

On the Structure of the Stem of *Rhynchoptetalum montanum*
(Fresen.) *. By F. O. BOWER, M.A., F.L.S.

[Read December 20, 1883.]

(PLATES XXXVI.-XXVIII.)

RHYNCHOPETALUM MONTANUM is a native of Abyssinia, growing in districts 11,000 to 13,000 feet above the level of the sea. It differs from the allied *Lobelias* in being a plant which lives through more than a single year. The small lanceolate leaves first formed are succeeded as the plant grows older by larger ones, arranged on a more complicated plan, while the earlier leaves are successively thrown off and wither. The stem, which meanwhile increases in bulk, is completely covered externally by the scars or bases of leaves which have thus been thrown off. These scars appear as diamond-shaped areas on the surface of the stem, and are covered by a thick layer of corky tissue, in which the ends of the vascular bundles of the leaf-trace (five in number) may often be clearly seen. As the stem increases in bulk, the corky covering is split and fissured, so that the outline of the leaf-scars becomes unrecognizable. In this condition the old stem is not unlike that of some Cycads in external appearance. The stem, growing thus for four or five years, gradually attains a considerable thickness (a specimen in the museum at Kew is about 5 inches in diameter); it is columnar in form, and is, in most cases at least, unbranched; it reaches a height of 12 to 15 feet.

Internally it is succulent, especially when young; older stems are of sufficient hardness and strength to be used in Abyssinia for building purposes.

Axillary buds appear in the axils of the leaves at an early stage; but they are not developed beyond the first stages until the leaves, in the axils of which they are placed, have fallen off. Some, but not all, of them grow actively, developing a tuft of leaves, and on their underside often forming roots, which establish themselves in the soil. These axillary buds, which often appear as though they were of adventitious origin, especially at

* De Candolle, 'Prodrômus,' vol. viii, p. 396. Fresenius, Bot. Zeit. Flora, Oct. 1838, p. 603, and figured by him, 'Museum Senckenberg.' iii. Taf. iv. Richard, Flora Abyss. vol. ii. p. 9. Figured from a Kew specimen, Bot. Mag. 5587.

the lower part of the stem, are undoubtedly of use in carrying on the life of the plant when the main axis, having flowered and fruited, dies down, as in the case of *Agave* (Richard, *l. c.*). They are used in propagating the plant artificially.

Not only is *Rhynchoptetalum* remarkable among the Lobeliaceæ for its size and external appearance, but also for its internal structure. *Lobelia macrostachya*, *L. splendens* var. *ignea*, and *L. Erinus*, also *Siphocampylus*, have been examined; but the structure of the stem of these plants was in each case found to be normal.

The early stages of development of the vascular system of the stem and leaves were studied in the young axillary buds above mentioned. It is assumed that the structure of these is not unlike that of young seedlings. The latter have not been investigated, since the available plants at Kew had all been derived as axillary buds from older plants, and not raised from seed.

In these young axillary buds the arrangement of the leaves is simpler and less crowded than on older axes; and therefore the vascular connexions of each leaf can be more accurately distinguished from that of its neighbours than is possible in older stems.

Successive transverse sections of such buds show that the first formed bundles are those which take a median course in the young leaf (*x* in figs.), and on entering the stem pass inwards and arrange themselves in the normal manner, in a more or less regular circle, about the centre of the axis. Shortly after these the first pair of lateral bundles of the leaf-trace are formed (*y* in figs.), which likewise run directly into the stem, perpendicular to its surface, then, curving suddenly towards the central bundle, they coalesce with it in the cortex at points nearly opposite one another, and at a short distance outside the ring of bundles above described. This coalescence of the first pair of lateral bundles of the leaf-trace with the central bundle seems to be the rule, though in the older stems such a connexion is not always to be made out, and it is possible that it does not always occur.

Almost simultaneously with the first pair, or slightly later, a further pair of lateral bundles appears (*z* in figs.), the connexions of which are less regular than those of the first-formed pair; they are, however, attached, in the majority of cases, and especially in young buds, to the bundles of the first pair. The minute structure and composition of the young bundles present no peculiarities worthy of special remark.

Thus we have in the young bud of *Rhynchoptetalum* a leaf-trace

consisting of five bundles, which enter the stem. In the cortex the lateral bundles fuse successively with the central bundle, which, pursuing a direct course towards the centre, finally ranges itself, with similar bundles from other leaves, in the central ring-like series, such as is normally found in Dicotyledonous stems.

