter of 1986-87). Apparently, a limited exposure to light during the night will upset the hormonal mechanism by which the plant perceives a decrease in daylength. Thus, beginning in late October, 1984, a subset of plants at the UW greenhouses were subjected to artificially shortened days of 8 to 10 hours by covering them with a black cloth each afternoon.

Flowers were hand-pollinated by removing the stamens and immediately brushing the dehiscing anthers against the inner surfaces of both stigma branches until pollen grains were visibly adhering to the stigma. Self-pollinations were performed within individual flowers, between flowers of the same plant, and between plants derived from a common source. Cross-pollinations were performed between plants derived from different sources. Primary crosses included various parental combinations and were sometimes complemented with reciprocal crosses. Pollinations were performed at different times during the day (and night), and between flowers of different ages. Because the failure of nutlets to develop normally leads to calyx abscission, colored thread markers were fastened to the bases of the pedicels. For example, purple thread attached to pedicels on the plant labelled Berkeley #1 signified that those pedicels bore flowers which were crossed on February 17, with pollen from various flowers on plants derived from Valdes' Cerro Quemado collection. Small paper packets were attached below calyces with developing nutlets in order to catch the mature fruits which otherwise might have fallen to the ground.

To study pollen germination and pollen tube growth, styles were collected from flowers which had been self or cross-pollinated between 4 and 18 hours earlier. The styles were fixed in FAA and stored in distilled water at approximately 5°C. They were cleared with 8N sodium hydroxide for 24 hours, then taken through several washes with distilled water, and stained with analine blue at a concentration of .01 percent for 4 hours. Fluorescence microscopy was performed with a Zeiss microscope equipped with a Zeiss UG1 excitation filter and 47,-65 barrier filters. The UV source was an Osram HBO 200W mercury vapor lamp. Staining and microscopy techniques were mostly according to Martin (1959) as modified by Stettler and Guries (1976). Styles were slightly crushed beneath a coverslip and observed whole in a darkened room. The callosic lining of the pollen tubes fluoresces bright yellow-green, but the amount and distribution of callose is variable between taxa (Martin, 1959). Scanning several species of Salvia showed that the pollen tubes come in and out of visibility for the length of the style, and can easily be distinguished from the two vascular bundles which fluoresce a uniform, much less brilliant yellow. Fluorescence was most visible at the stigmatic and ovary ends of the style, therefore an inability of the tubes to reach the ovary should have been readily detectable.

Pollen grains from FAA-preserved flowers on wild and greenhouse-grown plants were analyzed for cytoplasm stainability. Pollen was removed from dissected anthers in several drops of cotton blue-lactophonol, after which a drop of Hoyer's medium was added and coverslip applied. A grid was inserted into the ocular so as to divide the field of view into segments to facilitate counting. Sterile or aborted pollen grains did not take up the stain, and were also conspicuous by their shrunken size and shriveled form. The fraction of aborted pollen grains was tabulated as a rough percentage of total grains produced for several collections of <u>Salvia</u> species.

Nectar studies included an analysis of constituents, a study of daily secretion patterns, and also total volumes produced per flower. Flowers on greenhouse-grown plants from various sources were analyzed at various times during the day and night with the hope of gaining insight into the relationship between the flowers and their co-evolved pollinators. Calibrated micropipettes were inserted into the pool of nectar which accumulates at the base of the corolla tube, with nectar extracted by capillary action.

Certain flowers were tagged and periodically measured in order to ascertain the amount of nectar produced by an indivdual flower. The pattern of nectar secretion at the population level was studied by measuring as many flowers as possible at various time intervals. Asynchronous patterns of nectar secretion and the possibility that the sampling technique was destructive were two of several problems discussed below. Sugar concentrations were measured with an Extech model 2132 pocket refractometer, which provides the percentage of sugar in the water on a weight to weight basis. Several samples were also analyzed for sugar constituents (ratio) by Irene Baker at UC Berkeley. The nectar was spotted on Whatman #2 filter paper, the diameter of the spot outlined with four pencil marks, and the volume and percent sugar for each spot provided to Dr. Baker.

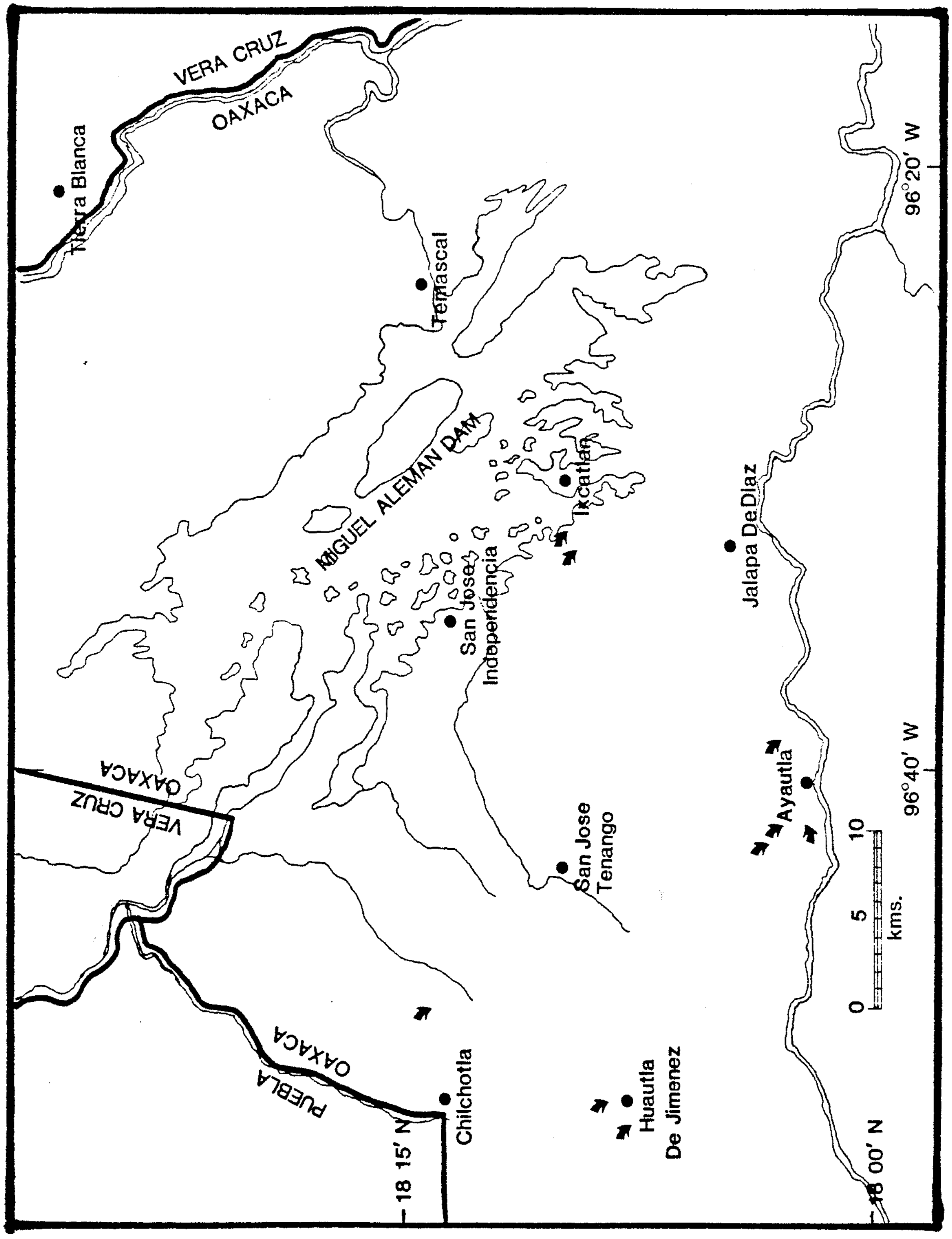
Young anther sacs were dissected and meiocytes squashed according to the technique described in Chapter Six. Meiocytes with a distinct number of chromosomes which were countable without the aid of "through-focusing" were photographed.

RESULTS AND DISCUSSION

Distribution, Ecology, and Flower Initiation

During the winter of 1984-85, approximately 15 populations of S. divinorum were located, though for the purpose of mapping their distribution, several populations are merged because of their close proximity (fig. 30). Salvia divinorum was first located (Reisfield & Solheim 1077) about 2 km. north of Huautla in a very wet, somewhat disturbed, shaded ravine at the edge of a coffee plantation. The coffee plantation apparently replaced a cloud forest, of which remnants include Liquidambar macrophylla Oerst. and Hedyosmum mexicanum Cordem. Plants were found growing along a streambank, with some stems trailing near or in water, rooting copiously at the nodes and sometimes along the internodes. Broken, trailing, and drooping stems were noticed to resume erect growth at the stem apex or by axillary branching, with new, vigorous shoots often arising from the axils of old, senescent stems. All living stems were observed to arise from stems which had since died, the dead stems lying on or in the ground, sometimes appearing as woody caudices. Many stems were cut, apparently by people who collected the leaves for

Figure 30: Distribution of <u>Salvia</u> <u>divinorum</u> Epl. & Jat. Arrows point to populations found during fieldwork in the winter of 1984-85. In addition to the locations shown, the type specimen was collected in (near?) San Jose Tenango. (Adopted from McMahon, 1973.)


VERA CRUZ
OAXACA
Tierra Blanca
Temascal
MIGUEL ALEMAN DAM
Ixcatlan
San Jose Independencia
Jalapa De Diaz
VERA CRUZ
OAXACA
San Jose Tenango
Ayautla
PUEBLA
OAXACA
Chilchotla
Huautla De Jimenez
96°20' W
96°40' W
18 15' N
18 00' N
0
5
10
kms.

medico-religious use. Several old, dried, inflorescence branches (rachises) were present but no fruit were found. Later, similar stands of plants (#'s 1091-92) were found in other ravines near Huautla.

The road from Huautla (1700 m.) to Ayautla (760 m.) takes about 10 hours to walk, and is copiously dotted with streams and wet ravines which were searched for populations of S. divinorum. A few such populations (#'s 1085, 1111, 1112) were finally found near Ayautla, and these again showed signs of past flowering, but all the old floral stems were entirely naked (developing fruit are enclosed by a persistent calyx, but failure of the nutlets to develop normally leads to calyx abscission). The plants were vigorously spreading along the rocky streambanks, and erect shoots emerged mostly from a thick litter composed of older decaying stems. One branch was noted to be completely severed, lying in shallow water and rooting along the internodes. An additional population in this area, chosen by a local shaman, Maria de la Oz Unda, to supply the leaves for the divinatory ceremony we had requested, grew among the trees of a coffee plantation. Although there was no running water at this site, the many epiphytic ferns and orchids suggested that this mountain slope is regularly clothed in fog. Similar stands of *S. divinorum* in "cafetals" were found near Huautla (*#1090*) and Cerro Quemado (*#1108*).

Flowering of *S. divinorum*, as in many forest understory species, is promoted by sunlight, and the extent of flowering of a given population is dictated by the amount of sunlight which penetrates the canopy. We saw our first flowering population of *S. divinorum* (*#1093*) near the village of Chilchotla (1200 m.). The plants colonized the banks of a broad, shaded ravine with several pools of standing water. The channel of the ravine was mostly without vegetation and almost certainly flooded during wetter periods. The vegetation suggested a transition between cloud forest (e.g., *Hedyosmum*, *Liquidambar*) and tropical evergreen forest (e.g., *Syngonium* and other Araceae), and climate data (Garcia, 1973) indicates that this area is extremely humid, with an average of 472 cm. of rain annually. This flourishing population of plants appeared to be clonal, spreading vegetatively in the same fashion as populations observed previously. Inflorescence rachises past the flowering stage were again entirely naked, and not a single mature nutlet was found. The beautiful white and violet flowering stems, found only in patches where sunlight penetrated the canopy, were very conspicuous. This observation suggests the main distinction between this and previous sites where populations of *S. divinorum* were found. The breadth of this ravine allows a greater penetration of sunlight, while the extreme humidity of the region prevents the habitat from drying out. It is this interplay between sunlight and humidity which apparently dictates the success and the extent of flowering of a given local population of *S. divinorum*.

Another flowering population (*#1109*) was found on a steep face of Cerro Alto, the mountain adjacent to the village of Ayautla. This trailside population formed a thick, shaded stand, and the crowded stems were over two meters tall. Flowering branches, up to three meters tall, rose above the rest and received filtered or direct sunlight. Valdes (1983) reported that he collected plants from Cerro Rabon, a somewhat more distant mountain, but our local guide, Pedro Diaz, insisted that he knows "*La Maria* very well, and in 40 years of walking Cerro Rabon, [he] never saw it up there."

