The Morphology of the Monocotyledonous Embryo and of that of the Grass in particular.

BY

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With ten Figures in the Text.

ABNORMAL COLEOPTILE.

SOME seedlings of *Zea Mais* were kindly placed at my disposal by Dr. E. J. Salisbury, in a number of which (he himself has observed ten in all) the coleoptile was forked, or divided into two equal parts for a short

FIG. 1. *Zea Mais* (Maize). Seedlings attached to grain, showing the forked coleoptile and the plumule grown beyond it. E. J. Salisbury photo. Slightly reduced.

distance from the apex (Figs. 1 and 2). The remaining organs of the seedlings were quite normal. I have myself raised a number of seedlings (from seed supplied by Dr. Salisbury) which show the same feature of the coleoptile.

As the above would seem to be an uncommon abnormality, it seems desirable to indicate what, in my opinion, is its probable meaning. This involves a brief discussion of the much-debated morphology of the different parts of the Grass-embryo, as also of the Monocotyledonous embryo in general. Every one is familiar with the structure of the Grass-embryo, so it need not here be described in detail. I will merely take each of the main parts in turn and give a brief historical account (a complete one is unnecessary, having been given by previous writers) of the views held as to their nature.

NATURE OF THE SCUTELLUM AND COLEOPTILE.

The *scutellum* is the hypogeal absorptive organ. Regel, Hofmeister, and Gris regarded it as of axial nature; Agardh as the tegument of the endosperm. The majority have held it to be either an entire cotyledon or part of one. Treviranus, Bischoff, Demoor, Le Maout et Decaisne, Hackel, Warming, Bruns, Coulter, belong to the first group. Those who regard scutellum and coleoptile (or plumular sheath) as together constituting the cotyledon include Mirbel, Cassini,'Raspail, Bernhardi, Klebs, Schlickum, Hanstein, Hegelmaier, Fleischer, Celakovsky, van Tieghem. In most of these last cases the scutellum is described as the lamina of the cotyledon, and the coleoptile as the sheathing portion, or else the ligule, or a pair of fused stipules.

Of these various views as to the nature of the scutellum, the last one, to which the majority subscribe, is almost certainly the correct one. Hanstein's excellent researches into the development have clearly demonstrated this, as both his description and figures indicate. He says: 'The earliest origin of the upper circular protective rim from a forwardly and downwardly directed outgrowth of the already differentiated first leaf unmistakably shows it to be a sheathing portion of the latter. This is confirmed by its subsequent growth around the anterior and lower side of
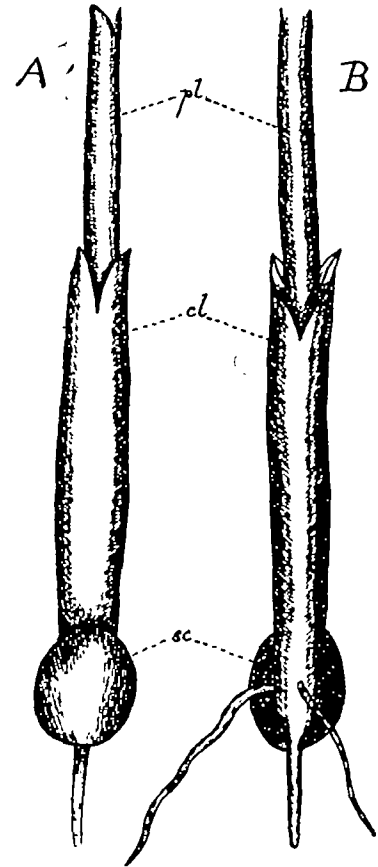

FIG. 2. *Zea Mais*. Seedlings with the grain removed, seen from the dorsal (A) and ventral (B) sides, showing the radicle, adventitious roots, scutellum (*sc*), forked coleoptile (*cl*), and plumule (*pl*).

