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U. S. DEPARTMENT OF AGRICULTURE.

DIVISION OF AGROSTOLOGY.

[**Grass and Forage Plant Investigations.**]

THE STRUCTURE OF THE CARYOPSIS OF GRASSES WITH REFERENCE TO THEIR MORPHOLOGY AND CLASSIFICATION.

BY

P. BEVERIDGE KENNEDY, Ph. D.

PREPARED UNDER THE DIRECTION OF F. LAMSON-SCRIBNER, AGROSTOLOGIST.

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LETTER OF TRANSMITTAL.

U. S. DEPARTMENT OF AGRICULTURE,
DIVISION OF AGROSTOLOGY,
Washington, D. C., May 4, 1899.

SIR: I have the honor to transmit herewith and recommend for publication as Bulletin No. 19 of this Division the manuscript of a report on the structure of the caryopsis of grasses, ordinarily termed the grain or seed. This report, prepared by Mr. P. Beveridge Kennedy, by special authorization through the Agrostologist, contains much of histological interest, but is of special value on account of the important facts brought out in the investigations relative to the morphology and classification of grasses. Mr. Kennedy was formerly assistant chemist in Toronto University, Canada, and for the past three years has been studying at Cornell University, devoting special attention to the investigation of grasses.

Respectfully,

F. LAMSON-SCRIBNER,
Agrostologist.

HON. JAMES WILSON,
Secretary of Agriculture.

INTRODUCTION.

The fruits and seeds of plants present characters which are less subject to variation than any of the other organs or parts. In consequence, these characters are of the highest importance in studying the classification and relationships of plants. They are employed in separating the larger groups, and in some cases ordinal characters are based upon them; and within many families the fruit affords the best differential characters for the separation of subtribes, and even genera. To what extent the fruit, or caryopsis, of grasses may be employed in determining the relationships of the various tribes and genera is to some extent indicated in the following paper. Enough is presented to show that the characters possess great value in this connection and clearly emphasize the interest and importance of a knowledge of the structure and morphology of the caryopsis of the different tribes of Gramineæ—a subject here treated for the first time in the English language.

The structure of the fruits of the cereals has been investigated to some extent at a number of the agricultural colleges and experiment stations, but the cultivated grains only represent three of the thirteen tribes of grasses.

F. Lamson-Scribner.

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HISTORICAL REVIEW.

The first writer to mention the fruits of grasses from a morphological point of view was Malphigi,[1] who described the embryos of *Triticum* and *Avena* in 1687. He regarded the scutellum as representing the cotyledon. Nothing further was written concerning the embryo of grasses for a hundred years, when Gaertner[2] described it in 1788. He studied a considerable number of species, especially in regard to the scutellum. The name "scutellum" was first used by him. He regarded the "vitellus" as a transition between the endosperm and the cotyledon. A. L. de Jussieu[3] in describing the grass fruit used the term "lobus" implying the cotyledon.

In the year 1808 Poiteau[4] concluded that the sheath in the embryo, called "vitellus" and "scutellum" by Gaertner, is a true cotyledon. He decided that the epiblast must be the rudiment of a second cotyledon, because of its position opposite to the cotyledon or scutellum. Richard[5] in the same year presented the view that the scutellum originates from the lower part of the radicle, and that therefore the scutellum is a lateral protuberance of the radicle. By imagining the plumule raised in such a manner that it stands at right angles to the long axis of the scutellum, he constructed an homology with the embryos of the *Naiadaceæ*, *Alismaceæ*, *Hydrocharidaceæ*, and *Nymphaceæ*. The word epiblast originated with Richard. He regarded it as a continuation of the root sheath, basing his opinion on a section cut obliquely through the embryo of *Oryza*.

In 1809 Kirbel[6] compared a number of embryos of the grasses in the resting and germinating stages with those of other monocotyledons. He believed that the scutellum represented a cotyledon and that the epiblast was a reduced cotyledon. In another work[7] Kirbel regarded

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[1] Opera omnia. 1687.

[2] De fructibus et seminibus plantarum. 1788.

[3] Genera plantarum secundum ordines naturales disposita. P. 28. 1789.

[4] Mémoire sur l'embryon des Graminées, des Cypéracées et du Nelumbo. 1808.

[5] Analyse des embryons Endorh. on. Monoc. et part de cel. d. Gr. 1808.

[6] Eléments de Physiologie végétable, r. I. 1809.

[7] Examen de la division des végétaux en Endorhizen et Exorhizes. 1810.

the plumule-sheath as belonging to the cotyledon, but in 1815 returned to his former view. Treviranus[1] opposed Richard's view and regarded the scutellum as a cotyledon. He speaks of the scutellum as enlarging itself the length of the seed and taking on a yellowish color, which is certainly not the case. Turpin[2] agreed with Mirbel that the embryo has two cotyledons. According to Cassini[3] the embryo of the grasses is composed of an axis, a cotyledon, one or two radicles, a plumule, and one or two "carnodes." His "cotyledon" is the plumule-sheath, while the "carnode," a name for the scutellum, he regards as a protuberance of the radicle. Raspail[4] compared the fruit and the flower. He believed that there was also an homology between the embryo and the culm. On examining the cotyledon he discovered a large nerve, joining the two nerves of the plumule-sheath at the base. From this he concluded that the scutellum is homologous to the peduncle of the aborted flower in the spikelet and to the sheath of the culm-leaf. He compared the plumule-sheath with the two-nerved palet in the spikelet and to the first leaf of the vegetative bud, and the endosperm to the flowering glumes of the spikelet and to bracts on the culm.

Dr. C. A. Agardh[5] in 1826 compared a longitudinal section of the embryo of *Ruppia* with the grass embryo and fruit, and found a great similarity between them. He regarded the entire endosperm of the grasses as the cotyledon, and the scutellum as a covering of the same. This, however, is impossible, as the scutellum never surrounds the endosperm. Bernhardi[6] believed that a cotyledon must, aside from its function of nourishment, also act as a protective organ to the young leaves. He therefore regarded the plumule-sheath as a cotyledonary-sheath and the scutellum as a cotyledon. Bischoff[7] also believed that the scutellum and epiblast are two cotyledons. He regarded the caryopsis as having an embryo with alternate cotyledons, without however giving any special grounds for this opinion. M. J. Schleiden[8] was the first to study the development of the grass embryo. According to him the scutellum and the plumule-sheath together form the cotyledon. He regards the epiblast as an outgrowth of the cotyledon, since it is connected with the main axis lower down than the cotyledon

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[1] Von der Entwickelung des Embryo und seiner Umhüllungen im Pflanzen-Ei. 1815.

[2] Mémoire sur l'inflorescence des Graminées. Ann. d. Mus. d'hist. Nat. 1819.

[3] L'analyse de l'embryon de Graminées, Jour. de Physique. T. 91. 1820.

[4] Sur la formation de l'embryon dans les Graminées. Ann. des Soc. Natur, Series 1, vol. 4, plates 13–14, 1824, 271–290. 1824.

[5] Über die Eintheilung der Pflanzen nach dem Cotyledon und besonders über den Samen der Monocotyledonen. 1 Nov. Act. C. B. C., T. XIII, P. I. 1856.

[6] Ueber der merkwürdigsten Verschiedenheiten des entwickelten Pflanzenembryo. Linnaea. 1832.

[7] Lehrbuch der Botanik I. 1834.

[8] Einige Blicke auf die Entwickelungsgeschichte des vegetale Organ bei den Phan., Wieg. Archiv. III, I. 1837.

itself. Adrien de Jussieu[1] differed from his father in the interpretation of the parts of the embryo, believing that the scutellum is not a true cotyledon but only a lateral appendage of the axis which resembles one. This view has been held by many up to the present time. Regel[2] considered the plumule-sheath the true cotyledon and the scutellum first as a stipule and again later as a bract from which the plumule arises laterally. In the same year Reisseck[3] advanced the opinion that the plumule-sheath is an axillary bud and that the cotyledon (Samenlappe) is an organ of the aborted terminal bud and the protecting leaf of the plumule, and that the epiblast is united with the cotyledonary-sheath, which is evidently also a part of the cotyledon. Lestiboudois[4] regarded the plumule-sheath as the cotyledon, but considered the scutellum of no significance, because only the former is traversed by fibrovascular bundles, hence resembling two leaves grown together.

Hofmeister[5] interpreted the embryo in different ways, describing the development of *Zea*. He called the scutellum the cotyledon and the plumule-sheath a part of it. A few years later, in another work,[6] he compared the so-called scutellum of the embryos of *Zea* ana *Andropogon sorghum* with the first leafless structures of *Zostera*. Demoor[7] investigated a large number of the fruits of grasses in the mature stage, and also their development. He regarded the scutellum as the true cotyledon of the grasses, and the plumule-sheath not as representing the ligule, but as a sheath of a primordial leaf. This would not, however, correspond to the alternating arrangement of the leaves of grasses, a difficulty which he bridges over by citing that there is no opening of the sheath in *Melica uniflora* because of the growing together of the two margins of the leaf. He admits, however, that he has not been able to observe this. J. C. Agardh[8] speaks of the embryo as sometimes presenting a thalloid form. Schacht[9] considered the scutellum as the cotyledon, the plumule-sheath as the first leaf, and the epiblast a part of the cotyledon.

Hofmeister,[10] writing again concerning the grass embryo, stated: "I still regard the scutellum of the grasses and the analogous structure

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[1] Sur les embryons monocotylédones. Compt. Rend. des Soc. de l'Acad. des Sciences, **9** : 15–31. 1839.

[2] Beobachtungen über den Ursprung der Stipeln. Linnaea, 17. 1843.

[3] Monocotylischer Embryo. Bot. Zeit. 1843.

[4] Phyllotaxie anatomique, Ann. des. sc. naturelles, ser. III, **10** : 15. 1848.

[5] Die Entstehung des Embryo der Phanerogamen. 1849.

[6] Zur Entwickelungsgeschichte des Zostera embryo. 1852.

[7] Note sur l'embryon des Graminées. Bull. de l'Acad. roy. des Sci. de Brux. 1853.

[8] Theoria system. plant. 1858.

[9] Lehrbuch der Anatomie und Physiologie der Gewachse. 2, 1859 und das Mikroscope, 224. 1862.

[10] Neue Beitrage zur Kenntniss der Embryobildung der Phanerogamen Abhand. der königl. sachs. Gesellschaft. d. Wien. 1861.

of *Zostera* as an outgrowth from the axis, and not as a leaf." In this he agrees with Adr. de Jussieu. A. Gris,[1] studying the embryo of *Zea* from a physiological standpoint, also regarded the cotyledon as a lateral expansion of the axis, modified in such a manner as to become the principal absorbing organ of the embryo.

Duchartre[2] stated that the embryo is remarkable in having an oval, flat, or slightly curved, bud-like expansion at its base, called by Gaertner the "scutellum." This organ directly adjoins the endosperm by its dorsal face. In front of it is another shoot, which Richard calls the "blaste." Le Maout and Decaisne[3] regarded the scutellum as a cotyledon, which is often split along its outer face, showing the radicle and plumule. The plumule is conical and composed of one to four primary convolute leaves. They regarded the plumule sheath as the first leaf of the plumule. Sandeen[4] investigated a large number of ripe embryos and concluded that the scutellum is a thallus formation and that the plumule is a protuberance of the axis.

Sachs[5] regarded the scutellum as an outgrowth of the axis beneath the cotyledon and the plumule-sheath as the cotyledon, enveloping the whole plumule like a mantle. Hanstein[6] studied the development of *Brachypodium* from the embryo sac to its maturity. He regarded the scutellum as a leaf and a cotyledon, and both the plumule-sheath and the epiblast as trichomatic projections. This is difficult to imagine. Van Tieghem[7] reviewed the subject, illustrating the parts of the embryos of *Triticum œstivum*, *Hordeum vulgare*, *Avena sativa*, *Phalaris canariensis*, *Zea mays*, and *Andropogon sorghum vulgare*, briefly stating his own objections to the views previously held. He considered that the scutellum and plumule sheath together represent the cotyledon, which has at its opposite side a small protuberance called the lobule or epiblast. Owing to the presence of two vascular bundles in the plumule-sheath, he calls it a double stipule united at the margins, and homologizes the scutellum and plumule sheath with the leaf and ligule.

Hegelmaier[8] discussed the grass embryo from its developmental history, giving excellent figures of *Triticum œstivum*. He also noted the occurrence of secondary roots in *Coix*, *Hordeum*, *Secale*, *Avena*, *Triticum*, and other genera, concluding with Van Tieghem that the

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[1] Recherches anatomiques et physioloques sur la germin. Ann. des Sci. naturelles, ser. 5, **2**: 1864.

[2] Eléments de Botanique. 1867.

[3] Recherches anatomiques et physioloques sur le germin. Ann. des Sci. naturelles, ser. 5, **2**: 1864.

[4] Bidrag till kaenn ed omen om Grasembryots byggnad och Utweckling. Acta Univers, Lundens, 1868.

[5] Lehrbuch der Botanik, 474. 1868. Eng. Trans. and revision by S. H. Vines, 1882.

[6] Die Entwickelung des Keimes der Monocot. and Dicot. Botanis, Abhand, 47. 1870. Taf. 14, figs. 11–21; Taf. 15–18.

[7] Sur les Cotyledons des Graminées. Ann. des Sci. naturelles, series 5, **15**: 723–276. 1872.

[8] Zur Entwickelungsgeschichte monocotylischer Keime, etc. Bot. Zeit. 1874.

scutellum and plumule-sheath together correspond to the cotyledon of the other monocotyledons. A. Stephen Wilson[1] held that the cotyledon of the grasses had not yet been correctly interpreted, and that the morphological interpretation lay in whether the two vascular bundles of the plumule-sheath represent the middle nerves of two leaves or whether they only occur to strengthen the organ. In comparing this with the leaves in the terminal bud of the rhizome of *Agropyron repens* he found a difficulty, owing to the latter being many-nerved. He believed that the scutellum certainly has the function of a cotyledon and is a nourishing organ for the embryo at germination, but whether the plumule-sheath is also a nourishing organ is left in doubt.