Several populations of *S. divinorum* (*#'s 1102-04*, *1106-08*) were found on the east-facing bluffs above the village of Cerro Quemado, on the western bank of the Aleman Dam. At roughly 300 to 400 m. elevation, these stands were scattered along a steep trail which winds between the peaks of Cerro Quemado and Cerro Camaron. Some plants were found in a slash-and-burn cornfield, and most of the associated vegetation was disturbed, replacing a tropical evergreen forest with _Brosimum_, _Dendropanax_, and _Urera_. Many flowering stems were found, these always in partial to full sunlight, sometimes dryed out to the degree that the leaves were badly wilting. Climatic data for the nearby village of Ixcatlan (Garcia, 1973) indicates that this area is considerably warmer than the highland regions of the Sierra Mazateca (the annual average temperature is 79°F in Ixcatlan), and the wilting plants indicated that they were at their limits of evapo-transpiration. On the other hand, these same populations included more flowering stems than any other, again indicating that flowering of _S_. _divinorum_ is promoted by sunlight, and perhaps the stress of drying out to a certain degree. This is reasonable in light of the heliotrophic nature of the genus in general, with mostly species of open ground and with brightly colored flowers. _Salvia_ _divinorum_, though, with its crisp, easily broken, hollow stems, is clearly a hydrophyte, and most aggressively colonizes sites which are dark and humid. Vigorous, flowering populations are found in conditions of marginal light, and in very humid areas (e.g., Chilchotla), the plants can "venture out of the shade" into the sunlight where they will flower.

Conditions which promote vegetative growth of *S. divinorum* are different than those which promote flowering, and this is reflected in the character and distribution of populations. The Mazatecs displaced by the Aleman Dam who now live in the low-lying "tierra caliente" on the eastern side of the dam have tried unsuccessfully to cultivate *S. divinorum* (Diaz, pers. com.). This region receives similar amounts of rainfall but is warmer, and consequently drier, than the highland areas of the Sierra Mazateca. Thus, in order to gather fresh leaves, some of these Indians travel by boat across the dam to the hillsides near Cerro Quemado, where I reported (above) the populations to be at their limit of evapo-transpiration. Throughout the higher, cooler regions inhabited by the Mazatec, flourishing populations may be found in shaded ravines near water, or on mountainsides continuously bathed in fog. In the latter type of site, often a hillside planted to coffee, *S. divinorum* is almost certainly introduced, and the Mazatecs do this by simply sticking a severed branch in the soil. Though the more remote, aggressive populations along watercourses seem not to have been planted, they may in fact have been introduced long ago. The Mazatecs do not distinguish between wild and cultivated populations, nor do they attach any significance to the flowers.

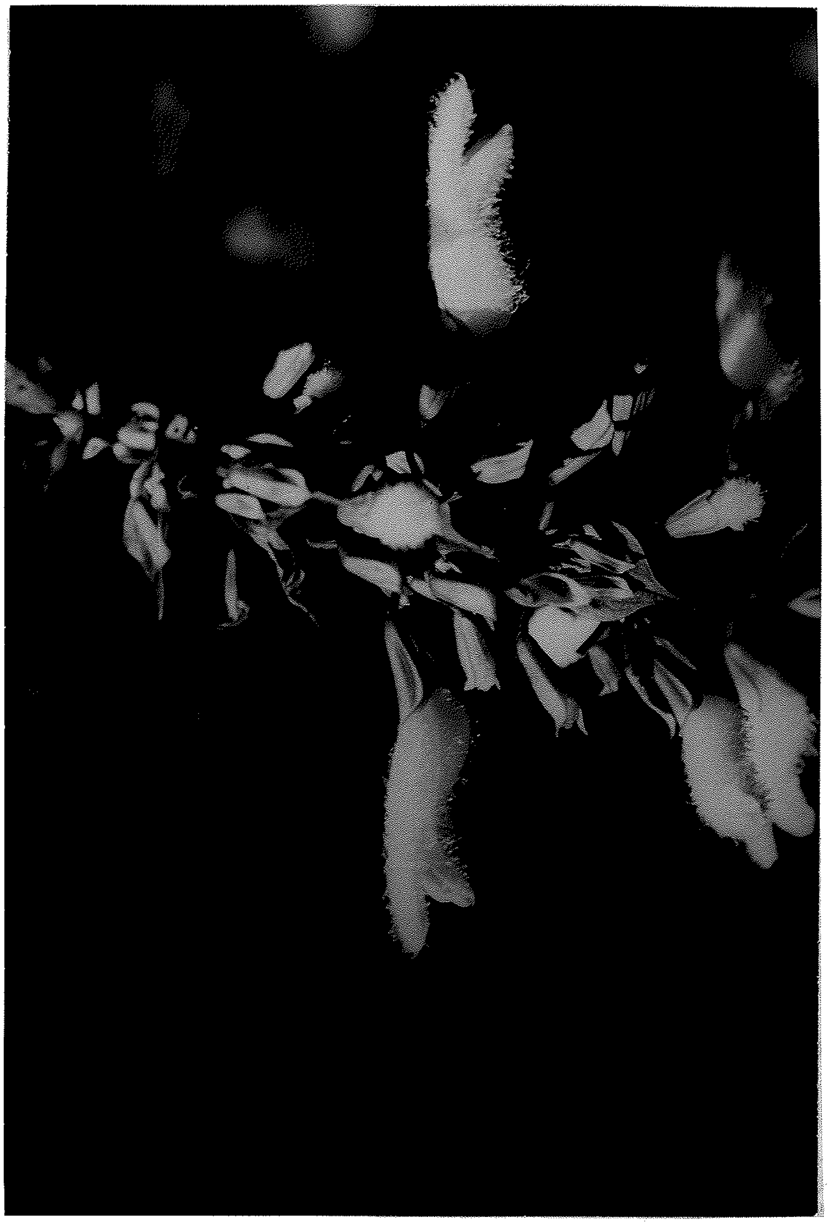
While Emboden (1979) reported that S. divinorum flowers only when the "branches" [stems] are seven feet or more in length, Valdes (Valdes, et al., 1987) concluded that plant height is a minor factor in flower initiation. In the Sierra Mazateca, most flowering stems are, in fact, very long, since the stems that elongate the most are most likely to receive direct sunlight. The stems of greenhouse-grown plants preparing to flower also elongate, a development which posed problems for the short day, black cloth treatment, as the height of the cloth had to be raised to fully 2 meters. Still, plants grown in the greenhouse received unfiltered sunlight, and those which were subjected to the short day treatment flowered profusely on branches of varying lengths.

Flower buds were first noted roughly two months after the beginning of the short day treatment, and the first flowers did not open until almost one month later. The nearly three month lag between the time the plants first perceived the stimulus to flower and the onset of flowering correlates with the results of Valdes (Valdes, _et_ _al_., 1987), but raises the question whether a critical threshold period is actually perceived by the plants. The type specimen was collected in flower by Hofmann and Wasson on October 8 (I am unaware of the collection flowering in August referred to by Valdes), which suggests that these plants perceived the stimulus to flower three months earlier, that is, in late June, during the period with the longest days of the year. The mechanism responsible for flower induction is apparently not as simple as our greenhouse and growth chamber experiments would suggest, and the actual induction of flower primordia probably involves several factors, including temperature and water regime. Perhaps the critical stimulus perceived by the plant is an increase in the length of the night _per_ _se_, an hypothesis which could easily be tested. Flowering plants have been collected from near Cerro Quemado in March, and Pedro Diaz, our local guide from Ayautla, insisted that _La Maria_ flowers all year long except in June and July, with flowers most abundant in March, April, and May, when it is the dryest. A local villager from Cerro Quemado also claimed that ska Maria flowers most abundantly in May, and in light of the conditions which promote flowering during the cool and wet winter, these assertions seem reasonable. Sunlight and the stress of drying out, to some degree, promote flowering in S. divinorum, and these conditions are most realized during the dry months from March until mid-May.

Co-evolved Pollinators

Although several flowering populations were finally found during the winter of 1983-84, at no time was a legitimate pollinator observed visiting the flowers. While poor flight conditions for Hymenoptera often prevailed, pollinators were also conspicuously absent during an entire, sunny, hot afternoon while flowers were collected near Cerro Quemado. Bumblebees were active in the area, but they ignored the white and violet inflorescences of S. divinorum as they do the scarlet flowers of many ornithophilous Salvia. The explanation for this behavior is suggested by the dimensions of the S. divinorum corolla, which more resemble those of ornithophilous salvias than melittophilous ones (figs. 14C, 31, 32). The sigmoid

Figure 31: Corolla of _Salvia_ _divinorum_ Epl. & Jat. (Photo by C. Lipke.)



Salvia divinorum

Figure 32: Flowering stem of _Salvia divinorum_ Epl. & Jat. (Photo by C. Lipke.)

corolla tube is 19 to 22 mm long, and measures only 2 mm by 1.5 mm at its narrowest point, near the throat. The lower lip, which is horizontally expanded to form a landing platform on bee flowers, is instead vertically oriented, with the middle lobe somewhat cupped, like those of classical hummingbird pollinated salvias. The sigmoid curvature of the corolla tube is uncommon in bee flowers, but characterizes several bird pollinated species of *Salvia*, such as those in sect. Flexuosae.

Data obtained from analyzing nectar constituents also suggests that the flowers of *S*. *divinorum* are pollinated by hummingbirds. As might be expected, the nectar sugar is sucrose dominant, as are most nectars from flowers pollinated by long-tongued bees, hawkmoths, or hummingbirds. Flowers on clonotypic plants yielded a nectar sugar composed of 86% sucrose, 10% fructose, and 4% glucose. This evidence is even less meaningful in light of the fact that the Labiatae, as a group, are characterized by sucrose-rich or sucrose-dominant nectar sugars (Baker & Baker, 1983).

The concentration of sugar *per se* in the nectar is somewhat more significant, especially because the preferences of long-tongued bees more resemble those of short-tongued bees than those of birds. While the corolla tube of S. divinorum suggests a co-evolved pollinator with long mouthparts, information concerning nectar sugar concentration (and the volume of nectar secreted) can help resolve further the identity of this long-tongued pollinator. Nectars sampled by Cruden, et al. (1981) from a spectrum of plants below 2400 m. showed that bee flowers produce more concentrated nectars (34.7%) than hawkmoth (22.6%) and bird-pollinated (23.8%) flowers. The concentration of nectar sugar produced by greenhouse-grown plants of S. divinorum was mostly between 21% and 23%.

In general, hummingbird flowers have low nectar sugar concentrations, but produce larger total quantities of nectar than bee flowers. The contrast in total nectar accumulation between bee and bird flowers is often dramatic, as evidenced by data presented by Cruden, et al. (1981) from hummingbird flowers (12.03 µl per flower) and bee flowers (2.81 µl per flower). Because of the interplay between pollinator adaptation, on the one hand, and the constraints of phylogenetic relationship, on the other (Baker & Baker, 1983), data presented by Cruden, et al. (1981) from several species of Salvia is especially useful for comparison with data obtained from S. divinorum. Ornithophilous species of Salvia sampled by Cruden, et al. included S. cardinalis (17.71 µl per flower), S. elegans (7.52 µl), S. greggi (3.49 µl), and S. pubescens (20.72 µl). Melittophilous species sampled included S. tiliaefolia (.015 µl per flower), S. reflexa (.14 µl), and S. cohuilensis (.53 µl). Despite the fact that nectar accumulation data obtained by intermittently sampling flowers of S. divinorum grown in the greenhouse is plagued with inconsistencies, there can be no question that the quantity of nectar produced suggests ornithophily. The measurements ranged from 8 to 16 microliters, though most flowers produced a total quantity of nectar near 9 microliters. Still, the methodology employed was crude, and several questions emerged, such as the possible negative effect of the intrusive sampling technique, the effect of nectar removal on secretion rates, and the effect of the time of secretion on the quantity of nectar produced, since flowering and nectar production were asynchronous.

No nocturnal visitors were observed during the overnight stakeout near flowering populations of S. divinorum at Cerro Quemado. Flowers opened asynchronously in the evening or during the night, and nectar production was also initiated asynchronously, mostly during the night. Virtually three of every four flowers had a hole punctured in the calyx and corolla tube, presumably by nectar robbers, and even many unopened flowers containing little or no nectar were pierced. At the first signs of dawn, under an overcast sky, a large hummingbird with a conspicuously decurved bill visited virtually every flower, jumping from flower to flower in an irregular fashion. It flew away in the direction of additional flowering stands of S. divinorum, and several minutes later returned and again visited most flowers. The nectar in most of the flowers was depleted by the bird, and pollen grains had been deposited on several stigmas. Two bumblebees were in the area but ignored the Salvia flowers. Roughly one hour after sunrise, it began to drizzle, and the stakeout had to be concluded.