the bud. It cannot therefore be regarded as an independent phyllome, for its main portion on the posterior side, judging by the plastic processes of its construction, arises, not from a shoot, but from an older leaf.' That is to say, the coleoptile clearly arises, in the early stages of the ontogeny, as part and parcel of the scutellum. This is illustrated by Fig. 3 (A–E), taken from Celakovsky's paper, and whose description of which I here quote. A shows the earliest stage in which the ligular outgrowth (here directed downwards) and the scutellum are clearly parts of one organ. ' In B the ligule is more developed and the angle between it and the scutellum has deepened, *a* is further separated from *c*, and the angle *a b c* is more obtuse than in A. In C *a b c* has become very obtuse, so that the ligule is only slightly connected with the scutellum. In D the growth occurring towards the plumule has caused *b* to fall into the line *a c*, whereby all connexion between the scutellum and the ligular sheath is lost. In E, owing to the continued extension in the hypocotyl or in the cotyledonary node, *a* has
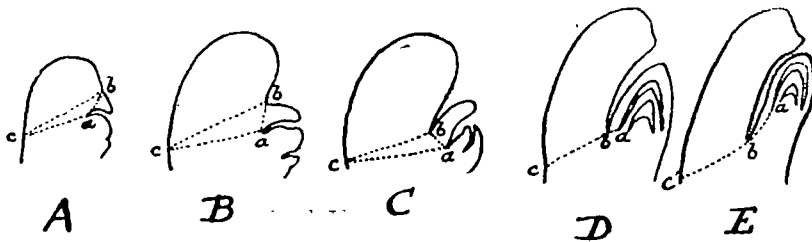

FIG. 3. A–E, Grass-cotyledon, showing successive developmental stages. *a c* = limit between cotyledon and hypocotyl; *a*, the angle made by cotyledonary sheath with plumule; *b*, the angle separating the ligular outgrowth from the scutellum in A, B. (From Celakovsky after Hanstein.)

become carried farther from *b* and *c* in the same direction, i.e. the base of the sheath becomes stretched along with the node, giving rise to the mesocotyl (*a b*).

'As a result of all these processes, the limit between leaf and axis continually changes. The cell-tissue, which in A–C is included in the dotted triangle, there occurs above the insertion of, and belongs to, the cotyledon ; in D the same tissue, increased in amount by growth, has come to form part of the hypocotyledonary node, and when a mesocotyl is formed and elongates, the outer basal tissue of the sheath forms part of the meso-cotyl and constitutes the outer foliar-base of the sheath.' It is thus seen how the sheath and the scutellum (lamina of cotyledon) become separated from one another so widely, losing every trace of connexion.

Hegelmaier also concluded, from his study of the development of *Triticum vulgare*, that scutellum and coleoptile together constitute the cotyledon.

Great importance may be attached to these developmental data of the embryo. It is to them we should turn for light on the morphology

of the parts concerned, and not to the later stages. In many Grasses the older condition is marked by the appearance, as above referred to, of the 'mesocotyl', i.e. an internode-like area becomes developed between the scutellum and the coleoptile. In some, e.g. *Zizania*, *Leersia*, *Oryza*, the mesocotyl is of very considerable length, and gives the exact impression of an internode (Fig. 4). Mere appearances, however, must not mislead us in this case. The early developmental history clearly shows that the coleoptile is part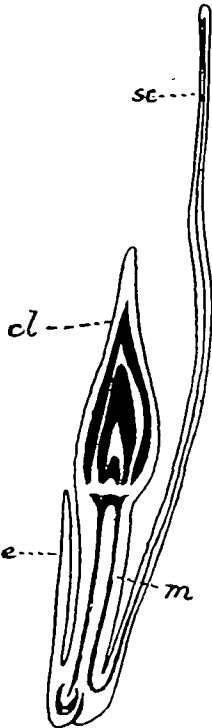 of the cotyledon (scutellum). Van Tieghem's anatomical researches showed that the mesocotyl was not an internode, but the first, abnormally extended node. Schlickum also, by the same method, concluded that the mesocotyl possesses hypocotyledonary structure (Fig. 5). Sandeen found that the very long mesocotyl of *Panicum* has the same structure as an adventitious root. It is only necessary to read the papers of the two first-named authors, containing a record of exact observations into the anatomical structure of the mesocotyl, in order to see that, whether it belong to the node or the hypocotyl, it cannot, in any case, belong to the epicotyledonary region. Celakovsky points out that inasmuch as the coleoptile is proved by the developmental history to be part of the scutellum, the mesocotyl must therefore represent a much-extended node. The anatomy supports this. There remain over no other valid reasons, save those resting on mere appearances, for regarding it in any other light. What has really occurred during the elongation of the node is that the base of the coleoptile has become congenitally concrescent therewith, the 'carrying-up' of the sheath being due to this fact, just as the 'carrying-up' of a bract on a peduncle is due to congenital fusion of its basal region with that organ. A perfectly analogous and parallel case to the mesocotyl of the Grass-embryo is, as Celakovsky points out, to be seen in the axial extension which separates the leaf-stalk of *Ficus elastica* from its ochreate stipular sheath, and which is doubtless due to the same cause.

FIG. 4. *Zizania aquatica.* Longitudinal section of embryo showing the scutellum (*sc*), epiblast (*e*), the elongated mesocotyl (*m*), and the coleoptile (*cl*). (After Bruns.)

