

THE ORIGIN OF MONOCOTYLEDONY

II. Monocotyledony in Grasses

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Recently Dr. Land and I published¹ the results of an investigation suggested by a specimen of *Agapanthus umbellatus*, one of the South African *Liliaceae*, possessing two good cotyledons. It seemed to us that if the seedlings of the same species are indifferently monocotyledonous or dicotyledonous, there must be some evident relationship between the two conditions. These two conditions of the seedling of *Agapanthus* were compared critically, and *Sagittaria* was included in the investigation because it has stood, along with *Alisma*, for the typical monocotyledonous embryogeny, in which the terminal cell of a filamentous proembryo is said to give rise to the single cotyledon, in contrast with the dicotyledonous embryogeny, in which the corresponding terminal cell produces the stem tip, and the cotyledons are distinctly lateral. No contrast would seem sharper and less capable of being confused with intergrades.

The result of the investigation, as recorded in the paper referred to, was to show us that there are no such rigid categories for cotyledony; that the cotyledonary apparatus is always the same structure, arising in the same way, and varying only in the details of its final expression. Briefly stated, the situation is as follows: In the embryogeny of both monocotyledons and dicotyledons, a peripheral cotyledonary zone gives rise to two or more growing points, or primordia; this is followed by zonal development, resulting in a cotyledonary ring or sheath of varying length. If both growing points con-

¹ Coulter, John M., and Land, W. J. G. The origin of monocotyledony. Bot. Gaz. 57: 509-519. pl. 28-29. 1914.

tinue to develop equally, the dicotyledonous condition is attained; if one of the growing points ceases to develop, the continued growth of the whole cotyledonary zone is associated with that of the other growing point, and the monocotyledonous condition is attained. In like manner, polycotyledony is simply the appearance and continued development of more than two growing points on the cotyledonary ring. It follows that cotyledons are always lateral structures, arising from the peripheral zone developed at the top of a more or less massive proembryo. This reduces cotyledony in general to a common basis in origin, the number of cotyledons being a secondary feature. The constancy in the number of cotyledons in a great group is no more to be wondered at than the same constancy in the number of petals developed by the petaliferous zone. This is a brief statement of the thesis of our previous paper, detached from the evidence upon which it was based.

It was our purpose to extend the investigation far enough to include all of the representative regions of monocotyledons, so that the conclusion could be tested sufficiently to lead either to its abandonment or to its establishment. This second paper deals with a study of the embryos of grasses, which have been examined more extensively, perhaps, than the embryos of any other monocotyledonous group. As a result of this extensive study there are available many accurate records in the form of good figures, giving the details of embryogeny in such a way that interpretation is almost as satisfactory as it would be from the actual material. Of course this use of illustrations has been checked by the direct inspection of more or less material.

The embryo of grasses early attracted special attention because it does not seem to conform to the plan of the ordinary monocotyledonous embryo. Certain structures appear that could not be accounted for, but they enriched terminology. As a consequence, the nature of scutellum, epiblast, and coleoptile became subjects of discussion. It was to be expected that

the embryo of grasses, with all of its unusual structures, would be interpreted in terms of a rigid conception of the monocotyledonous embryo; in other words, that the conventional monocotyledonous embryo would be read into the grass embryo. There is no better illustration of the compelling power of a preconception than this treatment of the grass embryos, for it so happens that they show all the intermediate stages between dicotyledony and monocotyledony.

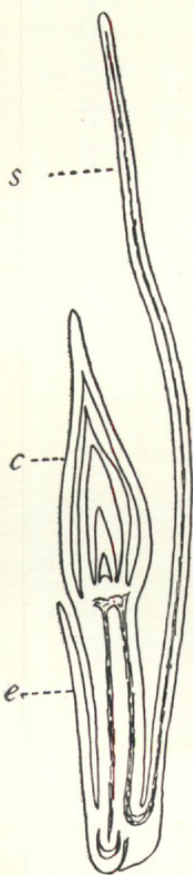


Fig. 2. Embryo of *Zizania aquatica*: s, scutellum; e, epiblast; c, coleoptile; $\times 11$. — After Bruns.

Very early in the history of this subject, the scutellum came to be recognized as a cotyledon. The corollary to this proposition, however, was that it must be recognized also as a terminal structure. Any one who has seen the vascular system of the embryo of corn (fig. 1), the most highly specialized of all grass embryos, with its distinct axial cylinder, made up of stem cylinder and hypocotyl cylinder, and the cotyledonary strands leading off from the intermediate cotyledonary plate, just as do the strands of any lateral cotyledons, will understand the great difficulties in the way of interpreting this cotyledon as a terminal structure.

