

PHYTOGEOGRAPHICAL NOTES ON THE GENUS
BRACHYPODIUM P. BEAUV. (GRAMINEAE)

by

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This paper is concerned with the probable time of origin and differentiation of species in the genus *Brachypodium*, which belongs to the so-called festucoid group of grasses. The festucoid grasses can be classified into about 140 genera, and they are generally arranged in six or seven tribes. The following tribes appearing in the system of Parodi (1961) are included in the festucoid group: Festuceae¹, Aveneae, Phalarideae, Agrostae, Monermeae and Triticeae (= Hordeae).

The festucoid group is characterized by a particular combination of morphological, anatomical, cytological and other microscopic features (see Prat, 1960; Stebbins and Crampton, 1961; Parodi, 1961). It is also characterized by being distributed in regions with a temperate or warm - temperate climate. In tropical or subtropical regions, they occur in the mountains or grow in the lowlands only during the cool season. We would expect that the restricted ecological requirements of this group would have some effect on the geographical distribution, but the species are found in all parts of the world where ecological conditions are favorable for their growth and survival.

Unfortunately, fossil records of festucoid grasses are scarce. Therefore, only the following types of evidence can be used to form a decision as to the age of a particular festucoid genus: (1) the present distribution patterns of the genera and of other plants, particularly woody plants, with which they are associated, and (2) studies on the geology and palaeobotany of the regions concerned. Several festucoid

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¹ Parodi (1961) includes the genera *Melica* and *Glyceria* in the tribe Festuceae. However, considering their cytological and morphological features, these genera are more naturally ascribed to the tribe Meliceae which should be excluded from the festucoid group.

genera, such as *Dactylis* and *Helictrotrichon*, have been recently discussed from these viewpoints by several authors (Stebbins and Zohary, 1959; Holub, 1962), but *Brachypodium* has not yet been investigated.

SPECIES AND RANGE OF BRACHYPODIUM

The genus *Brachypodium* has in the past been referred variously to the tribes Festuceae, Triticeae or Bromeae but is recently more often treated as a distinct tribe, Brachypodieae. The chromosome numbers reported for species of *Brachypodium* are listed in Table 1. As shown in this table, the numbers diverge considerably. They may have arisen from some structural changes, which bring about the loss or addition of chromosomes, during the course of their evolution. Even in our present limited knowledge of this field, the differences in chromosome features seem to be correlated with the subdivision of *Brachypodium* into subgenera or sections, or even into genera in a more restricted sense. But, this does not mean that *Brachypodium* as broadly interpreted could be considered a mixture of phylogenetically quite distant species. To judge from their morphological and anatomical features, the species with different chromosome numbers are rather closely related phylogenetically, and the tribe Brachypodieae is a well-defined evolutionary unit.

The subdivision of the collective genus *Brachypodium* into sections or genera has been discussed by several authors. Unfortunately, not many Eurasian species have been considered. Nevertheless, it would be appropriate to enumerate here the sections and genera previously described. (1) Sect. *Brachypodium* (= *Brachypodium* s. str.): perennial, with creeping rhizomes and shortly awned or mucronate lemmas. Nevski (1934) put *B. pinnatum* (L.) Beauv. and *B. rupestre* (Host) Roem. et Schult. in this section (together with an uncertain species, *B. villosum* Drob.), and Maire (1955) included in it *B. pinnatum*, *B. phoenicoides* (L.) Roem. et Schult. and *B. ramosum* (L.) Roem. et Schult. *B. ramosum* var. *arbusculum* Saint-Yves in known to have $2n = 18$ (Larsen, 1963). Its basic number $x = 9$ differs from $x = 7$ which has been found in *B. pinnatum* and *B. phoenicoides*. The systematic arrangement of these species needs further study. (2) Sect. *Leptorachis* (= Genus *Brevipodium* Löve and Löve): perennial, with $x = 9$ and abbreviated rhizomes and long-awned lemmas. Nevski (1934), Maire (1955) Löve and Löve (1961 a) included only *B. sylvaticum* (Huds.) Beauv. in this section. Larsen (1963) added *B. flexum* Nees, an African species, indicating its morphological and cytological similarity to *B. sylvaticum*. (3) Sect. *Festucopsis*: including *B. serpentinei* C. E. Hubbard, proposed by Hubbard (1935)

because of its unique features, such as densely caespitose habit, entire leaf sheaths of the innovations, setaceous filiform blades, minutely pubescent rachilla and 5-6-nerved lemmas. The basic chromosome number is $x = 7$. (4) Sect. *Trachynia* (= Genus *Trachynia* Link): annual, *B. distachyon* (L.) Beauv. with $x = 5$ as the type.