Gordon[2] studied the morphology of the inflorescence. He says that the node-like swelling at the base of the plumule-sheath occurs very generally in the grasses. It appears to be a part of the node, but in reality is only a circular swelling at the base of the closed sheath. The proper node lies underneath this swelling. The plumule-sheath must exercise a certain pressure on the axis, and if axillary buds are present this pressure must have a certain influence on the plumule. The author speaks of the well-known organ, which denotes the origin of a branch, and which is looked upon by most morphologists as a two-keeled simple "Vorblatt" (prophyllum), with its back turned toward the main axis. The axillary shoots in *Zea*, *Tripsacum*, *Coix*, and many others make a cavity or groove in the culm, showing that they have developed under pressure of the sheath. The tissue at the base of the culm remains soft and capable of growth for a long time as a basal vegetation point. In other grasses, such as *Arundo* and *Phalaris*, the axillary shoot does not press itself into the culm. In these the growing point breaks through the sheath to the light. In *Arundinaria* the sheath soon dries up and the growing point has nothing to hinder it. Attempting an analogy between the fruit and the spikelet, he concluded that the plumule-sheath represents two leaves grown together. Certain *Gramineæ*, he says, have one or two buds in the axil of the plumule sheath, each with a prophyllum.

Warming[3] regards the scutellum as the cotyledon and the plumule-sheath as an independent leaf, the latter because an internode is occasionally found. Klebs[4] agrees with Van Tieghem. Hackel[5] believes, as does Warming, that the epiblast is a rudimentary second cotyledon.

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[1] On the envelope of the plumule in the grass-embryo. Trans. and Proc. of the Bot. Soc. of Edinburgh. **13**: 457. 1879 (with plate).

[2] Etudes morphologiques sur la famille des Graminees. Revue des Sci. naturelles, Montpellier. 1879.

[3] Handbog i den Systematiske Botanik. Trans. by Potter. 1895.

[4] Beitrage zur Morphologie und Biologie der Keimung. Untersuch aus d. Bot. Institut der Lubingen.

[5] Echte Graser. Engler und Prantl. Pflanzenfamilien, **2**: 1887. 2. Eng. Trans. by Scribner and Southworth. 1890.

Regarding it as a cotyledon explains the peculiar position of the first leaf over the scutellum. Many authors, he says, regard the plumule-sheath as a part of the cotyledon, surely an incorrect idea. Lermer and Holzner[1] in an exhaustive histological treatise on *Hordeum vulgare* describe in detail the different parts of the fruit. They regard the scutellum as a shield-like expansion of the hypocotyl, acting as a special absorption organ, and the plumule as composed of four leaves inclosed in a plumule-sheath, but attempt no interpretation of the latter view.

Bruns[2] has investigated the grass embryo chiefly from a systematic point of view. He describes and figures a large number of genera of each of the tribes. He regards the scutellum as one cotyledon, and the epiblast as a second, much reduced on account of the great development of the former. He considers it of no consequence from a systematic standpoint whether or not the scutellum and the epiblast are regarded as two cotyledons, provided it is granted that they represent two leaves, as the cotyledons are the first two leaves placed together. The plumule sheath is the thickened first leaf of the plumule especially adapted for protecting the young leaves. It has no blade, a common characteristic of the lower leaves of grasses. Schlickum,[3] in comparing the cotyledons of the monocotyledons, says that when the cotyledon has assimilating functions to perform its lamina displays a differentiation into a nutrient portion, the haustor, and a conducting portion, the conductor. In the grasses the conductor is very rudimentary or entirely suppressed, while the scutellum is transformed into the haustor, which bears no resemblance to a foliage leaf. The epiblast is probably an outgrowth of the coleorhiza. When the cotyledon does not emerge above the soil its function is to take up, by means of the haustor, the nutrient substances present in the endosperm, and to protect the rudimentary leaves by the formation of a more or less developed cotyledonary sheath.

Finally, Celakovsky[4] reviews the work of previous investigators and criticises them especially in regard to the homology of the epiblast and plumule-sheath. He believes that the true morphological nature of the parts can only be determined by investigating along many different lines, and if all these lines point toward the same conclusion, then surely it must be the correct one. The writer investigates the fruit according to the four following lines: (1) Ontogeny; (2) taxonomy; (3) anatomy; and (4) progressive and retrogressive metamorphoses. He then attempts to find out where the scutellum and plumule-sheath are joined at the base; where they separate; and whether the plumule-

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[1] Beitrage zur Kenntniss der Gerste. Munchen, 1886. Extract by Brown and Morris Chem. Soc. Jour., vol. 57. 1890.

[2] Der Grasembryo. Flora, **76**: 1892.

[3] Morphologischer und anatomischer Vergleich der Cotyledon und ersten Keimblatter der Keimpflanzen der Monocotyledon. Bibl. botan. Heft. 35. 1896.

[4] Uber den Homologien der Grasembryo. Bot. Zeit., Sept. 1897.

sheath is inserted directly over the scutellum; and, finally, how the insertion of the plumule-sheath becomes separated so far from the scutellum through the elongation of the axis. He also homologizes the grass fruit with *Smilax*, *Potamogeton*, *Ficus elastica*, the mosses, and the leaf of the grasses. He regards the scutellum as the blade of the cotyledon, and as being homologous with the blade of the leaf. Over the scutellum is situated the plumule-sheath which is homologous to the ligule. The epiblast is the blade of an opposite second cotyledon.

SUMMARY.

The most important views of the different authors may be summed up as follows:

1. The scutellum is the cotyledon; the epiblast a second independent leaf; the plumule-sheath a third leaf; while the first true leaf is the fourth lateral appendage of the embryo.—(Malphigi, Mirbel, and Poiteau.)
2. The scutellum and the epiblast together form the cotyledon, the plumule sheath a second leaf, and the first true leaf becomes the third lateral appendage of the embryo.—(Schleiden, Shacht, and Decaisne.)
3. The plumule-sheath represents the cotyledon, the scutellum and epiblast being only expansions of the axis or of the radicle; and the first true leaf then becomes the second lateral appendage of the embryo.—(Richard, Adr. de Jussieu, Lestiboudois, Hofmeister, and Sachs.)
4. The scutellum is the central portion of the cotyledon, the epiblast an opposite appendage of it, and the plumule-sheath an ascending part in the form of a protective organ; the first true leaf then becomes the second lateral appendage of the embryo.—(Gaertner and Mirbel, at a certain time.)
5. The scutellum and the plumule-sheath together represent the cotyledon, and correspond to the blade and ligule of the culm-leaf; the epiblast is a protuberance of the cotyledon on the opposite side.—(Van Tieghem and Klebs.)
6. The sixth view is the same as the fifth, with the exception that the epiblast represents a second cotyledon opposite the scutellum.—(Celakovsky.)
7. The scutellum is one cotyledon and the epiblast is the other, the plumule-sheath being the first leaf of the plumule.—(Bruns.)

GENERAL DESCRIPTION OF THE FRUIT.

The embryo of grasses stands isolated from those of other monocotyledons in possessing two peculiar structures, the *epiblast* and plumule sheath. The following investigations were undertaken to determine the morphological significance and taxonomic value of these structures in the different tribes. Owing to the difficulties met with at the outset in securing a suitable method, the work is not so complete as at first anticipated.[1]

The fruit of the *Gramineæ* was described first by Mirbel under the name "cerium" and rechristened later by Richard "caryopsis."

Its contents at maturity consist largely of endosperm and embryo, the tissues of the nucellus, ovule, and ovary being almost completely displaced. The only remnants of the nucellus which are recognizable in the ripe grain are the empty cells which spring from the funiculus, and the epidermis of the nucellus, which is continuous as a very attenuated layer of cells around both endosperm and embryo. Of the walls of the ovary only the inner one persists as a double layer of cells forming the testa or true coat of seed. Within the nucellus are one to four layers of cells with highly cuticularized walls. In section they are somewhat rectangular in form and constitute the gluten cells which contain the closely packed aleurone grains.

Lying between the starch-containing portions of the endosperm and the embryo is a comparatively thick layer of compressed cells belonging to the scutellum. They are for the purpose of dissolving the starchy material of the endosperm during germination. The endosperm consists of thin-walled cells packed closely with starch granules, embedded in a fine mass of proteid material. These starch-containing cells each possess a nucleus which is not easily recognized.

The embryo is situated laterally and at the base of the seed. It is differentiated into the scutellum, the plumule, the radicle, and frequently the epiblast. The plumule is surrounded by the plumule-sheath, which sometimes has a slit-shaped opening on the side opposite to that of the scutellum. The plumule sheath is composed of a vegetation point and several layers of leaves. The radicle is inclosed in the lower part of the embryo, and at germination, before making its exit, must break through a protective mass of tissue, the coleorhiza, so called because it forms a kind of sheath around the radicle. Secondary radicles frequently occur in the mature and resting embryo. They arise in the axis usually just below the plumule.

The vascular system may be traced down into the primary radicle, and also into the scutellum, plumule-sheath, and plumule.

THE SCUTELLUM.

The name "scutellum" has been given to the cotyledon of the grasses because of its resemblance to a little shield. It has for its object the protection of the plumule and the absorption of nutrient materials from the endosperm.

---

[1] The author wishes to express his thanks to Prof. W. W. Rowlee for many helpful suggestions during the progress of the work; also to Profs. F. Lamson-Scribner and W. J. Beal for much valuable material, and to Prof. F. C. Harrison, of the Ontario Agricultural College, at Guelph, Canada, and to Messrs H. R. Carveth and O. Shantz for aid in the discovery of a method.

Observing a cross section of any embryo, one sees that the scutellum surrounds the plumule like a sheath. In *Zea* (figs. 4 A–F, Pl. I), *Andropogon* (figs. 10 A and B, Pl. II), and others the plumule is almost completely surrounded by the scutellum, so that only a narrow opening may be seen. A longitudinal section of *Andropogon saccharatus* (fig. 9, Pl. II) shows the scutellum so completely surrounding the plumule that it appears as if an epiblast was present. By observing a cross section, however, it is seen that the margins of the scutellum surround the plumule with the exception of a small slit (fig. 10 B, Pl. II). At a point toward the apex of the plumule sheath the scutellum bears a protuberance which projects over the plumule. This is especially distinct in *Lygeum* (fig. 25, Pl. IV), *Lolium* (fig. 75, Pl. VIII), and *Ammophila* (fig. 42, Pl. V). This part has been called the cotyledonary sheath (c. s.) to distinguish it from the plumule-sheath (pl. sh.).

At the base of the scutellum there is another protuberance in many embryos, such as *Avena* (fig. 44, Pl. V), *Triticum* (fig. 69, Pl. VII), *Anthoxanthum* (fig. 29, Pl. IV), *Uniola* (fig. 61, Pl. VII), *Bulbilis* (fig. 58, Pl. VI), and *Beckmannia* (fig. 60, Pl. VI). Sometimes a deep cleft occurs, appearing as a separation of the radicle. In some embryos the scutellum has a distinct sheath and a blade. A striking example of this may be seen in *Avena* (fig. 44, Pl. V), *Spartina* (fig. 53, Pl. VI), and *Zizania* (fig. 22, Pl. III).

The attachment of the scutellum to the axis varies considerably in different embryos. *Desmazeria* (fig. 63, Pl. VII) and *Anthoxanthum odoratum* (fig. 29, Pl. IV) have the attachment directly at the base of the plumule. In others there is a lengthening of the axis with the attachment at the base, leaving a very small proportion of the embryo to represent the hypocotyl: *Zizania* (fig. 22, Pl. III), *Homalocenchrus* (fig. 28, Pl. IV), and *Spartina gracilis* (fig. 53, Pl. VI).

The scutellum has at every point where it comes in contact with the endosperm a layer of peculiar oblong cells called the epithelial layer. Sachs regards it as corresponding to the somewhat similar layer found in the cotyledons of the palms, and to the young epidermis of *Ricinus* and many other seeds. The scutellum, therefore, may be regarded as part of the cotyledon.

THE EPIBLAST.

The peculiar organ, the epiblast of Richard, situated opposite to the scutellum, is not very well understood. Its occurrence in the *Gramineæ* is of much greater frequency than is generally supposed. Warming[1] describes the fruit of the grasses, but does not mention the epiblast. He figures a fruit of *Avena sativa*, but does not represent the epiblast, which is always present and quite distinct. Van Tieghem[2] speaks of the existence of a second cotyledon in a dozen or less of the genera of

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[1] Warming and Potter. 1895.

[2] Comptes Rendus heb. Lean. l'Acad. des Sci. **124** : 1896 and 1897.

the *Gramineæ.* Unlike the scutellum, the epiblast has no vascular system, and on this account much dispute has arisen over its morphological nature. This, however, is no proof against its leaf nature, as there occur many instances of reduced organs without fibrovascular systems.

Although the epiblast is usually very small in comparison with the scutellum, yet there are many grasses in which it reaches a considerable size. *Zizania aquatica* (fig. 22, Pl. III) has a well-marked epiblast extending from the base of the lengthened axis to about the middle of the plumule, or even further.

In the genus *Stipa* there are marked differences in the size of the epiblast in the different species. *S. tenacissima* (fig. 30, Pl. IV) has a very small one; in *S. pennata* it is long and attenuated; while in *S. richardsoni* (fig. 36, Pl. V) and *S. viridula* (figs. 32 and 33, Pl. IV) it is very large and broad. Sometimes the margin of the epiblast is curved or deeply keeled, although in the large majority it is straight. *Homalocenchrus oryzoides* (fig. 28, Pl. IV) has a very large epiblast which greatly resembles the form of the scutellum. It is large and broad at the base and has a shield-like appearance. A small protuberance occurs at the base similar to that in the scutellum.

