The Roots of *Psaronius*, Intra-Cortical or Extra-Cortical ?—A Discussion.

IN a preliminary note with the above title communicated last November to the Indian Science Congress and read before the recent Calcutta session (January 1935)[1], I wrote as follows:

"In the root-region of *Psaronius* generally two zones can be distinguished: an inner zone of relatively small roots which are very crowded and

sometimes flattened in consequence, with a 'packing' of thin-walled filamentous cells; and an outer zone of larger, obviously extra-cortical, free roots, which are not distorted by mutual pressure. The inner roots were formerly regarded as intra-cortical, but since 1902, after Farmer and Hill (see discussion in Scott, *Fossil Botany*, 1920, **1**, 271-275), the view has gained ground that they are also extra-cortical, the filamentous tissue being regarded as the compacted hairs derived from the roots themselves. This view was confirmed by Solms (1911)[2]" [and, I may add, accepted by the late Dr. D. H. Scott].

"After an examination of some material from Chemnitz[3] the writer has been led to believe that the intra-cortical view was after all the correct one, and that Stenzel's interpretation best meets the observed facts. Along the outer border of the inner zone the writer finds many places where there is an unmistakable compact periderm-like tissue, in places a dozen cells deep, with the cells serially arranged [see Figs. 1, 2]. This 'periderm' is not in a continuous band all round but this seems to be due to the fact that here and there the inner roots are bursting out through it so as to become free."

"The absence of leaf traces among the roots cannot be questioned but is explicable on Stenzel's view that 'the embedding tissue is a secondary zone, developed *pari passu* with the growth of the roots after the leaves had fallen' (Scott, p. 217)."

The object of the present communication is to bring forward some further facts in support of Stenzel's view. I confess that although Stenzel's interpretation probably offers the best available solution of the problem, even this at first seemed to me rather far-fetched. I knew of no other plant, living or extinct, which showed the unusual mode of growth visualised by Stenzel; and although I have had the main facts before me for over three years, I did not feel quite convinced.

However, as stated, my preliminary note was communicated in November, and I was hoping shortly to write a fully illustrated description of the facts, for whatever they might be worth, when indirect support for Stenzel's view came in from an entirely unexpected source, namely, a living member of the Liliaceæ, *Asphodelus tenuifolius*,