Soon after the lateral bundles of the leaf-trace become distinguishable, a new system of bundles of exclusively cauline nature is formed in the cortex. These may be called "cortical bundles" or "cauline peripheral bundles" ("Rindenstränge," *cf.* Mettenius, *Beitr. zur Anat. d. Cycadeen*). They first make their appearance as groups of small cells, resulting from the division of cells of the cortex. The central portions of these groups develop as xylem, the peripheral portions as phloem, while a slowly active cambium lies between them. The result in each case is the formation of a series of wedge-shaped bundles, which, being arranged radially round a centre, constitute together a cylindrical group. The xylem, which forms the greater part of these bundles, consists of spiral and pitted elements, surrounded by and imbedded in parenchyma, which is present in considerable quantity; in the phloem, also, much parenchyma is present, together with laticiferous vessels. The course which these bundles take is a more or less steep spiral, according to the arrangement of the leaves; they run almost at right angles to the parastichies in which the leaves are arranged, while their position is such that the median bundle of each leaf is always about halfway between two successive cortical bundles. The spiral cortical bundles are themselves connected with the lateral bundles of each leaf-trace; the exact point of junction varies, but is usually at or near the sharp curvature of the lateral bundle towards the central bundle of the leaf-trace, prior to their coalescence. The cortical bundles do not remain as single strands throughout their course, but here and there they separate into two or more strands, which soon fuse again to a single strand; they thus appear when isolated as a succession of loops of varying size (Pl. XXXVIII. fig. 4). In older stems, where the vascular system has been strongly developed, it has been possible to obtain vascular skeletons by the rotting of the parenchymatous tissues; and in these the connexions of the cauline and the common systems and the course of their constituent bundles have been more exactly observed. Part of such a skeleton is represented in fig. 4, in which are shown the steeply spiral

cortical bundles (*a, a*). These, as above noted, often split up and again coalesce, thus forming a series of loops. Further, the successive spirals are connected one with another by branch bundles, which run almost vertically (*b* in the figures). The space between them is thus cut up into a number of diamond-shaped areas; through the centre of each of these areas the central bundle of a leaf-trace passes on its course from the leaf (or leaf-scar) to the central ring of common bundles, thus describing a course in a direction perpendicular to the surface of the cylindrical network of cortical cauline bundles. As each bundle passes through the network, it gives off right and left branch bundles, which are the branches connecting the lateral bundles of the leaf-trace with the central bundle. These, as above described, are connected with the cortical system at or near to the point where they curve suddenly in their course. The result is that in old stems it appears as though lateral bundles of the leaf-trace were given off originally from the network of cauline bundles, whereas in reality the cauline system is of later origin, and connects the earlier-formed vascular systems of successive leaves one with another. The position of the four-sided leaf-scars and of the several bundles of the leaf-trace relatively to the network of cortical bundles will be readily understood on comparing figs. 4 & 5, Pl. XXXVIII.

Besides the bundles hitherto described, other smaller branch bundles may be seen in old stems traversing the outer portions of the cortex (fig. 2); the course of these does not appear to be constant, and has not been accurately followed.

As it grows older the stem increases in bulk. Judging from a single dry specimen of an old stem in the museum at Kew, this would appear to be chiefly due to a secondary increase of the bundles of the normal vascular ring, which, in the specimen in question, is nearly 2 inches in thickness. But the bundles of the cortical system, as well as the central bundles of the leaf-trace, also increase in bulk, and appear, in the large specimen at Kew, at least $\frac{1}{8}$ inch in diameter.

No system of cortical bundles was found, even in the oldest roots examined.

