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9. Plants were maintained in a growth chamber on a 16/8-hour light/dark cycle for the first 5 weeks and a 9/15-hour cycle thereafter, at temperatures of 27° and 19°C, relative humidities of 60 and 80 percent, and a photosynthetic photon flux density of 800 μE m^{-2} sec^{-1} measured in the photosynthetically active range. Plants were inoculated with *Rhizobium japonicum* strain 61A96 (obtained originally from J. Burton, Nitragen Co., Milwaukee, Wisc.) and grown in vermiculite in 6-liter pots. Plants were watered with a nutrient solution containing 4 m*M* $CoCl_2$, major elements as recommended by E. G. Bollard and reported by E. J. Hewitt [in *Sand and Water Culture* (Technical Communication 22, Commonwealth Agricultural Bureaux, Farnham Royal, Bucks, England)], and trace elements according to C. M. Johnson, P. R. Stout, T. C. Broyer, and A. B. Carlton [*Plant Soil* **8**, 337 (1957)].
10. Ribulosebisphosphate carboxylase activity was determined as described by G. E. Kleinkopf, R. C. Huffaker, and A. Matheson [*Plant Physiol.* **46**, 204 (1970)]. Ribulosebisphosphate carboxylase protein was determined after acrylamide gel electrophoresis and scanning the band in a spectrophotometer as described by B. J. Davis [*Ann. N.Y. Acad. Sci.* **121**, 404 (1964)]. Nitrogen fixation was estimated by acetylene-dependent ethylene production as outlined by G. J. Bethlenfalvay and D. A. Phillips [*Plant Physiol.* **60**, 419 (1977)]. Evolution of hydrogen by root nodules was not detected in any of the F_3 and F_4 plants tested. The parent Lee 68 showed delayed senescence compared to L63-1097, which exhibited normal senescence.

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Epidermal Patterns of the Lemma in Some Fossil and Living Grasses and Their Phylogenetic Significance

Abstract. *Morphological study of fossil grass anthoecia of* Berriochloa *and* Nassella *collected from Miocene-Pliocene strata in Kansas has revealed well-preserved epidermal structure. This seems to be the first micromorphological information known from fossil grass floral bracts. The epidermal pattern on the lemma in the fossils and their living counterparts are evidence in support of the view that the North American species of* Stipa *of the section* Hesperostipa *Elias and species of* Piptochaetium *have a common ancestry in* Berriochloa, *and that species of both taxa have been distinct from species of the* Nassella, Oryzopsis, *and other* Stipa *since at least the Miocene or Pliocene.*

Some of the most extraordinary plant fossils are the remains of fossil grass floral bracts (*1*) reported from the Late Tertiary High Plains strata of central North America (*2*, *3*). Genera previously described include *Berriochloa* (*3*–*5*), *Nassella*, and *Paleoeriocoma* of the tribe Stipeae (*6*), and *Panicum* and *Setaria* of the tribe Paniceae (*7*). Elias was one of the first to describe and compare the High Plains fossils with their modern counterparts (*3*). He developed preliminary evolutionary schemes on the basis of features of the floral bracts observable at low magnification (from ×10 to ×33) with a binocular microscope, for example, shape, size, and surface texture.

The classification of the grasses has been revolutionized by the introduction of microscopic characters from the internal and external anatomy and morphology of both vegetative and reproductive organs (*8*). The use of these characteristics, along with some traditional ones of gross morphology, has made it possible to produce a system of classification with high phylogenetic and predictive value. Among the micromorphological features utilized in the "new" systematics have been the features of the floral bracts of grasses (*9*). Collections of fossil grass anthoecia in Kansas have provided specimens that are well enough preserved to allow detailed study of the lemma epidermises. The epidermal features of the lemma can be used in determining relationships between some fossil and living grasses of the tribe Paniceae (*10*). I now present evidence that the epidermal patterns of the lemma, in several fossil and modern grasses of the tribe Stipeae, reflect systematic relationships and evolutionary trends dating from at least the Miocene or Pliocene epochs.

A diverse assemblage of three-dimensional silicified grass anthoecia, as well as borage nutlets, sedge achenes, and hackberry nutlets, have been collected from Tertiary strata in Ellis and Rooks counties, Kansas (*11*). The fossils were found in sands and silts of the Ogallala Formation. I studied the fossil-bearing strata (*5*) and dated them as Miocene to Pliocene on the basis of vertebrates associated with the fossil grasses.

