Cousins to the South: Amphitropical Disjunctions in Southwestern Grasses[1]

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The study of plant distribution can be a rewarding and stimulating endeavor. Such investigations can tell us much about the plants themselves—where they grow, why they grow there, what special adaptations they possess—and also much about their relationships to other organisms—the plant and animal communities in which they occur, the history of their association, and often some of the evolutionary processes leading to their development. This field of scientific investigation (termed biogeography or, when dealing with plants, phytogeography) involves more than just recording the geographic distribution of a particular species. The explanation of that distribution often requires a synthesis of data from many disciplines, including morphology, cytogenetics, physiology, reproductive biology, ecology, and geophysics. Thus, the careful researcher often finds himself at the heart of intriguing and many-faceted problems.

Some of the more interesting distribution patterns to be found in plants are disjunctions; that is, geographic range discontinuities where populations of plants are separated by large geographic gaps. Among the most fascinating disjunctions are those with widely separated intercontinental populations. For example, *Larrea tridentata* (Creosote Bush) occurs throughout the Chihuahuan and Sonoran deserts of North America; its close relative, *L. divaricata* (some consider the two to be one species), is found in the deserts of Peru, Bolivia, Chile, and Argentina. Also, *Plantago patagonica* (Plantain, Indian Wheat), a common component of the prairies and plains throughout much of western North America, may also be found in similar habitats in Argentina and Chile. Likewise, *Koeberlinia spinosa*, one of the pernicious crucifixion thorns, has identical populations of plants in the deserts of both North and South America. Indeed, Raven (1963) has listed approximately 160 plant species with amphitropical (on both sides of the tropics) range disjunctions such as these.

Pielou (1979), in an outstanding new text on biogeography, lists five ways that plants might achieve a disjunct distribution. 1) Through movements of the earth's crust, formerly adjacent land masses may be separated (continental drift). This helps explain the similar floras of certain regions of South America and Australia which were contiguous land masses before the separation of the continents. 2) Associated with the changing positions of the continents may be a climatic change. In a very widespread species, a climatic deterioration of the central portion of the range can leave the peripheral populations as disjuncts. 3) During the adaptation process of a species, geographic isolates may be differentiated from the parent species. If the selection forces acting on the isolates are similar, then they

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may evolve into more-or-less identical populations. Extinction of the ancestral species will leave only the disjunct descendants. A mechanism such as this is suggested by Raven (1963) for some species of *Acacia* found in the Chihuhuan and Sonoran deserts of North America and in the Chilean and Peruvian deserts of South America. 4) Many species of plants are adapted by a variety of ways to long-distance dispersal. Seeds of *Asclepias* (Milkweed) bear a light tuft of silky hairs at one end and are easily carried by the wind for several, or perhaps in open country, hundreds of miles. Some propagules of grasses have been found in the atmosphere several thousand feet above ground (Polunin, 1967); there is certainly a potential for long-distance dispersal in plants such as this. 5) A quick check of many floristic treatments will reveal many plant species reported only as ballast weeds in various ports. It is clear that man has played a significant role in the distribution of many plants, either introducing them deliberately for ornament or agriculture (for example, *Medicago sativa*, Alfalfa), or unwittingly in ballast, seed packets, packaging materials, or on transported animals. An interesting example of accidental dispersal involves *Cuscuta suaveolens*, a parasite of alfalfa that has followed this important crop plant around the globe.

Many grass species common in the Southwest exhibit remarkable amphitropical range disjunctions, with populations of plants in arid regions of both North and South America (Table 1). Many of these species have been discussed elsewhere (see Pielou, 1979; Raven, 1963; Thorne, 1972) and will not be considered here. But, it is instructive to analyze in detail the distribution pattern of one group of grasses prevalant in much of the Southwest, and to see what factors are brought to play in determining this pattern.