Unfortunately, no up - to - date comprehensive revision of the species of *Brachypodium* has been published, though Saint - Yves (1934) studied all of the species in Europe and the Mediterranean region. However, the total number of *Brachypodium* species can be estimated at 14 to 18. An outline of their geographical distribution is presented below. Fig 1 shows the general range of *Brachypodium*.

EUROPE AND THE MEDITERRANEAN REGION: Species of *Brachypodium* are widespread in this area. *B. sylvaticum* and *B. pinnatum* are found throughout most of Europe and Northwest Africa. *B. distachyon*, *B. phoenicoides* and *B. ramosum* are common in Northwest Africa and southern Europe. There are two species with quite restricted ranges; *B. boissieri* (Boiss.) Nyman endemic to the Sierra Nevada of Spain, and *B. serpentini* in Albania. In the Mediterranean region and Europe several taxa are also found which are treated as either distinct species or as varieties of species mentioned above; *B. rupestre*, *B. caespitosum* (Host) Roem. et Schult., *B. mucronatum* Willk., etc.

ASIA: *B. sylvaticum*, *B. pinnatum* and *B. distachyon* are also found in Asia. *B. distachyon*, which is adapted to the Mediterranean climate, extends from the Mediterranean region to northwestern India. *B. pinnatum* occurs from Europe to the Dahurian region of East Siberia. *B. sylvaticum* is widely distributed in Eurasia and is found from Europe to Japan and southward to the mountains of Ceylon and Malaysia. Several varieties of *B. sylvaticum* are known in Asia; var. *gracile* (Weigel) Keng in China, var. *luzoniense* (Hack.) Hara in Malaysia to Himalaya, var. *involutum* (Buse) Jansen in Java, var. *pubifolium* (Hitche.) Jansen in New Guinea, etc. Besides these widespread taxa, *B. kawakamii* Hayata, a species with distinctive morphological features, is found in the mountains of Formosa. *B. kawakamii* has a caespitose habit, slender and hard rhizomes, densely hairy lemmas and rachilla, and very slender culms of which the upper part is nodding and bears usually one spikelet at the tip. *B. kawakamii* is distant from all the other species found in Asia and seems to be a relict.

AFRICA: In the mainland of Africa (except the northern part) are found two species of *Brachypodium*, *B. flexum* and *B. bolusii* Stapf. *B. flexum* occurs in South Africa and in mountains of tropical East Africa, the Cameroon Mountains and Clarence Peak of West