The observations described can in no way be considered evidence for the co-evolution between S. divinorum and a species of hummingbird, especially in light of the many supposed melittophilous salvias which are visited by the opportunistic birds (discussed in Chapter Seven). Still, the dimensions of the corolla, the nectar constituents, and the amount of nectar produced per flower, all suggest the ornithophilous syndrome. On the other hand, the white corolla color, the sporadic and infrequent flowering of populations during most of the year, the great amount of nectar robbing, and the apparent complete lack of fruit set, suggest that the relationship between plant and pollinator has not been "fine-tuned" by natural selection. Certainly, the distribution of populations throughout the ecologically diverse region inhabited by the Mazatec is anthropogenic, and unrelated to any pollinator.

The Barrier to Fertility

The apparent complete lack of successful fruit formation by S. divinorum in the Sierra Mazateca can potentially be due to several types of failure. Since the species is vigorous in the vegetative phase of its life cycle, the earliest process which might potentially be aberrant is the differentiation of the reproductive organs and the spores which they produce. The irregular pairing or segregation of chromosomes during meiosis, or disturbances during some stage of gametophyte development, might result in the inviability of the haploid generation. Viable pollen grains must be transported by an animal vector to a receptive stigma, onto which they must adhere, and subsequently germinate. This requires that a functional male flower dust an animal with pollen in a way that it will be successfully deposited on the stigma of a functional female. The materials of the pollen grain (as well as substances derived from its sporophyte parent) must then harmoniously interact with materials on the stigma surface and underlying papillae. A pollen tube must successfully navigate its way through the transmitting tissue of the style, reach the ovary, and penetrate the micropyle of the ovule. Each of these steps depends on the harmonious interaction between the male gametophyte and the tissues of the female sporophyte. After the pollen tube deposits the sperm nuclei into the embryo sac, a breakdown may occur during fertilization or during the subsequent development of the seed. Endosperm failure or embryo abortion could occur if the tissues of the maternal sporophyte, endosperm, and embryo are incompatable in any way. Finally, a failure of the mechanism which prevents calyx abscission during fruit development would result in premature abortion of developing nutlets. Although the precise cause(s) of the observed sterility of <u>S</u>. <u>divinorum</u> is still not clear, we can, at this point, narrow down the range of potential stages during which irregularities are manifested.

Meiocytes from anthers of S. divinorum flower buds were suitable for chromosome counting during the first and second metaphase. No irregularities in pairing were observed, and the species was found to be diploid with a gametic number of 11 (fig. 26), which is the number most common in species of subg. Calosphace. Nevertheless, many examples of species are known (see Stebbins, 1958) in which chromosome pairing appears normal, but meiosis breaks down in the later stages and pollen grains fail to develop. This may be due to the presence of minor, non-homologous regions, too complex to observe, on chromosomes which are associated in spite of their lack of homology (cryptic structural hybridity). Even when the parental chromosome complements are perfectly paired, meiosis may break down due to disharmonious interaction of parental genes which affect the timing of meiotic cycles, or the necessary metabolic processes. This type of genic sterility (also called diplontic sterility) is, in reality, often combined with some degree of chromosome non-homology (haplontic sterility), and can cause aberrations at various stages in the development of a hybrid or its offspring (Stebbins, 1958, 1971). While disturbances of meiosis are often due to hybridity, similar irregularities can also be due to other factors. For example, lethal or deleterious genes harbored by an outbreeding population may become expressed upon inbreeding. In this case, the detriment to the plant would depend upon the type of action of the given deleterious gene(s).

Another index of genetic or cytological abnormalities is the fraction of pollen grains which abort, or lack cytoplasm, and therefore do not stain. A failure during the late stages of meiosis or during gametogenesis would normally lead to unviable pollen grains, often reflecting a disharmonious interaction of parental genes, usually indicating hybridity. A scan of pollen from preserved flowers of *Salvia sessei* (*Reisfield 1252*), *S. flaccidifolia* (*#1218*), and *S. mexicana* var. *minor* (*#1244*), revealed that virtually all the pollen grains took up the stain. Pollen grains from greenhouse-grown plants of *S. divinorum* (mixed collections) were much less viable, with 882 (56%) of the 1587 pollen grains observed aborted. Pollen from flowers of *S. divinorum* collected at Cerro Quemado (*Reisfield 1142*) showed a similarly low degree of fertility relative to other *Salvia* species, with 1592 (53%) aborted pollen grains out of 3027 observed. The failure of roughly one half of the pollen grains to develop indicates that the haploid stage in the life cycle of S. divinorum is partially sterile, due to causes as yet undetermined. Haplontic and/or diplontic sterility of interspecific hybrids is often similarly manifested, and hybridity seems likely. Inbreeding depression, of which the effects are mostly manifested in the diploid, is not commonly responsible for pollen abortion. Still, the inviability of the haploid stage in the life cycle is only partial, and can not explain why the plants in Mexico apparently set no seed. Whatever genetic or cytological irregularity is causing the pollen grains to abort may well also cause failure in other developmental stages.

Hand pollinations in the greenhouse clearly showed that the chief barrier to fertility in S. divinorum is not a failure to be pollinated. Of a total of 108 self-pollinations (108 stigmas dusted with pollen from the same plant or genetically identical plants), only 11 mericarps developed fully into dark, indurate, viable nutlets. Since each pollinated flower could potentially yield four nutlets, the 11 fruit represent 2.5% of a total potential yield of 432 fruit. Of 190 cross-pollinations, only 24 (3%) nutlets fully matured from a potential of 760 fruit. Most of the calyces abscised between 5 and 10 days after pollination, and quite often one or two (sometimes more) mericarps were noticed to be developing before the calyx and ovary fell from the plant. Several of the mature fruit were germinated in the UW greenhouses, where normally vigorous seedlings developed into plants indistinguishable from their parents. Each pollination was carefully performed, and there was some difficulty getting the grains to adhere to the stigma. Still, many viable pollen grains which were deposited on receptive stigmas did not lead to fruit set, indicating some failure after this stage in the life cycle of S. divinorum.

It has been suggested that S. divinorum is self-sterile (Valdes, 1983; Valdes, et al., 1987) which, if true, would explain the observed failure to set fruit. Individual populations all seem to be clonal, and plants of adjacent populations could feasably be genetically identical. Given the anthropogenic distribution of S. divinorum throughout the region inhabited by the Mazatec, it is also quite possible that many distinct populations are derived from a single source. Such a situation would explain why artificial cross-pollinations resulted in no greater fruit set than self-pollinations, since the so called crosses would, in reality, be between genetically identical plants. Even if the plants were not genetically identical, a common self-incompatability factor shared by the functional male and female plants would prevent successful fertilization. This type of self rejection, though, seems to be rare in Salvia (few studies have been done), and also could not account for the reduction in pollen fertility.

Further resolution of the problem was obtained by studying pollen germination and tube growth through styles of hand pollinated flowers. Of 39 styles observed, 13 (33%) had four or more pollen tubes which traversed the entire length of the style, reaching the ovary. Three or more pollen tubes reached the ovary in almost one half the styles observed. Of the twenty styles in which four or more pollen grains or tubes were observable at all, 14 had three or more pollen tubes which reached the ovary. Also, no difference was noted between the self and supposed cross-pollinations.

In classical, genetic self-incompatability systems, the site of pollen tube inhibition is on the stigma surface or somewhere in the style. A pollen grain may fail to germinate, or produce a tube which grows abnormally and is soon occluded by callose, or produce a tube which is eventually rejected by the transmitting tissue of the style (Heslop-Harrison, 1975). Although this type of active inhibition of the pollen tube may not be the only form of genetic mate discrimination in plants (see Mulcahy, 1983, 1984), the best understood self-rejection systems (called oppositional systems) do involve observable changes (e.g., swelling) in the growing tip of the pollen tube. I did not observe any such abnormalities, and no sort of occlusion was found anywhere in the style. A barrier to fruit set is apparently encountered after pollen tubes reach the ovary, at some point between the time the tube enters the micropyle of the ovule and the early development of the embryo.

SUMMARY AND CONCLUSIONS

<u>Salvia</u> <u>divinorum</u> is endemic to the Sierra Mazateca, and its overall, present distribution is clearly anthropogenic, with cultivated, semi-cultivated (weedy), and possibly wild populations all confined to the region inhabited by the Mazatec Indians. Thus within this region, stands have been

found in ecologically dissimilar areas, including dark, wet ravines at 1800 m., and sunny, disturbed trailsides at 400 m. In its vegetative phase, S. divinorum is very vigorous, and populations are clearly clonal. While populations flourish most in shaded, humid sites, flowering is promoted by sunlight and perhaps warmer temperatures. The plants may flower at any time during the year except June and July, but do so only sporadically, and only rarely are flowers abundant. Greenhouse-grown plants subjected to short day conditions, on the other hand, flower profusely.

The dimensions of the corolla suggest ornithophily, and the only pollination event observed involved a single hummingbird. The constituents, sugar concentration, and quantity of nectar produced, fit with the ornithophilous syndrome. Still, the anthropogenic distribution, the unusual character and phenology of flowering, the high degree of nectar robbing, and apparently complete failure to set fruit, suggest that hummingbird visits to the flowers in their present range are opportunistic, and not a product of co-evolution between plant and pollinator.

Salvia divinorum is diploid with n=11, and meiotic pairing seems quite normal, but some stage of gametogenesis is irregular, as roughly one half of the pollen grains abort. Since flowering is so sporadic, pollination may be undependable, and also, pollen does not adhere to the stigma as well as one would expect. Once a viable pollen grain germinates on a receptive stigma, pollen tubes are able to negotiate their way to the ovary, and there is clearly no active inhibition of the pollen tube like that which characterizes traditionally recognized, genetic self-incompatability systems. Some event or process after the pollen tube reaches the ovary is aberrant, though the precise nature or cause of the failure is unclear. Since calyces often abscise while the included nutlets are developing, post-zygotic embryo abortion or endosperm failure is probable. Whether this is due to inbreeding depression, hybridity, or a late acting (delayed) self-incompatability reaction is difficult to know. The latter is unlikely, especially because gametogenesis and other stages of the life cycle are also irregular, and one would think that the various aberrations have a common cause. Inbreeding depression is often the fate of taxa which become closely associated with man, and could potentially cause the observed irregularities.

Finally, the various anomalies which characterize S.

divinorum might perhaps be best explained as due to hybridity. However, except for the well known case of *Salvia apiana* and *S. mellifera* (sect. Audibertia) introgression, the effects of hybridity within the genus are not well understood. When floral isolation between these two Californian species breaks down, the resulting hybrids exhibit reduced pollen fertility and reduced seed set (Grant & Grant, 1964), as does *S. divinorum*. Disturbances due to hybridity in plants are well known (see Levin, 1978; Grant, 1971; Stebbins, 1958, 1971). They can be manifested at any point in the development of the sporophyte or gametophyte, and have been variously categorized: hybrid weakness, inviability, sterility, and breakdown, are types of disturbances caused by disharmonious genic or chromosomal interactions.

Disturbances at various stages in the life cycle of *S. divinorum* do suggest hybridity, but unfortunately, additional evidence is lacking. To none of the almost 500 species that comprise the Neotropical subg. Calosphace (Epling, 1939a) does *S. divinorum* show any obvious affinity, nor is intermediacy between two known species evident. Although the various character states for *S. divinorum* are encountered at one place or another within subg. Calosphace, I have been unable to identify two species, out of the hundreds, which, when crossed, might produce offspring which look like _S_. _divinorum_.

The Mazatecs say that "_La_ _Maria_ speaks with a quiet voice," which may explain, in part, why many issues concerning this enigmatic plant remain unsolved. Whether of hybrid origin or an inbred cultigen, questions regarding taxonomic affinities, fruit abortion, native distribution, and pharmacology, await yet to be addressed, before the aura of secrecy which enshrouds _La_ _Maria_ is to be lifted.

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APPENDIX I

SALVIA L. SUBG. CALOSPHACE (BENTH.) BENTH.

Listing of species as treated by Epling, 1939 in his revision published in Feddes repertorium specierum novarum regni vegetabilis. Species names in parentheses were reduced to synonomy by Epling in his unpublished (and unfinished) manuscript.