The structure which presented the greatest difficulty, however, was the epiblast, usually defined as a small scale "opposite" or "over against" the

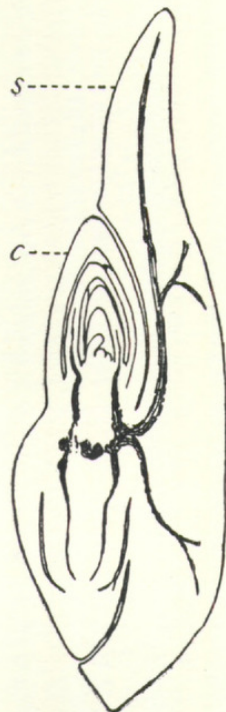


Fig. 1. Embryo of *Zea Mays*: s, scutellum; c, coleoptile; the vascular cylinder of the embryo is shown, made up of stem cylinder and hypocotyl cylinder, also the lateral origin of the cotyledon (scutellum) from the cotyledonary vascular plate; opposite the vascular connection of the cotyledon there appears a group of procambium cells, marking the origin of another cotyledonary strand connected with the suppressed second cotyledon (epiblast); $\times 18$.

cotyledon. The definition is accurate, for the epiblast occupies exactly the place of a second cotyledon opposite the large and

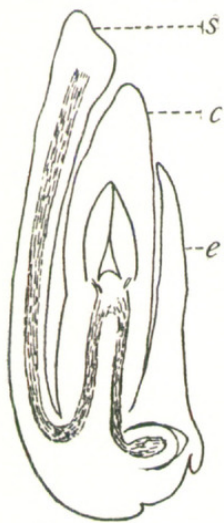


Fig. 3. Embryo of *Leersia clandestina*: s, scutellum; e, epiblast; c, coleoptile; $\times 44$. — After Bruns.

functional one (fig. 2). If some one had found an epiblast vigorous enough to establish vascular connections, this debated structure would long since have been accepted as a second cotyledon, for the definition of it always emphasized the fact that it is a scale in the right position for a cotyledon, but with "no vascular strands."

So obvious is the interpretation of the grass embryo when an epiblast is developed that Porteau in 1808, Mirbel in 1809, Turpin in 1819, and Bischoff in 1834, all called the epiblast a rudimentary cotyledon. The submergence of this idea seems to have been due to Schleiden, who in 1837 dissented from this view, and it disappeared from literature. It reappeared in 1897, when Van Tieghem, in

his paper on the embryo of grasses and sedges,¹ reiterated it, based chiefly upon the study of vascular connections.

Any series of sections, cross or longitudinal, through the embryos of grasses, shows the following facts: the so-called scutellum or functional cotyledon arising from the peripheral cotyledonary ring or sheath which surrounds the apex of the embryo, and establishing vascular connections laterally with the cotyledonary plate; the epiblast in a similar relation to the coty-

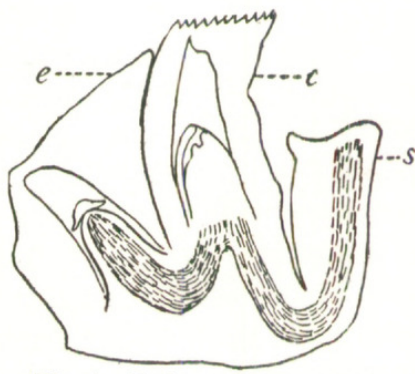


Fig. 4. Embryo of *Oryza sativa*: s, scutellum; e, epiblast; c, coleoptile; $\times 22$. — After Bruns.

ledonary ring on the opposite side, and varying in development from a structure somewhat smaller than the large cotyledon, to complete suppression; and the apex of the

¹ Van Tieghem, Ph. Morphologie de l'embryon et de la plantule chez les Graminées et les Cypéracées. Ann. d. Sci. Nat., Bot. VIII. 3: 259-309. pl. 14-16. 1897.

embryo, continuing beyond the cotyledonary ring or sheath, and producing a variable number of leaves.

The early appearance and rapid development of these leaves seems to account for the abortion of one of the growing points. I am convinced that if grass embryos had been the only monocotyledonous embryos studied; we should never have heard of terminal cotyledons.

Some common grasses, whose embryos have been figured by Bruns,¹ may be used to illustrate stages in the abortion of the second cotyledon. The abortion always is

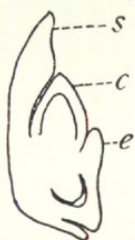


Fig. 6. Embryo of *Leptochloa arabica*: s, scutellum; e, epiblast; c, coleoptile; X 44. — After Bruns.

accompanied by the diversion of the growth of the whole cotyledonary zone in connection with the growing point that remains active; so that growing tissue is not suppressed, but develops as one structure rather than as two.

