TERTIARY GRASSES AND OTHER PRAIRIE VEGETATION FROM HIGH PLAINS OF NORTH AMERICA.[1]

MAXIM K. ELIAS.

ABSTRACT.

The results of field research of 1933 indicate that the remains of grasses and other herbs, some of which were described by the writer in 1932, are of utmost importance as index fossils in the late Tertiary deposits of Nebraska and the surrounding territory. The remains of fossil herbs in the form of husks of grasses and nutlets of Boraginaceae have been collected in great numbers in more than a score of localities, and the succession of floral zones proves to be invariably the same. The writer has succeeded in tying of the majority of his floras with the horizons in which some of the best known vertebrate remains have been collected. According to the modern interpretation of the age of these vertebrate faunas, the floral zones of the writer range from middle Miocene to middle (and probably even to upper) Pliocene. A new genus of fossil grasses, *Stipidium,* is described, and the general trend of evolution of Stipideae is outlined.

INTRODUCTION.

The existence of fossil remains of prairie grasses was first recognized in 1931 (2, p. 150). The fossils come from the late Tertiary deposits of the High Plains region, and as yet they have not been collected outside of this area. Field research in 1933, which was conducted largely on a grant from the Marsh Fund of the National Academy of Sciences, proved that the remains of grasses (and other herbs), mostly in the form of hollow husks, furnished by far the most important fossil material for stratigraphic studies of the late Tertiary continental formations.

OCCURRENCE.

The fossil grass husks are comparatively very common and are beautifully preserved, being apparently buried not far from their place of growth. The remains can be found at almost any outcrop, provided it is large enough to show several successive beds, as the remains are not found in all beds of the geologic sections but are scattered along certain horizons; rarely they are concentrated in small spots, measured by inches in diameter, or fill up small pockets in the rock.

The succeeding horizons, which contain the same leading types of herbs, constitute natural stratigraphic zones. The

[1] Published by permission of the State Geologist, Kansas Geological Survey.

thickness of these zones is measured in scores of feet. The succession of these floral zones proves to be the same everywhere within the studied areas in western Nebraska, northwestern Kansas and adjacent part of Colorado. The same assemblages of plant remains were also found on reconnaissance trips to south-central South Dakota and north-central Texas.

PREVIOUSLY KNOWN FOSSIL GRASSES.

Fossil grasses have previously been not entirely unknown to science (4, 5, 8, 9), grass-like remains being occasionally collected among the foliage and fruits of the late Cretaceous and Tertiary arboreal plants (which comprise the bulk of paleobotanical collections). These remains, however, consist of fragmentary linear leaves and herbaceous stems and culms, rarely accompanied by imprints of crushed paniculate fertile shoots. The classification of these imperfect remains with this or that living genus of grasses is in most cases quite arbitrary. The references by the famous Baron Heer of some of the best grass remains of this kind from the European late Tertiary to the living *Oryza* and *Panicum* were severely and justly criticized by other high authorities on living and fossil plants, and at best are considered not proved. Only the presence of *Arundo*, *Phragmites*, and perhaps of *Bambusa* in the late Cretaceous and Tertiary beds was considered as being established on sufficient fossil evidence. The living representatives of these grasses are tall water-loving species which dwell along the shores of ponds and streams. The association of their fossil relatives with the arboreous vegetation permits no doubt that in the late Cretaceous and Tertiary times they grew in the same environment.

PRESERVATION AND ASSOCIATION OF FOSSIL PRAIRIE GRASSES.

The beautifully preserved husks of grasses in the late Tertiary formations of the High Plains are remains of an entirely different kind and origin. They are not imprints, but are siliceous petrifactions, the silica of which, at least in part, is the original mineral skeleton of the plant. They are embedded not in clays or other fine sedimentary material, where most known fossil plant imprints are found, but are restricted almost exclusively to sands and unsorted grits, the separate pebbles in the latter being up to 1 cm. in diameter. The only nonherbaceous plant, the remains of which is found in association with the grasses, is hackberry (*Celtis*), a typical xerophitic tree, sometimes dwarfed to a shrub, which is now infrequently found in ravines and valleys of the High Plains. Other plant remains of the fossil association belong to several herbaceous genera of the Borage family and to *Yucca* (provisional reference of two forms of fossil trunks), which are also distinct xerophites. The whole assemblage undoubtedly represents the remains of the late Tertiary prairie vegetation, with which we only now begin to make a real acquaintance.