1. Sect. Axillares
   1. S. axillaris Moc. & Sesse

2. Sect. Microphace
   2. S. occidentalis Sw.
   3. S. misella Kunth
   4. S. riparia Kunth (=S. misella)
   5. S. setosa Fernald
   6. S. monantha Brandegee
   7. S. pseudoprivoides Epling

3. Sect. Tomentellae
   8. S. vinacea Wooton & Standley
   9. S. pinguifolia Wooton & Standley (=S. ballotaeflora)
   10. S. ballotaeflora Bentham
   11. S. cuspidata R. & P.
   12. S. Gilliesii Bentham
   13. S. Lorentzii Griseb. (=S. gilliesii)
   14. S. chorianthos Epling (=S. retinervia)
   15. S. retinervia Briquet
   16. S. calolophos Epling (=S. gilliesii)
   17. S. Bangii Rusby
   18. S. Humboldtiana Dietr.
   19. S. pruinosa Fernald
   20. S. Goldmanii Fernald
   21. S. fruticulosa Bentham
   22. S. rubropunctata Robins. & Fernald (=S. parryi)
   23. S. Parryi Gray
   24. S. candicans M. & G.
   25. S. Coulteri Fernald (=S. candicans)

4. Sect. Purpusiana
   26. S. Purpusii Brandegee

5. Sect. Cucullatae
   27. S. clinopodioides Kunth

6. Sect. Fernaldia

28. S. albo-caerulea Lind.

7. Sect. Caducae
    29. S. subincisa Bentham
    30. S. tehuacana Fernald

8. Sect. Lavanduloideae
    31. S. scaposa Epling
    32. S. Teresae Fernald
    33. S. helianthemifolia Bentham
    34. S. guadalajarensis Briquet
    35. S. moniliformis Fernald
    36. S. remota Bentham
    37. S. cryptodonta Fernald
    38. S. stricta Sesse & Moc.
    39. S. longifolia Willd.
    40. S. muscarioides Fernald
    41. S. lavanduloides Kunth
    42. S. Agnes Epling

9. Sect. Sigmoideae
    Subsect. Eusigmoideae
    43. S. platyphylla Briquet (=S. nepetoides)
    44. S. crucis Epling
    45. S. nepetoides Kunth
    Subsect. Cymulosae
    46. S. dryophila Epling
    47. S. alamosana Rose
    48. S. chapalensis Briquet
    49. S. quercetorum Epling
    50. S. inconspicua Bentham
    51. S. thyrsiflora Bentham
    52. S. chalarothyrsa Fernald
    53. S. dasycalyx Fernald (=S. thyrsiflora)

10. Sect. Punctatae
    54. S. Pavonii Bentham
    55. S. punctata R. & P.

11. Sect. Corrugatae
    56. S. ochrantha Epling
    57. S. corrugata Vahl
    58. S. styphelus Epling
    59. S. bullulata Bentham

12. Sect. Discolores
    60. S. discolor Kunth

13. Sect. Uliginosae
   61. S. urticifolia L.
   62. S. arizonica Gray (=S. glechomaefolia)
   63. S. Forreri Greene (=S. glechomaefolia)
   64. S. setulosa Fernald (=S. glechomaefolia)
   65. S. oreopola Fernald (=S. glechomaefolia)
   66. S. villosa Fernald (=S. glechomaefolia)
   67. S. pusilla Fernald
   68. S. glechomaefolia Kunth
   69. S. prunelloides Kunth
   70. S. pseudocomosa Epling
   71. S. laevis Bentham
   72. S. unicostata Fernald
   73. S. nana Kunth
   74. S. tricuspidata Mart. & Gal.
   75. S. rostellata Epling
   76. S. firma Fernald
   77. S. veronicaefolia Gray
   78. S. Lozani Fernald
   79. S. assurgens Kunth
   80. S. prunifolia Fernald
   81. S. sinaloensis Fernald
   82. S. uliginosa Bentham
   83. S. curta Epling (=S. uliginosa)
   84. S. congestiflora Epling (=S. uliginosa)
   85. S. lachnostachys Bentham
   86. S. procurrens Bentham
   86a. S. hamulus Epling
   86b. S. Hintonii Epling

14. Sect. Micranthae
   87. S. tenella Sw.
   88. S. thomasiana Urb. (=S. uliginosa)
   89. S. parciflora Urb. (=S. uliginosa)
   90. S. prostrata Hook.
   91. S. serotina L.
   92. S. podadena Briquet
   93. S. caymanensis Millsp. & Uline
   94. S. micrantha Vahl
   95. S. Fernaldii Standl.
   96. S. insularum Epling (=S. Fernaldii)
   97. S. pseudoserotina Epling (=S. Fernaldii)

15. Sect. Rhombifoliae
   98. S. occultiflora Epling
   99. S. rhombifolia R. & P.
   100. S. paposana Philippi

16. Sect. Siphonantha
    101. S. Lobbii Epling
    102. S. cyanocephala Epling
    103. S. pichinchensis Bentham

17. Sect. Macrostachyae
    104. S. speciosa Presl
    105. S. macrostachya Kunth
    106. S. atrocalyx Epling
    107. S. psilostachya Epling

18. Sect. Hastatae
    108. S. macrophylla Bentham
    109. S. Funkii Briquet
    110. S. sagittata R. & P.
    111. S. rhodostephana Epling
    112. S. rumicifolia Kunth
    113. S. scutellarioides Kunth
    114. S. palaefolia Kunth

19. Sect. Standleyana
    115. S. cacaliaefolia Bentham

20. Sect. Blakea
    116. S. costaricensis Oersted
    117. S. vitifolia Bentham
    118. S. mendax Epling
    119. S. patens Cav.
    119a. S. subpatens Epling

21. Sect. Wrightiana
    120. S. arborescens Urb. & Ekm.
    121. S. strobilanthoides Wr.
    122. S. densiflora Bentham

22. Sect. Gardoquiflorae
    123. S. Buchii Urb.
    124. S. brachyloba Urb.
    125. S. selleana Urb.

23. Sect. Bracteata
    126. S. herbacea Bentham

24. Sect. Glareosae
    127. S. reflexa Hornem.
    128. S. emaciata Epling
    129. S. hirsuta Jacq.
    130. S. potus Epling

25. Sect. Potiles
    - 131. S. hispanica L.

26. Sect. Mitratae
    - 132. S. lasiantha Bentham
    - 133. S. altimitrata Epling

27. Sect. Phoeniceae
    - 134. S. hirtella Vahl

28. Sect. Mineatae
    - 135. S. exserta Griseb.

29. Sect. Rubescentes
    - 136. S. melaleuca Epling
    - 137. S. colombiana Epling
    - 138. S. rubescens Kunth
    - 139. S. orthostachys Epling

30. Sect. Biflorae
    - 140. S. squalens Kunth
    - 141. S. tubiflora Smith
    - 142. S. striata Bentham
    - 143. S. oppositiflora R. & P.

31. Sect. Cylindriflorae
    - 144. S. quitensis Bentham
    - 145. S. hirta Kunth
    - 146. S. trachyphylla Epling
    - 147. S. Sprucei Briquet
    - 148. S. mucidistachys Epling
    - 149. S. praeclara Epling
    - 150. S. Heerii Regel
    - 151. S. psilantha Epling
    - 152. S. cylindriflora Epling
    - 153. S. hapalophylla Epling
    - 154. S. Haenkei Bentham
    - 155. S. Rusbyi Britton
    - 156. S. integrifolia R. & P.

32. Sect. Brittonia
    - 157. S. cubensis Britton & Wilson
    - 159. S. speirematoides Wr.

33. Sect. Ekmania
    - 159. S. Tuerckheimii Urb.
    - 160. S. uncinata Urb.

  161. S. foveolata Urb. & Ekm.
  162. S. Ottoschulzii Urb. & Ekm.
  163. S. lachnaiclada Briquet
  164. S. Thormanni Urb.
  165. S. arduinervis Urb. & Ekm.

34. Sect. Subrotundae
  166. S. subrotunda St. Hil.
  167. S. coccinea Juss.

35. Sect. Sulcatae
  168. S. phaenostemma J.D. Smith

36. Sect. Flexuosae
  169. S. bella Briquet
  170. S. derasa Bentham
  171. S. pauciserrata Bentham
  172. S. calocalicina Briquet

37. Sect. Incarnatae
  173. S. cinnabarina M. & G.
  174. S. elegans Vahl

38. Sect. Iodophyllae
  175. S. iodophylla Epling

39. Sect. Chariantha
  176. S. perlonga Fernald
  177. S. Orbignaei Bentham

40. Sect. Membranaceae
  Subsect. Elscholtzioideae
  178. S. hyptoides Mart. & Gal. (=S. lasiocephala)
  179. S. lasiocephala Hook. & Arn.
  180. S. galinsogifolia Fernald (=S. lasiocephala)
  181. S. verecunda Epling
  Subsect. Lophanthoideae
  182. S. glabra M. & G.
  183. S. lophanthoides Fernald
  184. S. nitida Bentham
  185. S. Langlassei Fernald
  186. S. Sanctae Seem.
  187. S. lophantha Bentham
  188. S. zacuapanensis Brandegee (=S. mocinoi)
  189. S. Mocinoi Bentham
  190. S. rubiginosa Bentham
  191. S. Mexiae Epling

41. Sect. Flocculosae
   192. S. cognata Urb. & Ekm.
   193. S. incumbens urb. & Ekm.
   194. S. chionophylla Fernald (=S. chamaedryoides)
   195. S. chamaedryoides Cav.
   196. S. coahuilensis Fernald
   197. S. serpyllifolia Fernald (=S. chamaedryoides)
   198. S. thymoides Bentham
   199. S. cedrosensis Greene
   200. S. Cruikshanksii Bentham
   201. S. sarmentosa Epling
   202. S. griseifolia Epling
   203. S. inornata Epling
   204. S. lycioides Gray
   205. S. macellaria Epling
   206. S. Greggii Gray
   207. S. Muelleri Epling
   208. S. cyanotropha Epling
   209. S. flocculosa Bentham

42. Sect. Tenuistachya
   210. S. Cavonii Urb.
   211. S. primulaeformis Epling

43. Sect. Scorodonia
   212. S. breviflora Moc. & Sesse
   213. S. reducta Epling
   214. S. Keerlii Bentham
   215. S. pannosa Fernald
   216. S. ramosa Brandegee
   217. S. variana Epling
   218. S. melissodora Lag.
   219. S. rupicola Fernald
   220. S. aequidistans Fernald
   221. S. tepicensis Fernald
   222. S. paupercula Epling
   223. S. occidua Epling

44. Sect. Uricae
   224. S. amarissima Ort.
   225. S. Urica Epling

45. Sect. Rudes
   226. S. sphacelifolia Epling
   227. S. cardiophylla Bentham
   228. S. cordata Bentham
   229. S. propinqua Bentham
   230. S. durifolia Epling

231. S. lucida Briquet
232. S. rosmarinoides St. Hil. (=S. nervosa)
233. S. nervosa Bentham
234. S. ovalifolia St. Hil.
235. S. caaguazensis Briquet
236. S. brevipes Bentham
237. S. viscida St. Hil.

46. Sect. Farinaceae
238. S. platycheila Gray
239. S. amissa Epling
240. S. similis Brandegee
241. S. pallida Bentham
242. S. farinacea Bentham
243. S. lanicalyx Epling
244. S. azurea Michx.
245. S. leptophylla Bentham
246. S. heterotricha Fernald (=S. leptophylla)
247. S. oblongifolia Mart. & Gal.

47. Sect. Malacophyllae
248. S. loxensis Bentham
249. S. malacophylla Bentham (=S. loxensis)
250. S. platystoma Epling (=S. rypara)
251. S. sophrona Briquet
252. S. tiraquensis Briquet (=S. rypara)
253. S. rypara Briquet
254. S. stachydifolia Bentham
255. S. rhinosina Griseb.