In *Zizania aquatica* (fig. 2), the so-called epiblast is very conspicuous, arising as distinctly from the peripheral cotyledonary ring as does the so-called scutellum, and attaining at least one-quarter to one-third of its length. This unusual development of the second cotyledon is associated with the fact that the stem axis above the cotyledons develops a long internode, so that the first leaves begin to appear at an unusual distance from the origin of the cotyledons. In fact, in this case the length of the second cotyledon is approximately the length of the first internode, and where the leaves begin this cotyledon ends.

In *Leersia clandestina* (fig. 3), the second cotyledon (epiblast) approaches the large cotyledon in length even more



Fig. 5. Embryo of *Spartina cynosuroides*: s, scutellum; e, epiblast; c, coleoptile; X 13. — After Bruns.



Fig. 7. Embryo of *Triticum vulgare*: s, scutellum; e, epiblast; c, coleoptile; X 22. — After Bruns.

¹ Bruns, Erich, Der Grasembryo. Flora 76: 1-33. pl. 1-2. 1892.

than does that of *Zizania*, and all the connections of the various organs show a lateral origin for the cotyledons, and a terminal origin for the "coleoptile," a structure made up chiefly of leaves arising from an indistinctly differentiated stem-tip region.

Oryza sativa (fig. 4) is interesting in the relation of the parts of the embryo, the "scutellum" and "epiblast" being opposite and well-balanced structures, between which the prominent plumule (a name expressing the real character of the "coleoptile") is evident.

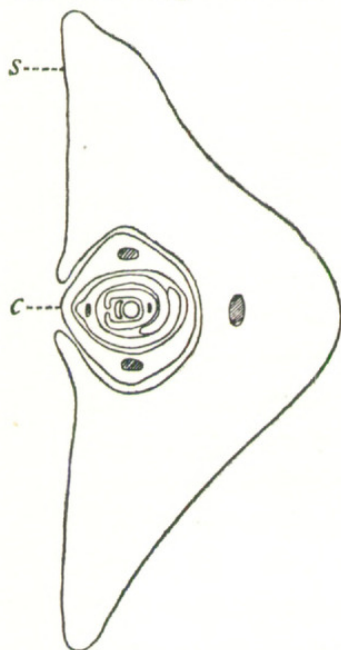


Fig. 8. Transverse section through cotyledon (s), showing it embracing the plumule (c) of *Zea Mays*: the plumule shows three distinct leaves and the terminal stem tip; the succession of opposite vascular bundles indicates that a bundle opposite that of the cotyledon is missing, but its rudiment is evident in a lower section; $\times 20$.

relation to the functioning cotyledon, and the relation of both to the plumule are evident.

In *Leptochloa arabica* (fig. 6) and in *Triticum vulgare* (fig. 7), the epiblast remains very small, but the significant connections are evident.

It is in the embryo of *Zea Mays* that this reduction series reaches its extreme expression in the complete disappearance of the epiblast or second cotyledon (fig. 1), whose position is indicated merely by more or less protuberant

In *Spartina cynosuroides* (fig. 5), the small cotyledon (epiblast) is less prominent, but its

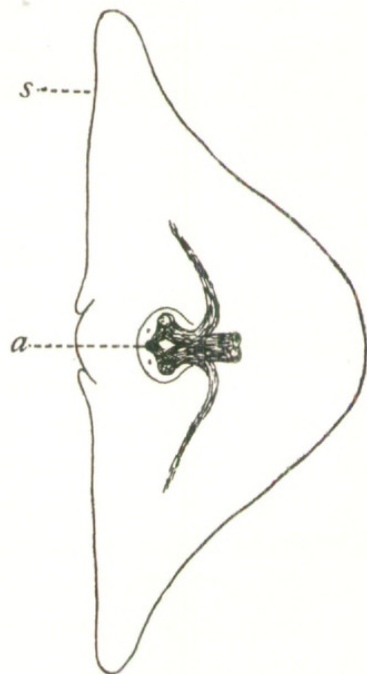


Fig. 9. Transverse section through the cotyledonary plate of *Zea Mays*: the functioning cotyledon (s) does not overlap a small protuberance, which represents the site of the missing cotyledon (epiblast), as indicated also by the appearance of a procambium mass (a), which is the rudiment of a former vascular connection; $\times 20$.