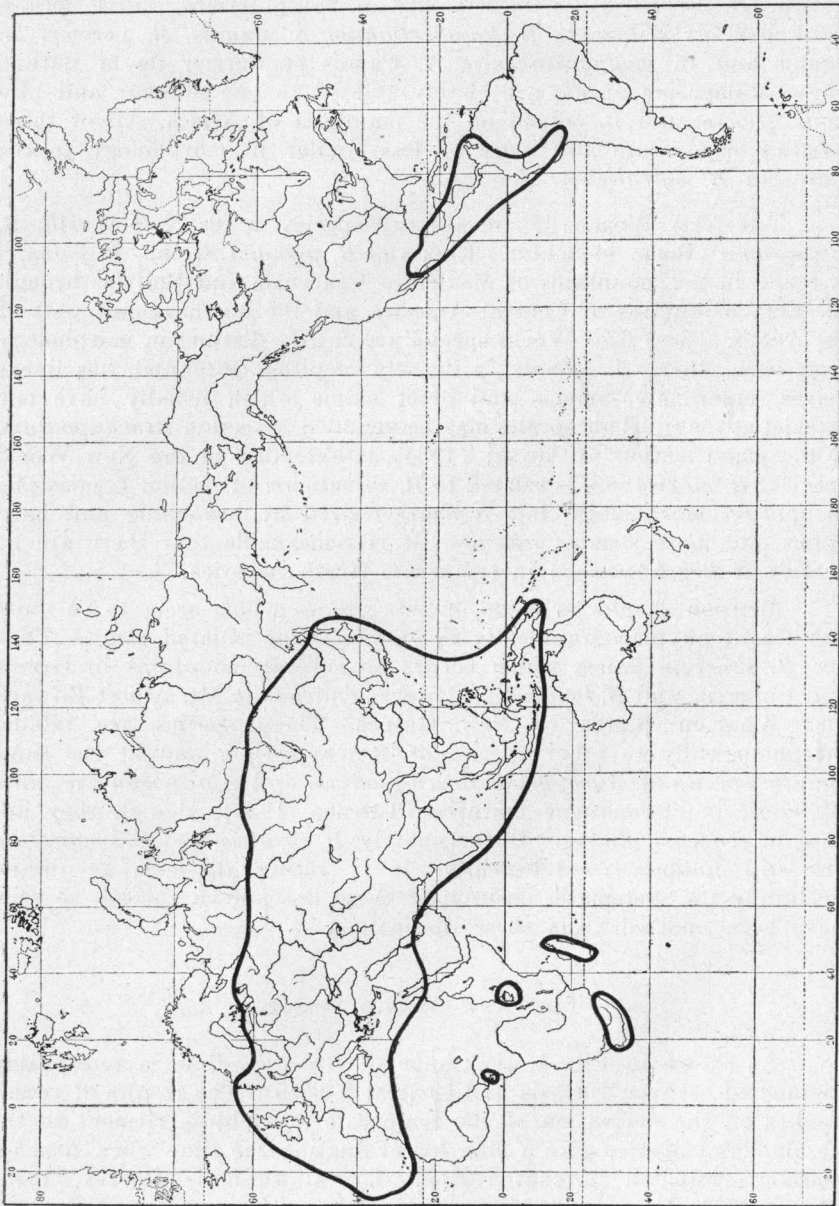


Fig. 1. Range of the genus *Brachypodium*

Africa. *B. bolusii* is distributed only in South Africa. Three species are known in Malagasy; *B. humbertianum* A. Camus, *B. perrieri* A. Camus and *B. madagascariense* A. Camus et Perrier de la Bathie. These Malagasian species are closely related to one another and also to *B. flexum* and *B. bolusii* on the mainland of Africa. All of these African species are also more or less similar in morphology to the Eurasian *B. sylvaticum*.

THE NEW WORLD: There are two species in the New World, *B. mexicanum* (Roem. et Schult.) Link and *B. pringlei* Scribn. *B. pringlei* is found in the mountains of Mexico to Venezuela and Bolivia through the high mountains of Central America and the northernmost part of the Andes. These New World species are clearly distinct in morphology from each other. *B. pringlei*, a densely caespitose perennial, has linear leaves, mucronate lemmas and erect culms which usually have one spikelet at the tip. This species may be included in section *Brachypodium*, if the classification of Nevski (1934) is extended to the New World species. *B. mexicanum* is related to *B. sylvaticum* of section *Leptorachis* in spikelet morphology, but is characterized by branching and hard culms and more slender racemes. It is remarkable that there are no species of *Brachypodium* in temperate North America.

Mention should be made of two species which seem to be quite significant phytogeographically in view of their isolated ranges. They are *B. sanctum* Janca which occurs on several mountains in Greece and Bulgaria, and *B. longisetum* Hitchc., endemic in Mt. Albert Edward and Wharton Range of New Guinea. These species are related morphologically to other species of *Brachypodium* and at the same time to species of *Agropyron*. *Brachypodium* and *Agropyron* are quite different in chromosome features (Tateoka, 1956), though they are close in gross morphology. Unfortunately, *B. sanctum* and *B. longisetum* are still unknown cytologically. It is rather difficult to decide definitely the systematic position of these less known species, so they have been omitted from these discussions.

THE NEW WORLD SPECIES

As shown in Fig. 1, the range of *Brachypodium* is remarkably disjuncted between Eurasia and Central America. The results of recent studies on the derivation of the temperate mesophytic element in the highlands of Mexico give a clue for evaluating the time when *Brachypodium* originated in that region. Several authors (Deevey, 1949; Sharp, 1953; Dressler, 1954) state that the majority of the temperate elements in the Mexican mountains arose by southward migration from America in recent geological time, such as during the pluvial

stages of the Pleistocene. However, Steyermark (1950), McVaugh (1952) and Braun (1955) have found various floristic evidence which contradicts such an interpretation, and they have advanced the hypothesis that the temperate element must have existed there a much longer time. These two opposing views have been critically examined by Martin and Harrell (1957) who studied the distribution of terrestrial vertebrates in connection with floristic relationships between eastern North America and Mexican mountains. They conclude that only a small portion of the temperate biota could have migrated during the Pleistocene. This opinion is further substantiated by Axelrod (1960) and Graham (1965).