Bruns's arguments in support of the internodal character of the mesocotyl are easily refuted in the light of the known facts: his conclusions are based solely on the mere appearance presented by the mature embryo, without any reference to the important facts of the development.

Coulter has recently given vigorous support to the same theory as that held by Bruns, viz. that the mesocotyl is the first internode of the epicotyl, thus bringing his view that the epiblast is a second cotyledon into line with the rest of the morphology. This article is an astonishing one for two reasons. Firstly, because his deductions are based, like those of Bruns, entirely on the outward appearance of the advanced embryo; the mesocotyl *looks like* an internode succeeding two apparent cotyledons, therefore it must *be* an internode! Secondly, the important developmental and anatomical facts disclosed by Hanstein, van Tieghem, and Schlickum are completely ignored; the article by this last author and the very important one by Celakovsky are not cited, the entire treatment of the subject being thus one-sided. It seems to me a pity that the writings of these previous workers should have been over-looked, especially as the conclusions involved are rather important.

Schlickum, as a result of his investigations, finds that the Grass-seedling essentially resembles in all its morphological parts that of other Monocotyledons, and a continuous series of transitional forms between the two can be instituted. He says that the coleoptile differs in no essential point from the cotyle-
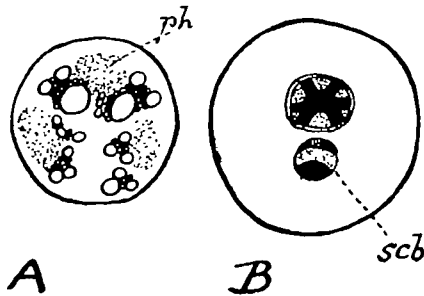

FIG. 5. A. *Panicum miliaceum.* Transverse section of vascular system of mesocotyl. *ph* = phloem (diagrammatic). B. *Oryza sativa.* Ditto. *scb* = bundle destined for scutellum. (After Schlickum.)

donary sheath of other Monocotyledons, such as *Canna* and *Carex*. Just as in the case of other investigated Monocotyledons, there exists a great difference, e.g. in *Oryza* and *Panicum*, between the structure of the coleoptile and that of the first plumular leaf-sheath, whilst, on the other hand, the first and second plumular leaf-sheaths exhibit only trivial differences between themselves. He states further that 'as the rudiment of the coleoptile arises in the tissue complex which is becoming the scutellum, I must, as does also Hegelmaier, agree with Hanstein, and like him, on the basis of developmental data, equate the scutellum with the haustorium and the coleoptile with the cotyledonary sheath of other Monocotyledons'.

From what has been stated above there is obviously no foundation for Bruns's and Coulter's view that the mesocotyl is the first internode of the epicotyl and that the coleoptile is the first plumular leaf. The possession by the coleoptile of two widely-separated vascular strands which are situated much nearer to the two margins than they are to each other, strongly suggests a ligular structure formed by the union of stipules. If this organ represented an independent (first plumular) leaf this type of venation would

certainly not occur, but, instead, there would be two or three veins placed at equal distances from each other and from the margins. This ligular (stipular) character is further suggested by the seedlings observed by me with a forked coleoptile, this forking being a most natural occurrence in a leaf with this venation, and representing, in my opinion, a partial reversion to the primitive stipular condition of the coleoptile. Regel mentions the interesting and, in this connexion, important fact that the ligule of the foliage-leaf of *Festuca spadicea* is bifid. *Ammophila* and *Bromus* also have bifid ligules. The position, viz. on the same side as, and opposed to, the cotyledon, as also (as above stated) the mode of development, of the coleoptile (especially in those Grasses which, like the Maize, are devoid of a mesocotyl) are still further features in support of its homology with the ligule of the foliage-leaf in this order. How much better it is to trust to these comparative data than to those exhibited by the advanced embryo considered by itself.

Nature of the Epiblast.

Turning now to the vexed question as to the nature of the 'epiblast', we find that Poiteau, Mirbel, Turpin, Hackel, Warming, Bruns, van Tieghem, and Coulter regard it as a second cotyledon. This is owing chiefly to its position opposite the supposed lateral main cotyledon or scutellum and at the base of the supposed internode (mesocotyl). It appears widely separated from, and without connexion with, the scutellum, and as it occupies the same relative position as the latter on the opposite side of the primary node, it is best regarded, according to this view, as a second independent leaf or cotyledon.