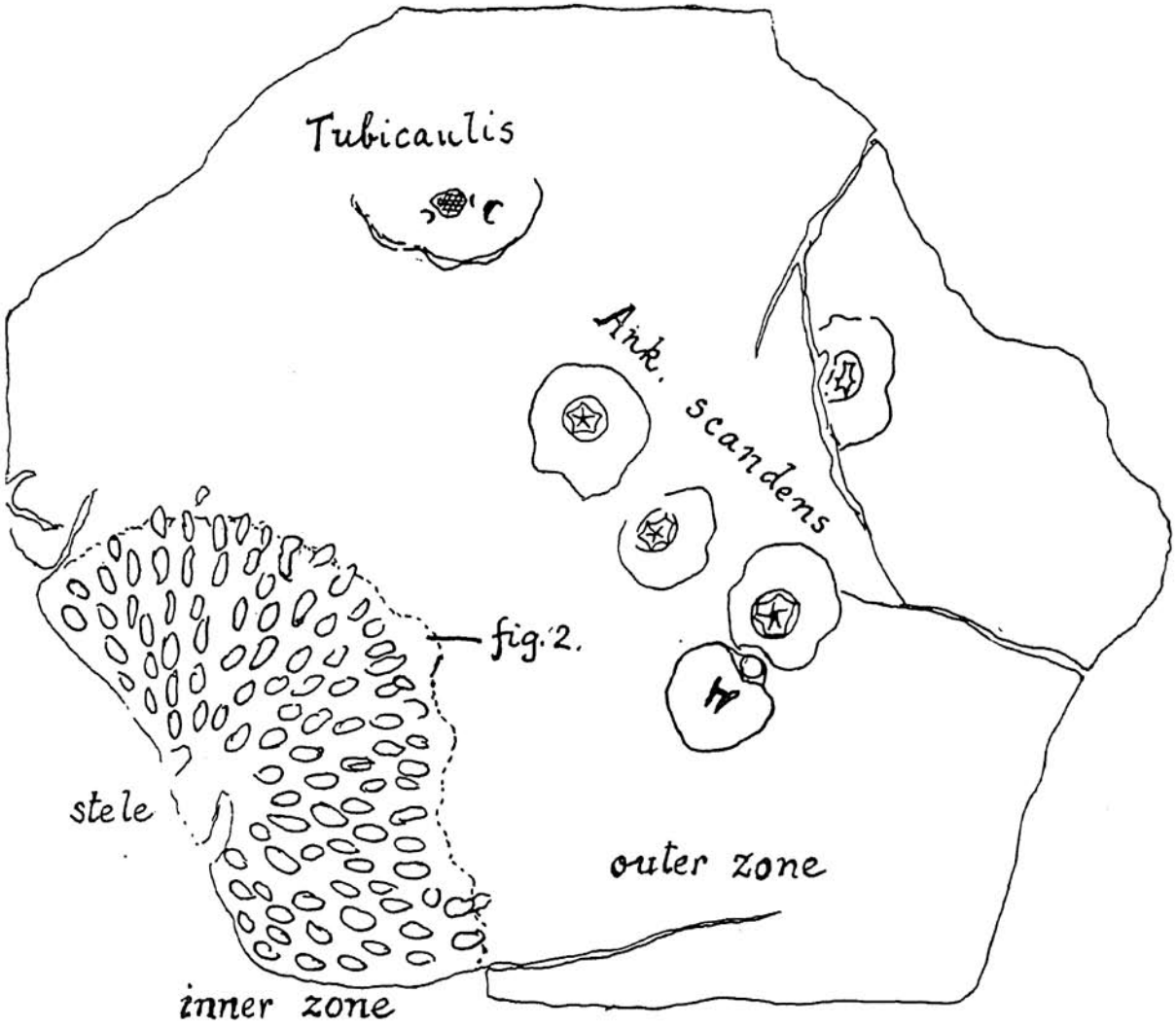

Fig. 1.

Outline sketch (diagrammatic) of cross-section of *Psaronius* sp., showing the position of the periderm (dotted line). Among the extra-cortical roots (outer zone) are several epiphytic stems and roots of *Ankyropteris scandens* and *Tubicaulis Berthieri*. Nat. size.

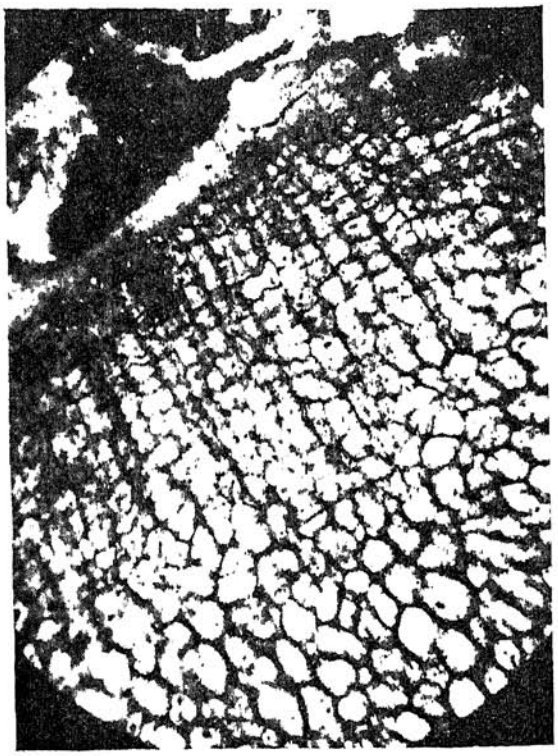

Fig. 2.

Part of the periderm, a dozen cells deep (from the same specimen). × 60.

Early in January I came to know of a paper by Mr. K. R. Mehta, M.Sc., of Benares, describing the root-system of this common weed.[1] At my request Mr. Mehta very kindly sent me a few of his original sections, which I supplemented by sections cut from plants collected in Lucknow. I was thus able to confirm his observations in the main, although the structure seems more complicated than he describes, and deserves more detailed investigation. The facts, so far as I have been able to gather them from hand-sections, are briefly as follows:

In *A. tenuifolius*, unlike the condition in most monocotyledons, there is one main root (*r.r.* in Fig. 1) which persists and behaves somewhat like the tap-root of a dicotyledon. The younger roots, whose relation to the main root still needs elucidation, grow vertically down through the cortex of the latter, rather like the intra-cortical roots of a *Lycopodium*. But they soon become so crowded that they begin to distend the main root, which meanwhile has already provided for an increase in girth through the activity of a peripheral cortical cambium (*m.p.* in Fig. 4). Thus a secondary outer cortex of thin-walled radially arranged cells (comparable to that here described in *Psaronius*) is formed. Some of the later