48. Sect. Flavidae
256. S. decurrens Epling

49. Sect. Dusenostachys
257. S. biserrata M. & G.
258. S. flaccidifolia Fernald
259. S. atrocaulis Fernald
260. S. recurva Bentham
261. S. concolor Lamb.
262. S. madrensis Seem.
263. S. monclovensis Fernald
264. S. lepida Epling
265. S. oligocantha Dusen

50. Sect. Donnellsmithia
266. S. Collinsii J.D. Smith
266a. S. infuscata Epling
267. S. Shannoni J.D. Smith

268. S. Kellermanii J.D. Smith

51. Sect. Pennellia
   269. S. Pennellii Epling

52. Sect. Atratae
   270. S. semiatrata Zucc.

53. Sect. Fendlera
   271. S. axilliflora Epling

54. Sect. Polystachyae
   Subsect. Australes
   272. S. tonalensis Brandegee
   273. S. sacculus Epling
   Subsect. Sacculus
   273a. S. durantiflora Epling (=S. sacculus)
   274. S. connivens Epling (=S. sacculus)
   275. S. obtorta Epling (=S. obtorta)
   Subsect. Polystachya
   276. S. lenta Fernald (=S. polystachya)
   277. S. igualensis Fernald (=S. polystachya)
   278. S. polystachya Ort.
   279. S. compacta Kuntze (=S. polystachya)
   Subsect. Glabratae
   280. S. brachyodonta Briquet
   280a. S. perblanda Epling
   281. S. filipes Bentham
   281a. S. decora Epling
   282. S. plurispicata Epling

55. Sect. Urbania
   283. S. tortuensis Urb.
   284. S. montecristina Urb.
   285. S. subaequalis Epling
   286. S. calaminthifolia Vahl
   287. S. mornicola Urb. & Ekm.
   288. S. saccifera Urb & Ekm.
   289. S. hotteana Urb. & Ekm.
   290. S. subglabra Urb.
   291. S. praeterita Epling
   292. S. brachyphylla Urb.

56. Sect. Carneae
   293. S. pseudogracilis Epling
   294. S. gracilis Bentham (=S. membranacea)
   295. S. membranacea Bentham
   296. S. iodochroa Briquet (=S. membranacea)

297. S. simulans Fernald (=S. membranacea)
297a. S. ionocalyx Epling
298. S. carnea Kunth
299. S. debilis Epling (=S. Killipiana)
300. S. Killipiana Epling

57. Sect. Angulatae
Subsect. Tiliaefolia
301. S. rhyacophila Epling (=S. leptostachys)
302. S. leptostachys Bentham
303. S. urolepis Fernald
304. S. uruapana Fernald
305. S. tiliaefolia Vahl
306. S. obvallata Epling (=S. tiliaefolia)
307. S. personata Epling
308. S. penduliflora Epling
Subsect. Glumacea
309. S. caudata Epling
310. S. roscida Fernald
311. S. fallax Fernald
312. S. arthrocoma Fernald
313. S. remissa Epling
314. S. fusca Epling
314a. S. languidula Epling
315. S. mucidiflora Fernald
316. S. prasiifolia Bentham
317. S. aliena Greene (=S. prasiifolia)
Subsect. Fruiticosae
318. S. perplicata Epling
319. S. myriantha Epling
320. S. haitiensis Epling
321. S. intonsa Epling
322. S. arenaria St. Hil.
323. S. itatiaiensis Dusen
324. S. nemoralis Dusen
Subsect. Rudes
325. S. consimilis Epling
326. S. laxispicata Epling
327. S. sphacelioides Bentham
328. S. angulata Bentham
329. S. longimarginata Briquet
330. S. bogotensis Bentham
331. S. albiflora Mart. & Gal.
332. S. mazatlanensis Fernald
333. S. Seemannii Fernald
334. S. longispicata Mart. & Gal.
335. S. fluviatilis Fernald
336. S. xalapensis Bentham

Subsect. Hiantes
337. S. drymocharis Epling
338. S. Alvajaca Oersted
339. S. amplifrons Briquet
340. S. membranicalyx Epling
341. S. perlucida Epling
342. S. ocimifolia Epling
Subsect. Scutellarioideae
343. S. flaccida Fernald

58. Sect. Ampelophyllae
344. S. ampelophylla Epling
345. S. amethystina J.E. Smith

59. Sect. Maxonia
346. S. festiva Epling
347. S. comayaguana Standl.
347a. S. chiapensis Fernald
348. S. umbraticola Epling
349. S. natalis Epling
350. S. pteroura Briquet
351. S. Maxonii Epling

60. Sect. Insignifoliae
352. S. pansamalensis J.D. Smith

61. Sect. Briquetia
353. S. umbratilis Fernald
354. S. mexicana L.
355a. S. atropaenulata Epling
355. S. lamiifolia Jacq.
356. S. ecuadorensis Briquet

62. Sect. Umbratiles
357. S. obumbrata Epling
358. S. silvarum Epling

63. Sect. Fulgentes
359. S. pulchella DC.
360. S. fulgens Cav.
361. S. lineata Bentham
361a. S. modica Epling
362. S. dichlamys Epling
363. S. microphylla Kunth

64. Sect. Pavonia
364. S. revoluta R. & P.
365. S. Macbridii Epling

65. Sect. Nobiles
    - 366. S. gesneraeflora Lindl. & Paxton
    - 367. S. adenophora Fernald
    - 368. S. disjuncta Fernald
    - 369. S. balaustina Pohl
    - 370. S. articulata Epling
    - 371. S. Benthamiana Gardn.
    - 372. S. Hilarii Bentham
    - 373. S. rivularis Bentham
    - 374. S. persicifolia St. Hil.
    - 375. S. salicifolia Pohl
    - 376. S. Sellowiana Bentham
    - 377. S. macrocalyx Gardn.

66. Sect. Muricatae
    - 378. S. scabrata Britton & Wils.

67. Sect. Erythrostachys
    - 379. S. Regla Cav.
    - 380. S. pubescens Bentham (=S. sessei)
    - 381. S. Sessei Bentham
    - 382. S. libanensis Rusby

68. Sect. Silvicolae
    - 383. S. miniata Fernald
    - 384. S. ianthina Otto & Dietr.
    - 385. S. guaranitica St. Hil.
    - 386. S. atrocyanea Epling

70. Sect. Cardinales
    - Subsect. Tubiformes
    - 387. S. cardinalis Kunth
    - 388. S. stolonifera Bentham
    - Subsect. Ventricosae
    - 389. S. siguatepequensis Standl. (=S. Karwinskii)
    - 390. S. Karwinskii Bentham
    - 391. S. Holwayi Blake
    - 392. S. Wagneriana Polak.
    - 393. S. involucrata Cav.
    - 394. S. puberula Fernald

71. Sect. Conzattiana
    - 395. S. aspera Mart. & Gal.
    - 396. S. oaxacana Fernald
    - 397. S. pexa Epling

72. Sect. Sphacelioides

398. S. subhastata Epling

73. Sect. Leonuroideae
    399. S. plumosa R. & P.
    400. S. formosa L'Herit.

74. Sect. Skeptostachys
    401. S. Regnelliana Briquet

75. Sect. Asperifoliae
    402. S. scabrida Pohl

76. Sect. Hoehneana
    403. S. grewiaefolia S. Moore
    404. S. altissima Pohl

77. Sect. Leucocephalae
    405. S. leucocephala Kunth

78. Sect. Tuberosae
    406. S. oxyphora Briquet

79. Sect. Longiflorae
    407. S. vestita Bentham
    408. S. tubulosa Epling
    409. S. acuminata R. & P.
    410. S. Dombeyi Epling
    411. S. scandens Epling
    412. S. lachnostoma Epling
    413. S. Weberbaueri Epling

80. Sect. Brandegeia
    414. S. blepharophylla Brandegee
    415. S. oresbia Fernald
    416. S. angustiarum Epling

81. Sect. Pruinosae
    417. S. Rosei Fernald

82. Sect. Palmerostachys
    418. S. Palmeri Gray

83. Sect. Killipiana
    419. S. erythrostoma Epling
    420. S. latens Bentham
    421. S. laurifolia Epling
    422. S. costata Epling

84. Sect. Peninsulares
   423. S. Marci Epling
   424. S. peninsularis Brandegee

85. Sect. Tubiflorae
   425. S. tubifera Cav.
   426. S. Pringlei Robins. & Greenm.
   427. S. microdictya Urb. & Ekm.
   428. S. eriocalyx Bert.
   429. S. jamaicensis Fawe.
   430. S. clarendonensis Britton
   431. S. secundiflora Rusby
   432. S. camaraefolia Bentham
   433. S. venulosa Epling
   434. S. pseudolantana Epling
   435. S. tortuosa Kunth
   436. S. moschata Kunth

86. Sect. Iodanthae
   437. S. iodantha Fernald
   438. S. Townsendii Fernald (=S. iodantha)
   439. S. arbuscula Fernald (=S. iodantha)

87. Sect. Purpureae
   440. S. curviflora Bentham
   441. S. Littae Vis.
   441a. S. Matudae Epling
   442. S. purpurea Cav.
   443. S. sordida Bentham
   444. S. rufula Kunth
   445. S. tolimensis Kunth

88. Sect. Floridae
   446. S. subrubens Epling
   447. S. florida Bentham

89. Sect. Albolanatae
   448. S. leucantha Cav.
   449. S. tomentella Pohl

90. Sect. Curtiflorae
   450. S. longistyla Bentham
   451. S. nervata M. & G.
   452. S. venosa Fernald (=S. excelsa)
   453. S. curtiflora Epling
   454. S. excelsa Bentham
   455. S. neovidensis Bentham
   456. S. mentiens Pohl

457. S. fruticetorum Bentham
458. S. tenuiflora Epling

91. Sect. Secundae
459. S. Dugesiana Epling
460. S. Herrerae Epling
461. S. mattogrossensis Pilger
462. S. melissaeflora Bentham
463. S. paranensis Dusen (=S. melissaeflora)
464. S. splendens Sellow
465. S. rufa Epling (=S. confertiflora)
466. S. confertiflora Pohl
467. S. secunda Bentham
468. S. occlusa Epling

APPENDIX II

KEY TO THE SECTIONS OF SALVIA SUBGENUS CALOSPHACE

From: A Revision of Salvia subgenus Calosphace (Epling, 1939). [Translated from the Latin of Carl Epling by Duane Kolterman and Aaron Reisfield].

1. Stamens exserted beyond the upper lip.

  2. Corolla tubes furnished within below the middle sometimes with 2 or 4 papillae, sometimes with paired transverse (longitudinal in sect. Mitratae) wrinkles [folds].

    3. Upper lip of the calyces chiefly 3-veined, rarely 5-7 veined (see also sect. Flexuosae, sect. Purpureae) ....86. Iodanthae

    3. Upper lip of the calyces 5-7 veined.

      4. Upper lip of the corollas mostly longer than the tube; hairs branched .... 26. Mitratae

      4. Upper lip of the corollas shorter than the tube.

        5. Tubes of the corollas scarcely invaginated at the base, sometimes narrowed below the papillae.

          6. Bracts persistent; calyces viscid on the outside with long extended glandular hairs...........................27. Phoeniceae

          6. Bracts deciduous; calyces glabrous if not red-villous, scarcely glandular.

            7. Stamens placed at the middle of the tube and below.........................36. Flexuosae

            7. Stamens placed at the throat.............. ....38. Iodophyllae

        5. Tubes of the corollas nearly straight, invaginated at the base below the papillae; stamens placed at the throat...............39. Chariantha

  2. Tubes of the corollas entirely naked within

(longitudinally sulcate-invaginate at the base in sect. Sulcatae and S. cinnabarinae).

8. Upper lip of the calyces chiefly 3-veined (see also S. tiliaefolia).

9. Styles pilose.

10. Veins of the calyces thickened at the base, reticulate-branched at the mouth; Mexican plants..............................81. Pruinosae

10. Veins of the calyces chiefly simple.

12. Stamens placed at the throat...88. Floridae

12. Stamens placed at the middle of the tube.........................29. Rubescentes

11. Mexican plants, with the lips of the calyces often aristulate [with small bristles]....................................90. Curtiflorae

9. Styles glabrous.

13. Tubes of the corollas 4-9 mm. long; flowers crowded in dense cylindric spikes; Cuban plants.............................21. Wrightiana

13. Tubes of the corollas 12-43 mm. long; flowers arranged either in racemes or in interrupted spikes, rarely crowded together.

14. Lower lip of the corollas almost lacking, much shorter than the upper lip.90. Curtiflorae

14. Lower lip of the corollas almost equalling the upper or longer.

15. Flowers opposite, arranged in racemes.

16. Corollas red or scarlet; leaves more or less narrowed at the base; Cuban plants (see also Ekmania)................32. Brittonia

16. Corollas blue; leaves deltoid-sagittate; Mexican and Central American plants (see also

<u>Blakea</u>)....................19. **<u>Standleyana</u>**

15. Flowers 3-9 in verticillasters arranged in interupted or congested spikes.

17. Bracts lanceolate, persistent; corolla tubes longitudinally sulcate-invaginate below, at the base; Guatemalan plants........................35. <u>Sulcatae</u>

17. Bracts deciduous or cauducous; corolla tubes entire.

18. Corollas zig-zag shaped, dark blue; northern Andean plants...................16. <u>Siphonantha</u>

18. Corollas red or scarlet, rarely yellow; Haitian-Dominican plants.......................33. <u>Ekmania</u>

8. Upper lip of the calyces 5-7 veined or more.

19. Tubes of the blue corollas 3.5-6 mm. long; posterior branch of the glabrous style usually shorter, even almost lacking.