In my opinion, it will not do to rely, as van Tieghem does, solely on the course of vascular strands for determining the nature of an organ. The conclusions of Bruns and Coulter, again, are based solely on superficial appearances. It is simply astounding that no deeper investigations into the comparative morphology of the organ concerned, nor into the results of researches of other authors in this connexion, have been thought necessary. Undoubtedly, if we are to judge by the *appearance* presented by such embryos as those of *Zizania* (Fig. 4), *Oryza*, and *Leersia*, the epiblast and scutellum are two lateral cotyledons, the mesocotyl is the first epicotyledonary internode, and the coleoptile is the first plumular leaf situated in its proper position (following the distichous arrangement) on the same side as, and directly over, the scutellum. Coulter does not seem to be aware of the existence of Celakovsky's able paper in which quite another side of this question is presented. Therein is to be found a comprehensive and most interesting discussion on the nature of the epiblast. As Coulter has passed it over, I will here give its gist.

Gärtner's view of the epiblast: 'lacinula e scutello oriunda', and van Tieghem's former view: 'une dépendance des bords de l'écusson' [scutellum], are really correct. Celakovsky adopts the natural and reasonable method of comparing the cotyledon with the foliage-leaf. Surely there could be no better plan than that ! As we have above seen, the developmental facts and anatomical structure of the mesocotyl show that the scutellum corresponds to the lamina of the foliage-leaf and the coleoptile to the ligule, the sheath of the foliage-leaf not being represented in the cotyledon except at the very earliest stage of all. The fact that scutellum and coleoptile are parts of the cotyledon is in itself sufficient to dispose of the idea that the epiblast represents a second cotyledon. The true nature of the epiblast is revealed by the following facts and deductions. The foliage-leaves of *Hordeum* (Fig. 6), *Triticum, Secale, Lolium*, and the larger leaves of *Oryza* possess peculiar sickle-shaped appendages to the base of the lamina. If these appendages were to become united on the opposite side of the axis, a structure would result comparable to the epiblast. This last is, however, in many cases (not in all) quite separate and distinct from the scutellum,[1] existing as an independent outgrowth on the opposite side of the axis. Celakovsky found, however, in certain robust leaves of *Oryza* that the appendages were completely separated from the leaf-blade,[1] more linear or lanceolate in shape, hardly curved, directed upwards, and provided with long, bristle-like cilia on the edge nearest that of the leaf-blade. Now if the leaf-sheath and ligule were closed structures (as occurs in species of *Melica*) then the distal margins of the two appendages would, like those of the sheath and the ligule, become united, and a single appendage would result,

FIG. 6. *Hordeum vulgare.* Base of lamina (*la*) of foliage-leaf, showing auricles (*a*). *li* = ligule; *s* = sheath. (After Celakovsky.)

situated opposite the leaf. Such a condition of things is realized in the seedling of *Oryza*, where the epiblast corresponds to the single appendage. The cause of the marked independence of scutellum and epiblast in many Grasses is that the latter, owing to the disappearance of the sheathing-base in the cotyledon, arises directly from the hypocotyl, so that its original connexion with the cotyledon could easily become obscured.

Further light is thrown on the origin of the epiblast by the contemplation of that of *Stipa*, which is deeply bifid into two equal parts (Fig. 7, A), at once suggesting its composition from two originally separate organs.

[1] As in the case of the mesocotyl, so also in that of the area separating the scutellum-base from the epiblast, and the leaf-blade from the appendages, we can postulate a congenital fusion of the foliar parts concerned with the axis.
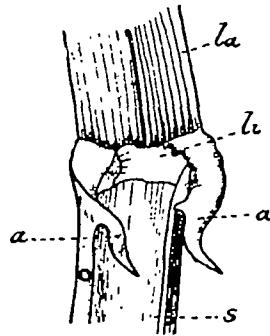
The epiblasts of *Koeleria*, *Eleusine* (Fig. 7, B), *Danthonia*, and *Brachypodium* show a similar structure. How Coulter can explain the structure of the epiblasts in these Grasses (figures of which are given by his favourite author Bruns) in favour of the latter being a second cotyledon is to me a mystery. Just as the forked coleoptile observed in certain seedlings of Maize is evidence of its compound nature, in the same way the bifid epiblast of *Stipa* and *Koeleria* is evidence of the compound nature of *this* organ.

Thus we see that counterparts of all the foliar structures of the seedling can be found for the searching in the foliar structures of the mature plant ; and, as a result of a careful comparative investigation, Celakovsky reaches the convincing conclusion that the epiblast also is part and parcel of the cotyledon, and that there are no natural or legitimate grounds whatever for regarding it as an independent foliar organ.
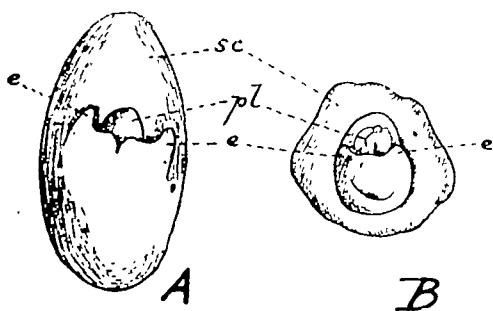

FIG. 7. A. *Stipa arenaria*. B. *Eleusine coracana*. Embryos showing bifid epiblasts (*e*) ; *sc.* = scutellum ; *pl.* = plumule. (After Bruns.)