A fact which seems to indicate that the epiblast has the same morphological value as the scutellum is, that it is inserted on the axis almost at the same height. Even in *Zizania* (fig. 22, Pl. III), where the axis elongates to a great length and the insertion of the scutellum is almost at the base of the embryo, the epiblast is inserted directly opposite.

The absence or presence of the epiblast appears to be fairly constant in the different tribes, and the presence of an epiblast in a tribe where the majority of the genera have none may indicate that it is not in its natural position. The tribes *Andropogoneæ* and *Maydeæ*, to conclude from the genera examined, might be regarded as being without an epiblast. The scutellum almost entirely surrounds the embryo, as may be observed in any of the cross sections figured, more especially among the *Maydeæ*. In the tribe *Zoysieæ* there occur genera without an epiblast, as *Nazia*, *Trachys*, and *Anthephora*, while *Zoysia* has a distinct one. The *Tristegineæ*, to conclude from *Beckera* and *Arundinella*, have no epiblasts. The *Paniceæ* appear to be without an epiblast, the only exception being *Olyra*, which has a very large epiblast covering the plumule. From its great resemblance to the embryos of *Leersia* and *Oryza* it seems probable that it should be placed with them, or should form a separate intermediate tribe. The *Oryzeæ* appear to have a very large epiblast. The *Phalarideæ*, so far as examined, vary, *Anthoxanthum* and *Phalaris* having small epiblasts, while *Ehrharta* has none.

The *Agrostideæ* examined, although varying greatly in their external form, all possess an epiblast. In the large majority it is small, but in some, as in *Stipa*, it is remarkably large, extending the whole length of the plumule. The *Aveneæ* also, so far as examined, all possess an epiblast. It is in the *Chlorideæ* that the most remarkable and varying formations of the embryo are to be found. *Eleusine* (fig. 52 A–D, Pl. VI) has a round nut-like fruit, with a small embryo having a very large epiblast; while *Spartina* (fig. 53, Pl. VI) has a long fruit, with the embryo extending almost the length of the seed, but with no trace of an epiblast. Between these occur the genera *Bulbilis* (fig. 58, Pl. VI), *Leptochloa* (fig. 56, Pl. VI), *Astrebla* (fig. 55, Pl. VI), *Cynodon* (fig. 57, Pl. VI), and *Beckmannia* (fig. 60, Pl. VI), each with an epiblast.

In the *Festuceæ*, a very large percentage of the genera have a well-formed epiblast, but in *Bromus* and some others it is absent. Among the *Hordeæ*, *Secale* (fig. 67, Pl. VII) and *Hordeum* (fig. 35, Pl. IV) are without an epiblast, while in *Lolium* (fig. 70, Pl. VIII) and *Triticum* (fig. 69, Pl. VII) it is present. *Elymus* (fig. 72, Pl. VIII) has a very light projection at the point where the epiblast is usually situated, and might be regarded as a transition stage between those with and those without an epiblast.

Among the *Bambuseæ* only the genera *Arundinaria* (figs. 74, 75, 76, Pl. VIII) and *Bambusa* have been examined. They possess very large broad epiblasts.

It appears, therefore, in most cases that the tribes *Maydeæ*, *Andropogoneæ*, *Zoysieæ*, *Tristegineæ*, and *Paniceæ* are without epiblasts, while in the *Oryzeæ*, *Phalarideæ*, *Aveneæ*, *Chlorideæ*, *Hordeæ*, *Festuceæ*, and perhaps, the *Bambuseæ*, it is usually present.

The following table will show that it is not correct to regard the epiblast as usually wanting in the Gramineæ.

MAYDEÆ.

Without epiblast.	*With epiblast.*
Euchlaena.	
Zea.	
Coix.	
Tripsacum.	

ANDROPOGONEÆ.

*Saccharum.[1]	
Andropogon.	

*SORGHUM.

*Erianthus.	
Apluda	

ZOYSIEÆ.

Perotis.	Zoysia.
*Trachys.	Nazia.
Anthephora.	

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[1] The genera starred (*) are taken from Bruns's work, not examined by the writer.

RISTEGINEÆ.

*Arundinella.
*Beckera.

PANICEÆ.

Paspalum.
Pennisetum.
Chætochloa.
*Panicum.
Tricholæna.
*Pennisetum.
*Berchtoldia (Chaetium).
Cenchrus.

ORYZEÆ.

Oryza.
Zizania.
Homalocenchrus.
Lygeum.
Pharus.[2]

PHALARIDEÆ.

*Ehrharta.

Phalaris.
Anthoxanthum.
Savastana.

AGROSTIDEÆ.

Stipa.
Phleum.
*Polypogon.
Sporobolus.
*Piptatherum.
Calamagrostis.
Eriocoma.
Oryzopsis.
Brachyelytrum.
Ammophila.
Milium.
Chæturus.
*Apera.
Lagurus.
*Aristida.
Cinna.

AVENEÆ.

Avena.
Arrhenatherum.
Danthonia.
Aira.
Holcus.

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[2] Van Tieghem. Ann. Sci. nat. Ser. 5, **15**: 240.

CHLORIDEÆ.

Spartina.

Leptochloa.
Eleusine.
Chloris.
Beckmannia.
Cynodon.
Astrebla.
Bulbilis.

HORDEÆ.

Secale.
Hordeum.
Asperella.

* Nardus.
Lolium.
Triticum.
* Aegilops.
* Lepturus.
Elymus.

FESTUCACEÆ.

* Boissiera.
* Schismus.
Bromus.
Gynerium.

* Echinaria.
Cynosurus.
Festuca.
Leptochloa.
Melica.
Koeleria.
Korycarpus.
Desmazeria.
Dactylis.
Poa.
Panicularia.
* Lamarkia.
* Avellinia.
Briza.
* Brachypodium.
Triodia.

BAMBUSEÆ.

Arundinaria.
* Bambusa.

THE PLUMULE-SHEATH.

This peculiar structure is found in all grasses, completely surrounding and protecting the plumule, with the exception of a small opening or slit toward the apex on the side opposite to the scutellum. At germination the young leaves break through this sheath, which soon afterwards dies down. The plumule-sheath always has two distinct vascular bundles situated laterally and slightly inclined toward the scutellum. Considerable controversy has arisen as to whether this organ is a part of the cotyledon or whether it represents the first true leaf of the embryo. This will be treated of later under the chapter on the homology of the parts. It usually originates directly under the plumule and close to the insertion of the scutellum, although it is widely separated from the scutellum in many grasses. See *Zizania* and *Homalocenchrus* (figs. 22 and 28, Pls. III and IV). Because of its thickness, it is specially adapted for a protective organ.

THE ROOT SYSTEM.

The large majority of the embryos of grasses have only one radicle, situated at the base of the embryo, usually in a vertical position, but sometimes turned obliquely, as in *Oryzopsis* (fig. 38A, Pl. V) and *Stipa richardsonii* (fig. 36, Pl. V), or, again, completely horizontal, as in *Eriocoma* (fig. 34, Pl. IV), *Oryza sativa* (fig. 27, Pl. IV), and *Eleusine* (fig. 52A–D, Pl. VI). In *Homalocenchrus oryzoides* (fig. 28, Pl. IV) it has a slightly upward tendency.

There are, however, embryos with numerous lateral roots. *Triticum æstivum* (fig. 69, Pl. VII) has four lateral roots, two on each side of the scutellum. *Zizania* (fig. 24O–Q, Pl. III) has three, situated directly under the plumule, a long distance from the main radicle. *Coix* (fig. 1, Pl. I) has four radicles, obliquely one above the other on the axis. In the illustration only three are seen, as they are not all in the same plane. *Hordeum vulgare* (figs. 65, 66, G and H, Pl. VII) has eight secondary radicles, three on each side of the scutellum and two in front. On germination the primary radicle is soon outstripped in growth by the secondary ones. Both the primary and secondary ones are surrounded by a compact mass of cells which form the coleorhiza or root-sheath.

Each radicle terminates in a rootcap, the cells of which appear as regular continuations of the rows of cells in the radicle. The rootcap can thus be distinguished from the coleorhiza, in which the cells are very irregular. The rootcap is not connected with the coleorhiza. The former is produced from the embryonic tissue, while the latter is derived from the preembryonic tissue and is connected with the lower part of the scutellum. In dissecting out the embryo the radicle or radicles, with their rootcaps, easily separate from the coleorhiza, leaving the latter at the base of the sockets in the lower part of the scutellum.

LATERAL BUDS.

In a number of genera of the tribe *Hordeæ* there is a lateral bud in the axil of the plumule-sheath: *Hordeum* (fig. 65, Pl. VII), *Triticum* (fig. 69, Pl. VII), *Elymus* (fig. 72, Pl. VIII), and *Secale* (fig. 67, Pl. VII). Bruns regards this as proving that the plumule-sheath must represent a leaf. Similar buds, however, may be found in Polygonum, Rumex, and a large number of plants with axillary stipules. Van Tieghem describes and figures lateral buds in *Avena sativa*, but it was not possible, after making many paraffin sections through different embryos, to discover them. This circumstance is remarkable in that *Avena* belongs to the tribe *Aveneæ*, while all other genera in which lateral buds have been found belong to the tribe *Hordeæ*. Bruns, however, figures and describes a *Bambusa* with a large lateral bud in the axil of the plumule-sheath.

THE FIBRO-VASCULAR SYSTEM.

The fibro-vascular system of the embryos of the *Gramineæ* may be considered under three main divisions, according to the manner and place of insertion of the plumule-sheath on the axis and its connection with the scutellum.

1. The plumule-sheath is inserted on the axis directly above the insertion of the scutellum: *Stipa* (fig. 36, Pl. V), *Phleum* (fig. 41, Pl. V), *Ammophila* (Fig. 42, Pl. V), and perhaps all of the *Agrostideæ*.

An example of this modification occurs in *Stipa viridula* (figs. 32 and 33, Pl. IV). A vascular bundle passes through the entire length of the scutellum. At the insertion of this bundle on the axis two branches are sent off from it which traverse the plumule-sheath (fig. 33, Pl. IV), while the main branch continues into the axis and then descends to the radicle. A little above this insertion numerous small bundles form and run up into the young leaves and vegetation point. As these different bundles are not all in the same plane, it is not possible to obtain a single section showing them. In any transverse section of the plumule, however, the bundles of the plumule-sheath may be seen quite distinctly.

In *Eriocoma cuspidata* (fig. 34, Pl. IV) the bundles ascend from the axis into the plumule-sheath, while in a cross section of *Stipa richardsoni* (fig. 37B, Pl. V), taken below the insertion of the scutellum on the axis, the vascular bundle may be seen entering the radicle. Again, in *Triticum* (fig. 69, Pl. VII) a bundle may be seen entering the first true leaf. *Hordeum* (fig. 65, Pl. VII) shows the bundles passing up into the second true leaf and the vegetation point, while several may be seen branching off from the axis into the secondary radicles. All the genera of the tribes *Agrostideæ* and *Hordeæ*, so far as examined, have this arrangement of their vascular systems.

2. The plumule-sheath is inserted on the axis at some distance from that of the scutellum, with which it is connected by a vascular bundle traversing the axis: *Zizania* (fig. 22, Pl. III) and *Homalocenchrus* (fig. 28, Pl. IV). The embryo of *Zizania aquatica* (figs. 22, 23 A and B, 24 A–T, Pl. III) has a remarkably long axis, which separates the insertion of the plumule-sheath and the scutellum to a very considerable degree. It will be noticed in the longitudinal section (fig. 22, Pl. III) that two vascular bundles traverse the axis, one terminating in the main radicle, while the other curves sharply round and traverses the long linear scutellum. The exceedingly large epiblast is devoid of any vascular system. In the transverse sections (fig. 24 A–T, Pl. III) it is found that in A, a section taken through the apex of the plumule-sheath, the two bundles have joined into one. In B they are beginning to separate, while in C and D they are entirely free. Figure E shows a section through the tip of the first leaf of the plumule, the plumule-sheath with its two widely separated lateral bundles surrounding it. Figures F–L illustrate sections taken through the plumule at different heights, showing the arrangement of the leaves with their bundles. The bundle in

the center of the leaf is always a little larger than the lateral ones. The bundle of the scutellum now appears distinctly in all sections taken through the region of the plumule. N represents a section taken directly underneath the plumule-sheath. The bundles of the sheath have united with those of the leaves and appear very irregular, with a secondary radicle appearing on each side. A little lower down a third secondary radicle is seen on the side of the axis next to the scutellum. The axis now for a considerable distance presents the appearance shown in P and Q, with two distinct, separate, vascular bundles in the center. At the base of the long axis one of these bundles situated nearest to the scutellum joins with the bundle of the latter, as in S, while the other continues down into the main radicle, as in T. This seems to prove conclusively that the plumule-sheath is not an independent leaf, but that it belongs to the scutellum.

There is no difference between this group and the first, represented by the *Agrostideæ*, except that between the insertion of the plumule-sheath and the scutellum there occurs a very long axis representing the first node.

3. The plumule-sheath is inserted on the axis at the base of the plumule, but its fibro-vascular bundles are not directly connected with that of the scutellum: *Zea*, *Coix*, *Pennisetum*, *Paspalum*, *Panicum*, and *Spartina*. *Zea mays* may be taken as typical of this arrangement of the vascular system, as shown by a series of sections from the radicle to the plumule (figs. 3, and 4 A–F, Pl. I). Fig. 4 A represents a cross section through the main, radicle. There are two systems of vessels, consisting of six large ones toward the center and about sixteen smaller ones on the outside, which, along with their conjunctive tissue, make up the central cylinder. Section B, taken somewhat higher up, above the region of coleorhiza shows the axis with its bundles beginning to form round the periphery of the central cylinder, the two systems of vessels remaining the same as in the radicle. The dark portions of the scutellum are sections through the lateral branches of the scutellum bundle. These peripheral bundles widen and come closer and closer to the center until they reach the condition figured in C, where there is an irregular mass of vascular strands and bundles with only a few of the vessels. Immediately above this the bundles arrange themselves round the periphery, leaving only a few in the center, while a vascular strand branches off and penetrates through the cortical parenchyma into the scutellum, where it divides into an ascending and descending branch, as in D. The large vessels have returned to their original position, while the smaller ones have become fewer, and are arranged irregularly nearer the center. At E, a section taken through the upper part of the scutellum, two radicles emerge from the axis to the right. Vascular bundles are found both in the periphery and in the center of the cylinder. The axis now continues in a regular form with its two systems of vessels and bundles arranged in the periphery,

until just below the plumule, where several bundles in the periphery unite on either side and branch off into the plumule-sheath. Soon numerous, bundles form in the center, until the whole axis is completely filled with them. These arrange themselves in a definite manner and run up into the leaves of the plumule.