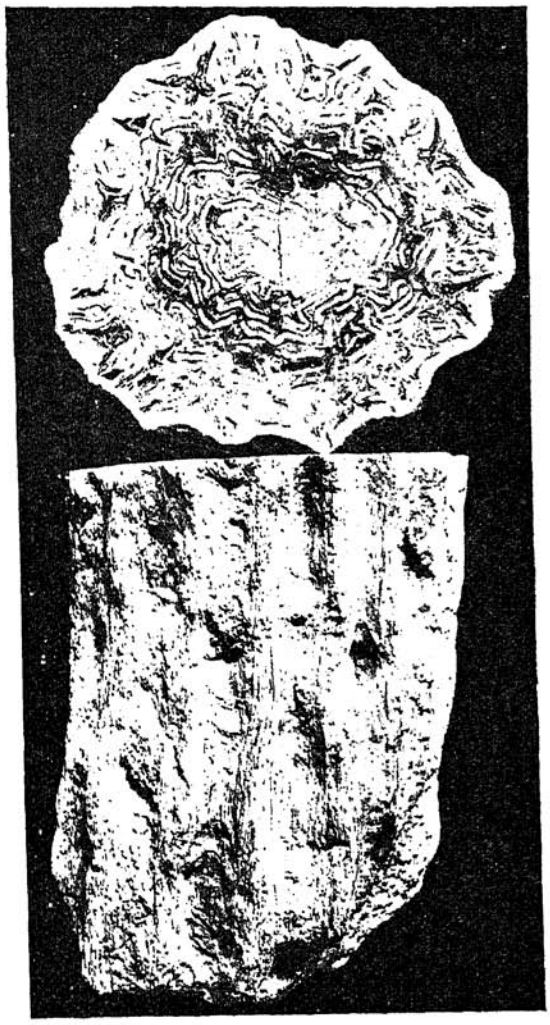

Fig. 3.

Psaronius infarctus: stem bereft of the intra-cortical root-zone, showing the scars of fallen leaves upon a decorticated surface in the region of the inner cortex. Photograph by A. R. Rao. ×3/10.

formed roots also contribute a little to the girth by partial periderms of their own. But it is a curious fact that *these partial periderms are developed only on their outer sides, where they are in contact with the main periderm* (*p.p.* in Fig. 4). The whole appearance strongly suggests that the formation of these partial periderms is induced by some contagious influence (? a hormone) emanating from the main periderm. The newly formed roots sometimes even grow down through the cortex of roots only slightly older than themselves (*r.r.* in Fig. 4). In a full grown plant a transverse section through the root system may show as many as a hundred or more intra-cortical roots packed round the centrally placed stele of the main root. These roots are as a rule so densely crowded that there is very little room left for any "packing tissue"; but the mode of development leaves no doubt whatever that any traces of such a tissue

that may be left can only belong to the cortex of the main root. *At the lower end of the plant the roots are seen breaking through the sheathing periderm*, either singly or in thongs of two or more, which become resolved into their constituents at still lower levels.

I ought to add here that the above interpretation has been confirmed by my colleague, Mr. A. R. Rao, who prepared at