Schlickum regarded the epiblast, owing mainly to the downward extension which it possesses,· as part of the coleorhiza. But Celakovsky points out that the scutellum has a similar outgrowth which is to be regarded as the foliar base of that organ, analogous to the similar outgrowth from the succulent leaf of some species of *Sedum*. The epiblast having become a quasi-independent foliar organ, it has come to form its own foliar base.

POSITION OF THE COTYLEDON.

Finally, we have to determine the *position* of the scutellum (cotyledon), whether it is terminal or lateral to the axis of the seedling.

As the construction of the Grass-embryo is essentially the same as that of other Monocotyledonous embryos, what is true of the latter must also be true of the former. The cotyledon must occupy the same position in both. This is an important point to remember. Now the excellent investigations of Hanstein, of Fleischer, and of Hegelmaier have clearly shown that the cotyledon of Monocotyledons is always *terminal*. Speaking of *Funkia*, Hanstein says : ' The cotyledon is laid down as a massive structure as a continuation in the same direction of the hypocotyl, before a trace of the growing-point exists.' Fleischer says of *Leucojum aestivum* that a terminal cotyledon arises from the entire upper portion of the

embryo; the growing-point occurs at the region between the upper and lower halves of the embryo. In *Juncus glaucus* he found that after the terminal cotyledon a succession of sympodially-formed foliage-leaves occurs, each arising out of the sheath of the preceding one, before any other organ exists at all besides these leaves. He states that this mode of development in *Juncus* appears to contain the key to the understanding of the construction of all Monocotyledonous embryos, for there occurs here several times in succession what occurs only once in the first development of the terminal bud of every Monocotyledonous plant. He points out that Strasburger's view that the ontogenetic development of the Monocotyledonous embryo represents a 'later adaptation', due to the cotyledon pressing the stem-apex to one side, is contradicted by the fact that the later cotyledon with the later hypocotyledonary segment constitute a morphological unity, completely corresponding to that of the Archisperms, which later becomes in its extension the shoot; that there is thus not the slightest trace of a lateral sprouting of the cotyledon from a pre-existing axis. 'That the axis exists before the cotyledon cannot be maintained, for it has no growing-point. On the contrary, the cotyledon exists before the commencement of activity of the growing-point. . . . It exists, however, not as a cotyledon, but as part of a thallus, which becomes a cotyledon only after the appearance of activity of a growing-point.'

Hegelmaier also, in *Canna indica*, notes the development of the first three plumular leaves without there being any stem-apex present at all. In *Pistia* he found that seven or eight plumular leaves arose, each out of the base of the preceding, in a spiral sequence, with no sign at all of a stem-apex. He says: 'The clearly terminal position of the cotyledon is merely a single phenomenon in a whole group of such, but one of the most striking of the group, for the following leaves, which are equally with the cotyledon (relatively) terminal, are laid down in somewhat closer approximation to the preceding leaf-apex and thus form a gradual transition to the production of a so-called bud-axis with its own growing-point.' He says that if the theory of the cotyledon assuming the place of an aborted stem-apex be extended, as it ought to be, to the plumular leaves (which arise in the same way as the cotyledon) it would lead to absurdities.

I would draw particular attention to the *sympodial* arrangement of the cotyledon and the first few plumular leaves in the embryos above-mentioned. It involves the complete absence of an epicotyledonary axis and of laterally placed leaves. Hence, neither the cotyledon nor the plumular leaves concerned can be lateral in position, and no evidence can be adduced to show that this is a secondary and derived condition of things.