There is no direct connection between the vascular bundle of the scutellum and those of the plumule-sheath, both originating from the peripheral bundles of the axis separately. The same condition occurs in all the genera of the *Maydeæ*, *Chlorideæ*, *Paniceæ*, and *Andropogoneæ* examined, with slight modifications as to the number and size of the vessels and bundles. This would seem to indicate that these tribes are closely related to one another, although it is not exactly in accordance with Hackel's classification of the tribes with reference to the *Chlorideæ.*

HOMOLOGY OF THE PARTS OF THE EMBRYO.

To what do the scutellum, epiblast, and plumule-sheath correspond; from what have they been developed; and to what parts of the leaf and spikelet of the grasses are they homologous?

The scutellum is at present generally regarded as the cotyledon, corresponding to the single cotyledon characteristic of the group of monocotyledons, but differing from them in not emerging from the caryopsis at germination.

The epiblast has been regarded in various ways by different authors. Bernhardi, Schleiden, Schacht, and, later, Van Tieghem, regard the epiblast as part of the cotyledon. Hanstein concludes that it is merely an insignificant trichomatic projection of the hypocotyl. The majority of writers, however, with Poiteau, Mirbel, and Bruns, regard it as a second rudimentary cotyledon, and in embryos in which it is wanting, look upon it as having become completely aborted.

Van Tieghem[1] in his new classification of the phanerogams based upon the ovule, revised his opinion concerning the epiblast, regarding it as a second rudimentary cotyledon, and explaining its partial or complete abortion as due to the pressure more or less exerted by the seed coat or pericarp upon the embryo. From this and other characters of the integuments and ovules he is led to believe that the *Gramineæ* are in reality dicotyledons, which have accidentally become monocotyledons.

In spite of the fact that there has never been found the slightest trace of a vascular system in the epiblast, yet it seems most reasonable to regard it as a second rudimentary cotyledon. One inclines to this view from the study of the perfectly developed epiblasts of *Homalocenchrus*, *Zizania*, and *Oryza*, where they are inserted on the axis opposite the insertion of the scutellum.

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[1] Comptes Rendus seanc. l'acad. des Sciences, **124**: 1896–97.

The plumule-sheath is, of all the organs of the embryo, the most striking and difficult to explain. Three very different theories are held regarding its interpretation. To the first we attach the names of Hofmeister and Sachs, who regard it as an outgrowth of the so-called hypocotyledonary internode.

The adherents of the second view regard it as an independent leaf belonging to the plumule and next in leaf arrangement to the scutellum. According to this the plumule-sheath, which is directly above the scutellum on the same side of the axis, would not correspond to the distichous arrangement of grass leaves; but if one regards the epiblast as a leaf, i. e., a second cotyledon, then the apparent disagreement is explained and the plumule-sheath becomes the third leaf alternating with the epiblast. Bruns, who is a strong advocate of this view, sees no reason why Hanstein should deny the independent nature of the plumule-sheath because of its origin.

Let us briefly follow the devolopment of *Brachypodium* according to Hanstein's investigations. The young embryo is at first a spherical mass composed of three with sometimes a fourth smaller cell. These cells divide several times in all directions and the embryo takes on a club-shaped form, becoming longer and narrower at the base. This many-celled body is at this time without distinct internal or external differentiation. The lower-most cell, which has now become considerably divided, later goes to form the suspensor, while the two upper cells form the embryo proper. Soon the internal differentiation of the radicle can be seen with its dermatogen, periblem, and plerome. The second stage of development takes place in the external part of the embryo. In the wall there occurs a depression which marks the division of the scutellum from the hypocotyledonary part. The tissue immediately above this depression is the cotyledon, from which a part of the plumule-sheath soon emerges, while that on the lower side forms the vegetation point with its later-developed leaves. The projection on the upper part of the embryo, i. e., on the upper side of the depression, shows again on its upper surface another depression similar to the first, thus forming a second projection. At the same time a projection in the form of a half collar has formed on the lower part below the vegetation point. These two projections stand opposite one another like lips. Finally they grow and their margins unite to form a complete cap over the plumule. The occurrence of a slit in the mature plumule-sheath is in all probability caused by the incomplete junction of the margins of these collar-shaped projections. The tissue above this second depression, which sometimes curves down to a considerable degree protecting the plumule, forms that part of the cotyledon known as the cotyledonary-sheath. Thus the origin of the plumule-sheath indicates that it must be a part of the scutellum. To regard the plumule-sheath as an independent leaf as Bruns has done, one must look upon it as arising from a stem and not from a primordial leaf, which, according to Hanstein's investigations, is evidently the case.

The third view is that the plumule-sheath is a ligule-like growth proceeding from the scutellum as an inseparable part. The existence of an intermediate part between the insertion of the plumule-sheath and that of the scutellum in many embryos, is relied upon by Bernhardi, Bruns and others as positive proof that there can be no connection between these organs. By many authors it has been called an internode, which latter always develops between two leaves and not between two parts of a leaf.

Bruns says that while in *Euchlæna* the two insertion points are near together, it hardly seems plausible in the case of *Spartina*, and especially of *Zizania*, to regard two organs which are so widely separated from one another as the same. The occurrence of a bud in the axil of the plumule-sheath also influences his conclusion that the plumule-sheath must represent a leaf.

From a careful study of the vascular system of the different tribes, together with Hanstein's investigations, one is led to believe with Van Tieghem and Celakovsky that the so-called internode between the plumule-sheath and the scutellum, occurring so distinctly in *Zizania* and *Homaloceuchrus*, and not at all in the genera of the *Agrostideæ*, is nothing but the first unusually lengthened node. The ligule-like growth, the plumule-sheath, is usually inserted directly over the scutellum and the plumule-sheath in the mature fruits of *Zizania*, *Homaloceuchrus*, and the *Chlorideæ*, or as in *Oryza* (according to Bruns and Schlickum) soon after germination.

The vegetative leaf of the grasses is composed of a sheath and blade and a more or less strongly developed ligule inserted at the point of junction of the sheath and blade. The ligule is usually small, without chlorophyll and stomata, and exclusively parenchymatous, but as Duval-Jouve[1] has shown in *Ammophila arenaria*, it attains a length of about 4 centimeters and possesses nerves with chlorophyll and stomata. The ligule thus represents a double sheathing axillary stipule.

Of the three parts of the leaf it is the sheath which develops last, by an intercalary growth, which raises up the blade and ligule.

Comparing the culm leaf with the scutellum and plumule-sheath, the cotyledonary leaf of the embryo, one finds that the latter has no sheath. Its sessile blade, however, elongates to form the scutellum, while the pumule-sheath, which is homologous with the ligule, attains a great size with vascular bundles similar to the ligule of *Ammophila arenaria*. It is provided with two prominent lateral nerves, which later acquire chlorophyll and stomata.

The homology of the parts may in the same manner be carried out in the spikelet. The awn of the floral glume, when present, is regarded as corresponding to the blade of the leaf, and therefore to the scutellum of the embryo. When the awn is inserted on the back of the

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[1] Anatomie de l'arete des Graminees Mem. de l'ac. des Sci. et lettres. Montpellier. 1871.

glume some distance from the apex, that part between the insertion and the apex is regarded as corresponding to the ligule, and, in consequence, to the plumule-sheath. That part of the glume below the insertion of the awn is regarded as the sheath of the leaf, while its analogous structure in the embryo has been arrested in its development.

Colomb,[1] who has investigated the stipules of many plants, also takes up the ligule and sees in it an analogy to the stipules of *Potamogeton* and *Smilax*. Celakovsky[2] makes a comparison between these, adding another plant, *Ficus elastica*. He carries his homology still further to the mosses, believing that the moss capsule is homologous to the cotyledon and the seta or their bases to the hypocotyl.

DETAILED DESCRIPTIONS OF FRUITS.

Tribe MAYDEÆ.

The fruits of the genera of this tribe are large, ellipsoidal or roundish, and inclosed, with the exception of *Zea*, in a hard capsule formed of the glumes or of part of the articulate rachis. They have a very large embryo, with the scutellum almost completely surrounding the plumule.

Coix lachrymæ-jobi L. (figs. 1, 2 A–G, Pl. I). The structure of the embryo of *Coix* resembles that of *Zea mays*, the main difference consisting in the former possessing four lateral radicles. Only three are shown in fig. 1, the fourth and uppermost one not being in the same plane. Fig. 2 A represents a transverse section through the upper part of the plumule, showing the plumule-sheath with its two bundles and the first and second true leaves in their normal position. A section through the base of the plumule (fig. 2 B) shows the plumule-sheath and a small part of the first, true leaf. Within is the axis with its numerous bundles which belong to the leaves of the plumule.

At C is the axis, with its numerous bundles and the plumule-sheath. Some of the bundles in the periphery of the central cylinder unite and branch off into the plumule-sheath on each side. A little lower down, between the insertion of the plumule-sheath and that of the scutellum the axis appears with its numerous bundles arranged in the periphery of the central cylinder (fig. 2 D). Fig. 2 E shows the scutellum inserted on the axis by its broad, fibrovascular bundle, at the same time cutting through the first lateral radicle on the opposite side. A number of ducts are scattered here and there in the axis. The axis terminates in the lowermost radicle, the central cylinder having six distinct ducts or vessels. Fig. 2 F shows a section through the upper part of the lowermost radicle and one of the lateral radicles, while G represents a section through the lowermost radicle. Each radicle is provided with a root-cap while the coleorhiza surrounds them all. The

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[1] Recherches sur les stipules. Ann. des Sci. nat. Ser. 6, **1**: 19. 1887.

[2] Ueber die Homologien des Grasembryo. Bot. Zeit., Sept., 1897.

scutellum entirely surrounds the remainder of the embryo, as may be seen in cross section or in the longitudinal section (fig. 1). There does not appear to be such a direct connection between the vascular bundle of the scutellum and those of the plumule-sheath, as in *Zizania* (fig. 22, Pl. III), *Homalocenchrus* (fig. 28, Pl. IV), and other embryos. The vascular bundle of the scutellum, as in the other genera of the *Maydeæ*, branches into two, one traversing the upper and the other the lower part of the scutellum, and these again sending off lateral branches. The leaves of the plumule are arranged as in all grass embryos.

Zea mays L. (figs. 3, 4 A–F, Pl. I).—The vascular system of *Zea* has already been described. The general structure of the embryo differs but little from that of *Coix*. Instead of four large lateral radicles it has one large main radicle (fig. 4 A) and two smaller secondary ones at the insertion of the scutellum bundle on the axis. The scutellum surrounds the remainder of the embryo like a mantle, the margins almost coming together, but separated by a long, narrow groove (figs. D and E). There is a deep cleft between the base of the scutellum and the coleorhiza (fig. 3).

Tripsacum dactyloides L. (figs. 5, 6, 7, A–B, Pl. I).—The embryo of *Tripsacum* is very similar to that of *Zea* and *Coix*, except that it has only one radicle. The axis is remarkably long and consists of a number of vascular bundles, as in *Coix*. About halfway down the axis the bundles in the periphery increase toward the center, presenting the same condition as in *Coix* and *Zea*, again returning to the periphery and disappearing as they approach the radicle. The insertion of the scutellum-bundle is not as in *Coix*, *Zea*, and *Euchlæna* at some distance from the plumule but directly under it, where the plumule-sheath also branches off (fig. 6). The scutellum-bundle soon after leaving the axis divides, one branch traversing the lower, and the other the upper part of the scutellum, while these in turn have lateral branches (fig. 6). Aside from these bundles connected with the vascular system there are conducting vessels running irregularly through the scutellum, apparently nourishing organs for the plumule and radicle, as they can be traced to be directly connected through the epithelial layer with the other parts of the embryo (fig. 6).

Euchlæna mexicana Schrad. (fig. 8, Pl. II).—The structure of the embryo of *Euchlæna* is almost identical with that of *Zea mays*, except that it has no secondary radicles and the insertion of the scutellum-bundle is at some distance from the plumule.

Tribe ANDROPOGONEÆ.

The fruits of the tribe *Andropogoneæ* have an embryo which is usually about half the size of the fruit itself. As in the *Maydeæ*, the scutellum almost completely surrounds the remainder of the embryo. By comparing the embryo of *Andropogon* (fig. 9, Pl. II) with *Zea* (fig. 3, Pl. I) one notices a striking similarity. The scutellum-bundle is inserted on the axis at some distance from the plumule, as in the majority of the *Maydeæ*.

Andropogon saccharatus (fig. 9, 10, A–C Pl. II).—The scutellum almost surrounds the plumule. The projection appearing in fig. 9 like an epiblast is only a longitudinal section through one of the margins of the scutellum. The scutellum-bundle is inserted on the axis at some distance from the plumule, while directly under the plumule two bundles branch off into the plumule-sheath. Fig. 10 A shows a section through the plumule with its plumule-sheath and bundles of the first true leaf, while fig. 10 B represents a section taken through the axis between the plumule and the insertion of the scutellum-bundle. Only one radicle is present with a large vessel in the center and five smaller ones around it in the central cylinder (fig. 10 C). There is a deep groove between the scutellum and the coleorhiza.