The grass genus *Bothriochloa*, familiar to many as "Bluestem," is common throughout much of the plains and rangelands of the western United States. These grasses were formerly included in the genus *Andropogon*, as the section *Amphilophis* (Hitchcock, 1951). A number of features (chromosome number and panicle morphology, among others) justify its segregation as a distinct genus, and it is so considered by most taxonomists throughout the world.

Bothriochloa may be roughly divided into two groups: those native to Australia, southern Europe, and southern and southwestern Asia (the Old World species); and those native to North and South America (the New World species). We will be concerned here with only the New World species (Table 2).

Most species of New World *Bothriochloa* are markedly amphitropical in distribution (Figs. 1–18). The distribution patterns are centered in the southwestern United States, Mexico, and the West Indies in North America; and in southern Brazil, Uruguay, Paraguay, and northern Argentina in South America. The two regions are at approximately equivalent latitudes of 25–35 degrees. Only *B. "parvispicula," B. saccharoides* var. *saccharoides*, and *B. alta* occupy interevening latitudes.

Table 1. Some grasses with amphitropical disjunctions in the semi-arid to arid lands of North and South America. Partially compiled from Raven (1963) and Thorne (1972).

Species	Distribution
Bouteloua aristidoides (H.B.K.) Grisb. var. *aristidoides*	Southwest US, Mexico; infrequent in Bolivia, Brazil, Colombia, Ecuador, Paraguay; common in northern Argentina
Bromus trinii Desv.	Coastal and intermountain US; Chile, Argentina, Peru, Bolivia
B. unioloides (Willd.) H.B.K.	Throughout southern half of US; temperate South America
Chloris ciliata Sw.	Texas, Mexico, Caribbean Islands; Argentina, Uruguay
C. crinita Lag.	Southwest US, northern Mex.; Argentina, Bolivia, Paraguay, Venezuela
C. pluriflora (Fourn.) Clayton	Texas, Mexico; Central America; southern South America
Cottea pappophoroides Kunth	Southwest Us, Mexico; Ecuador, Peru, Argentina
Digitaria insularis (L.) Ekmann	Southern US, Mexico; south to Argentina
Enneapogen desvauxii Beauv.	Southwest US, Mexico; Argentina, Bolivia, Peru
Eragrostis lugens Nees	Texas; Mexico; northern Argentina, southern Brazil
Leptochloa dubia (H.B.K.) Nees	Southern US, Mexico; Argentina
Muhlenbergia asperifolia (Nees & Mey.) Parodi	Midwest & western US, Mexico; southern South America
M. torreyi (Kunth) Bush	Southwest US, Mexico; Argentina
Panicum hirticaule Presi	Southwest US, Argentina; Chile
Phalaris angustata Trin.	Southern & Southwest US; southern South America
Schedonnardus paniculatus Steudel	Central Canada south to Texas and Arizona; Argentina
Scleropogon brevifolius Phil	Southwest US, central Mexico; Chile, Argentina
Stipa speciosa Trin. & Rupr.	Southwest US; Argentina, Chile
Stipa tenuissima Trin.	Southwest US, Mexico; Argentina
Trachypogon secundus (Pres1) Scrib.	Southwest US, Mexico; Argentina
Tripogon spicatus (Nees) Ekm.	Texas, Mexico; southern South America
Wilkommia texana Hitchc.	Southern Texas; northern Argentina

Distribution patterns such as this prompt several questions: How did the disjunction come about? When did the disjunction occur? What was the method of dispersal? And, in what direction was the dispersal? We will try to arrive at some plausible answers to these questions using evidence from morphology, cytogenetics, reproductive biology, dispersal mechanisms, ecology and habitat, and past geological events.

Table 2. Species of *Bothriochloa* native to the New World.