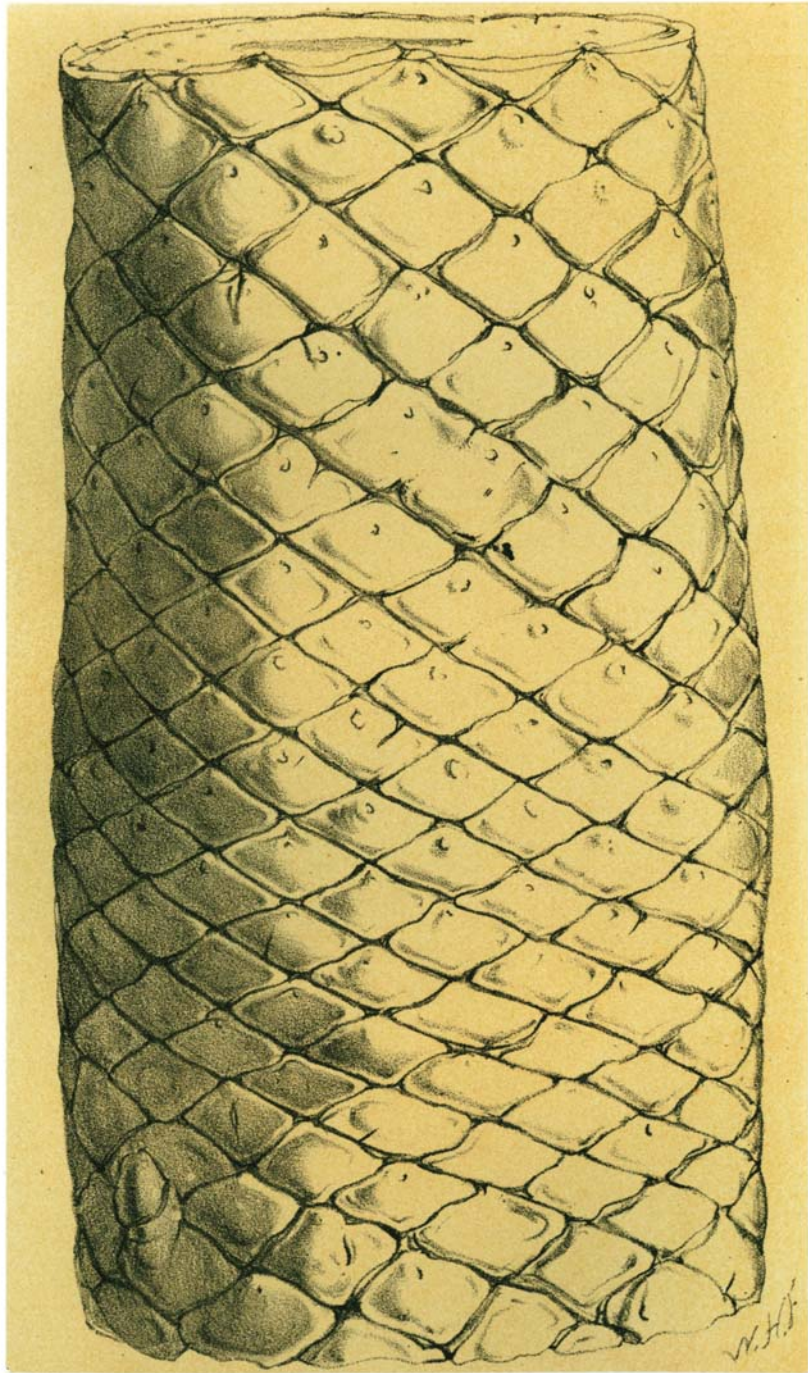
It remains to draw a comparison between this abnormal arrangement of bundles in *Rhynchopetalum* and that in other plants.

Among Dicotyledons, cortical bundles formed at an early period in the growing stem, and having a definite position relatively to

the bundles of the leaf-trace, are found only in comparatively few cases; and in many of those cases such cortical bundles may be regarded merely as branches or continuations of the common bundles of the leaf-trace, which ultimately enter the normal ring. This is the case in species of *Lathyrus*, in *Casuarina*, and many *Begonias*. In other instances the cortical bundles have a similar origin to those above cited; they, however, do not enter the ring, but form a cortical system connected with the ring by anastomoses at the nodes. This arrangement is found in the Calycanthæ and many Melastomaceæ. In a third series of succulent plants, including especially forms with reduced leaves, bundles are found ramifying in the cortex as in the lamina of the leaf; and, finally, in the winged Rhipsalidaceæ the common bundles of the leaf-trace are chiefly cortical and surround a central ring, which is for the most part cauline.