Fossils were picked by hand to free them from their enclosing matrix. Specimens of several described and undescribed fossil species of the grass genera *Berriochloa* and *Nassella* (Fig. 1, A to C) were coated with carbon and gold and examined with a scanning electron microscope (JEOL-35). A similar procedure was unsuccessful with modern counterparts of the fossils because the thick cuticle obscured the epidermal patterns and no entirely successful method was discovered for removing it for an examination of the underlying epidermal pattern. Lemmas of modern species of *Piptochaetium*, *Stipa*, *Oryzopsis*, and *Nassella* were cleared with 5 percent NaOH, treated with chlorine bleach, and stained with chlorozol black E. The prepared lemmas were then studied with light microscopy. Epidermal patterns of modern taxa revealed by light microscopy are presented in the form of line drawings rather than photographs so that tissues underlying the lemmatal epidermises do not obscure the essentials of the patterns (Fig. 2).

Among the fossil Stipeae examined were 15 species of *Berriochloa* and 4 species of *Nassella*. The basic lemma pattern of *Berriochloa* is one of long cells (*12*) with strongly sinuous, well-developed lobes (Fig. 1, E to G). Short cells are entirely absent. The observed lemma pattern of fossil *Nassella* contrasts sharply with that of *Berriochloa*. Short cells (silica or suberin cells) are abundant and the basic long cells have been reduced in length (Fig. 1D). Long cells have sinuous walls but not to the extent found in *Berriochloa*.

Included in the modern Stipeae examined were 21 species of *Piptochaetium*, 11 species of *Nassella*, 13 species of *Oryzopsis*, and 38 species of *Stipa*. Examination of the lemmas under a binocular microscope reveals that many extant species of *Piptochaetium* possess ridges and grooves. Higher magnification revealed that the lateral walls of the long cells are strongly developed and project above the central area of the cell (Fig. 2C). The exact mechanism for this modification is unknown. Modern species of *Nassella*, like their fossil counterparts, have an epidermal pattern consisting of greatly reduced long cells and an abundance of short cells (Fig. 2D). Species of *Stipa* examined could be assigned to a number of distinctive types. The most significant to this discussion is the pattern observed on *S. comata* Trin. and Rupr., *S. spartea* Trin., and *S. neomexicana* (Thurb.) Scribn., which com-

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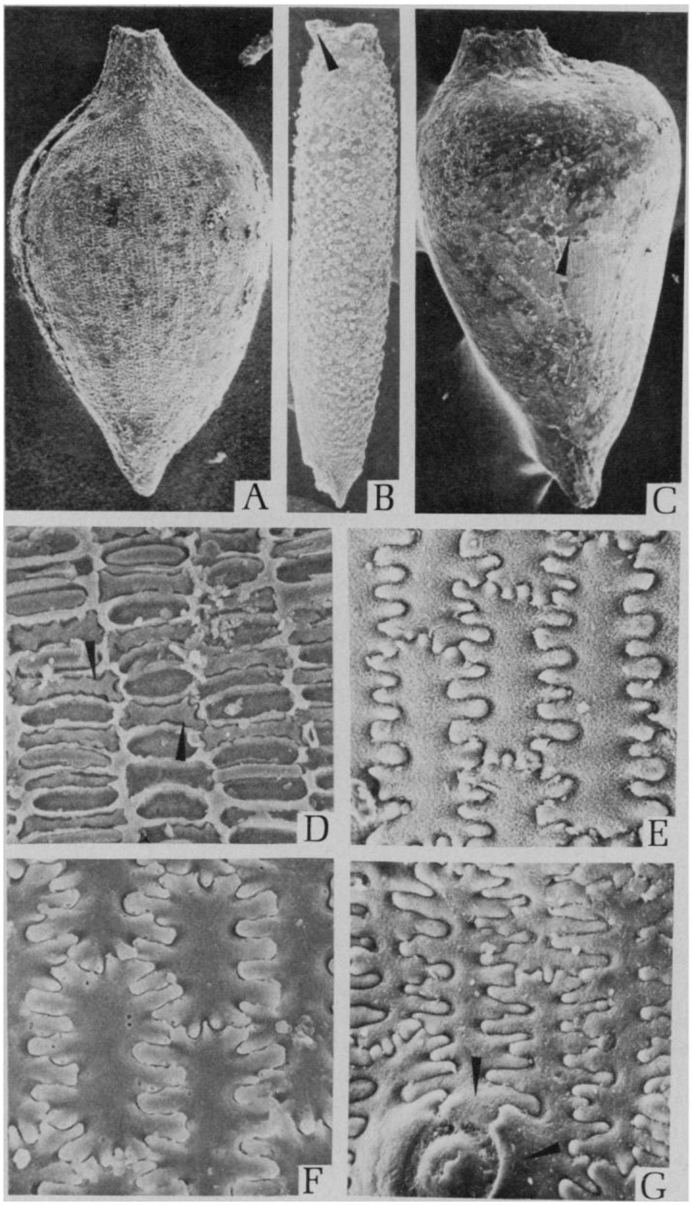
prise the North American species of the section *Hesperostipa* Elias. The pattern is characterized by well-developed long cells with strongly sinuous walls (Fig. 2, A and B) and the complete absence of short cells. No other species of *Stipa* examined had a comparable pattern. Species of the genus *Oryzopsis* are characterized by reduced long cells and an abundance of short cells that were almost exclusively of the silica type although some silica-suberized couples were also observed (Fig. 2F). In most respects they were similar to species of *Nassella* and certain other North American species of *Stipa* (for example, *S. robusta*, Fig. 2E).

