

## THE FLORISTIC SIGNIFICANCE OF SHRUBS COMMON TO NORTH AND SOUTH AMERICAN DESERTS\*

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IN southwestern United States and Northern Mexico, in North America, and in Argentina and Chile, and adjacent Bolivia and Peru, in South America, there are vast areas characterized by a low atmospheric humidity and a rainfall usually well under 20 inches annually. The climatic and edaphic conditions of these two regions are rather similar and so also is their general type of vegetation. Although some of the plant-formations in the two areas are superficially similar, their component species are almost completely different. Speaking generally we may say that the two desert floras show differences that suggest a different origin and history. This is certainly not unexpected since they are separated by about 3500 miles of wet tropics and lie in different hemispheres.

It is to be noted, however, that amid all the conspicuous differences between the two desert floras there are identities which indicate former connections and interchange. There are species growing in one desert area which have their closest relatives in the other; while there are actually some species which grow, in indistinguishable forms, in both of these far separated arid regions. Since the distinctive floras, characterizing each of the American desert areas could have developed only under isolation, our problem is to try to understand how they could have maintained their differences when the presence of certain species indicates that the floras have had some connection.

The plants whose present distribution is indicative of some direct floristic connection between the xerophytic floras of North and South America may be trees, shrubs or herbs. Curiously, however, the distributional behavior and general relationships of the herbs of this group are remarkably different from those of the trees and shrubs. Practically all of these rather numerous herbs belong to genera appearing to have had an origin and relatively modern evolution in North America. Their distributions fall into patterns revealing floristic affinities between particular regions in North and South America: thus we have species

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shared between California and Chile; between the Great Basin and the Argentine Andes and northern Patagonia; or between Texas and northern Mexico and northern and central Argentina. The woody species, which are less numerous, belong to groups that are usually well developed in Argentina. Many have characteristics suggesting that they are old desert elements. Their distribution on the two continents has not the stereotyped pattern noted in the distribution of the bicentric herbs. These surprising differences in relationship and distribution between the herbaceous and woody species, shared by the deserts of the two continents, give us every reason to believe that the plants date from two different periods of floristic interchange between the continents. I believe we are dealing here with two distinct problems. Since time will not permit a proper presentation of them both, it seems wise to limit this paper to a discussion of the nature and affinities of the shrubby flora that is shared by North and South American deserts.

The most famous shrub common to both American deserts is *Larrea divaricata*. In northern Mexico and in western United States (where it is called "Creosote Bush") this plant is the characteristic shrub over thousands of square miles of desert country; while in Argentina (where it is known as "Jarilla"), it is the characteristic element in the arid monte from northern Patagonia to Salta. Although this well known shrub may occupy more square miles in North America, it is clearly a South American type, for it has several congeners in the Argentine deserts and its family, the *Zygophyllaceae*, a world-wide group of chiefly desert shrubs, has one of its principal centers there. This shrub is so widespread and common and, where it occurs, seemingly such an integral part of the desert environment, that no one has suggested that it was not native where he has seen it flourish. An Argentine botanist may suggest that it was introduced into Mexico by the conquistadores, or a northern botanist may give it useless names, arguing that his plant ought to be different from that of the Argentine, but this only gives evidence of the convictions of local botanists of two continents that the plant is native to each of them.

Two other shrubs occur in indistinguishable forms in the deserts of both North and South America. *Atamisquea emarginata* is a companion of *Larrea* in the dry monte of western Argentina and with *Larrea* again it is present in a much more limited area about the Gulf of California in northwestern Mexico. And again there is *Koeberlinia spinosa* widely distributed, though not particularly common, in the deserts of northern Mexico and adjacent United States, and also present in a limited area of the dry chaco of Bolivia. *Atamisquea* and *Koeberlinia* are both very



well marked monotypes of the *Capparidaceae* and both have vegetative modifications stamping them as old desert types. Curiously *Atamisquea* is widely spread in South America and limited in distribution in North America, whereas *Koeberlinia* presents completely the reverse condition.

I need not explain that species commonly vary and that in any flora divided by a barrier some species usually remain constant, while other species tend to produce variants in each of the areas isolated. It is not unexpected that evidence of such behavior should be found in elements of a desert flora now divided by the wet tropics. A study of the two American desert floras shows that there are some species, such as *Larrea*, *Atamisquea* and *Koeberlinia*, which remain distinct after their range has become divided. It also shows the presence of a variety of paired species which because of their intimate relationship must have descended from some common ancestor once represented on both continents. The genus *Prosopis* gives some good examples. Here is a genus of desert shrubs and trees, with a few species in Africa and the Near East, more in North America, and the greatest number and variety of types in Argentina. In North America we have the characteristic desert trees the "Mesquites," a group of critical species usually called *Prosopis juliflora* or *P. chilensis*. The northern Mesquites are closely paralleled by a group of very similar, very closely related trees in Argentina where they are called "Calden" and "Algarrobo." Furthermore in *Prosopis* section *Strombocarpa*, the "Screwbeans," there are paired forms in *Prosopis cinerascens* of northern Mexico and *P. strombulifera* of Argentina. Cases similar to these may be cited in *Ephedra*, *Acacia*, *Caesalpinia*, *Condalia*, *Lycium* and other genera. These paired species had common ancestors and they point just as clearly as do *Larrea* or *Koeberlinia* to a shrubby element shared in common by the North and South American deserts.