It is clear that the case of *Rhynchoptalum* does not coincide exactly with any of these, since, as above stated, the cortical system does not consist of branches of bundles of the leaf-trace, but are cauline bundles. A closer comparison may, however, be drawn between the stem of *Rhynchoptalum* and that of *Cycas* as described by Mettenius*. There the girdle-like bundles of the leaf-trace are connected with one another by bundles, which pursue a nearly vertical course and together form an "accessory cortical system." They originate from a secondary meristematic activity of longitudinal rows of cells of the cortex, strands of small cells being thus formed, which develop into small vascular bundles with a radial arrangement of their elements round a centre. This is fundamentally the same process as has been above described for the cortical bundles of *Rhynchoptalum*. The chief difference between the two cases lies in this: that in *Rhynchoptalum* the cortical bundles run obliquely, and together form an approximately regular network with four-sided meshes, which bear a definite relation to the bases of the leaves, and therefore also to the bundles of the leaf-trace; in *Cycas*, however, the bundles of the accessory cortical system are not thus regularly arranged, and pursue an almost vertical course. In both cases the mode of origin is the same; and in both cases the

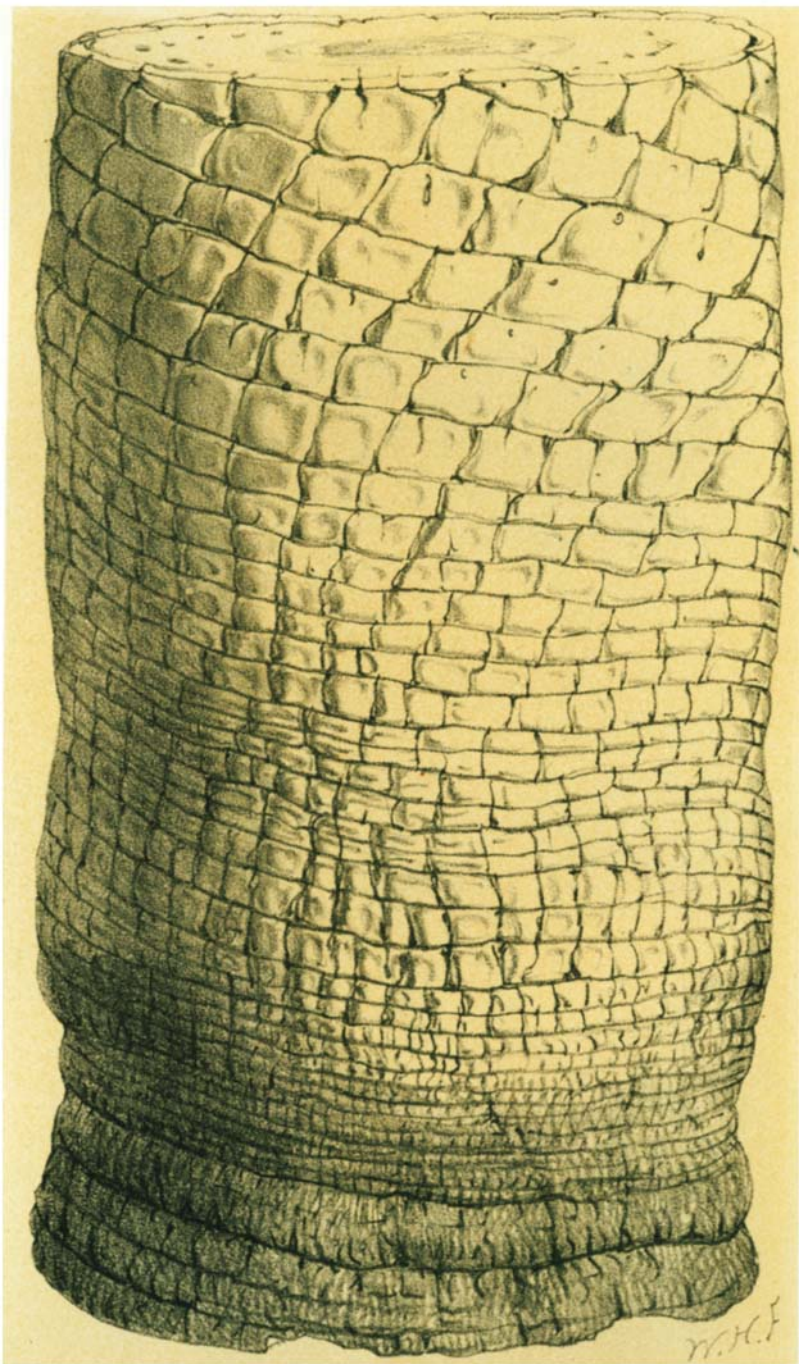
* On *Cycas circinalis*, cf. description by Miquel, 'Ueber d. Bau' &c.; on *Cycas circinalis*, Linnæa, Bd. xviii, p. 125. On *Cycas revoluta*, cf. Mettenius, "Beitr. z. Anat. d. Cycadeen," Abhandl. d. k. Sächs. Ges. d. Wissensch. vii. p. 567.