Apluda cristata (figs. 11, 12, Pl. II).—The embryo of *Apluda cristata* resembles those of the *Maydeæ* and *Chlorideæ*. There is no epiblast. The radicle appears as in fig. 12, with one large vessel and six smaller ones in the central cylinder. This arrangement continues through the axis until near the insertion of the scutellum, where vascular bundles appear. These continue through the lengthened node as far as the base of the plumule, where they send off branches into the plumule-sheath. The ring around the radicle in fig. 12 represents a cross section through the coleorhiza.

Tribe ZOYSIEÆ.

The *Zoysieæ* resemble on the one hand the *Andropogoneæ*, through *Trachys*, *Anthephora* (fig. 13 A–E, 1 Pl. II), and *Perotis* (fig. 15 A–D), and on the other hand *Oryzeæ* through *Zoysia* (fig. 14 A–D) and *Nazia*. Bruns, in a list of genera, represents *Nazia* without an epiblast, while in his figures he represents it with an epiblast, both in longitudinal and transverse sections. The scutellum in *Anthephora* and *Perotis* is inserted at some distance from the plumule, while in *Zoysia* it is inserted directly under it. The radicle of *Zoysia* is also curved in a horizontal direction like *Oryza*.

Tribe TRISTEGINEÆ.

Unfortunately no representatives of this tribe could be secured. Bruns, however, who has investigated the fruits of *Beckera* and *Arundinella*, found them to be without an epiblast, and similar to the *Zoysieæ*.

Tribe PANICEÆ.

The general appearance of the fruits of the *Paniceæ* is similar to those of *Andropogoneæ*. They are, with one exception, without an epiblast, and have the scutellum-bundle inserted at some distance from the plumule. *Olyra* is the only genus which has an epiblast. It is described and figured by Bruns, and differs in every respect from the other *Paniceæ*. The scutellum is broader than long, while the plumule is covered by a very large epiblast. A peculiarity mentioned by Bruns is that the radicle is hollowed out. Owing to the general appearance of the fruit and embryo, with its large epiblast and the insertion of the scutellum-bundle, also the fact that the flower is monœcious, would seem to indicate that it does not belong to the *Paniceæ*. It might, perhaps, be placed with the *Oryzeæ* or form an intermediate tribe with *Zoysia* between the *Paniceæ* and *Oryzeæ*.

Pennisetum spicatum (figs. 16, 17, 18, Pl. II).—The fruit of *Pennisetum* has a very large embryo. The scutellum surrounds the remainder of the embryo, although not to such an extent as in the *Andropogoneæ* and *Maydeæ*. The projection opposite the scutellum in fig. 16 is not an epiblast, but a longitudinal section through the margin of the scutellum. A single large radicle is present, which consists of one large vessel in the center and six small ones surrounding it in the central cylinder (fig. 18). The ring around the radicle represents the coleorhiza with its attachment to the scutellum. Fig. 17 represents a cross section through the plumule, showing the scutellum with its bundle and the plumule-sheath with its two lateral bundles. Within is the first true leaf. The scutellum-bundle is inserted on the axis at some distance from the plumule (fig. 18).

Chætochloa macrochæta (fig. 19, Pl. III).—The embryo of this nut-like fruit resembles in the main other *Paniceæ*. The insertion of the scutellum-bundle is, however, somewhat closer to the plumule. A deep cleft or groove is present between the scutellum and coleorhiza.

Paspalum pubiflorum glabrum (figs. 20, 21, Pl. III).—The embryo of *Paspalum* resembles that of *Pennisetum*, although much smaller. It possesses a large radicle, and its scutellum-bundle is inserted at some distance from the plumule.

Tribe ORYZEÆ.

To this tribe belong, among others, the genera *Homalocenchrus*, *Zizania*, and *Oryza*. Great variation occurs in the size and formation of the fruits. The embryo is usually small compared with the amount of endosperm, but in *Zizania* it attains a considerable size. All the genera belonging to this tribe have a well-marked epiblast.

Zizania aquatica (figs. 22, 23 A–B, 24 A–T, Pl. III) (see p. 21).—The fruit of *Zizania* is long and linear, with an epiblast which reaches three-quarters the length of the whole fruit. Figs 23 A and B show the relative size of embryo and endosperm; A through the plumule, and B through the axis or lengthened node. Figs. 24 A–T represent a series of sections through the embryo from the apex of the plumule-sheath to the main radicle. A and B show the two vascular bundles of the plumule-sheath, which at this point are united into one. At C and D they have become separated, while at E the plumule-sheath appears as a complete ring, inclosing the upper part of the first leaf. The opening in the plumule-sheath on the side opposite to the scutellum now appears for a short distance as shown at G. At H, I, and J it is again closed, and within is seen the arrangement of the leaves of the plumule. K shows the first appearance of the epiblast, while at M it has increased in size. Within the plumule-sheath and first leaf one sees the axis with its bundles which belong to the remaining leaves of the plumule. Immediately below the plumule are three secondary radicles represented in N and O. The embryo for a considerable distance presents a form similar to that shown at P. The vascular system in the region of the secondary radicles presents a confused mass, but here it consists of two regular strands which course the lengthened node. As they approach the insertion of the scutellum the inner one becomes larger until it unites with the bundle of the scutellum. R shows the attachment of the epiblast to the axis, the division being marked by a dotted line, while T is a section through the main radicle surrounded by its coleorhiza.

Homalocenchrus oryzoides (fig. 28, Pl. IV).—The fruits of *Homalocenchrus*, although much smaller and of a different form from that of *Zizania*, yet in the main possess the same structural characters of the embryo.

Lygeum spartum (figs. 25, 26 A–E, Pl. IV).—The embryo of *Lygeum* differs from the other genera of the *Oryzeæ* examined in having a very small epiblast. The insertion of the scutellum-bundle occurs directly beneath the plumule. Also at this point branches are sent off into the plumule-sheath (fig. 26 B). The radicle is here lengthened out to a considerable extent. Lateral roots also arise from the node, as in fig. 26 C and D. Fig. 26 E shows a section through the main radicle, while 26 C shows parts of the secondary radicles and the base of the epiblast.

Oryza sativa (fig. 27, Pl. IV).—Compared with the amount of endosperm, *Oryza* has a very small embryo. The epiblast is large and broad at the base. As in *Lygeum*, the insertion of the scutellum is at the base of the plumule. The large radicle is directed obliquely outward.

Tribe PHALARIDEÆ.

Of the *Phalarideæ* only *Phalaris* and *Anthoxanthum* (fig. 29, Pl. IV) were examined. These much resemble the *Agrostideæ*, having a small epiblast and a straight radicle. The scutellum-bundle is inserted at the base of the plumule-sheath.

Tribe AGROSTIDEÆ.

The *Agrostideæ* may be characterized as fruits with small embryos, always with an epiblast, which, however, varies greatly in size. The scutellum-bundle is inserted on the axis at the base of the plumule. Here it branches to the right and left, running up into the plumule-sheath. The short axis terminates in a single radicle. Among the peculiarities noticed in this tribe is the genus *Stipa*. *Stipa pennata* has a well-marked epiblast more than half the length of the plumule, while *S. tenacissima* (figs. 30 and 31, Pl. IV) has a very small epiblast. In fig. 31 the opening of the plumule-sheath is apparent. In *Stipa richardsoni* (figs. 36 and 37 A and B, Pl. V) the epiblast extends more than half the length of the plumule, and the radicle is directed obliquely outward. Although *S. viridula* (figs. 32 and 33, Pl. IV) has a very small fruit, yet its embryo has proportionately the largest epiblast.

Eriocoma cuspidata (figs. 34 and 35, Pl. IV).—The fruit of *Eriocoma* resembles that of *Oryzopsis*, but has a very large epiblast which extends the whole length of the plumule. The scutellum differs from *Oryzopsis* in having a groove at its base. This character, together with the long, densely hairy, flowering glumes, would warrant its being placed as a separate genus *Eriocoma*, which is regarded as a subgenus by Hackel.

Oryzopsis micrantha (figs. 38 A and B, Pl. V), *Phleum pratense* (fig. 41, Pl. V), *Cinna arundinacea* (figs. 39 and 40, Pl. V), and *Brachyelytrum erectum* (fig. 43, Pl. V) all have a well-marked epiblast. The last named can easily be recognized by a long, pointed projection proceeding from the pericarp. This projection contains no starch, and its presence is remarkable from the fact that it is the only fruit in which such a structure has been found. *Ammophila arenaria* (fig. 42, Pl. V) presents a peculiar appearance. Its cotyledonary sheath extends down to the apex of the plumule. The scutellum also branches into three in the upper part.

Tribe AVENEÆ.

The *Aveneæ* resemble the *Hordeæ* in the structure of fruits. The embryo is usually small compared with the amount of endosperm. Lateral roots occur in *Avena*. The scutellum-bundle is inserted at the base of the plumule and continues down into the axis in the form of a loop.

Avena sativa (figs. 44, 45, 46 A–B, 47 A–G, 48, Pls. V and VI).—Fig. 47 A–G, Pl. V, represents a series of transverse sections through the embryo from the plumule to the radicles. At A one sees the peculiar shape of the scutellum, with its vascular bundle, while within is the plumule-sheath, with its bundles, inclosing the first true leaf. B represents a section taken somewhat lower down in the plumule and shows the position of the second leaf directly opposed to the first. The scutellum-bundle branches at the base of the plumule, as may be seen at C, to form the bundles of the plumule-sheath. Part of the plumule-sheath is still present, while within is the axis with the first leaf and its bundles just beginning to differentiate. Figs. D, E, and F show the axis, and the epiblast which becomes larger toward the base. At E only one radicle is present while at F there are three. G shows the position of the four radicles. The main radicle is in the center with one on each side to the right and left, and a fourth smaller one in front.

A longitudinal section of this small radicle may be seen in fig. 48, Pl. VI. The scutellum-bundle forms a loop in the axis as in fig. 48, a strand branching off from it forms the central bundle of the first true leaf. Fig. 45, Pl. V, represents a section facing the embryo. The main radicle with its two lateral radicles to the right and left are all surrounded by a coleorhiza. Figs. 44 and 46 A and B, Pl. V, represent longitudinal and transverse sections through the whole fruit showing the relative size of endosperm to embryo.

Holcus lanatus (fig. 51, Pl. VI.), *Arrhenatherum elatius* (fig. 49), and *Danthonia spicata* (fig. 50) all have a small epiblast and a single terminal radicle with the scutellum-bundle inserted directly under the plumule.

Tribe CHLORIDEÆ.

The *Chlorideæ*, according to the characters of their embryos, are more closely allied to the *Andropogoneæ* than to the *Aveneæ* and *Festuceæ*, with which they are placed in Hackel's classification. The fruit varies considerably both in regard to its form and the structure of the embryo. There is a spherical nut-like fruit, as in *Eleusine* (fig. 52 A–D, Pl. VI), with a well-marked epiblast, and a long linear fruit with an embryo more than half the size of the fruit itself and without an epiblast, as in *Spartina gracilis* (fig. 53). The scutellum is inserted on the axis at some distance from the plumule.

Eleusine coracana (fig. 52 A–D, Pl. VI).—This peculiar nut-like fruit has an embryo with a very large epiblast. The radicle is in a horizontal direction, while a deep groove is present between the scutellum and coleorhiza. The insertion of the scutellum-bundle is close to the base of the plumule, while the axis between the plumule and radicle is very short. Fig. 52 A represents a longitudinal section through the embryo, while at B we see the plumule with the large epiblast protecting it.

Spartina gracilis figs. 55, 54 A–C, Pl. VI).—In contrast to *Eleusine* it has a long linear fruit with an embryo reaching almost its whole length. The general appearance of the embryo reminds one of *Zizania aquatica*, as the insertion of the scutellum is a considerable distance from the plumule-sheath. One single vascular strand courses the lengthened node until it sends off a branch to the scutellum, and then continues down into the very small radicle. Fig. 54 A, B, C show sections through the radicle, lengthened node, and plumule, respectively. It is a noteworthy fact that this is the only genus of the *Chlorideæ* examined which does not have an epiblast.

Astrebla pectinata (fig. 55, Pl. VI).—The embryo of *Astrebla* is very large, with a very small epiblast. A deep groove is present between the scutellum and the coleorhiza. The scutellum-bundle is inserted on the axis at some distance from the plumule. The axis terminates in a single radicle, which preserves its root structure until just before it reaches the insertion of the scutellum, where vascular bundles appear.

Beckmannia erucæformis (fig. 60, Pl. VI), *Bulbilis dactyloides* (figs. 58 and 59, Pl. VI), and *Leptochloa imbricata* (fig. 56, Pl. VI) have about the same characteristics.

Tribe FESTUCEÆ.

The embryo of the *Festuceæ* is usually small. There is, according to Bruns, great variation in the presence and absence of an epiblast in this tribe.

Uniola latifolia (fig. 61, Pl. VII).—A broad epiblast reaches about half the length of the plumule. The scutellum-bundle is inserted on the axis at some distance from the plumule, while the single radicle is turned obliquely outwards.

Desmazeria sicula (fig. 63, Pl. VII), *Cynosurus cristatus* (fig. 64), and *Panicularia aquatica* (fig. 62, Pl. VII) all have the epiblast well marked. The scutellum-bundle differs from that of *Uniola* in being inserted directly at the base of the plumule. The axis terminates in a single radicle.

Tribe HORDEÆ.

The tribe *Hordeæ* may be characterized as having large fruits. The embryo usually has several radicles and a lateral bud in the axil of the plumule-sheath. A transition seems to take place between those without an epiblast, as in Hordeum (fig. 65, Pl. VII), and those with a distinctly formed epiblast as in *Triticum* (fig. 69, Pl. VII).