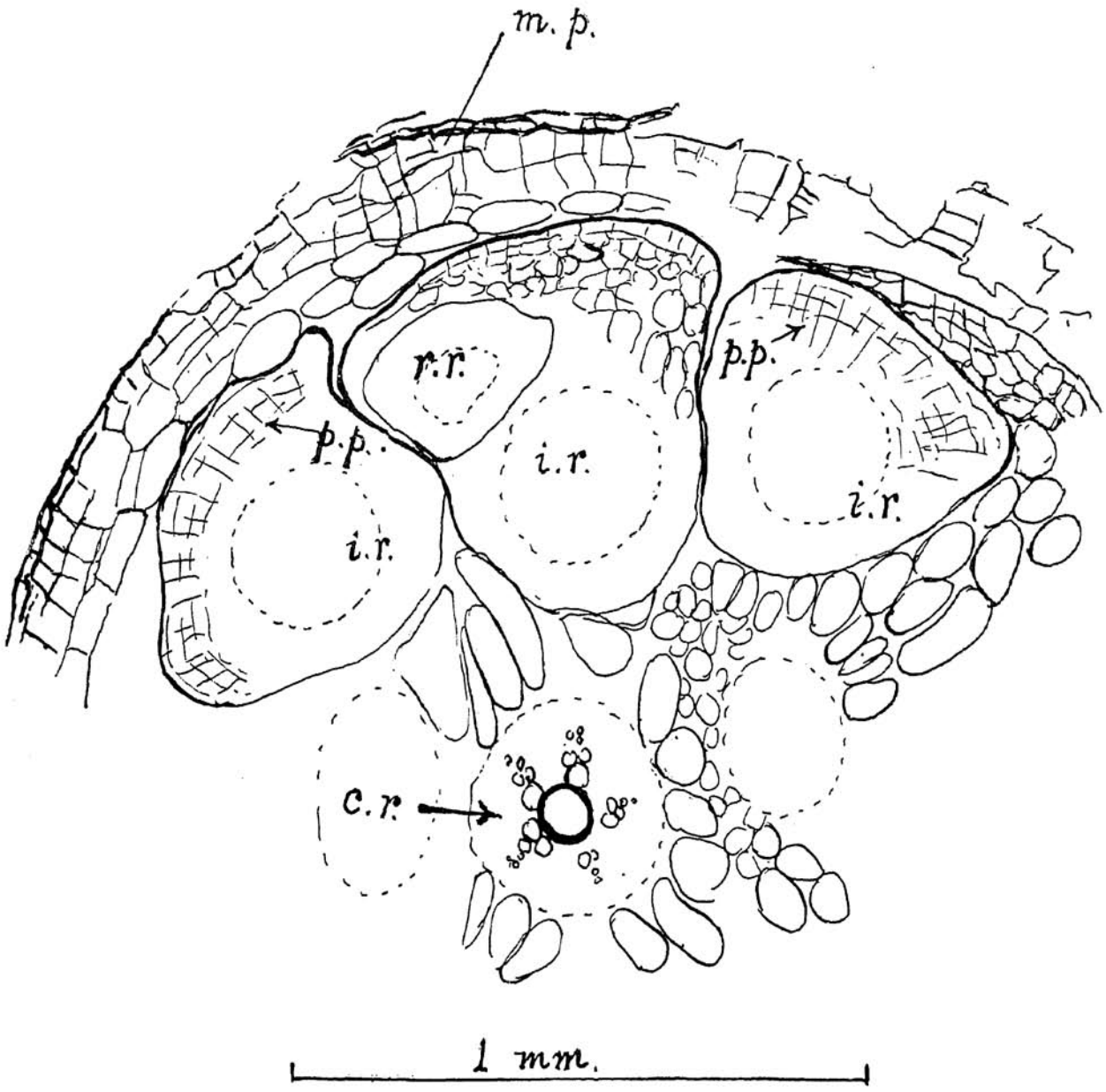

Fig. 4.

Asphodelus tenuifolius. Peripheral part of a transverse section of an old root, with periderms (*m.p.*), *intra-cortical roots* (*i.r.*) *with partial periderms* (*p.p.*) *on their outer sides;* (*c.r.*) central root ; (*r.r.*) root within root. Camera lucida sketch from a section sent by Mr. Mehta.

my request an independent series of sections. Similarly Mr. V. Puri of Agra, who kindly undertook to prepare some further sections for me, also arrived at essentially the same interpretation.

In presenting this necessarily brief description of the root system of *Asphodelus* I do not wish to claim that we have a complete solution of the *Psaronius* problem. But the discovery of this very unusual mode of growth in a modern plant certainly provides an interesting parallel to the condition seen in the Palæozoic genus which has so long puzzled palæobotanists. Mr. Mehta does not mention *Psaronius*, but the resemblance is obvious and full of significance from our present point of view. It has, at any rate, removed my own misgivings as to the far-fetched nature of Stenzel's interpretation which, without committing myself to details, I am now prepared to endorse. I now have little doubt that the roots in question are truly intra-cortical, although the exact nature of

the packing tissue is still obscure. Considering all the facts, and especially those brought forward by Solms-Laubach in 1911 (see his Fig. 5, p. 741) it seems the packing tissue in *Psaronius* after all does belong to the roots themselves, as first suggested by Farmer and Hill; although, as Stenzel contends, it was probably of secondary origin. At this point the analogy with the partial periderms of *Asphodelus* is particularly helpful. The true explanation thus seems to lie in a combination of the views of Stenzel, Farmer and Hill, and Solms.

Stenzel's idea that the leaves had fallen *before* the root-zone was developed is also substantiated by such specimens as the one shown in Fig. 3. Here leaf-scars are visible on a surface (probably in the region of the inner cortex) exposed by the decortication of the inner root-zone; whereas leaf-scars have never been observed, so far as I know, on any surface external to the root-zone.

We thus see that the newly discovered facts strongly support the view of this acute German observer, that the compact root-zone is truly intra-cortical. For us modern workers it is well to remember that Stenzel's conclusions were based not upon an examination of thin sections but only of polished surfaces examined in reflected light.

Once more, the pioneer's work has been vindicated, although it had long been held in question.

A fuller account of the subject here discussed will be published elsewhere.

University of Lucknow, B. SAHNI.
April 24, 1935.

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[1] *Proc. 22nd. Ind. Sci. Congress* (Botany Sec.), Calcutta, 1935.

[2] The literature is fully cited in Scott's *Studies in Fossil Botany*.

[3] Received in exchange from a private collector (Herr Guldner, a contractor of Chemnitz) during a European tour in 1930.

[4] Since published. *Jour. Ind. Bot. Soc.*, 1935, **13** (4), 271–275.