The relationships among the fossil Stipeae and their modern counterparts have been subject to several interpretations. Elias (*3*) believed *Stipidium* to be the forerunner of the modern genera *Stipa, Piptochaetium, Nassella*, and *Oryzopsis*, but was unable to determine the affinities of *Berriochloa*. Stebbins (*13*) and Williams (*14*) suggested that *Stipidium* and *Berriochloa* most closely resemble the modern genus *Piptochaetium*, thus eliminating from phyletic consideration the important genera *Stipa* and *Oryzopsis*. The above-mentioned workers recognized relationships among the fossil and living grasses on the basis of macromorphological anthoecia features such as shape, size, and surface textures; that is, the essential distinctions between genera (or sections) were the elongated, cylindrical anthoecia in *Stipidium, Stipa*, or *Piptochaetium* (section *Podopogon*), and the less elongated, generally robust anthoecia in *Berriochloa, Piptochaetium* (section *Eupiptochaetium*), *Oryzopsis*, and *Nassella*. My own observations and those of others (*15*) have shown conclusively that the features used by other workers are not sufficient for recognizing phyletic relationships or boundaries of taxa, especially at the generic level, for example, mature anthoecia of many *Stipa* are just as likely to be elongated-cylindrical as are mature anthoecia of *Piptochaetium* (*16*). When this occurs it is not possible to determine relationships with similarly shaped *Berriochloa*. Macromorphological features of the anthoecia alone are not considered a sound basis for assigning taxa at the generic level or for determining affinities among the fossil and related living Stipeae.

The evidence presented should be sufficient to determine both the systematics and phylogeny of the grasses studied. Among the fossil and living Stipeae examined there appear to be two basic lines of evolution suggested by the lemmatal cell patterns, as well as other anthoecial characteristics. In the *Nassella-Oryzopsis-Stipa* (for example, *Stipa robusta*)