Taxon[1]	2n	Distribution
B. alta (Hitchc.)	120	Texas, New Mexico; Bolivia, Argentina
B. barbinodis (Lag.) Herter	180	Southwest US, Mexico; Argentina, Uruguay
B. brasiliensis (Hack.) Heur	?	Southern Brazil, northern Argentina
B. campii (Swallen)	120	Southern Mexico; Ecuador
B. edwardsiana (Gould) Parodi	60	Texas; Argentina, Uruguay
B. exaristata (Nash) Henrard	60	Louisiana, Texas; Argentina, Bolivia, southern Brazil, Paraguay
B. hirtifolia (Presl) Henr.	60	Mexico
B. hybrida (Gould)	120	South Texas, northern Mexico
B. imperatoides Herter	60	Northern Argentina, southern Brazil, Uruguay
B. laguroides (Sw.) Herter	60	Mexico, Guatemala, Honduras, Panama; southern Brazil, Uruguay, northern Argentina, Paraguay, Chile
B. "parvispicula"[2]	(60)[3]	Northern Argentina, Bolivia, Chile, Peru, Ecuador, Colombia, Venezuela, Guatemala
B. reevesii (Gould) Gould	120	Central Mexico
B. saccharoides Sw. var. *saccharoides*	(120)	West Indies, southwestern Mexico, Central America south to Ecuador and Peru
B. s. var. *longipaniculata* (Gould) Gould	120	Texas, Louisiana, northern Mexico; possibly Argentina
B. s. var *torreyana* (Steud) Gould	60	Central & southwest US, northern Mexico; Argentina
B. schlumbergeri (Fourn.) Henr.	180	Mexico
B. springfieldii (Gould) Parodi	120	Southwest US; Argentina
B. wrightii (Hack.) Henr.	120	New Mexico, northern Mexico

[1]The nomenclatural status of many of these names is currently under re-evaluation. I have followed the most accepted usage, such as found in Gould (1975) and Burkart (1969).

[2]This taxon was originally named as *Andropogon saccharoides* subsp. *parvispiculus* Hitchc., but the combination in *Bothriochloa* has not yet been made. Preliminary studies indicate a close relationship to *B. alta*. Its correct disposition in *Bothriochloa* awaits further investigation.

[3]Chromosome numbers in parentheses were inferred from pollen diameters (Allred, 1979).