TYPES OF FOSSIL GRASS HUSKS.

The husks of two species of fossil grasses, as they are now recognized, were collected in Kansas as early as 1884 by John B. Hatcher, and described in the important pioneer work by E. W. Berry in 1928 (1, p. 2) as *Lithospermum fossilium glabrum* and *Lithospermum fossilium aristatum*. Their true nature as remains of grasses was established by the writer in 1932 (3, pp. 346-349), when he also described two new species of grasses collected by himself and referred to *Panicum* and *Stipa* (3, pp. 342-345). For the *glabrum* species, which was identified and re-described by him on his own material, a new generic name, *Berriochloa,* was introduced, while the species *aristatum* was questionably referred to the same genus. Now, after examining the cotypes of *aristatum*, which are deposited in the U. S. National Museum, the writer proposes to classify this species together with many new ones which he has collected under the new generic name *Stipidium*, a fossil grass closely related to the living *Stipa* or spear-grass.

MORPHOLOGY OF GRASS HUSKS.

Since the subject of fossilized husks of grasses is entirely new, a brief introduction to the morphology of the fertile parts of living prairie grasses, with which they are to be compared, is necessary. The grain of cereals and other living grasses is usually enclosed in a husk or protective cover and the two are dispersed together, forming what is commonly known as grass seed. The protective cover is usually made of two glumes or bracts, the fertile glume or lemma and the pale or palea. The two adhere closely to the grain, the palea from the inner side or the side facing the rachis, and the lemma from the outer side. The lemma is almost always larger than the palea. The lateral edges of the lemma usually overlap to greater or lesser extent the edges of the palea, and in some genera the palea is entirely enveloped by the lemma, as for instance in *Stipa*, the lemma of which is convolute. The palea is a part peculiar to all living grasses and is not duplicated in any other monocotyledons or other plants. The essential construction of the palea in grasses varies but little. It is almost invariably two-nerved, and when it appears as a one-nerved glume, the single nerve is believed to be made by fusion of the original two nerves.

The fossil husks of grasses under discussion consist of lemma and palea, the latter being distinctly two-nerved and showing otherwise all typical features pertaining to the palea of living grasses. It is the presence of typical palea overlapped by lemma which leads the writer confidently to recognize these fossil forms as husks of extinct grasses. Both lemma and palea are more or less distinctly striated longitudinally. They are smooth or tuberculate and may be covered by hairs. At the apices of the lemmas the tubercles are modified infrequently into sharp upright bristles. At the base of some husks a hairy callus is developed. All hairs and bristles, regardless of their location on the husk, point toward its apex.

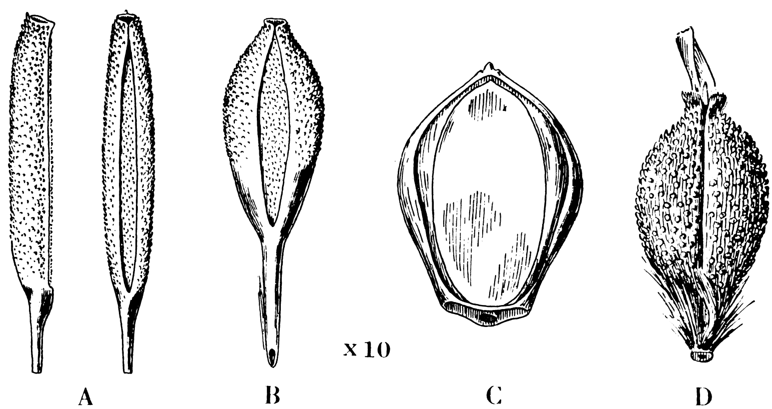
ORIENTATION OF FOSSIL GRASS HUSKS.