Hordeum vulgare (fig. 65, 66 A–H, Pl. VII). The fruit of *Hordeum vulgare* has many peculiarities not found in other grasses. There are two, and in some parts three, layers of gluten cells, while in nearly all grass fruits there is only one. This embryo often has, besides its main radicle, eight secondary ones, three on each side of the scutellum and two in front. In the axil of the plumule-sheath next the scutellum there is a large lateral bud (see p. 20). By examining figs. A–F it will be seen that the scutellum-bundle is composed of two strands which unite just before their insertion on the axis. The scutellum is inserted on the axis at the base of the plumule, a secondary radicle also emerging from it at this point, thus making the axis very short. At fig. 65 the bundles may be seen which belong to the first and second leaves and the vegetation point. Those of the plumule-sheath not being in the same plane are not represented. A transverse section through the upper part of the plumule (fig. 66) shows the opening in the sheath opposite to the scutellum and the two bundles situated laterally. Within is the upper part of the first true leaf. The scutellum shows a peculiar groove on its convex side next to the endosperm (fig. 66, A, B).

B shows a similar condition a little lower down through the plumule. At C and D the position of the first leaf opposite to the plumule-sheath, the second opposite the first, and the third opposite the second, according to the true distichous arrangement of all grass leaves may be noted.

E shows a section taken at the base of the plumule with the bundles in the axis which belong to the leaves of the plumule, also the two bundles of the disappearing plumule-sheath. At F the scutellum bundles are inserted on the axis. On the opposite side are two secondary radicles in the center of the bundles of the axis, while to the right and left appear the origin of the bundles of the plumule-sheath. At C the scutellum-bundles are no longer present, while three secondary radicles emerge from the axis. Four of the secondary radicles may be seen at H with the axis continuing down to form the main radicle. These radicles are all provided with a root-cap and surrounded by the coleorhiza. Although no epiblast is found here yet there is a slight prominence which might indicate its abortion.

Secale montanum (figs. 67, 68 A and B, Pl. VII).—The structure of the fruit of *Secale* resembles that of *Hordeum vulgare.* There is however only one secondary radicle. Not even a trace of an epiblast can be seen. The coleorhiza surrounds both radicles, forming a deep groove between them. At the base of the plumule-sheath next to the scutellum there is a lateral bud. The scutellum-bundle consists of a single strand, which is inserted on the axis almost directly at the base of the plumule. At this point branches are sent off into the plumule-sheath. The bundles in the axis belong to the leaves of the plumule while the axis continues down into the main radicle, a branch being sent off to the secondary radicle. Fig. 68 B represents a transverse section through the upper part of the plumule and A through the main and secondary radicles.

Elymus virginicus (figs. 72 and 73, Pl. VIII).—The fruit of *Elymus* has a very small embryo at the base of a long fruit. Although the epiblast is not present yet there is a slight elevation which might be regarded as a remnant of it. The scutellum-bundle consists of a single strand which curves around to the base of the plumule where it divides into three branches, two of them going into the plumule-sheath and the other continuing down into the axis and single radicle. A lateral bud is present in the axil of the plumule-sheath. Fig. 73 represents a transverse section through the upper part of the plumule.

Lolium rigidum (figs. 70, 71 A–C, Pl. VIII).—The embryo of *Lolium* resembles *Secale montanum* with only one large radicle. A lateral bud is present in the axil of the plumule-sheath.

Triticum æstivum (fig. 69, Pl. VII).—The fruit of *Triticum æstivum* has been so frequently described by previous writers that it is not necessary to treat it at length here. An excellent treatise by Bessey is to be found in Bull. 32 of the Nebraska Agr. Exp. Station, 1894. Its embryo has a small epiblast, a main radicle, and two secondary ones situated in front to the right and left. There is a prominent lateral bud in the axil of the plumule-sheath. In all other respects it resembles the tribe *Hordeæ.*

Tribe BAMBUSEÆ.

A small plant of *Arundinaria falcata* bloomed in the Cornell nursery during the summer of 1898. About a dozen fruits were secured and sections of the embryo made.

The fruit is oval and is covered by a pericarp, which easily separates from the endosperm and embryo. The embryo is small, with its scutellum almost completely surrounding the plumule (fig. 74, Pl. VIII). The vascular bundle traversing it is branched in all directions, as shown in any of the transverse sections (fig. 76 A–J, Pl. VIII).

The plumule-sheath differs from all other fruits of the *Gramineæ* investigated in having five vascular bundles instead of two. At its apex there is a well-marked slit or opening and only two vascular bunches (fig. 76 C). Figs. 76 D, E, F show the position of the five vascular bundles inclined toward the exterior side of the embryo.

The leaves have seven vascular bundles and are arranged as in all grass embryos (fig. 76 E). The epiblast is large and broad, but does not extend far up on the plumule. Toward the base it is rectangular in cross section (fig. 76 G, H). The axis terminates in one large radicle (fig. 76 K).

RELATIONSHIP AND SYSTEMATIC CONNECTION OF THE TRIBES.

Botanists disagree very generally as to which are the most primitive tribes of the grasses. The three great authorities on the subject are Hackel,[1] Bentham,[2] and Warming.[3] Their classifications are as follows:

BENTHAM'S CLASSIFICATION.

A. Panicaceæ.

Tribe I. Paniceæ.
II. Maydeæ.
III. Oryzeæ.
IV. Tristegineæ.
V. Zoysieæ.
VI. Andropogoneæ.

B. Poaceæ.

Tribe VII. Phalarideæ.
VIII. Agrostideæ.
IX. Isachneæ.
X. Aveneæ.
XI. Chlorideæ.
XII. Festuceæ.
XIII. Hordeæ.
XIV. Bambuseæ

HACKEL'S CLASSIFICATION.

A. Panicaceæ.

Tribe I. Maydeæ.
II. Andropogoneæ.
III. Zoysieæ.
IV. Tristegineæ.
V. Paniceæ.
VI. Oryzeæ.

B. Poaceæ.

Tribe VII. Phalarideæ.
VIII. Agrostideæ.
IX. Aveneæ.
X. Chlorideæ.
XI. Festuceæ.
XII. Hordeæ.
XIII. Bambuseæ.

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[1] Hackel, E. Echte Græser. Engler and Prantl, Pflanzenfamilien, 2^2: 2. Eng. trans. by Scribner and Southworth, 1890.

[2] Bentham, Geo. "Notes on Gramineæ," Jour. of the Linn. Soc., **19**: 14–134, 1881–82.

[3] Warming, E., and Potter, C., Systematic Botany.

WARMING'S CLASSIFICATION.

Tribe I. Bambuseæ.
II. Oryzeæ.
III. Maydeæ.
IV. Andropogoneæ.
V. Festuceæ.
VI. Aveneæ.
Tribe VII. Agrostideæ.
VIII. Phalarideæ.
IX. Chlorideæ.
X. Paniceæ.
XI. Hordeæ.

It will be noticed that Hackel's arrangement is in the main similar to that of Bentham, while Warming's varies, omitting the tribes *Zoysieæ* and *Tristegineæ*. Bentham, on the one hand, regards the tribes *Paniceæ*, *Maydeæ*, and *Oryzeæ*, while on the other, Hackel places the *Maydeæ*, *Andropogoneæ*, and *Zoysieæ* as the most primitive of the grasses. Warming, however, presents an entirely different view, and regards the *Bambuseæ* and *Oryzeæ* as the most primitive.

This great difference of opinion is probably due to the fact that the grasses have been largely studied from the basis of only a single character. Hackel[1] claims to have discovered the magic spell by which all difficulties must come to an end in regard to the arrangement of the genera of the *Andropogoneæ*, but it is to be doubted whether the same can be said of his arrangement of the tribes. The *Andropogoneæ* together with the *Maydeæ*, *Paniceæ*, *Tristegineæ*, and *Zoysieæ* without doubt represent a very natural group of the *Gramineæ*, but it is a question whether they are the most primitive. If one studies the *Andropogoneæ* from the standpoint of their resemblance to other Monocotyledons one is unable to find the slightest trace of such resemblances in any of the genera, while among the *Bambuseæ* and *Oryzeæ* there are many similarities.

The *Bambuseæ* are characterized as large, often tree-like, grasses, with woody, rarely herbaceous culms. The leaves are broad, sometimes compound and usually petioled. There are from three to six, or many, stamens while the prevailing number in the other *Gramineæ* is two or three. Usually three remarkably large lodicules[2] are present on the rhachilla. There is great variation in the structure and in the form of the fruit. Both Munro[3] and Hackel[4] use fruit characters to divide the different genera into sections. They may be classified as the berry-bearing and the true bamboos, the latter with linear or oblong-linear fruits, like those of *Avena* and *Triticum*, with a distinct furrow down one side and the scutellum visible below.

In the berry-bearing bamboos the caryopsis appears to be contained in an envelope somewhat analogous to the sac or perigynium which incloses the seed of *Carex*. In *Melocanna bambusoides* this covering

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[1] Hackel, E., Andropogoneæ. De Candolle's Monographie Phaner.

[2] Rowlee, W. W. The Morphological Significance of the Lodicules of Grasses. Bot. Gaz. **25**: 199–203. 1898.

[3] Munro, Memoir on Bambuseæ. Trans. of the Linn. Soc. XXVI:

[4] Hackel, E., Echte Græser. Engler and Prantl, Pflanzenfamilien, II^{2}: p. 92. Eng. trans. by Scribner and Southworth.

becomes very fleshy and the fruit attains the size of a large pear. *Schizostachyum acutiflorum* has very curious bundles of hairs on the scutellum, and the pericarp of the oblong fruit is quite loose and rugose. Some of the genera of the section *Triglosseæ* approach very closely in the structure of the spikelet the tribe *Paniceæ.*

The *Oryzeæ* may be compared with the *Bambuseæ.* In regard to their leaves there is a great variety of forms, from broad, ovate, petiolate leaves in *Pharus*, to long, linear ones in *Zizania*, and short, narrow leaves rounded at the apex in *Hydrochloa.* There is also great variation in the inflorescence. In some of the genera a number of bracts are arranged spirally around the main axis, while in others the inflorescence is inclosed in a spathiform envelope. The normal number of stamens is six, although they vary from one to eight. The pistil usually branches into two plumose stigmas, with occasionally a three-branched style, as in *Pharus.* The lodicules vary from 2 to 3. There are long, linear fruits, as in *Pharus*, and oblong-linear fruits, as in *Oryza.* The *Oryzeæ* therefore resemble the *Bambuseæ* in the following respects: (1) They show great variation in the structure of their fruit and spikelet. (2) Both have remarkably large epiblasts. (3) Some genera have the same number of lodicules. (4) *Pharus* has a style with three stigmas. (5) Many of the genera have broad petiolate leaves and transitions between these to linear ones. (6) They have to a great extent the same geographical distribution, the larger number of the genera being indigenous to tropical America. It would appear therefore that the *Oryzeæ* are closely related to the *Bambuseæ*, and that together they represent the most primitive of the grasses, thus bringing them nearer to the other Monocotyledons (e. g., *Palmaceæ*). So far as it has been observed there appears to be no similarity between the *Bambuseæ* and *Hordeæ*, although they are looked upon by both Bentham and Hackel as being closely allied.

The *Zoysieæ*, *Tristegineæ*, *Andropogoneæ*, *Maydeæ*, and *Paniceæ*, both according to the characters of the fruit and those of the inflorescence, according to Hackel's classification, form another natural group, joined to the *Oryzeæ* through the *Zoysieæ* and *Tristegineæ.* The *Chlorideæ*, although regarded by both Hackel and Warming as being removed some distance from the *Andropogoneæ*, are like them in their fruit characters.

The remaining tribes, *Phalarideæ*, *Agrostideæ*, *Aveneæ*, *Festuceæ*, and *Hordeæ*, from their fruit characters, form another group in the order named, which corresponds with the classification given by Hackel.

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EXPLANATION OF PLATES.

PLATE I.

FIG. 1. *Coix lachrymæ-jobi,* long. sec.; (x 7).
2 A–D. *Coix lachrymæ-jobi,* cross sec. of embryo; (x 9).
3. *Zea mays,* long. sec. of embryo; (x 5).
4 A–F. *Zea mays,* cross sec. of embryo; (x 14).
5. *Tripsacum dactyloides,* long. sec. facing embryo; (x 8).
6. *Tripsacum dactyloides,* long. sec.; (x 8).
7 A and B. *Tripsacum dactyloides,* cross sec.; (x 8).

PLATE II.

8. *Euchlæna mexicana,* long. sec. of embryo; (x 23).
9. *Andropogon saccharatus,* long. sec.; (x 19).
10 A–C. *Andropogon saccharatus,* cross sec.; (x 34).
11. *Apluda cristata,* long. sec.; (x 12).
12. *Apluda cristata,* cross sec.; (x 30).
13 A–E. *Anthephora elegans,* long. and cross sec.; (x 17).
14 A–D. *Zoysiæ pungens,* long and cross sec.; (x 12).
15 A–D. *Perotis latifolia,* long. and cross sec.; (x 17).
16. *Pennisetum spicatum,* long. sec.; (x 12).
17. *Pennisetum spicatum,* cross sec.; (x 16).
18. *Pennisetum spicatum,* cross sec.; (x 28).

PLATE III.

19. *Chætochloa macrochæta,* long. sec.; (x 13).
20. *Paspalum pubiflorum glabrum,* long. sec.; (x 20).
21. *Paspalum pubiflorum glabrum,* cross sec.; (x 12).
22. *Zizania aquatica,* long. sec.; (x 5).
23 A and B. *Zizania aquatica,* cross sec.; (x 10).
24 A–T. *Zizania aquatica,* cross sec. of embryo; (x 6).

PLATE IV.

25. *Lygeum spartum,* long. sec.; (x 6.5).
26 A–E. *Lygeum spartum,* cross sec.; (x 18).
27. *Oryza sativa,* long. sec.; (x 7).
28. *Homalocenchrus oryzoides,* long. sec.; (x 14).
29. *Anthoxanthum odoratum,* long. sec.; (x 23).
30. *Stipa tenacissima,* long. sec.; (x 20).
31. *Stipa tenacissima,* cross sec.; (x 24).
32. *Stipa viridula,* long. sec.; (x 14).
33. *Stipa viridula,* cross sec.; (x 42).
34. *Eriocoma cuspidata,* long. sec.; (x 17).
35. *Eriocoma cuspidata,* cross sec.; (x 43).