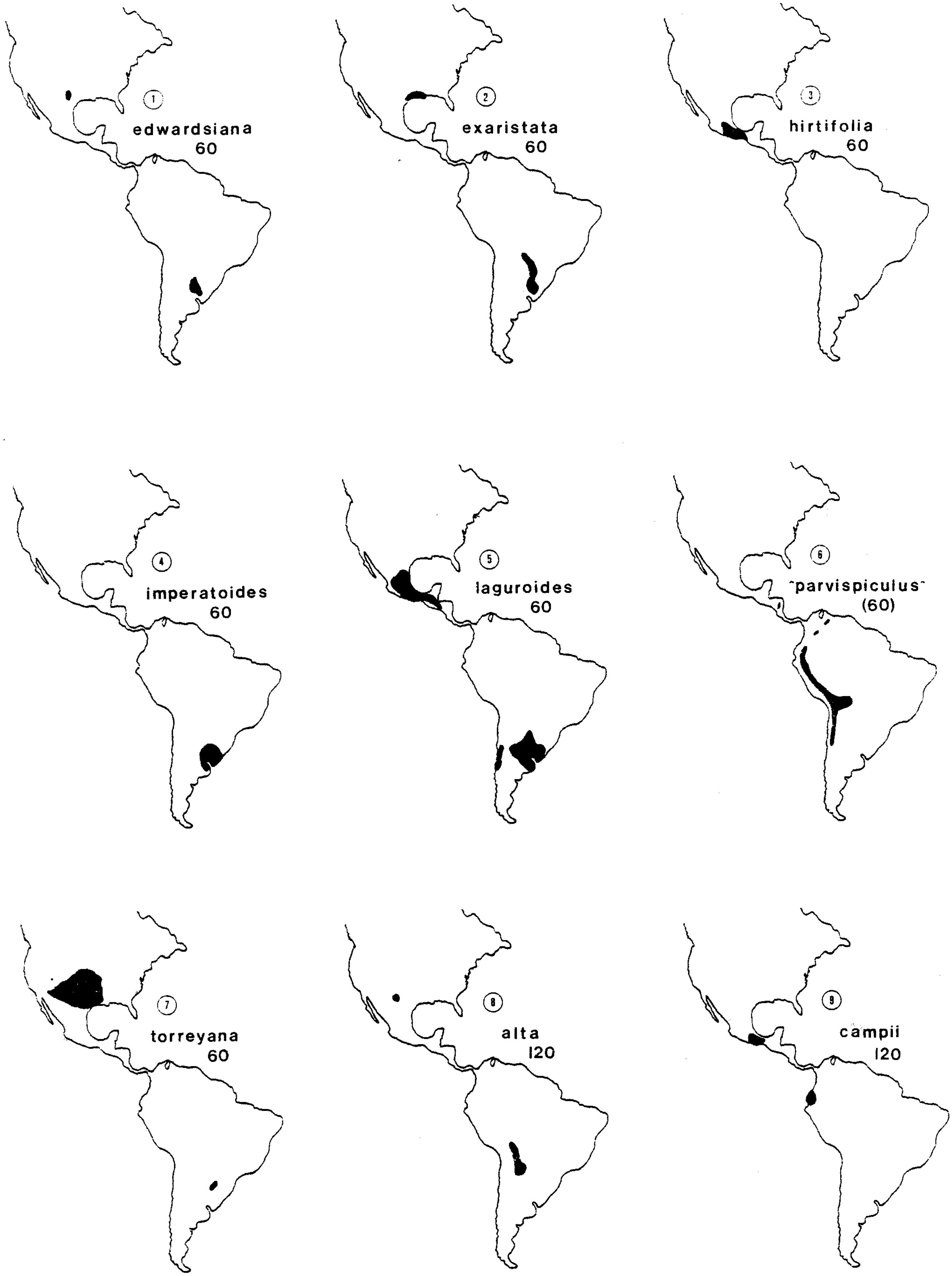
Morphology. Studies of the morphology of these species (Allred, 1979, and unpublished data) indicate that the disjunct populations are essentially identical. Plants of *Bothriochloa laguroides* from South America, for example, look just like the plants of this species from North America. Apparently, no visible evolutionary divergence has taken place. One would certainly expect to find some differences between populations that had been isolated for long periods of time. The absence of such differences implies that the disjunction was achieved in recent times.

Some *Bothriochloa* may be classed as vicarious species or vicariads. *B. alta*, for example, occupying a bicentric distribution, is very similar morphologically to *B. "parvispicula,"* which is restricted to the southern continent. The two vicariads appear to have been derived from the same genetic stock. *B. imperatoides* and *B. springfieldii* show a similar relationship. Comparative studies of these vicariads should help to determine if they are really separate species, or if they represent intermediate stages in the speciation process. The second conclusion would warrant their merger into a single species with two subspecies or varieties.