But the most fundamental evidence for the phylogenetically terminal position of the cotyledon has yet to be given. It rests on the sure and unequivocal basis of embryological data which are common to all the

divisions of vascular plants. In this connexion I cannot do better than quote Celakovsky :

'The cotyledon of Monocotyledons is, in my opinion, primitively single and terminal. The Monocotyledonous embryo is, before the bud and root are laid down, as Hanstein has stated, a simple thallus. This is completely homologous and equivalent to the sporogonium of Bryophytes in the embryonic state of the latter, as is shown by the similar mode of cell-division. The further construction of the thallus is indeed different from that of the sporogonium, corresponding to the phylogenetic advance from the earliest stage of the Thallophytes to the second stage of the Vascular Plants.' 'The simplest primitive metamorphosis, according to my repeatedly-expressed view, consisted in the development of the upper terminal portion of the embryo (which in the Mosses became the spore-capsule) as a purely vegetative assimilating organ, viz. a leaf, as occurs, according to Kny, in *Ceratopteris* among the Ferns before branching of any kind occurs, and the same thing is repeated in Monocotyledons. Just as the Moss-sporogonium becomes differentiated into two parts—the basal, sterile seta, and the terminal spore-capsule—in the same way is differentiated the embryonic thallus of Monocotyledons into the terminal leaf (cotyledon) and the basal stem-segment (hypocotyl), so that thus the Moss-capsule is phylogenetically homologous to the cotyledon, and the seta, or at any rate its basal portion, to the hypocotyl. In the embryonic thallus of *Ceratopteris* and of Monocotyledons, including the Grasses, the stem-bud arises laterally. . . . The embryonic thallus must be held to be the first segment (Glied) of the leafy shoot ; its hypocotyl represents at a later stage the first stem-segment of the further developed embryonic shoot, and its cotyledon the first leaf of the latter.'

The importance of this comparison of embryological structure in the different main plant-groups has never been adequately realized. The basis of comparison must be a perfectly sound one, as embryos are the least variable of all structures, and thus the most likely of all to reveal ancestral features. Hence, if the embryo of Monocotyledons and that of *Ceratopteris* exhibit the same construction as the sporogonium of Bryophytes, the conclusions deduced therefrom as set forth above are perfectly legitimate. The fact that Bryophytes are so distantly separated, in the genealogical tree of the Vegetable Kingdom, from Pteridophytes and Angiosperms can make not the slightest difference, for the embryo-structures, with their unvarying mode of development, constitute intimate connecting links at every stage.

The view above set forth could only be overthrown if it could be shown that the terminal position of the cotyledon in Monocotyledons and *Ceratopteris* has arisen as a secondary modification of the condition obtaining in Dicotyledons[1] and in other Ferns. There is, however, no real

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[1] The supposed two cotyledons of this class are, as Hegelmaier points out, present before there

evidence for such a thing, nor can any logical reason be given for supposing such a modification to have occurred. There is, on the contrary, plenty of evidence, some of which has been given above, for holding the opposite view, viz. that the cotyledon is primitively terminal.

A very important matter has yet to be referred to. It concerns the relative degree of development of the *lamina* and the *sheath* of the cotyledon in Monocotyledons. In the majority the lamina greatly overreaches in development that of the sheath. In the Dioscoreaceae and Commelynaceae, as Celakovsky points out, the state of affairs as described by Solms-Laubach is due to the fact that the sheath has developed at an earlier stage than, and consequently ahead of, the lamina (Fig. 10, A–C) ; *the apical portion of the embryonic thallus has been used up to form the sheath*, which appears in the form of a circular outgrowth ; there is *no shoot-growing-point present until a later stage* ; the lamina arises subsequently as a lateral outgrowth of the sheath.

Wherever in Monocotyledons the *appearance* of a second cotyledon is found, it can be traced to a special development of the cotyledonary sheath or of the basal portion of the lamina, which inevitably suggests a peripheral or lateral position of the one or two cotyledons. This it is which has mis-led Coulter into imagining that in the Grass-embryo either two or one, as the case may be, *lateral* cotyledons are present. The appearance is simply due to the very special development of the lamina of the cotyledon as a haus-torium and of its basal region in the form (where present) of the epiblast. The latter organ Celakovsky has shown to correspond to modified appendages of the lamina of the cotyledon ; the development shows that the coleoptile is the ligular portion of the cotyledon, and that the whole arises as a single organ, on essentially the same lines as in other Monocotyledons, before any other leaves or any trace of a stem-apex is present. Under these conditions it can be nothing else but *terminal.* Coulter himself states that no stem-tip is present even at quite a late stage. In the absence of a stem how is it possible, I ask, for the cotyledon or cotyledons to be peripheral or lateral ? Peripheral or lateral to what ? What is this ' peripheral zone ' he mentions from which the supposed two cotyledons arise on opposite sides ? It must be one of two things. : either (1) the earliest stage of the two first leaves (cotyledons) whose bases are united to form a sheathing structure, and whose position, of course, must be lateral to a stem ; or (2) it repre-sents a single cotyledon with its well-developed basal portion. Now (1) cannot possibly be the explanation, for at that stage there is a complete absence of any stem to which the cotyledons could be lateral ; for it is an absolute impossibility for two distinct cotyledons to exist without any axis to which they are attached. Hence (2) must be the true explanation,

is any trace of an epicotyledonary axis ; hence they cannot be two lateral cotyledons, but a single bifid terminal one.