The two species of husks, which were originally described by Berry and re-described by the writer, do not bear any bristles or hairs, but on some of the species recently collected by the writer and referred by him to the same genera (*Berriochloa* and *Stipidium*), hairs and bristles were observed. The orientation of these hairs and bristles permits determination of which end is the apex and which is the base of these forms, and as *glabrum* and *aristatum* have a construction very similar to the newly discovered hairy species, they must be oriented in the same way as the latter. By this reasoning the writer came to the conclusion that the orientation of *glabrum* and *aristatum*, as originally set by Berry, must be changed to exactly the opposite; thus, what was considered by Berry as awn in these forms is actually sharp callus, and what was recognized as hylum (or scar of attachment, author's term) is actually the apex of these husks.

As soon as the orientation of these fossil forms is changed, their relation to living genera of grasses can be satisfactorily established. When preserving the original orientation as set by Berry, it was difficult to classify *Berriochloa* with any of the established groups of living grasses and the writer provisionally placed this fossil genus among the Hordeae. With the change of orientation it became quite clear that the fossil genus *Berriochloa* (as well as the related genus *Stipidium*) does not belong to the Hordeae but to the group of the living *Stipa*, *Pitptochaetium*, *Oryzopsis* and others which constitute the subtribe Stipeae of the tribe Agrostideae.

THREE PRINCIPAL GENERA OF FOSSIL PRAIRIE GRASSES.

On the accompanying sketch the three principal genera of the so far discovered late Tertiary prairie grasses of the High



EXPLANATION OF PLATE

Seeds of representatives of three principal genera of fossil prairie grasses: A—*Stipidium* n. g., n. sp.; B—*Berriochloa* n. sp.; C—*Panicum elegans* Elias; and, for comparison, D—*Living Piptochaetium* sp. All figures are magnified 10 times.

Plains are illustrated. Figure A represents lateral and front views of the genotype of *Stipidium* n. gen. This is the smallest known species of the genus and comes from the type exposures of the lower Sheep Creek formation of western Nebraska, the well known vertebrate fauna of which is referred to middle Miocene. Figure B shows a front view of a typical species of *Berriochloa* from the same formation and locality. This early species of *Berriochloa* shows a very long slender callus, with few hairs still attached to it. A partly broken and apparently also fairly long callus is also well developed on the genotype of *Stipidium* (fig. A). This shows that the presence of a prominent hairy callus is an ancient feature of Agrostideae seeds, unlike the remarkable diversified awns of living *Stipa* and *Agrostis*, the development of which appendages seems to have occurred some time after middle Pliocene time (the observed related forms of this and earlier ages do not seem to bear any hard awns).

Figure C shows a front view of *Panicum elegans* Elias from the middle Pliocene beds of the Ogallala formation of Wallace County, Kansas, which was described in 1932 (3, p. 342).[2] The front views of the husks of all these figures show the palea (in the middle) overlapped by the edges of the lemma.

Figure D gives a front view of a seed of the living *Piptochaetium* sp. from Argentina (from the herbarium specimen 1,388,635, U. S. National Herbarium). The awn in this and other known species of *Piptochaetium* is flexuose and easily breaks away. Only the basal part of it is shown on the sketch. The large sharp bristle at the apex and between the edges of the lemma is protruding cuspidate apex of concealed palea. All sketches were prepared by the writer.

STRATIGRAPHIC DISTRIBUTION OF THE PRAIRIE PLANTS.