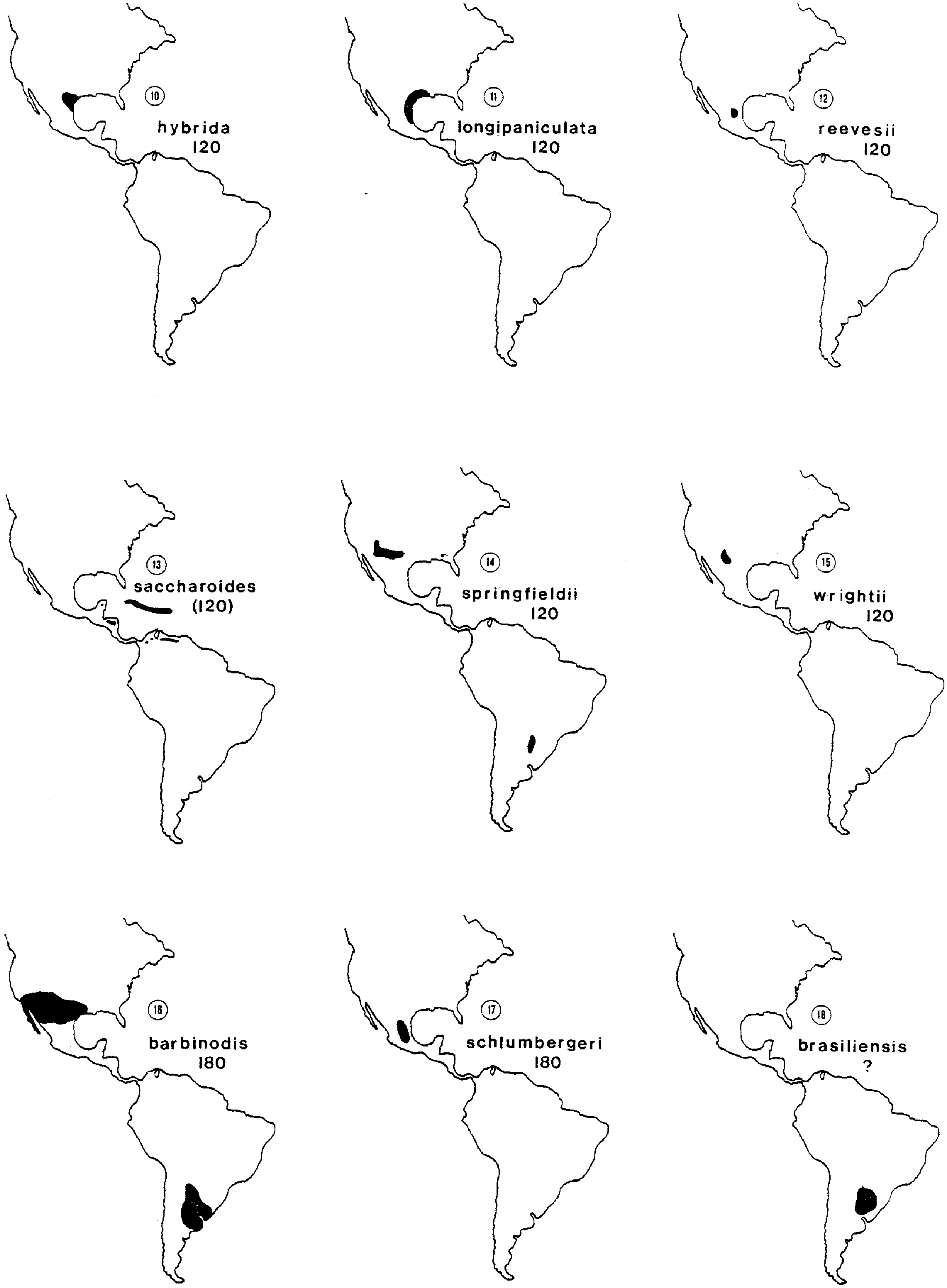
Cytogenetics. The study of chromosome numbers helps to refine the conclusions based on morphology alone. The New World *Bothriochloa* exhibit a remarkable polyploid superstructure with multiplication of a basic chromosome complement of 60 (Table 2). If we compare the distribution of the hexaploids (2n=60) with that of the duodecaploids (2n=120), we find that almost without exception the hexaploids are present in South America (and many also in North America), but most of the duodecaploids are restricted to North America. Assuming the lower polyploids to be ancestral to the higher polyploids, this distribution pattern suggests a South American origin for the complex, with migration proceeding northward. Raven (1963) suspects the same to be true of most desert plants with an amphitropical disjunction, in contrast to the presumed North American origin of many temperate (non-desert) and polar disjuncts.