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and the 'peripheral zone' represents the cotyledon with its well-developed basal portion, and this single cotyledon, in the absence of a stem, must, of course ; be terminal to the whole embryo, as the earliest stages of development show it clearly to be.   From all which it appears that Coulter's position with regard to this matter is ambiguous and illogical.

It having been deduced from all that has been set forth above that in Monocotyledons (all representatives of which have essentially the same type of embryo- and seedling-construction) the cotyledon is always single and terminal, the appearance of two lateral cotyledons in the Grass being due to the supervention of secondary modifications, the two remaining cases
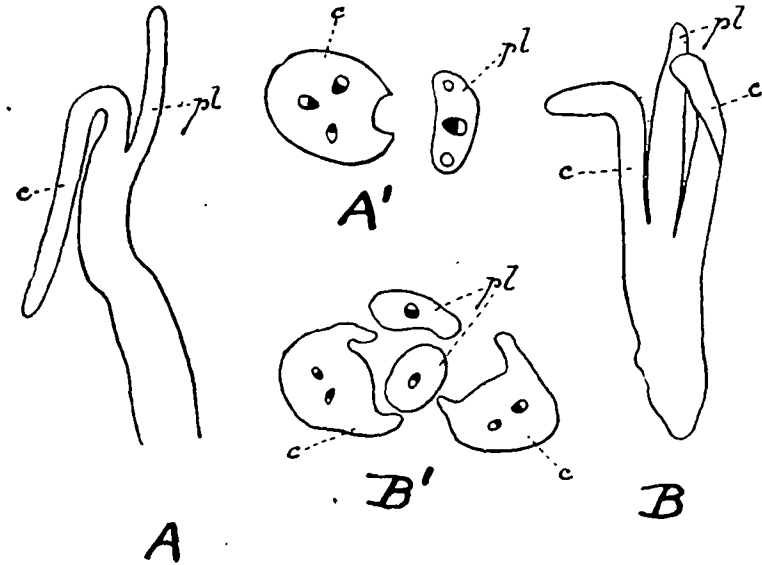

FIG. 8.   *Agapanthus umbellatus* (African Lily).   A = outline of normal embryo ; A' = transverse section of cotyledon (*c*) and plumular leaf (*pl*).   B = outline of dicotyledonous embryo.   B' = transverse section of cotyledons and plumular leaves.   (After Coulter and Land.)

which Coulter and Miss Farrell marshal, in the endeavour to demonstrate their thesis of primitive dicotyledony in all Angiosperms, can be easily dealt with.   I refer to the embryos of *Cyrtanthus* and *Agapanthus* in which two cotyledons occur.   Both cases can be quite well explained as accentuations of the condition met with in the Dioscoreaceae and Commelynaceae in which the development of the sheathing portion of the cotyledon sets in at an early stage, and proceeds to an equal degree with that of the lamina.

On the analogy of the Dicotyledons, if the orthodox view is held with regard to the morphology of the embryo of this class, then it is quite obvious that two cotyledons are present in these cases of *Agapanthus* and *Cyrtanthus*.   And it is a most rare and interesting observation to have made that in these cases a second cotyledon is formed by the excessive develop-

ment of the sheath of the other cotyledon. No previous case of the kind has ever been cited, so that the authors have every reason to make the most of it. I say that on the current view their conclusions as to the facts hold good. But the view I prefer to maintain here is that in Dicotyledons, owing to the complete absence, in the majority of cases, of an epicotyle-donary axis, two cotyledons cannot possibly be present, but only a single terminal cotyledon which has deeply divided. This argument, therefore, also applies to the cases of *Agapanthus* and *Cyrtanthus*, although in these the appearance of two cotyledons is due to quite another cause, which constitutes the sole importance of the observation.

That no phylogenetic significance attaches to the phenomenon can be deduced from the fact that only a *single* seedling of *Agapanthus*, according to Coulter and Land's account, possessed two cotyledons (Fig. 8). To suppose that a unique instance, the only example ever known, would be likely to exhibit the character of the ancestors of the whole group is to my mind next door to an impossibility.

If this had been the ancestral feature, instances would certainly be much more numerous, not only in this genus, but in others as well.

The phenomenon must therefore represent a *new*, aberrant departure, of progressive, not reversionary, nature.