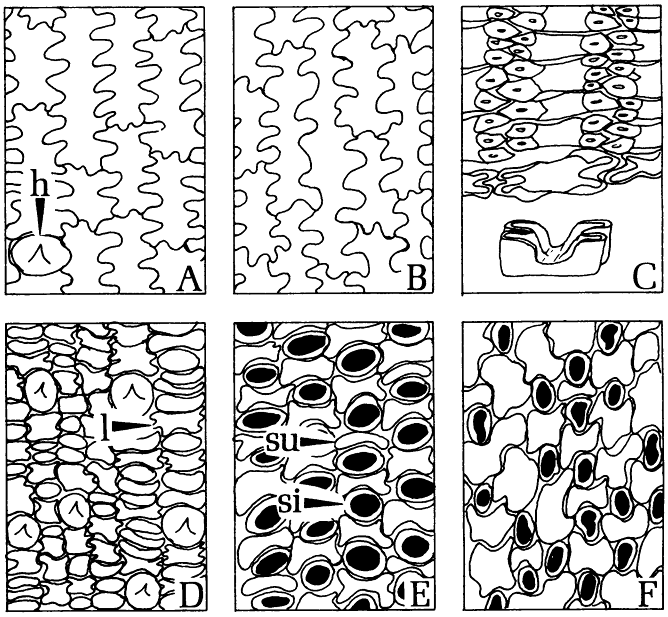


Fig. 1 (left). (A) *Nassella* undescribed sp., lateral view (× 36). (B) *Berriochloa* undescribed sp., lateral view, showing abundant hooks on lemma surface and well-developed palea prow (arrow) (× 20). (C) *Berriochloa minuta* Elias, lateral view. Portions of the lemma surface are obscured by fossilized cuticle (arrows) (× 33). (D) Lemma surface detail of the specimen in (A). Reduced long cells show typical sinuous cell walls (arrows), while the crescent to oval shaped short cells have smooth walls (× 585). (E) Lemma surface detail of specimen in (C). Long cells have well-developed interlocking cell walls (× 585). (F) *Berriochloa maxima* Elias lemma detail showing long cells (× 585). (G) Lemma surface of *Berriochloa brevis*. Long cells show well-developed "buttress" lobes (arrows) adjacent to a hook (× 585). Fig. 2 (above). Lemma epidermal patterns. (A) *Stipa comata* Trin. and Rupr. (B) *Stipa neomexicana* (Thurb.) Scribn. (C) *Piptochaetium stipoides* (Trin. and Rupr.) Hackel. Lower part of figure shows a single long cell in lateral view. (D) *Nassella trichotoma* (Ness) Hackel. (E) *Stipa robusta* (Vasey) Scribn. (F) *Oryzopsis hymenoides* (R. & S.) Ricker (all figures × 255). *l*, Long cell; *h*, hook; *si, su*, short cells, silica and suberin cells, respectively.

line the trend was toward a specialized epidermal pattern in which the long cells are greatly reduced and the short cells (silica and suberized cells or silica-suberized couples) are abundant. This contrasts with the *Berriochloa-Piptochaetium-Stipa* (section *Hesperostipa*) line in which only long cells are present. The reason for the differences in the patterns is unknown, but the fact that these lines have been divergent for a significant period of geologic time is clearly indicated by the patterns of the fossil and living species.

My findings also indicate that species of *Piptochaetium* and North American species of *Stipa* (section *Hesperostipa*) appear to have a common origin in species of the fossil genus *Berriochloa*. However, intermediate forms of Late Pliocene and Pleistocene grasses are not available, and the origin of the characteristic lemma pattern of *Piptochaetium* is unknown. At some time during the late Pliocene or Pleistocene *Stipa* (section *Hesperostipa*) and *Piptochaetium* became generically distinct.

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References and Notes

1. In grasses the flower is normally enclosed by two bracts, the lemma (lower) and palea (upper). In many grasses these floral bracts are indurate at maturity and enclose and protect the caryopsis ("grain"). The lemma and palea devoid of the flower is termed the anthoecium. Only the anthoecia are preserved as fossils.
2. E. W. Berry, *Proc. U.S. Natl. Mus.* **73**, 1 (1929); M. K. Elias, *Univ. Kans. Sci. Bull.* **20**, 333 (1932); A. B. Leonard, *ibid.* **38**, 1393 (1958); E. C. Galbreath, *Trans. Ill. State Acad. Sci.* **67**, 366 (1974).
3. M. K. Elias, *Geol. Soc. Am. Spec. Pap. (Reg. Stud.)* **41**, 1 (1942).
4. M. K. Elias [(*3*); personal communication, 1975] believed that the differences between *Stipidium* and *Berriochloa* were artificial and that these genera would eventually be united. I have recently united the genera (*5*) retaining the genus *Berriochloa* for all fossils previously assigned to *Berriochloa* or *Stipidium*.
5. J. R. Thomasson, thesis, Iowa State University (1976).
6. The tribe Paniceae is a group of predominantly tropical to subtropical grasses. It includes cultivated crops such as millets and sorghums, and weedy grasses known as sandburs, foxtails, and crabgrasses.
7. The tribe Stipeae is a group of grasses widely distributed in temperate, tropical, and subtropical regions of the world. It includes many grasses commonly referred to as needlegrasses, needle-and-thread grasses, and ricegrasses. Many are common constituents of grasslands of North and South America where they are valuable forage grasses.
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11. A detailed report on the systematics of the fossils is in preparation.
12. Epidermal cells of grass leaves and floral bracts are classified as long cells or short cells, the former generally much longer than wide and frequently having sinuous lateral walls, and the latter as wide as or wider than long, measured on the longitudinal axis of the blade or floral bract. Short cells are usually distinguished as either silica cells if a silica-body fills the lumen, or a suberin cell when the walls are impregnated with suberin. In my experience there seems to be little correlation between the pattern of long and short cells on the leaf epidermis and the pattern of long and short cells on the lemma and palea epidermises.
13. G. L. Stebbins, Jr., *Ecol. Monogr.* **17**, 149 (1947); *Taxon* **24**, 91 (1975).
14. D. L. Williams, *J. Biogeogr.* **2**, 75 (1975).
15. L. R. Parodi, *Rev. Mus. La Plata Secc. Bot.* **6**, 213 (1944); *Darwiniana* **7**, 369 (1947); ——— and F. Freiser, *Cienc. Invest.* **1**, 144 (1947); J. I. Valencia and M. Costas, *Bol. Soc. Argent. Bot.* **12**, 167 (1968).
16. The genera *Stipa* and *Piptochaetium* are distinct on the basis of palea characteristics: the former has a smooth palea, while the latter has a grooved and keeled palea into which the edges of the lemma lock. I have examined thousands of specimens of *Berriochloa* and have never seen one with a distinctly grooved and keeled palea, although I have seen some with slight medial depressions. The origin of the groove in modern *Piptochaetium* is unknown.
17. Supported by grant BMS 74-13324 from the National Science Foundation and by the Bessey Microscopy Facility, Iowa State. I thank R. W. Pohl, P. Elsner, J. L. Horner, J. A. Holman, R. J. Zakrewski, and R. M. Hunt for cooperation and assistance. I also thank M. G. Netting and J. H. McAndrews for personal intervention in support of my field studies.

