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ADVENTITIOUS BUDDING AND BRANCHING IN *CYCAS*,

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[7 FIGURES IN THE TEXT.]

WHILE I was in Japan (1907-1909) I had the opportunity of examining numerous specimens of *Cycas revoluta* living in the open, some of which were very old. Many of these were much branched in an irregular way. A photograph of some examples of the kind is given by Miyoshi<sup>1</sup> in his series of habit photographs of Japanese plants, and there are some drawings in Wieland's<sup>2</sup> work on the fossil cycads; while mention is made of branching Cycads by Caldwell<sup>3</sup>, Pearson<sup>4</sup> and others.

The brief notices of the subject in the literature, however, had not prepared me for the frequency or the extent of the branched plants, which were often much more like bushes than like "palms." One specimen in particular was most noteworthy, and as it seems greatly to exceed, in the quantity of its branching, those hitherto mentioned. I give a small sketch of it (Fig. 8) which is traced from a photograph.



Fig. 8. A sketch of the much branched *Cycas* at Yejiri, traced from a photograph. The plant bore twenty-six huge male cones the year this photograph was taken, and had also innumerable crowns of leaves without cones.

The sketch does not show nearly all the detail of the plant, and gives but a poor idea of the enormous extent of the complex of branched trunks. The thick axes curve about in many directions and are propped up with strong supports, while the leaves of the

<sup>1</sup> Miyoshi, M. "Atlas of Japanese Vegetation," phot. 31.

<sup>2</sup> Wieland, G. R. "American Fossil Cycads," Carnegie Institute of Washington, 1906.

<sup>3</sup> Caldwell, O. W. "Microcycas calocoma," Bot. Gaz. 44, Aug., 1907.

<sup>4</sup> Pearson, H. H. W. "Some South African Cycads: their Habitats, Habits and Associates." Rep. Brit. Assoc., York, 1906.

leafy crowns interlock all over the surface. I counted twenty-six huge male cones on this plant on one of my visits to it. I had occasion to spend several days studying this and other plants in the neighbourhood and thus visited it more than once, though I was investigating another feature in it. I soon noticed the remarkable little bulbils which seemed to be growing all over the thick trunks. These varied much in size, and were to be found everywhere on the tree, even down to the very base of the oldest trunk. These buds, nearly full size, are seen in Fig. 9, (i), (ii), (iii) and (iv), in several of their early stages. Fig. 9 (iv) shows a complete isolated "bud," natural size, of the type commonest on the parent tree. The smaller buds, like that in Fig. 9 (i) were also numerous, but largely hidden between the armoured scales of the corrugated leaf-bases.

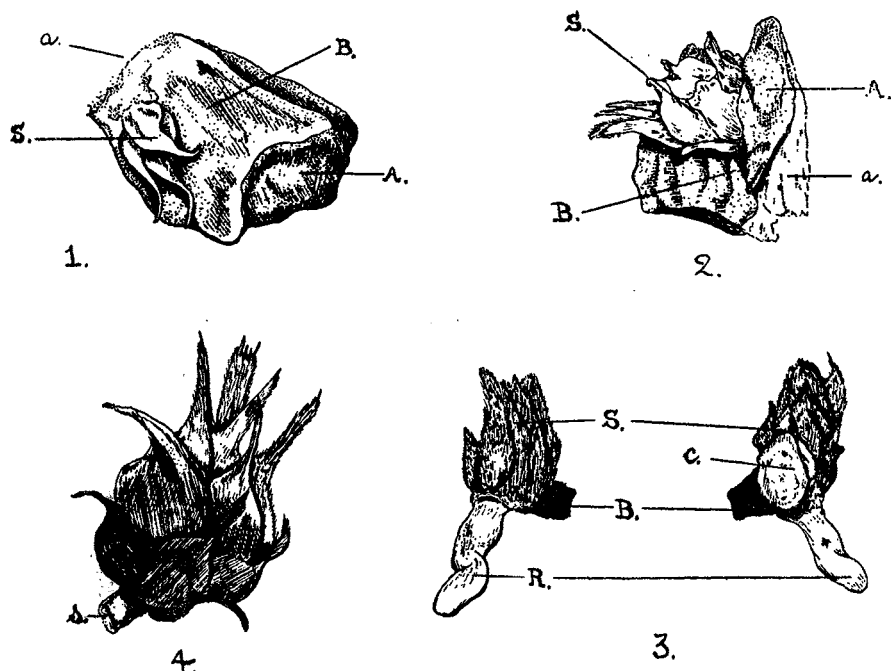


Fig. 9. A. Outer end of leaf base. B. Upper surface of leaf-base. a, end of leaf-base torn away from the stem-cortex.

(i.) Leaf-base detached, with a small "bud", s, growing on its upper surface.

(ii.) Older "bud" with hard outer scales and hairy inner ones seen between two leaf-bases.

(iii.) Two views of another "bud;" s, shoot with hairy scales, c, lateral attachment of the sprout to the leaf-base, R, root of sprout growing into the air.