W.Hood Fitch lith.

RHYNCHOPETALUM MONTANUM.

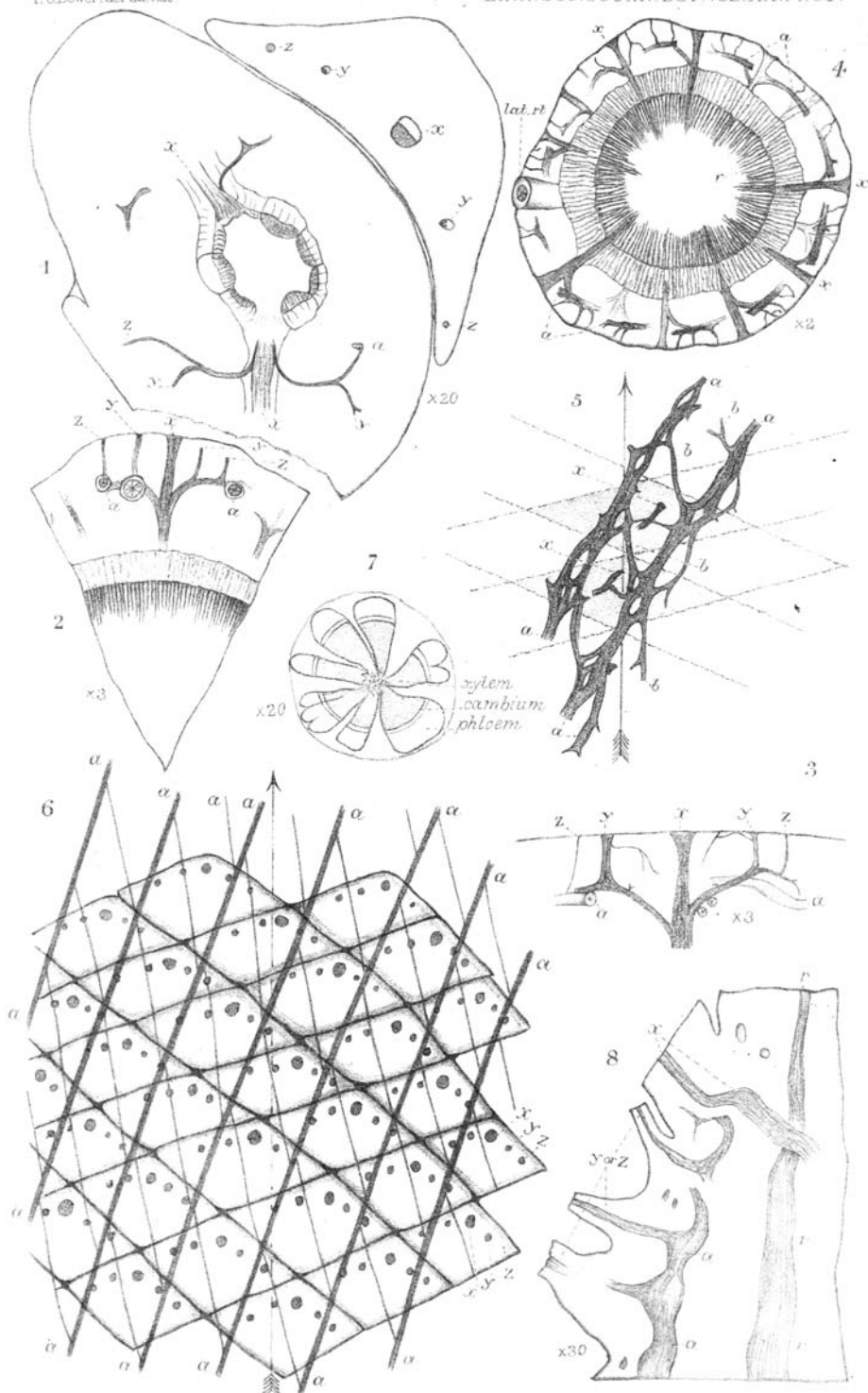
Hanhart imp.



W.Hood Fitch lith.