Reproduction. Available evidence for about two-thirds of the species indicates that these grasses reproduce sexually with a self-compatible pollinating system (Allred, 1979: Gould, 1956, 1957; deWet et al., 1963). Self-compatibility bestows a great advantage to any colonizing species: a single propagule may effectively establish a new colony of plants. Dependence on other plants for cross-pollination or on specialized pollinators is eliminated. Self-compatibility accounts in part for the weedy tendencies of many *Bothriochloa*. They are common along roadsides and other disturbed area where competition to an invading seedling is reduced. The successful introduction of a single plant in such areas establishes a permanent seed source for a future population.

Seed production is apparently high in this group of grasses (Allred, 1979). It is estimated that a single inflorescense of Silver Bluestem (*Bothriochloa saccharoides* var. *torreyana*) might contain as many as 160 viable seeds; a mature plant will produce about 3–4 such inflorescences in a growing season; this results in a potential of about 550 viable seeds being produced each year by one plant. Even a very low seedling establishment percentage of 0.5% could result in a population of 30 plants in 3 years time, from a single introduction.



Figures 1–9. *Distribution maps for New World species of Bothriochloa. Chromosome numbers follow the names and are placed in parentheses if inferred from pollen diameters.*



Figures 10–18. *Distribution maps for New World species of Bothriochloa. Chromosome numbers follow the names and are placed in parentheses if inferred from pollen diameters.*

Figure 19. *Propagule of Bothriochloa. Left: pedicel. Center: spikelet (with seed) with pedicel and rachis. Right: rachis.*

Apomixis (the production of seed without fertilization of gametes; ie., asexually) has not been reported in the New World *Bothriochloa*, although it is extremely common in the Old World species (de Wet et al. 1963). The occurrence of apomictic reproduction would further enhance a plant's colonizing ability, as the vagaries of wind pollination would be circumvented, and seed production would approach 100% efficiency.

Self-compatibility and high seed production do not, by themselves, implicate one method of disjunction over another. But, the predominance of these two biological features accord with a hypothesis of long-distance jump dispersal involving few propagules.

Dispersal Mechanisms. The dispersal unit, or propagule, in *Bothriochloa* is a compound structure comprising a spikelet with seed, a section of rachis, and a pedicel (Fig. 19). The rachis and pedicel are densely plumed with soft, white, silky hairs. The whole structure is extremely light and easily airborne and rafted by the wind.

As Darlington (1957) pointed out, it is easy to underrate the potential of wind as an agent of dispersal. A small propagule of *Bothriochloa* has an extremely large surface to weight ratio when compared to that of larger objects. As size increases, surface increases by the square, but weight increases by the cube. With our immense size (when compared to a *Bothriochloa* propagule!), it is difficult for us to appreciate the extreme effect wind may have on very small, light objects. Surface winds are certainly capable of lifting the plumed propagules of *Bothriochloa* above the ground and into atmospheric zones of rising air currents, where they may be carried for long distances.

Long-distance dissemination by wind offers one mechanism for the disjunction in *Bothriochloa*. On both continents, the arid and semi-arid regions inhabited by *Bothriochloa* are located at the Horse Latitudes (Fig. 20). These are zones of descending air masses that become warm and accumulate moisture rather than deposit moisture. Consequently, much of the land area in the Horse Latitude are deserts. Conceivably, propagules from South America could be transported northward by the