20. Leaves spade-shaped; flowers opposite; rudders of the stamens half as long as the connectives (see also <u>Blakea</u>) ....18. <u>Hastatae</u>

20. Leaves ovate or deltoid-ovate; flowers 2-6 or more in verticillasters; rudders of the stamens subequalling the connectives.

21. North American herbs; flowers subtended by small persistent or late deciduous bracts....... .... 4. <u>Micranthae</u>

21. South American annual herbs; flowers subtended by small caducous bracts............. ....15. <u>Rhombifoliae</u>

19. Tubes of the corollas 10-43 mm. long (see also <u>S. regla</u>).

22. Styles glabrous

23. Corollas blue or white (rarely rose).

24. Flowers opposite, solitary, in the axils of deciduous bracts; leaves mostly hastate or sagittate (see also Standleyana and Blakea)..........................18. Hastatae

24. Flowers 3-6 or more in verticillasters; leaves ovate or ovate-cordate.

25. Zig-zag shaped tubes of the corollas recurved-ascending; connectives of the stamens connected nearly at the middle......................16. Siphonantha

25. Corolla tubes straight; stamen connectives connected nearly at the base, the rudder consequently shorter in proportion.................17. Macrostachyae

23. Corollas scarlet.

26. Rudders of the stamens drawn out into an acute tooth at the connection.

27. Argentinian plants; bracts deciduous..... ....28. Mineatae

27. Brazilian plants; bracts conspicuous and persistent................74. Skeptostachys

26. Rudders of the stamens entire.

28. Flowers opposite, solitary, in the axils of deciduous bracts.

29. Cuban plants with chiefly elliptical leaves; stamens placed at the throat (see also Ekmania)..............32. Brittonia

29. Andean plants with chiefly deltoid leaves; stamens placed at ther middle of the tube....................30. Biflorae

28. Flowers 3-6 in verticillasters (more rarely opposite).

30. Mexican and Central American plants

with the calyces, excluding the tails, 3-7 mm. long.

30. South American plants (except *S. coccinea*) with the calyces 6-20 mm. long.

31. Brazilian plants (*S. coccinea* is widely distributed).....34. *Subrotundae*

31. Andean plants; posterior branch of the style longer than the anterior (excluding *S. quitense*)......................................31. *Cylindriflorae*

31. Haitian-Dominican plants; posterior branch of the style short, even lacking.....................33. *Ekmania*

22. Styles pilose or hirtellous.

32. Stamens placed at the middle of the tube. ....29. *Rubescentes*

32. Stamens placed at the throat.

33. Tubes of the corollas 4 times as long as the calyces; Mexican plants ...37. *Incarnatae*

33. Tubes of the corollas 2 times as long as the calyces.

34. Lips of the calyces attenuate; posterior branch of the style very long.......................................90. *Curtiflorae*

34. Lips of the calyces acute; posterior branch of the style shorter...34. *Subrotundae*

1. Stamens entirely included within the galea.

35. Upper lip of the calyces chiefly 3-veined.

36. Corolla tubes furnished within, at the base, with 2 or 4 papillae, sometimes wrinkles [folds] (see also *Invaginatae* species following [?]) [corrected by Epling (1941) to read: (see also *Hoehneana* and species following)]

37. Lower lip of the corollas patently longer than the upper.

38. Corollas rose or red-purple, rarely pale; petioles of the leaves almost equaling the blades; pedicels of the mature calyces mostly 3-4 mm. long or more..............................56. Carneae

38. Corollas blue; the petioles mostly half as long as the leaf blades; pedicels of the mature calyces mostly 1-2 mm. long; the glomerules consequently crowded.........................54. Polystachyae

37. Lower lip of the corollas subequal in length or shorter than the upper (see also Polystachyae).

39. Tubes of the usually blue corollas often constricted below the middle below the papillae, consequently ventricose above [swollen especially on 1 side]; 6-11 mm. (rarely 13 mm.) long.................................59. Maxonia

39. Tubes of the rose-purple or scarlet corollas gradually enlarged above, nevertheless scarcely ventricose, 15-22 mm. (rarely 10 mm.) long (see also S. erythrostoma).

40. Leaves ovate, rounded at the base, sometimes rounded narrowed; corolla rose-purple..........................87. Purpureae

40. Leaves narrowly ovate or elliptic, narrowed at the base, also extenuated, shortly petiolate; corollas scarlet ....83. Killipiana

36. Tubes of the corollas epapillate within, neverthless frequently invaginated.

41. Posterior branch of the style patently shorter than the anterior, sometimes lacking.

42. Lips of the corollas subequal in length, the shortest of the genus [?], with the appearance of Gardoquia; stamens placed at the middle of th tube........................22. Gardoquiiflorae

42. Lips of the corollas 5-40 mm. long; stamens

placed at the throat.

43. Styles glabrous; leaves mostly hastate or deltoid; flowers opposite............................20. Blakea

43. Styles pilose; leaves oval or oblong, rounded or narrowed at the base; flowers 3 or more in verticillasters................42. Tenuistachya

41. Posterior branch of the style attenuate and twice or 3 times as long as the anterior (those of sect. Secundae frequently subequal in length).

44. Anterior branch of the style patently hollowed out [in a curve] and truncate at the apex; rudders of the stamens oblong-deltoid, 2 or 3 times longer than the upper part of the filament........................8. Lavanduloideae

44. Anterior branch of the style entire, acute; rudders of the stamens either entire or at the connection drawn out into a small acute tooth, extended or retrorse, by no means is the tooth rising upward [i.e. not bent up].

45. Island plants, chiefly Haitian, with leaves largely 1-3 cm.....................55. Urbania

45. Continental plants (Angulatae, S, haitensis, S, lamifolia, and also Tubiflorae excepted) with larger leaves.

46. Hairs branched.

47. Flowers in the axils of the leaves; Venezualan plants ....53. Fendlera

47. Flowers arranged in compact spikes; Chihuahuan plants........82. Palmerostachys

46. Hairs simple (but not S, fluviatilis); flowers arranged in interrupted spikes.

48. Stamens placed at the middle of the tube ....29. Rubescentes

48. Stamens placed at the throat and rarely

(Secundae and Curtiflorae) between the throat and the middle of the tube.

49. Lower lip of the corollas curved inwards, concave, either shorter than or subequal in length to the upper, sometimes almost lacking; stamens placed between the middle of the tube and the throat (except S. venosa).

50. Mexican plants (see also Briquetia). ....90. Curtiflorae

50. Brazilian plants.......91. Secundae

49. Lower lip of the corollas deflexed; stamens placed at the throat.

51. Lower lip of the corollas shorter than or subequal in length to the upper.

52. Corollas rose-purple (see Briquetia).

53. Cuban plants......66. Muricatae

53. Lower [Baja] Californian plants. ....84. Peninsulares

53. Continental or Island plants (see also Carneae, S. pseudogracilis, and also Pruinosae).

54. Styles glabrous, leaves oblong-lanceolate........68. Silvicolae

54. Styles pilose, leaves mostly ovate..............85. Tubiflorae

52. Corollas dark blue (see also Dusenostachys and Polystachyae)...... ....61. Briquetia

51. Lower lip of the corollas longer than the upper.

55. Corolla tubes 15-21 mm. long.

56. South American plants; leaves rotund-cordate....58. Ampelophyllae

56. North American plants.

57. Leaves oblong-ovate, truncate at the base; Mexican plants..............51. Pennellia

57. Leaves elliptical, distinguished by acutely incised-serrulate margins; Guatemalan plants..........60. Insignifolia

55. Corolla tubes 3.5-14 mm. long (14-17 mm. long in S. flaccida with persistent bracts; see also Polystachyae).

58. Calyces glabrous or hirtellous, nevertheless scarcely farinaceous [farinose, i.e. mealy] on the outside..............57. Angulatae

58. Calyces with minute appressed hairs on the outside, densely farinaceous (chiefly Texan plants) or lanulose [somewhat wooly] (chiefly Coahuilan plants), the mouth subtruncate.........46. Farinaceae

35. Upper lip of the calyces 5-9 veined or more (nevertheless see sometimes Purpureae, Tubiflorae, Maxonia, Killipiana, and Rubescentes).

59. (p. 42) Flowers arranged in glomerules subtended by persistent, rarely late-deciduous bracts, or in the axils of the leaves.

60. Geniculate rudders of the stamens more or less deltoid and drawn out into an upward rising, rarely obscure tooth (see also Blakea).

61. Anterior branch of the style patently sigmoid-flexuous [sigmoid = S shaped, flexuous = zig-zag shaped]............................9. Sigmoideae

61. Anterior branch of the style sometimes deltoid,

sometimes concave, more often arcuate [curved like a bow], by no means sigmoid.

62. Styles glabrous (see also Uliginosae and Membranaceae)....................2. Microsphace

62. Styles pilose.

63. Upper lip of the calyces hooded, 2 times overtopping the lower; thick herbs...........................5. Cucullatae

63. Lips of the calyces subequal in length.

64. Perennial herbs, moderately small, sometimes prostrate; anterior style branch flattened-deltoid............13. Uliginosae

64. Stoloniferous shrubs or subshrubs with frequently branched hairs; anterior style branch moderately attenuate, scarcely flattend-deltoid.............3. Tomentellae

60. Rudders of the stamens either entire or broadened at the connection into a retrorse, sometimes extended tooth.

65. Hairs branched.

66. Corolla tubes naked within..41. Flocculosae

66. Corolla tubes furnished within with paired papillae.

67. South American plants....73. Leonuroideae

67. Mexican plants............71. Conzattiana

65. Hairs simple.

68. Small low-growing perennial herbs, with small leaves for the most part 5-10 mm. long; flowers 1-3 arranged in the axils of the leaves............................1. Axillares

68. Moderately large herbs or shrubs, rarely delicate.

69. Corolla tubes scarlet or rose, 13-35 mm. long or more.

70. Flowers arranged in the axils of the uppermost leaves (see also *Secundae*).

71. Corolla tubes furnished within at the base with paired papillae.

72. Andean plants with pilose styles (see also *Killipiana*)........73. *Leonuroidea*

72. Mexican plants with glabrous styles. ....71. *Conzattiana*

71. Tubes of the corollas naked within; plants of Mexico.............65. *Nobiles*

70. Flowers arranged in the axils of persistent bracts (see also *Nobiles*, *S. neovidensis* and *S. vestita*).

73. Lower lip of the corollas patently longer than the upper; Mexican plants....................80. *Brandegeia*

73. Corolla lips subequal in length or the lower shorter; South American plants.

74. Tubes of the corollas entire.

75. Lower lips of the corollas deflexed, 10-12 mm. long...............74. *Skeptostachys*

75. Lower lips of the corollas curved inwards, 1.5-5.5 mm., rarely 8-9 mm. (*S. splendens*) long....................91. *Secundae*

74. Tubes of the corollas strongly invaginated toward the base.....................76. *Hoehneana*

69. Tubes of the blue, rarely white corollas 2.5-9 mm. long (23-24 mm. in *S. Atrocyanea*).

76. Styles chiefly glabrous, rarely sparsely

hispidulous.

77. Posterior branch of the style patently shorter than the anterior (see also _Blakea_).

78. Continental plants, erect, annual, with leaves mostly elliptic-oblong....................24. _Glareosae_

78. Chiefly island plants (of the Galapagos and the Antilles, rarely Florida and the Yucatan), mostly annual, with leaves largely deltoid-ovate and round....................14. _Micranthae_

77. Posterior branch of the style patently longer than the anterior (see also _Glareosae_)

79. Styles articulated above the nutlets; Columella of the gynobase densely beset with sessile glands, persistent..25. _Potiles_

79. Styles articulated between [among] the nutlets; columella of the gynobase eglandulose. ....40. _Membranaceae_

76. Styles more or less villose.

80. Anterior style branch concave, truncate at the apex; annual herbs.......................23. _Bracteata_

80. Anterior style branch moderately acute, scarcely excavated, by no means truncate; perennial herbs or shrubs.

81. Corolla tubes 23-24 mm. long; Bolivian plants..........69. _Coeruleae_

81. Corolla Tubes 6-9 mm long.

82. Flowers arranged in compact spikes; South Mexican and Guatemalan plants (see also _S. breviflora_)..................................50. _Donnelsmithia_

82. Flowers arranged in interrupted spikes.

83. Leaves subsessile; Bolivian plants (see also Farinaceae).........................47. Malicophyllae

83. Leaves borne on petioles 1-4 cm. long or more; North American plants ([but] S. pallida is from Argentina) ....46. Farinaceae

59. Flowers subtended by caducous or deciduous bracts.

84. Geniculate rudders of the stamens more or less deltoid and drawn out into an upward rising rarely obscure tooth (see also Discolores).