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Lunar Tidal Acceleration Determined from Laser Range Measures

Abstract. *Lunar laser range measures covering the period 1969 to 1976 have been used to determine the anomalous secular acceleration in the mean longitude of the moon, commonly attributed to the effect of tidal friction in the earth. The acceleration determined is −24.6 ± 1.6 arc seconds per century squared, against an atomic time scale, where the uncertainty is the formal standard deviation of the solution. The realistic uncertainty is surely larger, as evidenced by the ensemble of solutions performed with various models and observation sets. The determined value is in good agreement with the conventional value and with several recent determinations by other methods. An attempt to determine the rate of change of the mean distance, essential for separating the tidal effect from a time variation of the gravitational constant, yielded no significant result, because the observations still span too short a time.*

The longitude of the moon shows an acceleration that is not explained satisfactorily by the techniques of classical celestial mechanics. This fact, well known for more than two centuries, continues to provoke both scientific activity and controversy. The question is not only astronomical but geophysical and cosmological as well, since the cause of the acceleration is now commonly thought to be frictional dissipation in the earth, but it will also contain a contribution due to a time variation of the gravitational constant G, if such exists. As we have discussed elsewhere (*1, 2*), there are other possible sources of contamination for a purely geophysical interpretation, but this is beyond the scope of this report.

Since the basic observed fact is an acceleration in longitude, the most obvious technique for studying it is by means of measures of angular position of the moon. In the Taylor's series expansion of the mean longitude L

$$L = L_0 + \dot{L}_0(t - t_0) + \tfrac{1}{2}\ddot{L}_0(t - t_0)^2 + \cdots \qquad (1)$$

the parameter of interest is $\ddot{L} = 2\dot{n}$ (*3*), where n is the "sidereal mean motion" (*4*). This parameter, or rather the correction to the adopted value, has been studied by means of observations of lunar and solar eclipses, equinox passages, meridian transits, and stellar occultations. The currently adopted conventional value of the "tidal" contribution of $\ddot{L}$ is −22.44 arc sec/cy^2 (cy = century); the results of recent studies of angular position observations range from −18 to −42 arc seconds (*5*). One must ask why the disparity is still so large.

One of the basic difficulties in this problem has been the lack of explicit partial derivatives with respect to the mean motion of the lunar orbit, which should be regarded as independent of the customary six Keplerian elements of the orbit. In some studies, the lack has been overcome by application of Kepler's third law

$$a^3n^2 = G(E + M) \qquad (2)$$

relating the mean motion with the mean distance a, the universal gravitational constant G, and the mass $E + M$ of the earth-moon system. The assumption that $G(E + M)$ is constant gives, to first order

$$2\delta\dot{n}/n = -3\delta\dot{a}/a \qquad (3)$$

Thus, derivatives for $\ddot{L}$ can be obtained from the readily available derivatives with respect to the mean distance. Van Flandern's attempt (*6*) to estimate $\dot{G}$ was an early warning signal that this is not sufficient. In that work, an attempt was

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