My examinations of the festucoid grasses in Central America indicate the following ratios: the total of the species spontaneously occurring in Central America is 91, of which 69 (75,8 %) are endemic, 7 (7,7 %) are common to North America, 12 (13,2 %) are common to South America, and the remaining 3 species (3,3 %) virtually cosmopolitan. The high proportion of endemics is striking. The majority of the festucoid grasses in Central America inhabit the mountains of Mexico and Guatemala, and the occurring farther south, as in Panama and Costa Rica, are much fewer in number. Therefore, the majority of the species occupy an area which is almost equi-distant from North and South America. Nevertheless, the totals above show that the species common to South America are more numerous than those common to North America. In Mexico are found many festucoid grasses which have no counterparts in North America: examples are *Briza rotundata* (H. B. K.) Steud., *Chaetotropis elongata* (H. B. K.) Björkman, *Cinna poaeformis* (H. B. K.) Scribn. et Merr., *Deschampsia pringlei* Scribn., *Helleria livida* (H. B. K.) Fourn., *Metcalfia mexicana* (Scribn.) Conert, *Peyritschia koelerioides* (Peyr.) Fourn., and *Trisetum virletii* Fourn. Further, some of these species, such as *Metcalfia mexicana* and *Trisetum virletii*, have unusual or primitive morphological features (Conert, 1960; Tateoka, 1964a & unpub.). These observations agree with the thesis that the montane flora of Mexico may be of ancient origin and that it has not been greatly changed by dispersals which occurred in response to climatic changes during the Pleistocene.

As stated by Braun (1955), Martin and Harrell (1957) and Axelrod (1960), the arid environments prevailing in southwestern United States and northern Mexico may have greatly obstructed the exchange of temperate mesophytes between highlands of Mexico and more northern, particularly northeastern, temperate areas. The arrival of temperate mesophytes to Mexico may principally predate the development of the arid environments. Axelrod (1960) suggest that the connection of the biota between the Appalachian region and the Mexican highlands would go back to the Early Tertiary, because the Madro-Ter-

tiary geoflora occupying the intervening arid region was already well developed in the Oligocene. The ancient origin of the arid climate of Mexico has been pointed out also by Rzedowski (1962). Braun (1955) and Martin and Harrell (1957) conclude that the majority of temperate mesophytes reached the highlands of Mexico by the mid-Cenozoic at the latest and that they were isolated there by the subsequent development of arid environments.

The two species of *Brachypodium* found in the New World often grow in association with temperate mesophytic trees, most of which are components of the Arcto-Tertiary flora. It is very likely that *Brachypodium* arrived in Mexico together with these trees. Considering their ecological nature, it is hard to conceive of *Brachypodium* species invading arid areas with high temperature. The possibility of long distance dispersal across the arid zone is very remote in the case of *Brachypodium*, because this genus is at present completely lacking in temperate North America. Therefore, we can conclude that *Brachypodium* has existed in Mexico at least since the mid-Cenozoic.

SPECIES OF THE MEDITERRANEAN REGION

Historical vicissitudes of the vegetation of the Mediterranean region, where species of *Brachypodium* are most abundant, have been reviewed by various authors on the basis of numerous investigations of palaeobotany, phytogeography, geology and palaeoclimatology (Stebbins and Zohary, 1959; Axelrod, 1960; Kraüsel, 1961; and others). It is known that the oldest elements of the modern flora of the Mediterranean region date back to the middle of the Tertiary period, and that the subtropical elements, which formerly occupied this area, gradually disappeared from the region during the Pliocene epoch, survivals from the Tertiary being well preserved in a few areas, such as the Canary Islands. If *Brachypodium* really is an ancient grass, we can expect to find phytogeographical evidence to indicate an old history of this genus in the Mediterranean region. The three species (*B. ramosum*, *B. boissieri* and *B. serpentinii*) will be discussed in relation to this assumption.