85. Anterior style branch patently sigmoid-flexuous; tubes of the corollas papillate within..............................9. Sigmoideae

85. Anterior branch of the style either arcuate or flattened-deltoid, sometimes concave or flat, nevertheless scarcely sigmoid.

86. Corolla tubes patently invaginated at the base.

87. Andean plants with corrugated leaves.....................................11. Corrugatae

87. Mexican plants with large, moderately smooth leaves...................6. Fernaldia

86. Tubes of the corollas scarcely invaginated, sometimes constricted or furnished within with papillae.

88. Caducous annual herbs [caducous leaves?], often weak [slender]..............7. Caducae

88. Perennial herbs

89. Styles strongly flattened at the apices, anterior branch subdeltoid...13. Uliginosae

89. Styles scarcely flattened; anterior branch arcuate, scarcely deltoid.

90. Hairs branched (except S. Ballotaeflora).............3. Tomentellae

90. Hairs simple.

91. Peruvian plants with hirsute styles. ....10. Punctatae

91. Mexican plants with glabrous styles. ....4. Purpusiana

84. Rudders of the stamens either entire or at the connection furnished with a small extended or retrorse tooth.

92. Stamens placed between the middle of the corolla tube and the throat; corolla lips short, the middle lacinia [fringe or lobe] of the lower [lip] incurved-concave (see also Albolanatae and Rubescentes).........................91. Secundae

92. Stamens placed at the throat.

93. Posterior branch of the style patently shorter than the anterior; corollas always blue.

94. Tubes of the corollas 20-33 mm. long.............................69. Coeruleae

94. Tubes of the corollas 3-6 mm. long; chiefly annual erect herbs.

95. Upper lip of the calyx 7-veined; bracts mostly persistent; chiefly insular herbs, also in Florida and the Yucatan.............. ....14. Micranthae

95. Upper calyx lip 5-veined; bracts mostly deciduous, sometimes persistent; continental plants.

96. Leaves mostly elliptical-oblong; Mexican plants..............24. Glareosae

96. Leaves mostly deltoid; Andean plants..

..........................15. <u>Rhombifoliae</u>

93. Posterior style branch patently longer than the anterior (see also <u>S</u>. <u>chorianthos</u>).

97. Corolla tubes more or less constricted [narrowed] or patently invaginated ,mostly furnished with papillae or 2 or 4 wrinkles [folds] at the base (see also <u>Flocculosae</u>, <u>Privoideae</u>, <u>Rudes</u>, and <u>S</u>. <u>consimilis</u>).

98. Styles glabrous.

99. Corollas scarlet or yellow-golden.

100. Mexican plants with the flowers either in short racemes or in the axils of the uppermost leaves, mostly opposite................71. <u>Conzattiana</u>

100. Peruvian plants with the flowers arranged [?] in showy interrupted spikes...................62. <u>Umbratiles</u>

99. Corollas blue or purple.

101. Corolla tubes 42-45 mm. long...... ....79. <u>Longiflorae</u>

101. Corlla tubes 13-14 mm. long

102. Corollas dark blue; calyces large, of the size of the flowers; Peruvian plants.................12. <u>Discolores</u>

102. Corolla tubes whitish, the lips dark blue; Mexican plants.52. <u>Atratae</u>

98. Styles pilose or villous, sometimes hirtellous.

103. Hairs branched.

104. Peruvian plants; corolla tubes 13-23 mm. long (see also <u>Cardinales</u>)................64. <u>Pavonia</u>

104. Mexican plants; corolla tubes 3.5-9

mm. long.................43. Scoradonia

103. Hairs simple.

105. Corolla tubes mostly blue, sometimes white, 5-15 (rarely 18) mm. long.

106. Corollas yellowish, stems decurrent-villous at the angles [corners]; Brazilian herbs.................................. 48. Flavidae

106. Corollas blue, rarely whitish; stems scarcely decurrent-villous; plants chiefly Mexican (see also Maxonia).

107. Leaves deltoid or ovate (oblong-lanceolate in S. occidua; see also S. similis).

108. Corolla tubes white, 13 mm. long; chiefly with the dark blue lower lip shorter than the upper.. ....52. Atratae

108. Corollas uniform in color, blue or pale, lower lip patently longer than the upper.

109. Corolla tubes patently invaginated at the base.................................44. Uricae

109. Corolla tubes entire.........................43. Scorodonia

107. Leaves linear or oblong; stems rarely besprinkled with rather long eglandular hairs. ....46. Farinaceae

105. Tubes of the red or scarlet or sometimes rose colored corollas 15-35 mm. (rarely 13-14 mm.) long (see also Purpureae and also Killipiana)

110. South American plants.

111. Corollas strongly invaginated at the base, by no means laterally saccate [pouch or bag-shaped]............................76. <u>Hoehneana</u>

111. Corollas laterally impressed [sunken]-saccate at the base; herbs with tuber-bearing roots.................................78. <u>Tuberosae</u>

110. North American plants.

112. Upper corolla lip subequaling or longer than the lower.

113. Corolla tubes invaginated, epapillate. .....84. <u>Peninsulares</u>

113. Corolla tubes furnished within with paired papillae, sometimes invaginated, sometimes entire.............70. <u>Cardinales</u>

112. Upper corolla lip patently shorter than the lower.

114. Corollas constricted at the base, but scarcely furnished with papillae...........80. <u>Brandegeia</u>

114. Corollas more or less invaginated at the base and furnished within with paired papillae............63. <u>Fulgentes</u>

97. Corolla tubes chiefly entire, sometimes gently constricted or invaginated, by no means furnished within with papillae unless with very minute ones.

115. Hairs branched.

116. Tubes of the red-purple corollas 20-28 mm. long................77. <u>Leucocephalae</u>

116. Tubes of the corollas 3.5-18 mm. long.

117. Corolla lips subequal in length with

the middle lacinia [fringe, lobe] incurved................89. *Albolanatae*

117. Lower corolla lip patently longer, spreading.

118. Leaves for the most part elliptic-oblong, frequently ovate, rarely deltoid, mostly entire or obscurely crenulate.............41. *Flocculosae*

118. Leaves for the most part deltoid, more rarely deltoid-oblong, sometimes ovate, more often bullate [blistered]-rugose [wrinkled]......43. *Scorodonia*

115. Hairs simple (hairs of the calyces of *S*. *hilari* branched)

119. Corollas scarlet or red with the tubes for the most part 25-90 mm. (rarely 12-22 mm.) long (see also *S*. *greggii*, *S*. *macellaria*, and *S*. *subhastata*).

120. Calyces inflated, subglobose, more or less venulose, mostly red..................67. *Erythrostachys*

120. Calyces tubular, by no means inflated.

121. Styles glabrous (see also *Umbratiles*, *subrotundae*, and *S*. *rivularis*)............79. *Longiflorae*

121. Styles pilose (see also *Subrotundae*, *Incarnatae*, *S*. *weberbaueri*, and *S*. *Tuberosae*)

122. Tall shrubs, rarely perennial herbs (see also *Tubiflorae* and *S*. *dugesiana*)..............65. *Nobiles*

122. Perennial herbs to 1 meter in height with few simple stems; Brazilian plants....75. *Asperifoiae*

119. Corollas for the most part blue,

rarely yellowish (S. madrensis), rarely red (S. greggii), or white-rose [pink] (S. subhastata), frequently whitish, with tubes for the most part 4-20 mm. (rarely 20-30 mm.) long.

123. Annual herbs with styles chiefly glabrous, sometimes very sparsely setose [bristly] in front [on the anterior side], (see also Purpusiana). ....24. Glariosae

123. Perennial herbs or shrubs with pilose or hirtellous styles

124. Lips of the corollas proportionately shorter [than contrasting couplet?], the middle lacinia of the lower lip incurved-concave; flowers white. ....89. Albolanatae

124. Lower lip of the corollas moderately deflexed, by no means incurved-concave (see also Coeruleae)

125. Corolla tubes 4-11 mm. (11-22 mm. in S. cognata, S. ovalifolia, and S. rhinosina) long (see also S. biserrata, S. monclovensis, and S. discolor).

126. Leaves for the most part deltoid or ovate, rounded or truncate at the base, often bullulate (see also S. consimilis).

127. Andean plants with leaves moderately smooth, below, softly pubescent.....47. Malacophyllae

127. Mexican plants with leaves mostly bullulate, for the most part clothed with branched hairs............43. Scorodonia

126. Leaves chiefly oblong or elliptic, more rarely linear,

sometimes ovate.

128. Pasture dwelling plants, Brazilian-Argentinian (one Sinaloan)............45. _Rudes_

128. Andean or Mexican plants.

129. Calyces appressed-hirtellous on the outside, sometimes glabrous. ....46. _Farinaceae_

129. Calyces clothed with short extended frequently glandular hairs on the outside (see also _Tomentellae_).41. _Flocculosae_

125. Corolla tubes 12-30 mm. (11 mm. in _S_. _biserrata_ and _S_. _monclovensis_; see also _S_. _discolor_)

130. Mexican plants.

131. Flowers dark blue; leaves large, ovate or rotund-ovate.........49. _Dusenostachys_

131. Flowers white-rose; leaves subhastate....72. _Sphacelioides_

130. Brazilian plants.

132. Upper lip of the corollas 6-7 mm. long, shorter than the lower.........49. _Dusenostachys_

132. Upper lip of the corollas 14-15 mm. long, longer than the lower.............69. _Coeruleae_

AMENDMENTS TO THE KEY

Further work by Epling after his major treatment (1939a) was presented in a series of Supplementary Notes on American Labiatae (Bulletin of the Torrey Botanical Club; Brittonia), beginning in 1940 and ending with No.10 in 1968 upon Epling's death. Amendments to the key to sections are for the most part designed to accomodate newly described species, but some new combinations of species are the results of Epling's increased understanding of various groups as more and better collections of plants were made available to him.

1940. Supp. Notes I. Bull. Torrey Bot. Club. 67:516. A new section is described (Lanatae) to accomodate the new species S. leucochlamys:

87. Andean plants with corrugated leaves..11. Corrugatae

87. Mexican plants

 87a. Leaves 2 cm. long, more or less corrugated, gray-hirsute above, densely white tomentose below......................................11a. Lanatae

 87a. Leaves elliptic, 10-20 cm. long, glabrous..................................6. Fernaldia

1940. Supp. Notes I. Bull. Torrey Bot. Club. 67:519. A new section is described (Pedicillata) to accomodate the new species S. pallealis.

1940. Supp. Notes I. Bull. Torrey Bot. Club. 67:530. A new section is described (Hintoniana) to accomodate the new species S. praestans:

6. Bracts persistent; calyces viscid outside, with long extended glandular hairs..................................27. Phoeniceae

6. Bracts deciduous.

 7. Stamens placed at the middle of the tube and below.

....................................36. Flexulosae

7. Stamens placed at the throat.

7a. Styles glabrous; lower corolla lip subequaling or shorter than the upper.

7b. Flowers opposite, arranged in racemes; glabrous plants of Orizaba...........................38. Iodophyllae

7b. Flowers 6 in verticillasters, in interupted spikes; sparsely villous plants of Guerrero.........................38a. Pedicillata

7a. Styles pilose; lower corolla lip nearly twice as long as the upper...................63b. Hintoniana

1941. Supp. Notes II. Bull. Torrey Bot. Club. .8:557: The sectional limits of Corrugatae are broadened to include a new species (S. pseudorosmarinus)

64. Stoloniferous shrubs or subshrubs with frequently branched hairs; anterior style branch moderately attenuate, scarcely flattened-deltoid.

64a. Corolla tubes strongly invaginated at the base; leaves with the habit of Rosmarinus....................11. Corrugatae

64a. Corolla tubes moderately ventricose, nevertheless scarcely invaginated unless obscurely furnished within with paired oblique [?] wrinkles [folds]..........3. Tomentellae

60. Rudders of the stamens either entire...

1941. Supp. Notes II. Bull. Torrey Bot. Club 68:558. A new section is described (Gentryana) to accomodate the new species S. trichostephana.