The fossil prairie flora of the High Plains, as collected and identified up to date,[3] consists of about 18 species belonging to two tribes (Paniceae and Agrostideae) of grasses (only four of which were previously described), five species of Boraginaceae herbs (four of which were described), one species (described) of hackberry (*Celtis*), two species of trunks which are provisionally classified as *Yucca*, and a few seeds which have not been identified as yet. The Boraginaceae herbs are very common in the Pliocene, but have not been collected as yet in the Miocene. They furnish the most important and widely distributed index fossils for zoning of the

[2] The age of these Wallace County beds was assigned to the lower Pliocene on the ground of interpretation of their rich vertebrate fauna (2, pp. 153 and 160-161). Now, however, R. A. Stirton, who is studying the entire problem of the age of North American late Tertiary faunas, refers the same Wallace County fauna to the middle Pliocene (oral communication by Dr. R. A. Stirton), which view is here accepted.

[3] Detailed description of the new species is in preparation.

lower and middle Pliocene. The succession of *Krynitzkia coroniformis* zone by *Biorbia fossilia* (ex *rugosa*) zone above was found to be faithfully repeated in a great many localities along the North Platte River and other areas in Nebraska, in northwestern Kansas, and in eastern Colorado. Grasses can be used for zoning of the beds below the *Krynitzkia coroniformis* zone, as indicated by the few collections made in undoubted Miocene strata.

GENERAL TREND OF EVOLUTION OF THE STUDIED GRASSES.

Perhaps the most important scientific result of the studies of the fossil vegetation of the prairies is the first glimpse that it provides on the evolution of some grasses through Miocene and Pliocene ages. All collected grasses belong to the tribe Paniceae and to the subtribe Stipeae of the Agrostideae (there are 14 tribes of living grasses). Only Stipeae have been found in the Miocene and lower Pliocene (in the sense now accepted by R. A. Stirton), while Paniceae have been found so far only in the middle Pliocene and in apparently higher beds (earliest late Pliocene?) from which no vertebrates have been collected. The Stipeae, which range through the whole studied section, show a very distinct evolutionary development, as their husks indicate. These husks show a general change from an open lemma of the Miocene to closed lemma of lower and middle Pliocene, and finally to convolute lemmas as in the living *Stipa* and *Aristida*, a few convolute types appearing, however, in the middle Pliocene. The earliest known (middle Miocene) husks of this tribe of grasses, which are classified as *Berriochloa* and *Stipidium*, are very small and can barely be seen with the naked eye among the sand grains of the containing rock. Although some slightly larger forms were also collected in the Miocene, these and still larger species become very common only in the lower Pliocene, where the smallest species of *Stipidium* disappear.[4] The largest known representatives of this tribe of grasses are *Berriochloa glabra* and *Stipidium aristatum*, which appear still later, in the middle Pliocene. None of the living nearest relatives of these forms seem to be as large as these middle Pliocene species. The evolutionary increase in size of the fossil Agrostideae, as

[4] The smallest species of Miocene *Berriochloa*, however, do not become extinct, but through evolutionary changes are connected to the living species of *Piptochaetium*, the husks of which are of about the same size (compare figs. B and D).

revealed by the material from the High Plains, is probably more than coincidental with the well known general increase in size, through the geologic ages, of horses, camels and other herbivores which fed on these prairie grasses.

AGE OF THE STUDIED FLORAS.

The age of the discovered floral zones was established exclusively with the help of the few best known vertebrate faunas from the High Plains, which were studied by Osborn, Matthew, and their associates and successors. The quarries from which these faunas have been collected were carefully re-located and the plant remains were collected directly from the vertebrate-containing beds and, whenever possible, from the beds above and below them in the local geologic sections.

The following well known faunas are now securely tied with the floral zones:

(1) The middle Miocene fauna from the section of lower Sheep Creek formation 18 miles south of Agate Springs. Here the plant remains have been collected from the very same outcrop which gave Osborn his types of *Merychippus isonesus secundus*, *M. isonesus tertius*, *M. isonesus quartus*, and *M. isonesus quintus*.

(2) The fauna from the famous Sternberg quarry of Long Island, Phillips County, Kansas, formerly referred to lower Pliocene; now considered by R. A. Stirton to be middle Pliocene.