Two varieties of *B. ramosum* can be recognized, var. *arbusculum* and var. *ramosum* (= var. *roemeri* and var. *gigas* sensu Saint-Yves, 1934). Var. *ramosum* is common in northwestern Africa and southern Europe, and var. *arbusculum* is endemic to the Canary Islands. Var. *arbusculum* is remarkable not only in its isolated range but also in occupying areas with a subtropical climate. Larsen (1963) notes that var. *arbusculum* occurs in the coastal region of Gomera, Hierro and the northeastern promontory of Tenerife. The large montane areas of the islands which have a more moderate climate contain no strains

of var. *arbusculum*. Var. *ramosum* is also entirely lacking here (Saint-Yves, 1934) although the ecological conditions of the uplands of the Canaries are just as favorable for var. *ramosum* as in Morocco and Oran where it is quite common (Maire, 1955).

The patterns of distribution indicated above strongly contradict the hypothesis that seeds of *B. ramosum* could be transported between the Canaries and the mainland of Africa by any available agent. Far more likely is the hypothesis that var. *arbusculum*, or a form closely related to it, already existed when exchange of biota between the Canaries and the African mainland was possible by aid of intermediate masses of lands or of a continuous land connection. Circumstantial evidence suggests that such a connection was finally broken in the Miocene epoch (Hagen, 1914; Stebbins and Zohary, 1959). It may be logical to assume that var. *arbusculum* or its ancestral form, which survives in the area with a subtropical climate, migrated along the coast of southwestern Europe, North Africa and the Canaries in the Miocene or earlier, and probably persisted in southwestern Europe and northwestern Africa until the subtropical element was eliminated from these areas during the Pliocene epoch. The isolated occurrence of var. *arbusculum* in the Canaries can therefore be explained as a relict, and this variety or a form closely related to it must have existed in the Mediterranean region at least in the Miocene epoch.

Brachypodium boissieri is endemic to the Sierra Nevada in southern Spain and grows on limestone soils at the altitude of 900 - 2.200 m. The palaeogeography of the area surrounding the Sierra Nevada is relatively well known. The Sierra Nevada, being largely composed of crystalline schists, belongs to the old Betic-Riffian Massif and was never covered by water throughout the Cenozoic Era (Furon, 1941; Gignoux, 1955). The flora of the Betic-Riffian province is known to include a number of endemic species (Meusel, Jäger und Weinert, 1965), and it is quite probable that many old species inhabit this area. The results of taxonomic investigations of the festucoid grasses support this assumption. In their studies of the genus *Trisetum*, Chrtek and Jirasek (1963) and Chrtek (1965) state that the subgenus *Glaciotrisetum*, which consists of two species endemic to the Sierra Nevada, may represent the last remnants of a previously more vigorous species assemblage. The genus *Homalachne* is composed of two Spanish species, one of which (*H. caespitosa* Pilger) is endemic to the Sierra Nevada (Paunero, 1955). *Homalachne* is related to the genus *Deschampsia* on the one hand, and is very close to the genus *Holcus* on the other. Among these three genera, *Deschampsia* is the most primitive in morphology. *Holcus* is characterized by such specialized features as shining and firm lemmas, elongated and bent rachilla between the glumes and the lowest floret, usually dimorphic florets; the spikelets

articulated below the glumes and finely hairy pedicels. Nevertheless, judging from its species composition and geographical distribution, *Holcus* seems to have appeared not later than the Late Tertiary. *Homalachne* is less specialized than *Holcus*, and the origin of *Homalachne* may predate that of *Holcus*.

The conspicuous endemism of *Brachypodium boissieri* suggests that it may be either a newly evolved taxon or a relict. If this species were a neo-endemic, it would have had no time to expand its area outside the Sierra Nevada. Even such taxa as some varieties of *B. distachyon*, which might be of a recent origin, are not so limited in range as *B. boissieri*. It is unlikely that *B. boissieri*, which is clearly separated from all the other species in its combination of morphological and leaf-anatomical features, has evolved more recently than such varieties. The possibility still remains that *B. boissieri* could have acquired a particular ecological specialization which limits its area to the Sierra Nevada. *B. boissieri* grows, however, at medium altitudes on limestone soils which may not be rare in the Iberian Peninsula and Northwest Africa. The most likely hypothesis is that *B. boissieri* is a relict which has survived in the Sierra Nevada together with such festucoid taxa as *Glaciotrisetum* and *Homalachne*.

Finally, *B. serpentini*, which is endemic to Albania, may also be a relict of great age. Markgraf (1948) has confirmed that it occurs only on serpentine soils of Albania where Tertiary relicts are particularly frequent. Hubbard (1935) points out the isolated systematic position of *B. serpentini*, the close relatives of which may be extinct.