PLATE V.

FIG. 36. *Stipa richardsoni,* long. sec.; (x 17).
37 A and B. *Stipa richardsoni,* cross sec.; (x 24).
38 A. *Oryzopsis micrantha,* long. and cross sec.; (x 14).
38 B. *Oryzopsis micrantha,* long. and cross sec.; (x 29).
39. *Cinna arundinacea,* long. sec.; (x 10).
40. *Cinna arundinacea,* cross sec.; (x 50).
41. *Phleum pratense,* long. sec.; (x 18).
42. *Ammophila arenaria,* long. sec.; (x 20).
43. *Brachyelytrum erectum,* long. sec.; (x 6).
44. *Avena sativa,* long. sec.; (x 5).
45. *Avena sativa,* long. sec. facing embryo; (x 6).
46 A and B. *Avena sativa,* cross sec.; (x 10).
47 A–G. *Avena sativa,* cross sec. of embryo; (x 13).

PLATE VI.

48. *Avena sativa,* long. sec. of embryo; (x 13).
49. *Arrhenatherum elatius,* long. sec.; (x 11).
50. *Danthonia spicata,* long. sec.; (x 17).
51. *Holcus lanatus,* long. sec.; (x 20).
52 A–D. *Eleusine coracana,* long. and cross sec.; (x 13).
53. *Spartina gracilis,* long. sec.; (x 9).
54 A–C. *Spartina gracilis,* cross sec.; (x 16).
55. *Astrebla pectinata,* long. sec.; (x 20).
56. *Leptochloa imbricata,* long. sec.; (x 27).
57. *Cynodon dactylon,* long. sec.; (x 31).
58. *Bulbilis dactyloides,* long. sec.; (x 18).
59. *Bulbilis dactyloides,* cross sec.; (x 18).
60. *Beckmannia erucæformis,* long. sec.; (x 26).

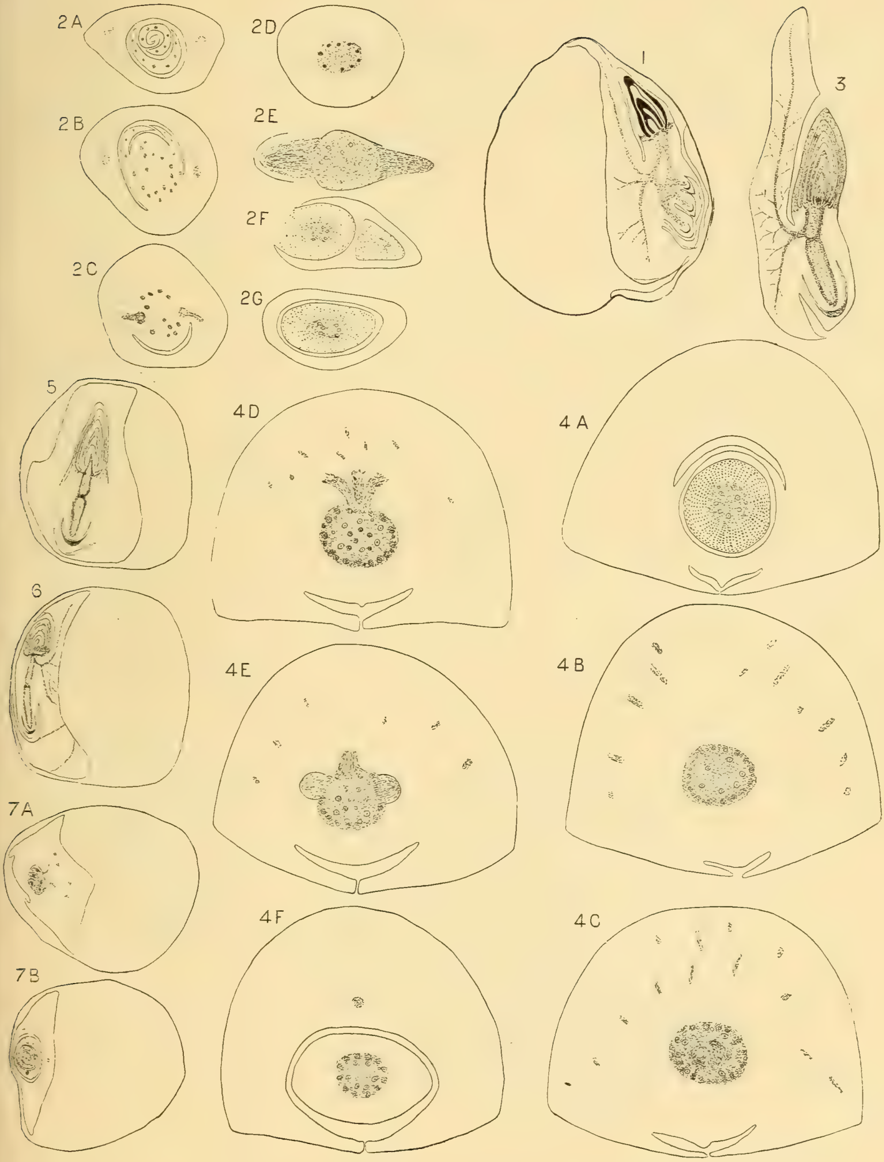
PLATE VII.

61. *Uniola latifolia,* long. sec.; (x 10).
62. *Panicularia aquatica,* long. sec.; (x 17).
63. *Desmazeria sicula,* long. sec.; (x 17).
64. *Cynosurus cristatus,* long. sec.; (x 16).
65. *Hordeum vulgare,* long. sec. of embryo; (x 9).
66 A–H. *Hordeum vulgare,* cross sec. of embryo; (x 18).
67. *Secale montanum,* long. sec.; (x 15).
68 A and B. *Secale montanum,* cross. sec.; (x 14).
69. *Triticum æstivum,* long. sec. of embryo; (x 13).

PLATE VIII.

70. *Lolium rigidum,* long. sec.; (x 16).
71 A–C. *Lolium rigidum,* cross sec.; (x 24).
72. *Elymus virginicus,* long. sec.; (x 11).
73. *Elymus virginicus,* cross sec.; (x 32).
74. *Arundinaria falcata,* long. sec. of embryo parallel to scutellum; (x 19).
75. *Arundinaria falcata,* long. sec. of embryo; (x 16).
76 A–K. *Arundinaria falcata,* cross sec. of embryo; (x 29).

PLATE I.



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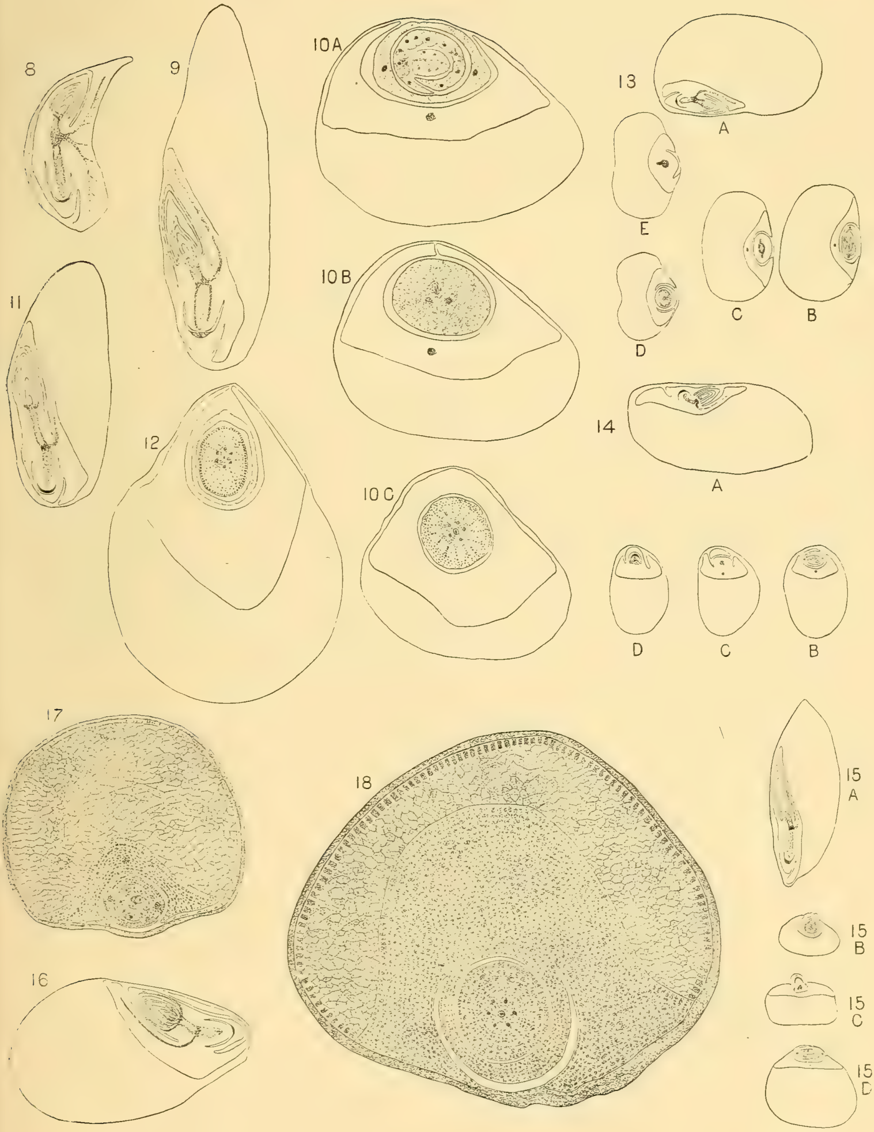

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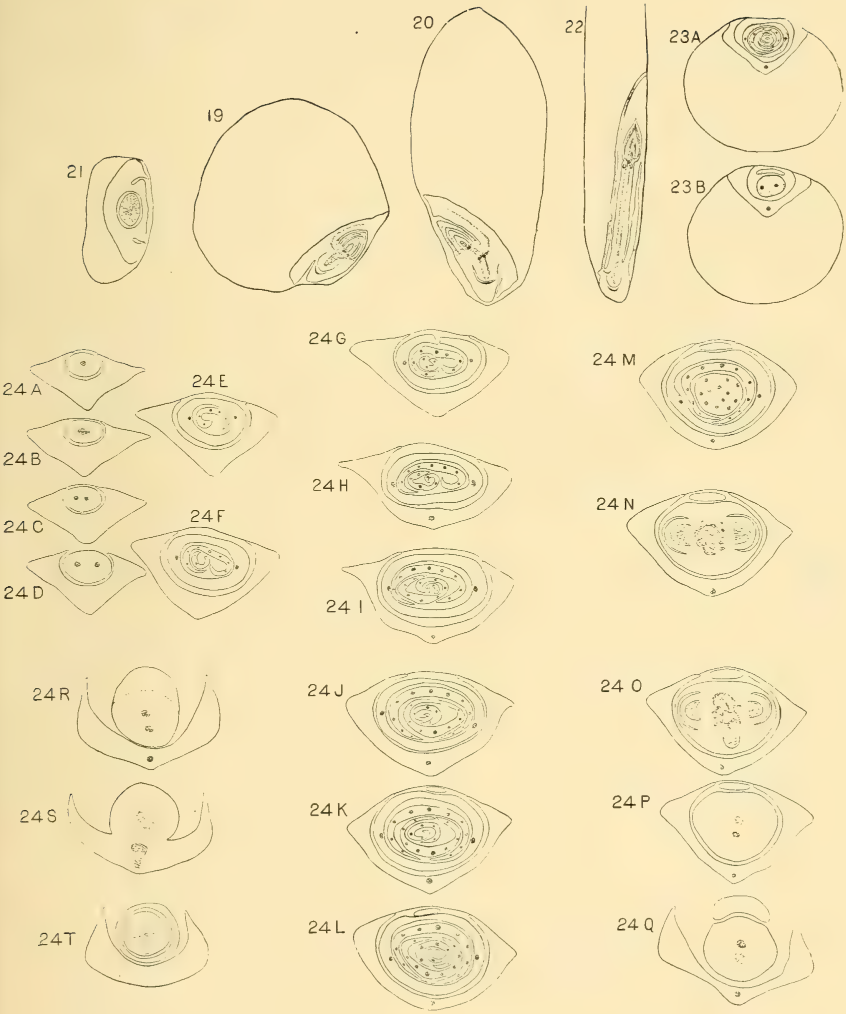