RHYNCHOPETALUM MONTANUM

Hanhart imp.



cortical system thus formed is permanent and capable of secondary increase.

In *Cycas* the occurrence of this system of accessory bundles in the cortex may be regarded as a response to a physiological need. The vascular bundles being the chief and most rapid channel of transfer of water and of nutritive materials, if *Cycas* were dependent only upon the girdle-like bundles of the leaf-trace for this transfer between stem and leaf, the channel would be very long and indirect. The accessory cortical bundles act in this case as short cuts, so to speak, reducing the distance which must be traversed, and at the same time making the vascular connexions of the massive cortex much more complete.

It can hardly be doubted that the bundles of the cortical system of *Rhynchopetalum* have a similar physiological function, though it must be confessed that the requirements are not so great as in the case of *Cycas*.

In conclusion, it may be again noted that, not only in internal structure but also in external appearance the old stem of *Rhynchopetalum* resembles that of some Cycads. This is especially true for the lower portions of the old stem, where the increase of girth has been accompanied by the formation of fissures in the outer tissues, so as to obliterate the scars of the leaves. Such a case of similarity of stems of plants belonging to distinct classes should serve as a warning to palæontologists. It can easily be imagined that even a well-preserved fossil specimen of the stem of *Rhynchopetalum* might pass as that of a Cycad, and *vice versa*.

DESCRIPTION OF THE PLATES.

Lettering used throughout:—*a*=main cortical bundles; *b*=secondary branches; *r*=normal ring of bundles in the stem; *x*=median bundle of leaf-trace; *y*=first pair of lateral bundles of leaf-trace; *z*=second pair of lateral bundles of leaf-trace.

PLATE XXXVI.

Upper portion of an old stem of *Rhynchopetalum montanum* seen from outside; the spiral lines running over the leaf-scars indicate the position of the spiral cortical bundles.

PLATE XXXVII.

Lower portion of the same stem as in foregoing Plate, showing the gradual obliteration of the leaf-scars by formation of longitudinal fissures.

PLATE XXXVIII.

Fig. 1. Thick transverse section of a young shoot, made transparent with potash

and glycerine, and showing the vascular system of three leaves; the cauline cortical bundles have hardly begun to make their appearance. $\times 20$.

- Fig. 2. Section through the periphery of an older stem, showing the connexions of the five bundles of a single leaf-trace (x, y, z) and their position relatively to the cortical bundles, $a a$. $\times 3$.
- Fig. 3. A similar section, showing in addition the irregular cortical bundles, the course of which was not followed.
- Fig. 4. Thick transverse section of a stem; the parenchyma has been partly dissected away, and then made transparent with potash and glycerine.
- Fig. 5. View from without of a small part of the system of cortical bundles of an old stem which had lost all the soft parenchyma by rotting. The dotted lines indicate the position of the leaf-scars relatively to the bundles.
- Fig. 6. View of the diamond-shaped leaf-scars from without, showing the five bundles of each leaf-trace; behind is drawn a diagram of the network of bundles of the cortical system; the arrow shows the direction of the main axis.
- Fig. 7. Transverse section of a single circular group of cortical bundles; the parenchyma at the periphery is pressed out of shape by the increase in bulk of the group of bundles. $\times 20$.
- Fig. 8. Longitudinal radial section of stem, showing the relative positions of bundles of leaf-trace (x, y, z), cortical bundles (a), and the normal ring (r). $\times 20$.

On the Development of Starch-grains in the Laticiferous Cells of the Euphorbiaceæ. By M. C. POTTER, B.A., St. Peter's College, Cambridge. (Communicated by Dr. S. H. VINES, F.L.S.)

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THE Euphorbiaceæ are characterized by possessing numerous laticiferous cells in the ground-tissue of their stems and leaves; these, in addition to containing latex, also contain large quantities of starch-grains, peculiar and irregular, known as rod- or bone-shaped. These grains appear to have been first observed by Meyen* about the year 1836.

As regards the formation of starch, Crüger† says:—

“All starch-grains come from the protoplasmic layer, which lines the inner wall of the cell as long as it is capable of development, and as long as protoplasm exists in the cell. In all starch-grains where the layers are distinctly formed, and a

* ‘Ueber die Secretions-Organe der Pflanzen:’ Berlin, 1837. Schleiden’s ‘Principles of Botany,’ p. 20.

† “Westindische Fragmente, Drittes Fragment,” Bot. Zeitung, 1854.