SPECIES OF ASIA AND AFRICA

As described earlier, the *B. sylvaticum* complex occurs not only in temperate Eurasia but also in the mountains of Tropical Africa, South Africa, Malagasy and Malaysia. It is likely that the *B. sylvaticum* complex originated somewhere in Eurasia and that it spread eastward to New Guinea and southward to South Africa and Malagasy. Migration between Malagasy and the mainland of Africa can be recognized in several festucoid genera. In Malagasy the festucoid group is poorly developed, and only 23 species in nine genera inhabit this island according to my preliminary study (Tateoka, 1964 b). Although a large majority of these species are endemic to the island, they are more or less related to the montane grasses in East and South Africa. Such connections are particularly obvious in *Festuca*, *Pseudobromus*, *Anthoxanthum* and *Brachypodium*. Likewise, the festucoid grasses in New Guinea are related to those in the northern and western

parts of Malaysia, and the connection of the festucoids between New Guinea and Australia is much weaker (Tateoka, 1965). The dispersal of the *B. sylvaticum* complex to the mountains of the tropical and subtropical regions must have been quite slow considering its strict ecological requirements. A long period of time was doubtlessly needed for this complex to attain its present wide range.

B. kawakamii, endemic to the mountains of Formosa, has very distinct morphological features which clearly separate it from all the other species. Many temperate plants which are the components of the Sino-Japanese flora also inhabit the mountains of Formosa. In such plants are various accompanying woody species of which fossil counterparts have been discovered in Europe of the Middle and Late Tertiary age (Tralau, 1963). It seems probable that *B. kawakamii* previously has a much wider, and further studies on the relations of this and the Mediterranean relict species should be of interest.

ORIGIN OF BRACHYPODIUM

It will be evident from the above descriptions that species of *Brachypodium* were already well developed in the middle of the Tertiary and that they spread in both Central America and the Old World at least by the Middle Tertiary.

The time of origin of *Brachypodium* should be related to its remarkable disjunction between Eurasia and Central America. It may be possible to account for this type disjunction by the theory of continental drift combined with the hypothesis of a palaeotropical zone (Maekawa, 1964 & 1965). The possibility that wider lands at the low latitudes were available for migration across the Atlantic and the Pacific Oceans has recently been stressed by Axelrod (1960) and van Steenis (1962). According to a classical explanation (Chaney, 1947), disjunction as found in *Brachypodium* can be interpreted as follows. *Brachypodium* was spread throughout the high latitudes of the Northern Hemisphere when climates in these areas were not so severe as at present. Later, it shifted southward in response to a subsequent trend toward a cooler and less humid climate, and was eliminated from the interrupted areas.

Any of these hypotheses demands the existence of *Brachypodium* at least by the Early Tertiary. In view of the fact that the Angiosperms were in full development in the Middle Cretaceous, it seems probable that the origin of *Brachypodium* dates back even into the Cretaceous period. The place of origin of *Brachypodium* is quite obscure, and it seems still premature to advance a hypothesis about it.

SUMMARY

The phytogeography of *Brachypodium* has been discussed. There are estimated to be 14 to 18 species. Their ranges are outlined. The general range of *Brachypodium* shows a remarkable disjunction between Central America and Eurasia. A historical explanation for this disjunction, combined with considerations as to the inter-relationships of existing species, leads to the conclusions that species of *Brachypodium* were well developed by the middle of the Tertiary period and that they spread in both Central America and Eurasia at least by the Middle Tertiary. Phytogeographical investigations on the floras of mountains in Mexico and the Mediterranean region lend support to the above conclusions. The origin of *Brachypodium* most probably dates back to the Early Tertiary or even to the Cretaceous period.

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TABLE 1

CHROMOSOME NUMBERS OF BRACHYPODIUM *

<i>B. serpentini</i> C. E. Hubbard	14
<i>B. pinnatum</i> (L.) Beauv.	28
<i>B. phoenicoides</i> (L.) Roem. et Schult.	28
<i>B. distachyon</i> (L.) Beauv.	30
<i>B. ramosum</i> (L.) Roem. et Schult. var. <i>arbusculum</i> Saint-Yves	18
<i>B. sylvaticum</i> (Huds.) Beauv.	18
<i>B. flexum</i> Nees	18
<i>B. mexicanum</i> (Roem. et Schult.) Link	38

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