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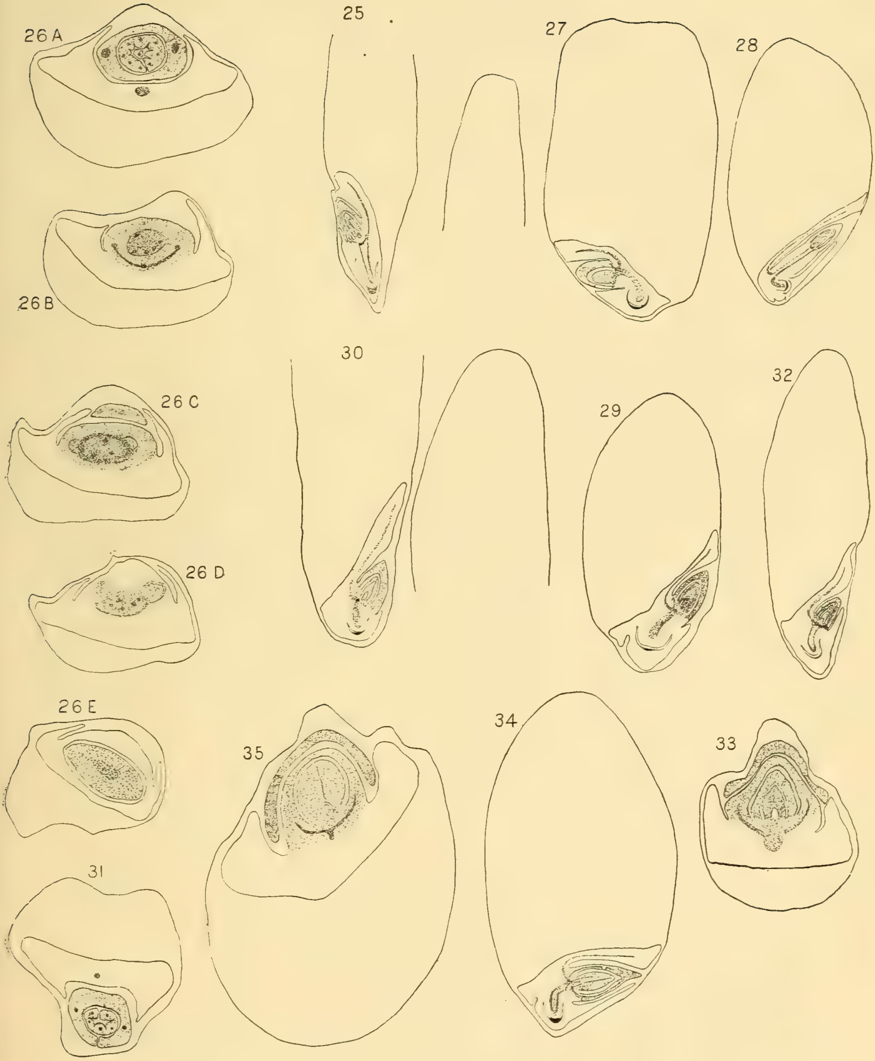

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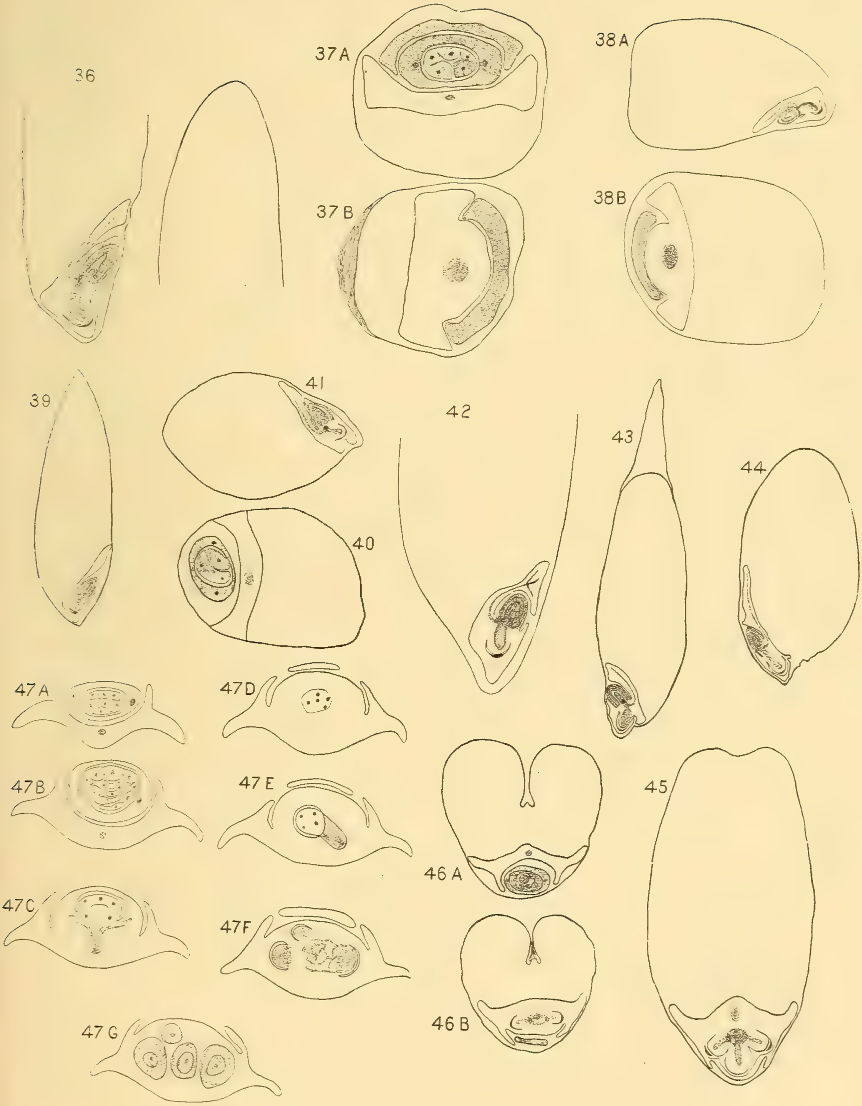

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PLATE VI.

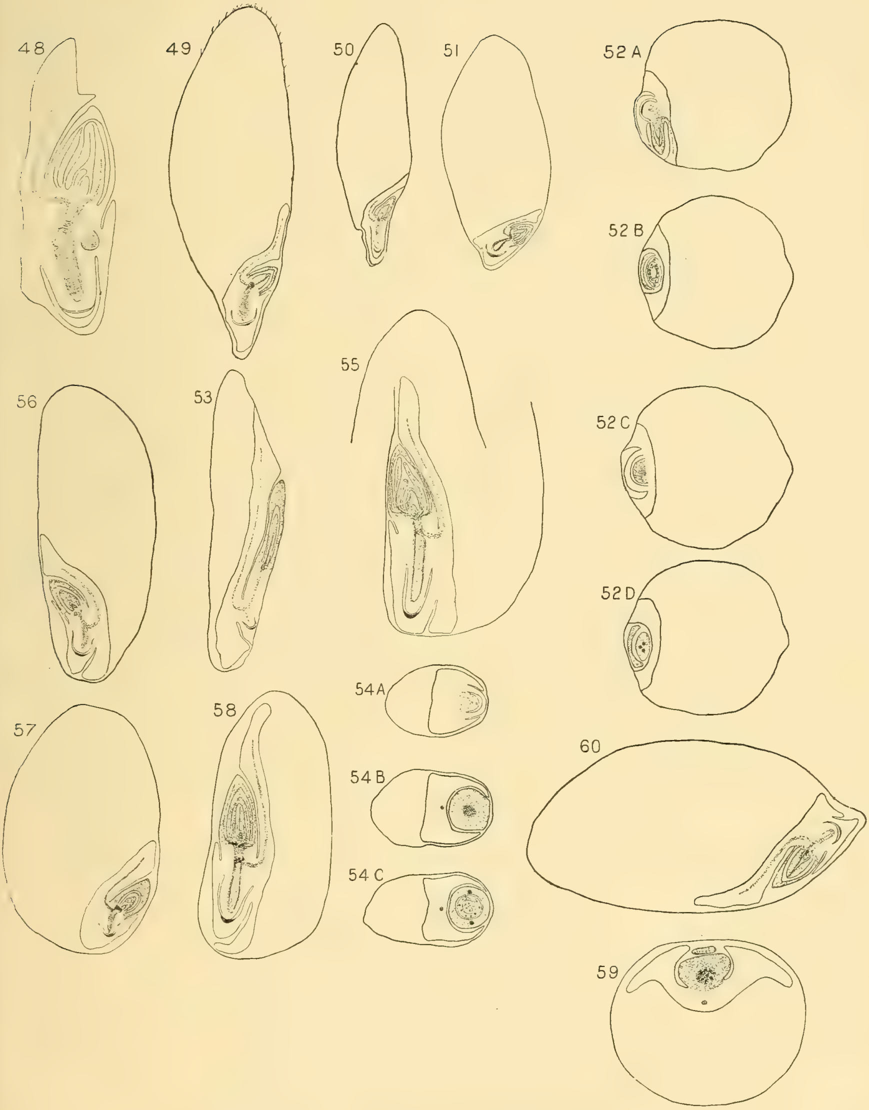

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PLATE VII.

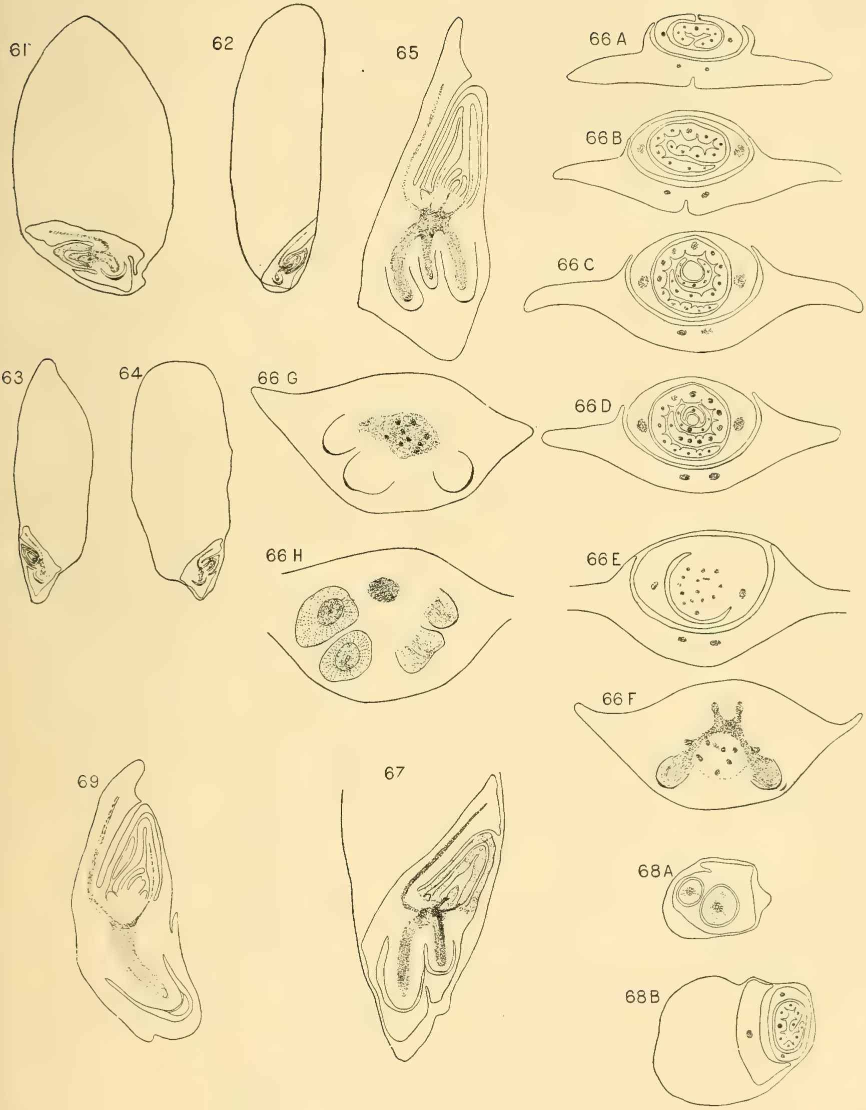

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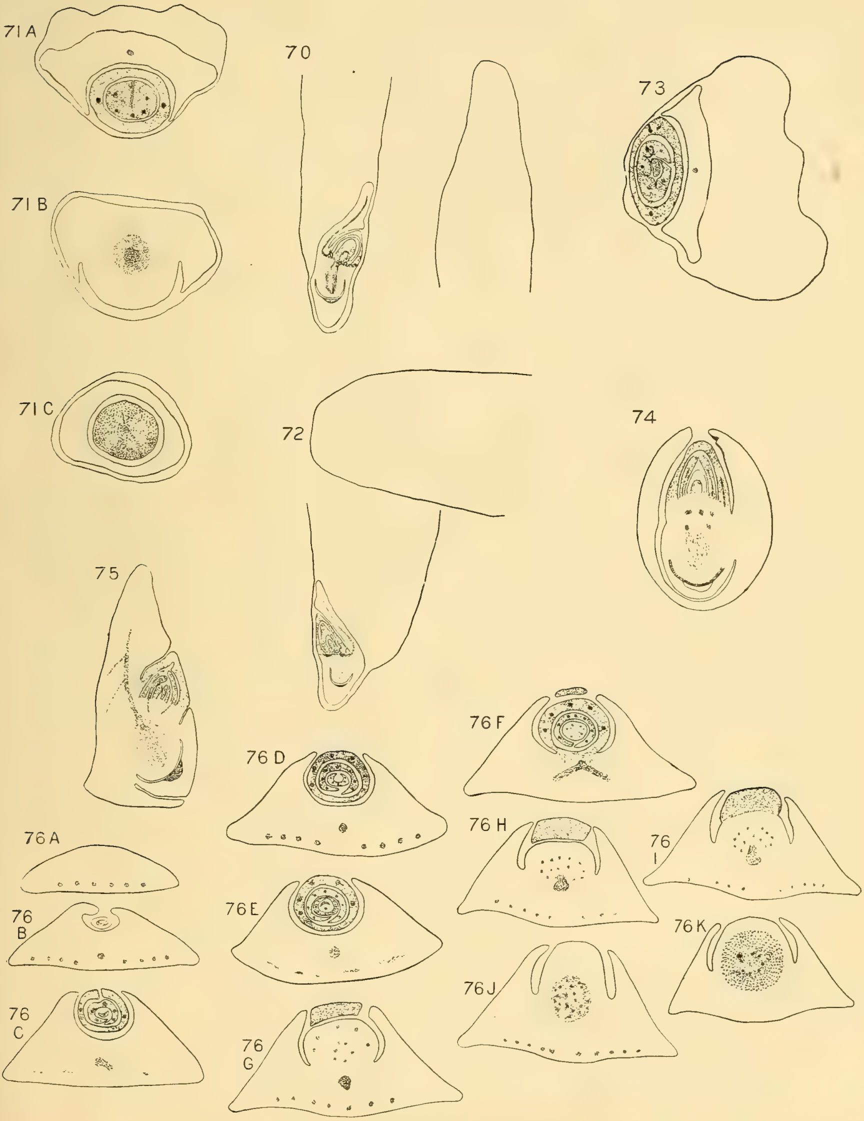
PLATE VIII.



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