tissue and by the very obvious vascular relations. A cross-section of this very specialized embryo is instructive (figs. 8 and 9). The large functional cotyledon is seen originating on one side, embracing the vascular axis of the embryo and more or less overlapping the other side, where in most grasses the second cotyledon (epiblast) appears. Moreover, in the section of the centrally placed plumule, with its succession of leaves, a section of the stem tip may be seen, clearly representing the axis of the embryo, with no suggestion of a lateral origin. A transverse section through the cotyledonary plate (fig. 9) shows some tissue developed at the site of the missing cotyledon (not overlapped by the functioning cotyledon). This is emphasized by the appearance of a mass of procambium at the base of the protuberance, which in other grasses develops into the epiblast. This procambium is distinctly a rudiment of a former vascular connection.

Some idea of the frequency with which the second cotyledon appears among the grasses may be obtained from the excellent work of Bruns on the grass embryo, published in 1882, and from the work of Van Tieghem, already cited, published in 1897. Bruns examined 82 genera, representing 12 tribes. In 29 of these genera epiblasts were present, and the genera represented 9 of the 12 tribes. The tribes in which no epiblasts were found were *Oryzeae*, *Agrostideae*, and *Aveneae*. The situation in the *Agrostideae* is noteworthy, for 13 genera were examined, and no trace of an epiblast found. *Festuceae* may be mentioned, for 20 of its genera were examined, and only 4 of them were found to possess epiblasts. Taking Bruns' results as a whole, they indicate that approximately 40 per cent of the grasses still develop a second cotyledon to a stage that enables it to be recognized under ordinary inspection as a definite structure.

The work of Van Tieghem included a somewhat wider range of forms, 91 genera being examined, and 61 of these showed epiblasts. This suggests that perhaps in as many as two-thirds of the grasses a second cotyledon is more or less obvious. In any event, it is certain that the grasses as a whole exhibit a remarkable number of transition stages from dicoty-

ledony to monocotyledony; and this fact strongly supports the view that grasses are a comparatively primitive assemblage of monocotyledons.

It is not difficult to explain the prolonged misconception concerning monocotyledony. When the first detailed studies of monocotyledonous embryogeny were made by Hanstein, and supplemented by Famintzin, a form (*Alisma*) with a filamentous proembryo was selected. If a form with a massive proembryo had been selected for these early investigations, there would probably have been no misconception, for in such proembryos the peripheral (that is, lateral) cotyledonary zone is so evident that it could hardly have escaped recognition. Since that time, embryogeny that starts with a filamentous proembryo has been regarded as the typical embryogeny, and all other kinds of proembryos have been dismissed as exceptions. In the case of this filamentous proembryo, it was observed that the terminal cell passed into the quadrant and octant stages, and later a terminal cotyledon appeared. It seemed safe to conclude that the terminal cell had developed the terminal cotyledon. The inference was true so far as it went, but it failed to recognize the fact that the terminal cell develops other structures as well. With the origin of the terminal cotyledon disposed of, the conclusion was confirmed by the appearance at its base of a notch, from which arose the stem tip. What could be more obvious than that the stem tip is lateral in origin, and therefore must arise from the cell of the proembryo behind the terminal one? In this way the conventional embryogeny of monocotyledons was established, and the relation of monocotyledony to dicotyledony became completely obscured.

The facts not observed in these earlier investigations are as follows: The terminal cell of the proembryo forms a group of cells; the peripheral cells of this group develop the cotyledonary ring or sheath, on which two growing points appear. One of these growing points soon ceases to be active, and the whole zone develops in connection with the other growing point; but at the base of the growing cotyledon a notch is left by the checking of the other growing point. This notch

is really the space between the two very unequal cotyledons, which surround the real apex of the embryo. The apex of the embryo is at the bottom of the notch, and not at the tip of the large embryo. This apex soon begins to form leaves, and the so-called stem tip appears issuing from the bottom of the notch, in a relation apparently lateral only because the two cotyledons are so unequal. Furthermore, when the stem tip is examined, it is found not to be a stem tip, but a cluster of leaves whose rapid development has aborted one of the growing points on the cotyledonary zone. All this is very obvious in grasses, and is equally obvious in any massive proembryo, but it escaped the earlier observers of filamentous proembryos.

The general conclusion is that monocotyledony is simply one expression of a process common to all cotyledony, gradually derived from dicotyledony, and involving no abrupt transfer of a lateral structure to a terminal origin.

This paper was prepared in collaboration with Dr. W. J. G. Land, who also supplied the material and made the illustrations.



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