I have given examples of species and paired species whose present distribution indicates the floristic connection between the deserts of two continents. I have been applying the criteria of systematic botany. Fully realizing that it must be applied with caution, I wish now to present another type of evidence bearing on this floristic problem. This evidence is morphological.

Among the plants inhabiting the deserts of the southern hemisphere, the so-called "adaptive" modifications in vegetative structure are more numerous, more common, and tend to be more extreme than those found among plants of northern deserts. All the desert shrubs of the southern arid regions are not unusual in form, but in each of the southern desert areas, South Africa, Australia and South America, many shrubs do present extreme vegetative modifications. They show various patterns



of these epharmonic forms and rather characteristic styles of them on each of the southern desert areas. Notable in South America is the tendency for leaf-reduction and short-shoots, with the development of shrubs that are leafless, or those knobby from short-shoots and dense leaf-clusters. We have stems covered with scale-like leaves. Spine-tipped leaves are unusually frequent. Branches are commonly divaricate and spinescent. Resinous secretions coating the herbage with a glutinous redolent varnish are also of wide occurrence. These so-called "adaptive" modifications occur singly or in combinations on a variety of South American desert shrubs representing a large number of plant-families. The desert plants possessing these characteristic modifications are not closely correlated with any particular desert environment. They grow with plants of less unusual habit on the puna of Chile, the chaco and monte of Argentina and on the steppes of Patagonia in varying edaphic and climatic conditions. As in Australia and South Africa, these epharmonic forms, beautiful examples of convergent evolution, can be explained only as environmental selection at some period in the past. Shaped for special conditions they remain serviceable after the special need for them has vanished. Correlated with particular episodes in the history of a flora, these growth forms may be as characteristic elements in a flora as any particular species or genus. Preserved by scattered conservative species, these growth forms may well point to the former association of their ancestors, and, as a badge, perhaps permit us to recognize some of their fraternity now present in northern deserts.

I have mentioned the resinous secretions that give a fragrant glutinous varnish to a great variety of South American xerophytes. This seems a rather characteristic development in the southern deserts. It is present in *Larrea*, which has a species in North America, and significantly no other genus of the *Zygophyllaceae* has developed it, though the family has shrubs in all the major deserts of the world. Comparable resinous varnishes are present on North American species of *Flourensia*, *Aplopappus*, *Viguiera*, *Baccharis*, *Grindelia*, *Gutierrezia* and *Dodonaea*. Is it not significant that these genera are all represented in the deserts of South America? Similar varnishes also occur in *Selloa* and *Chrysothamnus*, endemic to North America, but, as all botanists will agree, these are genera with very close relatives in *Gutierrezia* and *Aplopappus* which do have representatives in the south. I do not wish to infer that these varnishes are developed only in those groups having relatives in southern deserts. In North America these varnishes are present in *Eriodictyon* and certain desert *Rosaceae* that have no evident relations with the South American desert flora. However, I can not refrain from



attaching some meaning to the fact, that those shrubby North American desert plants which do develop the varnish (in the great majority of cases) are those whose genus is represented in the deserts of South America or, at least, has a very close relative there.

A study of the leafless or nearly leafless shrubs of the northern desert produces further interesting facts. This type of shrub has only three extreme examples in North America. They are the species of three monotypic genera. Two of them are so distinct that they have been treated as monotypic families. *Holocantha* has a sporadic occurrence in the deserts from southern California southeastward into Mexico; *Canotia* is known from scattered stations in Arizona; while, *Koeberlinia* is rather frequent over a large area in northern Mexico and adjacent United States, and, in South America, is local in one small area in the western chaco of Bolivia. We have here three species agreeing in a very similar highly specialized habit, interrupted distribution, and isolated systematic position, all indicative of old species. They have no obvious relationship in North America. Their habit, however, which sets them apart in North America, is not unusual in South America. In fact it is remarkably simulated in the southern continent, particularly by various colletioid *Rhamnaceae*. Perhaps in the range of *Koeberlinia* we may have a clue to the significance of all this. Here we have a very distinct, highly specialized old species that is widely spread in the desert of one continent and local in the other. Should this old species disappear from its small area in Bolivia it would become restricted to North America, and there, perhaps as does *Holocantha* and *Canotia*, reveal its former connections with the southern desert flora only in its stubborn maintenance of an ancestral growth form.