FIG. 9. *Cyrtanthus sanguineus.* A. Exterior view of young embryo. B. Longitudinal section through the centre of A. C. Exterior view of an older embryo. *c* = lamina of cotyledon; *s* = sheath of cotyledon. (After Miss Farrell.)

The same argument applies to *Cyrtanthus*; although the two cotyledons may occur as a normal feature of the genus (Fig. 9), yet the features of a single genus cannot be taken as indicative of the characters, whether modern or ancestral or both, of the whole class; they are much more likely to be progressive and novel.

That the embryos of one or two members of a modified order like the Amaryllidaceae, with its inferior ovary and other idiosyncrasies, would exhibit more ancestral characters than those of members of less modified orders is in the highest degree improbable. They are more likely, in agreement with the other advanced characters of the order, to show a progressive type of construction.

One may securely conclude, therefore, on all these grounds that the extra structure, opposed to the cotyledon, in these two genera is without doubt a second cotyledon, the result of the very exceptional development of
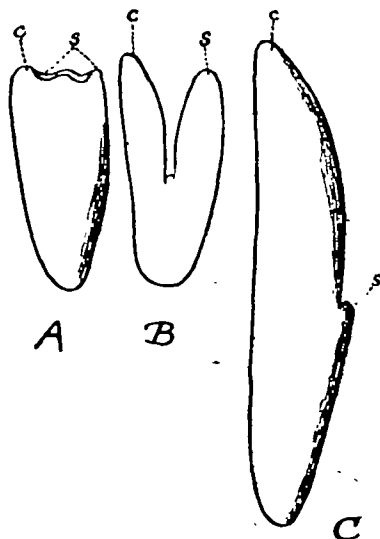
the sheath of the first one; but that the theoretical deductions drawn from this fact by Coulter and Land and Miss Farrell cannot in any way be accepted.

The same conclusions may be drawn with regard to the embryo of Dioscoreaceae and Commelynaceae (Fig. 10); it may be regarded as exhibiting a progressive feature; the former order is certainly a very
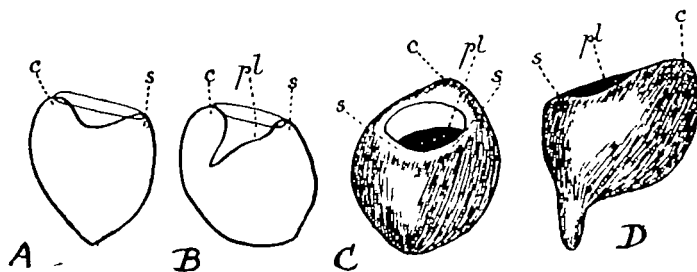

FIG. 10. A and B. *Heterachtia* (Commelynaceae). Outline of young embryo (plumular axis completely absent). C. *Tinnantia* (Commelynaceae). Young embryo. D. *Tamus communis* (Dioscoreaceae). Young embryo. *c* = cotyledonary lamina; *s* = sheath; *pl* = indication of plumule. (After Solms-Laubach.)

specialized one, and as regards the latter it is in several ways more specialized than the closely allied order Liliaceae, which is more typical of Monocotyledons generally.

CONCLUSIONS.

1. The *scutellum* is the lamina of the cotyledon, corresponding to that of the foliage-leaf of the Grass. That part of the cotyledon which corresponds to the *sheath* of the foliage-leaf is only present at an early stage of development, and later becomes completely obscured.

2. The *coleoptile* is part of the cotyledon, viz. that which is represented in the foliage-leaf by the *ligule*; this is clearly demonstrated by the early developmental stages of the embryo. The vascular anatomy and the abnormal forking strongly suggest a ligular structure.

3. The *epiblast* is part of the cotyledon, corresponding, as deduced by means of comparative morphological treatment, to the *auricles* of the base of the lamina of the foliage-leaf in certain Grasses.

4. The cotyledon of the Grass differs in no *essential* feature, either as regards its development or morphological construction, from that of other Monocotyledons.

5. The *mesocotyl*, as shown by the above facts with regard to the coleoptile, and by its anatomical structure, is the elongated primary node.

6. The *position* of the cotyledon in all Monocotyledons, as shown by the facts of development, there being no epicotyledonary axis present

on its first formation, is always *terminal,* and is the natural continuation and termination of the hypocotyl.

7. The balance of development of the cotyledonary lamina and sheath may vary in favour of the latter in certain cases, and at certain stages of the ontogeny, as in Dioscoreaceae and Commelynaceae.

8. In certain instances, as in a seedling of *Agapanthus* and in *Cyrtanthus* (both belonging to the Amaryllidaceae), the sheath may develop, at one stage or another, into a second cotyledon. This is not an ancestral, reversionary character, but a novel and progressive one.

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