(iv.) Older "bud" which has a short axial portion, s. This bud was in active growth, the inner hairy scales protecting small leaves,

As even the Tokio botanists to whom I mentioned my preliminary observations did not seem to have given the buds special attention, it appeared worth while to record the following facts about them.

The "buds" arise, apparently at any time and quite irregularly on the leaf-bases all over the older plants of *Cycas revoluta*. I counted back from the crown 228 whorls, and at this level found many of the small and flourishing buds growing on the leaf-bases all round the trunk.

Behind this region the whorls became indistinct and it was difficult to count accurately, but there must have been at least another 100 whorls, and even there the leaf-bases were fresh and bore "buds." Externally the old leaf-bases of *Cycas* appear to have entirely dried up and hardened, and they form, as is often described, a corrugated armour round the stem. As they were still capable of budding I cut into them and carefully examined their condition. The external blackened part is very hard and protected by several layers of cork; between it and the inner still fresh part of the leaf-base, are five or six areas cut off by successive active zones of cork. This is seen in Fig. 10.

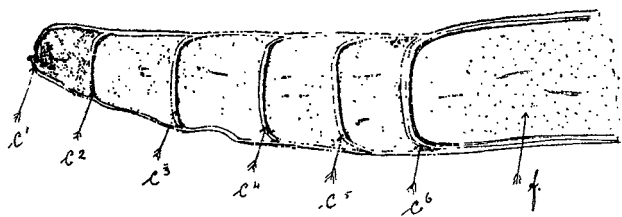


Fig. 10. Section through an old leaf-base showing successive zones of cork,  $c^1$ ,  $c^2$ , etc., and the persistent base,  $f$ , packed with starch.

The zones between the cork layers contain much tannin, but the persistent base behind is fleshy and quite juicy and fresh. The cells in the latter region are packed with starch grains, and the vascular bundles and mucilage canals are all quite normal. It is from this fresh, basal portion that the "buds" spring.

The manner of their growth and the course of the vascular system in these buds is very various, but all the many I examined seemed (it was in some cases difficult to determine this absolutely) to arise from the leaf-base itself and *not* from the axis, or to be in any way connected with the axis at first. In some cases this is perfectly evident, as in Fig. 9 (i), where the "bud" lies on the surface of the leaf-base some distance from the axis. Without injuring the trees

in a way that was not permissible it was not possible to collect all the material I should have liked; but I cut into the axis in several places and found leaf-bases still about an inch thick bearing buds which had no traces going back to the axis. In this connection an old wound on one of the trees should be mentioned. This wound had cut out an area of the leaf-bases about six inches square, leaving the axis itself exposed. No buds were formed in this region, though the leaf-bases round bore many, and some of these had exposed roots such as are shown in Fig. 9 (iii.) r and Fig. 11.



Fig. 11.

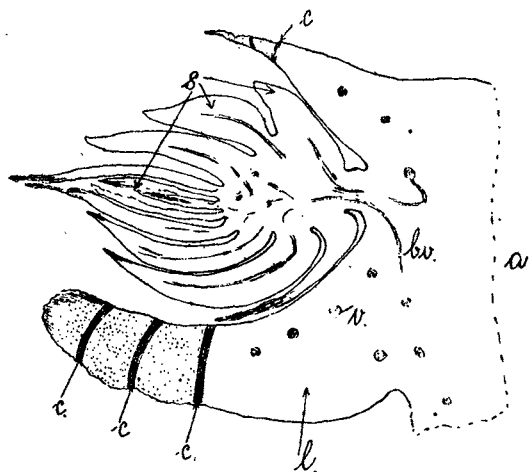


Fig. 12.

Fig. 11. Sketch of one of the irregular roots which stand out externally from the buds growing on the leaf-bases. Some roots like this tend to penetrate the bases again after growing for some time in the air. *l*, end cut off from the "bud," *t*, smooth tip standing out in the air.

Fig. 12. Diagram of a section through a "bud" and the leaf-base from which it has arisen. *a*, axis of parent plant. *l*, leaf-base with zones of cork *c*, and vascular bundles *v*. *bv*, bundles running out from the "bud" and dying away in the leaf-base. *s*, scales of the "bud."

Series of sections show that the "buds" are really attached to the leaf-bases. They arise in general on the upper surface of the base and grow directly upon it with no root or even definite constriction. The vascular cylinder of the bud tends to run through the flesh of the leaf-base for only a short distance, but may even penetrate an adjacent base. In any case it soon dies out, sometimes without seeming to connect definitely on to any of the vascular strands of the leaf-base. The diagram in Fig. 12 shows the attachment of such a "bud." This drawing is made from a longitudinal section through the whole structure.

The "bud" here has a slight constriction at the base, which carries it out a little from the leaf-tissue on which it is seated. Such an axial portion is clearly seen also in the larger "bud" illustrated in Fig. 9 (iv), *s*. The "buds" are generally entirely sessile however. The vascular strand running up each of them, and in the bases immediately below, is circular, with a fair development of wood in the case of the larger "buds." This strand does not continue very far in the tissues of the leaf-base and seems to end there blindly while the buds are still small.