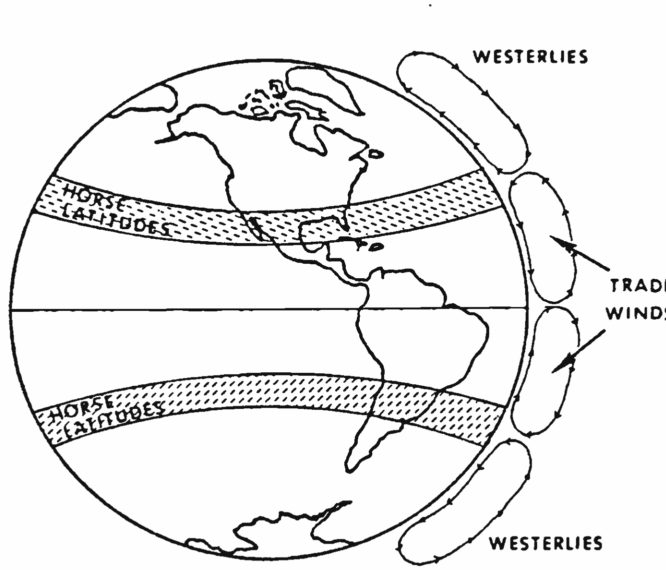


Figure 20. *Position of the Horse Latitudes and atmospheric wind currents in the New World.*

tradewinds and deposited in a favorable environment by the descending air masses at the Horse Latitudes.

Birds have been proposed as dispersal agents to explain similar amphitropical distributions in other plant groups (Cruden, 1966; Raven, 1963). This would require the seed to be either carried outside the body, by adhesion to mud, debris, or feathers, or to be carried internally and to be resistant to digestion or breakdown. There is some controversy concerning the actual effectiveness of long-distance transport by birds, with Löve (1963) summarizing the arguments against, and Ridley (1930) and Polunin (1967) stating the case for.

In either case, *Bothriochloa* do not appear to be candidates for long-distance bird dispersal. In view of the significant adaptations developed for wind transport, it would seem unlikely that a second suite of adaptions for bird dispersal would evolve independently.

Ecology and Habitat. Most of the New World *Bothriochloa* are distinctly weedy, comprising a major floristic component of disturbed or modified environments. In North America, at least, they are common along highways and ditchbanks, near agricultural fields, in old fields and abandoned lots, and wherever man has bared the soil and disturbed the habitat. Most species also form an integral, though not a dominant, part of prairies, savannahs, and deserts throughout the Southwest. These are all "open" habitats in which establishment following long-distance dispersal is made easier.

The prairies and desert grasslands of North America apparently originated only since Pliocene times, roughly 10–12 million years ago (Axelrod, 1958; Dix, 1964). This means the disjunction of North and South American *Bothriochloa* was also achieved during the last 10 million years, when the climatic and vegetational factors in the Southwest would have been similar to what they are now. The present widespread distribution of many *Bothriochloa* species (Silver Bluestem, for example) has resulted from an expansion of an earlier restricted range,

Bothriochloa springfieldii *in West Texas.*

undoubtedly heavily influenced by man's disturbance of the habitat.

Past Events in Geologic Time. A study of the geologic history of the earth (see Kummel, 1970, for an excellent treatment) discloses many, often drastic, changes in the earth's crust, the position of continents, climate, and the life forms that inhabited various regions. Many of these changes affected only indirectly the distribution of *Bothriochloa* in the New World, but some can be brought to bear on our case study.

Several different times during their long history, portions of the North and South American continents were covered by the sea. During the late Cretaceous period, a vast epicontinental sea inundated roughly what is now the great plains region of the Midwest, stretching from the gulf coast to the Arctic, and divided North America completely in two. By about this same time, the oceans had also encroached upon the east and west coasts of South America (Fig 21). Smaller seas have covered various portions of both continents since that time, generally flooding the coastal shelf areas. The latest inundation of these coastal areas probably took place during the Pleistocene, with the furthest advance inland presumably coinciding with the last warm interglacial period about 8–10 thousand years ago.

The distribution patterns of *Bothriochloa* seem to be concentrated in these areas of past epicontinental seas. Such taxa as *B. exaristata* and *B. imperatoides* are currently somewhat restricted in range to coastal (or once-coastal, in South America) areas and have failed to extend their ranges.