There are only a few other North American examples of the leafless habit to discuss. We may note that there are northern species of *Euphorbia*, *Pedilanthus* and *Asclepias* which exhibit this habit. These plants seem to have no relation to the southern desert flora. Perhaps significantly, they are more suffrutescent herbs than true woody shrubs. A fine example of the leafless shrub, however, is found in *Acanthothamnus*, a Mexican monotype, and this, it will be noted, is closely related to *Schaefferia*, a genus present in the deserts of both North and South America. Various northern species of *Ephedra*, *Hoffmanseggia*, *Cercidium* and *Baccharis* have the leafless habit more or less developed. These are all members of genera represented in the southern desert.

When it is realized that most of the North American species showing such modifications, as the glutinous varnish and the leafless habit, are members of genera also represented in South America, where we know

that these types of vegetative modifications are frequent and characteristic, we must be prepared to admit that, at least in many instances, these habits must have spread to North America. These are old habits of a flora now characteristic of South America. Introduced into North America by species during periods of floristic interchange, these habits now persist among descendants of the migrants. That these modifications are present in various northern members of genera, whose species no longer remain identical or very similar on the two continents, is simply evidence of a long period of diversification following the time when American desert shrubs were exchanged between the continents. It is one of the good reasons for thinking that this spread of shrubby elements must have occurred in the distant past.

Thus far in my remarks I have been presenting some of the evidence which points to the presence in the deserts of North America of floristic elements which apparently are a part of a flora now well represented in arid South America. I believe that we are concerned with a very old American desert flora formerly shared by both continents. In South America it is now relatively well preserved but in North America it lingers in a few recognizable remnants.

Since most biologists appear to think of geological climates only in terms of ice-ages and wet, usually tropical, conditions, perhaps I should emphasize the fact that deserts are an old earth-feature. The world must have always had its deserts, at least those just outside the tropics. There has always been moist ascending air, and rain, near the equator, and descending dry air, and aridity, at about latitude thirty. Desert floras may well have an age and continuity comparable with the floras of the wet tropics. Many groups of plants such as the *Zygophyllaceae* and *Chenopodiaceae* have probably been evolving on deserts, at least, since Mesozoic time. And these may be relatively recent xerophytes as compared to *Ephedra* and *Welwitschia*.

I have mentioned that the deserts of the southern hemisphere are richer in striking growth-forms than are the deserts north of the equator. Since there is no general difference in age or rigor between northern and southern desert areas, other factors than mere environment must account for the habitual peculiarities of their floras. Let us examine conditions in the southern hemisphere. All the extra-tropical portions of the three great habitable land-masses are dominated by arid climates and xerophytic floras. These areas are widely separated from one another and from Antarctica. Their xerophytic floras are not open to recruits from large and varied temperate floras occupying large adjacent land-areas. During the cooler and wetter epochs of earth-history, species



in these southern regions could slowly modify to meet new conditions, for they were not promptly placed in competition with aggressive and adaptable new-comers spreading from extensive temperate floras of higher latitudes. Open chiefly to recruits coming from the tropics, these southern desert floras could preserve many old types, not merely primitive species and genera, but also particular growth-forms which had been once highly adaptive and, though out-moded, were still generally serviceable in a conservative flora.

Under present conditions the unbroken belt of wet tropical forest forms a real and very effective barrier to the exchange of elements between northern and southern deserts. It is probable, however, that during dry warm epochs an exchange might have been effected along relatively arid coastal strips similar to, but more extended and drier than those now present in western Central America, Ecuador and Peru. Any such route, however, would present equal opportunities for species expanding northward as well as southward, yet among the shrubs showing the floristic connections between northern and southern deserts none has characters or relationships which mark it as a northern type, whereas most of them do have the affinities and characteristics of the flora of South America. This absence in the southern deserts of shrubs of evident northern affinity, is most significant. The shrubby flora found unequally represented in the deserts of two continents must have been assembled and spread before the characteristic North American shrubs had appeared in the northern deserts.

That this South American desert flora was assembled early and perhaps had special opportunities for spread, is indicated by the present distribution of the species of several genera now shared by America and Africa. In their distribution these species are not only examples of the floristic connections between the deserts of America, they are also examples of the former floristic interchange between deserts of northeastern and southwestern Africa, and, even, between the deserts of Africa and America. There is *Fagonia* in the Mediterranean, northern Mexico and Chile; there is *Thamnosma* of northern Mexico, Socotra, Somaliland and South Africa; and there are *Menodora* and *Hoffmanseggia* of northern Mexico, South America and South Africa; all genera of marked xerophytes with close species separated on the deserts of three continents. These scattered species are obviously elements of a widely spread desert flora that now lingers in desert-outposts north and south of the equator in America and Africa. An American desert flora that includes such elements may well date from early Tertiary time.

We have every reason for believing in the past existence of a widely

distributed American desert flora. All the evidence indicates that, relatively isolated and free from competition, it has persisted in South America, while in North America, diluted by new xerophytes originating in the northern temperate lands it has been giving way before their competition. Here we have the explanation of the affinities that are shown by certain northern desert shrubs with the distant flora of southern South America. These shrubs are remnants of an old American desert flora which has found a haven in South America, but has been decimated in the more keenly competed desert terrains to the north.

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