8. Upper lip of the calyces with 5-7 veins or more.

19. Corolla tubes 3.5-6 mm. long; the posterior branch

of the glabrous style short, even almost lacking.

20. Leaves spade-shaped; flowers opposite, blue; procumbent Columbian herbs (see also _Blakea_)..................................18. _Hastatae_

20. Leaves ovate or deltoid-ovate; flowers 2-6 or more in verticillasters.

21. Thick perennial herbs of Sinaloa, the branches clothed with branched hairs; corollas rose-purple.............................21a. _Gentryana_

21. Small herbs, often annual, clothed with simple hairs; corolla blue.

21a. Stamens scarcely exserted out of the upper lip; North American plants unless of the Galapagos Islands.................14. _Micranthae_

21a. Stamens moderately exserted; Andean plants. ....16. _Rhombifoliae_

19. Corolla tubes 10-43 mm. long ....

1941. Supp. Notes II. Bull. Torrey Bot. Club 68:559. _S. praeclara_ is transferred from sect. _Cylindriflorae_ to sect. _Mineatae_.

27. Argentinian or Bolivian plants.........28. _Mineatae_

1941. Supp. Notes II. Bull. Torrey Bot. Club 68:560. Sections _Scorodonia_ and _Uricae_ are combined.

106. Corollas dark blue, rarely whitish or rose-purple; stems scarcely decurrent-villous; plants chiefly Mexican.

107. Lower lip of the blue or whitish corollas longer than the galea (see also 59a. _Nivalis_; corollas white to white-pilose)

108. Leaves sometimes oblong-lanceolate or linear and the bracts often deciduous, sometimes ovate,

nevertheless the bracts are more often persistent; corolla tubes naked within (except S. leptophylla and S. similis)........................46. Farinaceae

108. Leaves ovate or deltoid (oblong-lanceolate in S. occidua); bracts deciduous; corolla tubes furnished within at the base with paired wrinkles [folds] or papillae, rarely naked. ....43. Scorodonia

107. Lower lip of the dark blue or rose-purple corollas subequal in length or shorter than the galea.

109. Leaves deltoid, bullulate [somewhat blistered or puckered]; corolla tubes white, lips blue...............................52. Atratae

109. Leaves ovate-elliptic, narrowed at the base (rounded in S. festiva); corollas scarcely bicolored..............................59. Maxonia

1941. Supp. Notes II. Bull. Torrey Bot. Club 68:565. Epling had previously overlooked the fact that the stamens of S. amethystina are seated between the middle of the corolla tube and the throat, thus the limits of sect. Ampelophyllae are broadened, and the key is changed in 2 places.

48. Stamens placed either at the middle of the tube or between the middle of the tube and the throat.

48a. Corollas blue, patently invaginated below the middle............................58. Ampelophyllae

48a. Corollas red or scarlet, entire..29. Rubescentes

92. Stamens placed between the middle of the corolla tube and the throat.

92a. Lips of the corolla short, the middle fringe [lobe] of the lower [lip] incurved-concave (see also Albolanatae and Rubescentes); tubes entire ....91. Secundae

92a. Lower lip of the blue corolla longer than the upper and patently deflexed [bent down]..............................58. Ampelophyllae

1941. Supp. Notes II. Bull. Torrey Bot. Club 68:565. A new section is described (Nivalis) to accomodate the new species S. Leninae.

1941. Supp. Notes II. Bull. Torrey Bot. Club 68:568. A new section is described (Latentiflorae) to accomodate the new species S. opertiflora.

39. Corolla tubes 6-13 mm. long; Mexican and Central American plants.

39a. Leaves narrowed on both sides; Corolla blue or rose..................................59. Maxonia

39a. Leaves truncate-rotund at the base; corollas white, white-pilose....................59a. Nivalis

39. Corolla tubes 15-27 mm. long (in S. purpurea [?] sometimes 10-12 mm. long; see also the Colombian species S. erythrostoma).

40. Corollas rose-purple or scarlet.

40a. Leaves mostly rounded at the base, rarely narrowed..............................87. Purpureae

40a. Leaves narrowed or extenuated at the base toward the petioles; Corollas scarlet; Colombian plants. ....83a. Latentiflorae

1944. Supp. Notes III. Bull. Torrey Bot. Club 71:490. S. madrensis is transferred from sect. Dusenostachys to the new section Longipes.

84. Rudders of the stamens either entire or furnished at the connection with a small extended or retrorse tooth.

92. Stamens placed between the middle of the corolla tube and the throat (see also Albolanatae and Rubescentes).

92a. Pedicels 2-6, rarely 10 mm. long; South American plants except S. dugesiana....91. Secundae

92a. Pedicels mostly 10-20 mm. long; Sinaloan plants with yellowish flowers...............29a. Longipes

1944. Supp. Notes III. Bull. Torrey Bot. Club 71:492. A new section is described (Steyermarkia) to accomodate the new species S. grandis.

113. Corolla tubes furnished within with paired papillae, sometimes invaginated, sometimes entire.

113a. Leaves moderately membranaceous, ovate or cordate, borne on petioles 1-10 cm. long..............................70. Cardinales

113a. Leaves coriaceous [leathery], lance-elliptic, glabrous, borne on petioles 3-8 mm. long..............................70a. Steyermarkia

1944. Supp. Notes III. Bull. Torrey Bot. Club 71:493. S. scandens is removed from sect. Longiflorae in favor of the newly described section Weberbaueria.

101. Corolla tubes 42-45 mm. long.....79a. Weberbaueria

1947. Supp. Notes IV. Bull. Torrey Bot. Club 74:516. S. perlonga is removed from sect. Pavonia in favor of the newly described section Nelsonia, and the limits of sect. Pavonia are broadened to include the newly described species S. orbignaei. The key to sections is ammended in 3 places.

5. Corolla tubes nearly straight, invaginated at the base below the papillae; stamens placed at the throat....................................39. Nelsonia

103. Hairs branched.

104. Peruvian or Bolivian plants; corolla tubes 13-24

mm. long (see also
<u>Cardinales</u>)............................64. <u>Pavonia</u>

111\. Corollas strongly invaginated at the base, by no means laterally-saccate [pouch or bag-shaped].

111a. Large leaves rounded or cordate at base;
Brasilian plants........................76. <u>Hoehneana</u>

111a. Leaves oblong, attenuate at
base....................................64. <u>Pavonia</u>

111\. Corollas...

1950\. Supp. Notes V. Brittonia 7(3):133. The limits of sect. <u>Longipes</u> are broadened to accomodate the newly described species <u>S</u>. <u>gracilipes</u> (with 3-veined upper calyx lip).

56\. South American plants; leaves round-cordate.

56a. Corollas dark blue, the tubes invaginated at the
base...............................58. <u>Ampelophyllae</u>

56a. Corollas white, tubes entire
....29a. <u>Longipes</u>

1950\. Supp. Notes V. Brittonia 7(3):135. A new section is described (<u>Platycheilos</u>) to accomodate the newly described species <u>S</u>. <u>expansa</u>. The section is close to <u>S</u>. <u>azurea</u> (<u>Farinaceae</u>) in habit and <u>S</u>. <u>herbacea</u> (<u>Bracteata</u>) in style structure, and sought in the key to sections either near <u>Farinaceae</u> or <u>Glareosae</u>.

APPENDIX III

AMENDED DESCRIPTION OF SALVIA DIVINORUM EPLING & JATIVA-M.

Salvia divinorum Epl. & Jat., Bot. Mus. Leaflets, Harvard University 20(3):75. 1962. Type: Mexico, Edo. Oaxaca, San José Tenango, 8 Oct. 1962, *Albert Hofmann* & *R. Gordon Wasson s.n.* (LA, holotype; LA in UC, ECON, isotypes).

Perennial herb, mostly 0.5-1.5 m tall vegetatively, the flowering stems 1-2(-3) m tall, the taller stems decumbent for part of their length; stems often trailing along rocky streambanks, sometimes in running water, rooting copiously at the nodes and sometimes along internodes, with broken, trailing, and drooping stems resuming erect growth at stem apices or by axillary branching, the new, vigorous shoots often arising from axils of old, senescent stems, these decaying or dead stems often appearing as woody caudices.

Stems quadrangular, with flanged angles, hollow, fleshy and crisp, translucent, breaking easily, hirtellous, green.

Leaves opposite, elliptic to ovate, acuminate to caudate at the apex, attenuate at the base, the petioles scarcely differentiated from the blade, 10-25(-30) cm long, 5-10 cm wide, glabrous above, sparingly glandular-punctate below; margins irregularly serrate or crenate-serrate, to entire at the base.

Racemes simple, erect, 30-40 cm long, with 2-4 cm long internodes; cymules with 3-6(-12) flowers each; rachis hirsute, glabrate.

Bracts sessile, concave, ovate, rounded at the base, acuminate-caudate at the apex, 1-2(-3) cm long, 0.6-1 cm wide, mostly violet, tardily deciduous.

Pedicels erect, slender, hirsute, violet, 4-9 mm long.

Calyx gradually widened above, 10-12 mm long, with subequal lips, glandular-hispid along the veins in bud, glabrate to glandular-puberulent throughout, violet; upper lip 1.5 mm long, with 3 major veins.

Corolla sigmoid, 28-32 mm long, densely villous with multicellular translucent hairs 0.5-2 mm long especially on upper and lower lips, glabrous within, white, drying brown in herbarium material, the lips becoming tinged blue with age; tube 19-22 mm long, 2 mm high by 1.5 mm wide at the narrowest point near the throat; galea (upper lip) 8-9(10) mm long; lower lip cupped, 5 mm long, 7 mm wide when flattened out, the middle lobe emarginate.

Stamens included within the galea, inserted near the throat, glabrous, white; connectives somewhat rigid, slightly arcuate, 15-16 mm long, 17-18 mm long when flattened out, the rudders 10-11 mm long, entire; anthers 2 mm long; pollen white.

Style 27-32 mm long, densely bearded below the stigma, white; posterior (upper) stigma branch exserted beyond the galea and curling upward, 2 mm long, 2.5 mm long when flattened out; anterior branch sometimes slightly exserted from the galea, somewhat carinate, 1.5 mm long.

Gynobase horn 3 mm long, 1.2 mm wide, glabrous, white.

Nutlets 1.8-2 mm long, 1(1.2) mm wide, somewhat pyriform, minutely tuberculate, dark brown, to date never collected in the wild.

Endemic to the Sierra Mazateca, Oaxaca, Mexico, at elev. of

300-1800 m, in primary and secondary growth of cloud forest and tropical evergreen forest, many populations cultivated or semi-cultivated (weedy), often spreading vegetatively along streambanks, flowering sporadically from September to the following May.

Specimens examined: Mexico, Edo. Oaxaca, Sierra Mazateca: 2 km north-northwest of Huautla market, Jan. 6, Reisfield & Solheim 1077 (WIS); 1 km southwest of Huautla market, Jan. 15, Reisfield & Solheim 1090 (WIS); ca. 2 km southwest of Huautla market, Jan. 15, Reisfield & Solheim 1092 (WIS); Huautla, Wasson s.n. (ECON); Huautla, Nov. 24, Bunnell s.n. (LA in UC); Huautla, Sept., Gomez-Pompa 500-E (GH); Cuauhtemoc, ca. 4 km northeast of Santa Maria Chilchotla, Jan. 16, Reisfield & Solheim 1093 (WIS); La Soledad, ca. 3.5 km west-northwest of Ayautla, Feb. 13, Reisfield & Solheim 1111 (WIS); Cerro Alto, ca. 2 km northeast of Ayautla, Feb. 13, Reisfield & Solheim 1109 (WIS); Cerro Camaron: ca. .75 km east of Cerro Quemado, Feb. 9, Reisfield & Solheim 1103 (WIS), 1 km east of Cerro Quemado, Feb. 9, Reisfield & Solheim 1106 (WIS), 1 km east of Cerro Quemado, Oct. 27, Reisfield 1242 (WIS); Cerro Quemado, March 2, Valdes & Paul s.n. (MICH); Univ. of Michigan Botanical Gardens, cultivated from material obtained at

Cerro Quemado, Nov. 17, April 20, Valdes s.n. (MICH); California State University, Hayward, cultivated from material of uncertain origin, Jan 24, Wilcox s.n. (ECON); Northridge, California, cultivated at San Fernando Valley State College from material of uncertain origin, Emboden s.n. (ECON).

APPROVED Hugh H. Iltis

Date Oct. 14, 1987