The extensive glaciation that took place in North America during the Pleistocene had the effect of compacting the climatic and vegetational zones, and of pushing these zones southward toward the equator. Glaciations in South America, though not as extensive, may have had similar effects, although much of the shift in zonation may have been east-west rather than north-south. The

Bothriochloa barbinodis, *Cane Bluestem, in West Texas.*

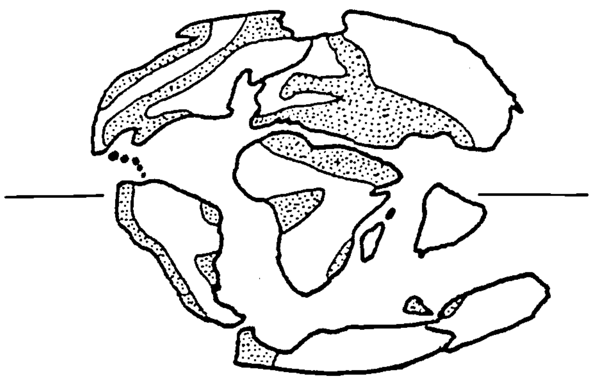


Figure 21. *Position of the continents at late Cretaceous. The stippled areas show the locations of past epicontinental seas. Redrawn from Pielou (1979).*

result was that suitable habitats in North and South America were closer together than they are now, and the chance for floristic exchange was at its greatest.

Conclusions. The disjunction of the New World *Bothriochloa* is most likely a recent event. Speciation within the group has apparently proceeded by way of polyploidy events, a rapid process compared to the gradual differentiation of populations through natural selection and reproductive isolation. Even though the disjunct populations are separated by nearly 5000 kilometers, the disjunction is recent enough that no morphological differentiation has taken place. The prairies and desert regions inhabited by these grasses originated by at least the Pliocene, but were accessible to uninterrupted invasion only since post-Pleistocene times when the sea retreated for the last time. Increasing aridity and the expansion of open habitats provided suitable environments for invading grasses such as *Bothriochloa.* Greater species diversity and the relative deficiency of higher polyploids (2n=120, 180) in South America also implies a southern origin with migration proceeding northward.

Long-distance dispersal is made possible by the extremely light, feathery propagules of nearly all species of *Bothriochloa.* They are easily airborne and capable of being carried long distances by the atmospheric wind currents. Because of self-compatibility and high seed production, even a single propagule could give rise to an established population. The efficiency of wind dispersal is attested by such widespread taxa as *Bothriochloa barbinodis* (Cane Bluestem) and *B. saccharoides* var. *torreyana* (Silver Bluestem). The latter taxon has made its way over the Rocky Mountains westward into eastern Utah, and up the Colorado River drainage into southern Utah, both distant outposts from the main geographic assemblage in the Great Plains and Southwest. This range extension into Utah is represented by only a very few plants at two stations, and apparently occurred during the last half-century. The populations were discovered in 1972 and 1978 in areas that were well-collected in the past, and are restricted to disturbed ground along major highways. In addition to wind dispersal, man's activities are probably playing a role in the current distribution of *Bothriochloa.* Open environments where competition is at a minimum are constantly being made available, and human transport to these environments, along the major roadways, is likely.

The factors involved in the distribution of *Bothriochloa* are typical of most of the desert amphitropical grasses that we find in the Southwest. It is unusual, however, to find a genus in which so many of the species possess such a remarkable bicentric distribution. The Old World species of *Bothriochloa* also pose several interesting questions. Why is it that the two groups are so completely separated on different continents, yet have maintained enough similarity to be classed in the same genus? Has long-distance dispersal also played a role in their distribution, or must we invoke some other causative agent? And, when did the two groups separate, was continental drift involved, and will further biogeographic studies shed some light on the origin and development of this interesting genus? A detailed study of *Bothriochloa* will not only provide some answers to these questions, but, it is hoped, suggest new questions as well.

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