(3) The fauna from Beecher Island, south of Wray, Yuma County, Colorado. This is the rich fauna described by H. J. Cook. Formerly referred to lower Pliocene; now considered by R. A. Stirton to be middle Pliocene.

(4) Two faunas from the vicinity of Valentine, Cherry County, northern Nebraska. The collections of plants were made at the time when R. A. Stirton was opening old and new quarries in order to prove that two distinctly different zones of vertebrates are developed here: one of early Pliocene age, the other of late Miocene age. With the coöperation of Stirton and his crew, a goodly number of plant remains was collected from both zones, which were also found to occupy distinctly different stratigraphic positions in the local geologic section.

STUDIED PLANTS AS "INDEX FOSSILS."

After being tied in the most precise way to the important and recently carefully revised faunal zones of the High Plains, the floral zones can now be used for determination of the age of rocks in those numerous outcrops from which no vertebrate remains have been collected or in which they have not been found in sufficient number or were not well preserved. In coöperation with the Nebraska Geological Survey, the floral zones of the Ogallala formation were successfully carried through the outcrops of this formation along the North Platte River from Paxton to the vicinity of Scotts Bluff, and with the help of these zones some important structural features along this valley were discovered.

The Ogallala formation of Darton is a very useful geologic unit, but its uniform lithology prevented the possibility of its being zoned until the plant remains provided the necessary zone markers. Now, with the help of these zones, the total thickness of this formation can be determined more accurately. It proves to be 475 feet, whereas formerly it was believed to be only 200 to 250 feet thick, since in no single locality is the total thickness of the formation exposed.

TABLE OF FLORAL ZONES.

Floral zones as determined by the most typical plants: Zones	Subzones	Geologic age as indicated by the vertebrates
Zone of *Celtis* cf. *willistoni* (Cockerell) 175′	Upper subzone of *Echinochloa* n. sp. Lower subzone	Probably late Pliocene (Vertebrate fauna unknown)
Zone of *Biorbia fossilia* (ex *rugosa* (Berry) about 100′	Upper subzone of *Panicum elegans* Elias Lower subzone of *Krynitzkia chaneyi* Elias	Probably late medial Pliocene Medial Pliocene
Zone of *Krynitzkia coroniformis* Elias about 100′		Early medial Pliocene Late early Pliocene
Zone of *Stipidium* n. sp. 100′		Earliest early Pliocene Latest late Miocene
?		Late Miocene
Zone of a very small *Stipidium* n. sp. 70′		Medial Miocene

SELECTED BIBLIOGRAPHY ON FOSSIL AND LIVING GRASSES

1. Berry, E. W.: Fossil nutlets of the genus *Lithospermum*: Proc. U. S. Nat. Mus., vol. **73**, art. 13, pp. 1-3, 1928.
2. Elias, M. K.: Geology of Wallace County, Kansas: Bull. Univ. Kansas, State Geol. Survey, Bull. 18. See pp. 149-152, 1931.
3. Elias, M. K.: Grasses and other plants from the Tertiary rocks of Kansas and Colorado: Contributions to the Paleontology of Kansas, No. 1, Sci. Bull., Univ. of Kansas, vol. **33**, pp. 333-368, 1932.
4. Gardner, J. S.: Fossil grasses: Proc. Geol. Assoc., vol. **9**, 1885-1886, p. 441, 1886.
5. Hackel, E.: Gramineae, in Engler and Prantl, Die Naturlichen Pflanzenfamilien, II Teil, 2 Abt., 1887.
6. Hitchcock, A. S.: Text-book of grasses, Macmillan Co., New York, 1914.
7. Hitchcock, A. S.: Genera of grasses of the United States: U. S. Dept. Agric., Bull. 772, 1920.
8. Hollick, Arthur: New fossil grass from Staten Island: Bull. Torrey Bot. Club, vol. **24**, pp. 122-124, 1897.
9. Lesquereux, Leo: Contribution to the fossil flora of the Western Territories: Rept. U. S. Geol. Survey Terr., vol. **7**, See pp. 85-91, 1887.

WASHINGTON, D. C.