"Buds" like that shown in Fig. 9 (iii) are much more rare. As seen in the figure, it is attached rather laterally to the parent leaf-base, see B., Fig. 9 (iii) and the "bud" with its root looks very like a seedling with a thick primary root and a sucker on one side. Although there was no opportunity for making experiments with the living plants, it seems likely that these are the buds which might be detached and grow independently.



Fig. 13. Longitudinal section through one of the "buds" which has persisted for a long time. *s*, fresh apical portion; *os*, old outer scales with decaying tips cut off by zones of cork, *c*, and with thick bases packed with starch.

Comparatively few large roots such as are figured in Fig. 11 are to be found on the trees. Their behaviour is uncertain, and in several instances I noted that they penetrated the leaf-bases again after running for two or three inches in the air.

The structure of the "buds" themselves has been indicated already in the figures. A young "bud" such as is shown in Fig 9. (i) *s*, is composed of only two or three soft scales, but the older "buds" are well armoured as they are exposed and seem to be

prepared to spend a long time dormant. The outer scales are very hard and spiny and the inner, unfolding ones are covered with dense hair. They reach a considerable size, double that shown in Fig. 9 (iv) before they unfold the small green foliage leaves (cf. Fig. 14, *b* and *c*) which appear in the development of active buds, but these are laid down while they are still about the size of the "bud" in Fig. 9 (ii).

Many of the small "buds" show signs of having been vegetating between the leaf-bases for a long time, and their outer scales are much blackened and dried up. Such a one is shown in Fig. 13 cut in longitudinal section. This diagram shows the small fresh apex and the old scales behind it which have become very thick and fleshy. The latter are filled with starch at the base, and the decaying tips are cut off by several successive zones of cork, *c*.

The power to cut off almost any part of its tissue and grow behind the separating layer is a remarkable feature of the Cycads. Solms Laubach<sup>1</sup> noted the persistency of the leaf-bases, and figured some which are cut off by three successive layers of cork; while even the seeds will continue to grow<sup>2</sup> when the internal aborting portions are cut off by a corky layer. This power serves the "buds" in good stead and enables them to linger on almost indefinitely.

These buds have so far been described merely as phenomena interesting in themselves. Their real importance, however, lies in the fact that they appear to be the clue to the real nature of most of the "branching" in *Cycas*. Without overlooking the possibility of other methods of branching, the behaviour of the buds makes it clear that probably the great majority of "branched" plants are simply those in which one or more of these adventitious "buds" developed from the leaf-bases, had grown till it rivalled the main axis. Such plants as the one figured in Fig. 14 are exceedingly common in Japan, and show the stages of the process.

The Japanese pot specimen figured by Wieland (*loc. cit.*) in his Fig. 10, p. 39, as a *hoso*-type will be now recognised as an excellent example of the branch-forming growth of these buds. While such plants are much cultivated by Japanese gardeners, they also nip off the buds and grow them as independent plants.

Once my attention was attracted to these buds I found that

<sup>1</sup> Solms Laubach, Graf zu. "Die Sprossfolge d. *Stangeria* u. d. übrigen Cycadeen." Bot. Zeit., 1890, cf. p. 226, Taf. II., Fig. 2.

<sup>2</sup> Stopes, M. C. "Beiträge z. Kenntnis d. Fortpflanzungsorgane d. Cycadeen," Flora, 1904, cf. p. 446 and 453.

they were almost universal in the older specimens of *Cycas* in Japan, and that nearly every "branch" showed signs of having arisen in the beginning from one of them. According to the position of the prospering bud, the kind of branching varies, and when the bud develops near the apex, once it has reached a diameter comparable to that of the main stem, it gives the plant much the appearance of a dichotomous trunk. When the "bud" increases to such an

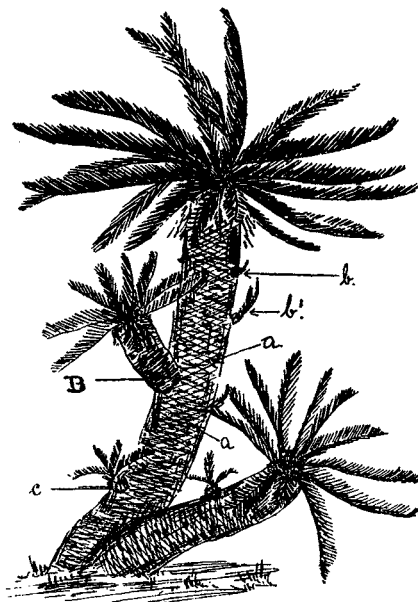


Fig. 14. A *Cycas* showing the beginning of the so-called branching. At *a* are the small "buds" between the leaf-bases. At *b* one enlarged, at *b* (i.) one bearing a few foliage leaves. A large "bud" with a full crown of leaves is seen at *c*, while it is evident that the "branch" *B* is simply a further growth of a "bud" similar to *c*.

extent of course, strong woody connections are formed with the main axis, and the leaf bases, on which it originated are crushed back, so that the mature appearance of the plant is identical with what it would have been had the axis itself branched, and may well deceive anyone into believing this to be the case.

These observations were made while travelling in Japan with a Grant from the Royal Society, which, though allotted for other work, was the means of bringing about the present minor investigation.

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