NOTES ON THE ANATOMY OF SOME SILICIFIED FERNS FROM THE CRETACEOUS OF GERMANY.

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From a recent tour in Europe Professor Sahni brought with him on loan the type specimens of some silicified fern stems from the Dresden, Berlin and Breslau museums. These specimens had already been described by several of the older authors, e.g., Corda, Cotta, Goeppert, Renault and Stenzel. But at Professor Sahni's suggestion I undertook a re-investigation of the material, with the result that some new points have come to light.

Protopteris Cottai Corda.

The type specimen of Protoptetris Cottai Corda, described by Cotta, Corda, Schimper, Stenzel and others, is part of the stem of a tree fern, found as a pebble near Grossenhain in Saxony (Fig. 1). It is probably of Cretaceous age. Corda's description and figures are on the whole very accurate but for the following points.

(a) Leaf-trace.—The outline of the leaf-trace is of the shape indicated in Fig. 2 and not so simple as shown in Corda's figures. The plicate lower part of the leaf-trace is very clearly seen in one of the leaf scars. This plicate base which is a characteristic feature of the Cyatheaceae (in the wide sense, including the Dicksonieae) is not mentioned in any of the previously published descriptions; it would further strengthen the Cyatheaceous affinity of the Protopteris Corda seems to be fairly clear.

It is not impossible that as in the living Cibotium Barometz the continuous horse-shoe shaped leaf-trace with a wavy base split up in the distal parts of the rachis into a number of strands. This is suggested by a comparison with Cibotiocalis Tateiwa, a Cretaceous fern from Japan which has leaf-traces of Cibotium Barometz type and which Ogura assigns to the Dicksonieae. In view of these facts the Cyatheaceous affinity of Protopteris Cottai Corda seems to be fairly clear.

1 I take this opportunity of expressing my sincere thanks to Professor Gothan (Berlin), Professor Wanderer (Dresden) and Professor Soergel (Breslau) for the loan of these fossils, and for many other kindnesses received during my tour.—B. Sahni.
(b) **Pericycle.**—Externally to the phloem there is a discontinuous zone, usually one or two cells thick, and consisting of large columnar cells. In places the columnar elements are replaced by a large number of smaller isodiametric cells. I am inclined to interpret this zone as a pericycle; it occurs on both the inner and outer sides of the stele—a fact which has been noticed recently by Edwards—and not only on one side as figured by Corda. Stenzel has described a similar layer of cells in *Caulopteris arborescens* Stenzel under the name "Stützscheide". A similar layer of cells occurring in *Fasciostelopteris Tansieii* has been considered as a pericycle by Stopes and Fujii. Edwards has also described a large celled pericycle in *Paradoxopteris*.

An endodermis is not clearly seen.

(c) **Cortical and medullary roots.**—A striking feature of this fern which, as Gothan points out, is also seen in modern tree ferns, is the large number of cortical and medullary roots. It is well known that some of the roots in *Psaronius* are (according to one view at least) truly intra-cortical. In some species of *Lycopodium*, e.g., *L. Selago*, *L. pithyoides*, *L. phyllanthum*, *L. Hamiltonii* and *L. serratum*, the intra-cortical roots arise at the stem apex and travel down through the cortex, emerging at a lower level. I think that the large number of roots met with in the cortex of *P. Cottai* Corda are of a similar nature. These roots of *P. Cottai* may be compared with those figured by Ogura in the cortex and pith of *Cyathocaulis nakiongensis* and *Cibotiocaulis Tateiwa*, two Cyatheoid ferns from the Cretaceous of Japan.

The question is whether these roots (which presumably all belong to the *Protopteris* itself) became intruded during the life of the plant or after its death. The general downward course of the roots suggests that the stem must have been standing erect (and not lying flat on the ground) when the roots invaded the tissues. I, however, agree with Gothan that it was a partly degenerating ground tissue into which these roots bored their way, because some of the roots are surrounded by cells in various stages of decay. Remarkably well-preserved root hairs are developed wherever the roots are not hemmed in by the parenchyma. Evidently the roots were functional when they thus became intruded.

Although root traces can be seen arising from the stele, still, I am inclined to consider that some of these medullary roots are really the extra-cortical roots which, growing downwards, must have met the upper ends of

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2 Chowdhury (MSS). I am deeply indebted to my friend Mr. N. P. Chowdhury who very kindly showed me the manuscript and slides of his monograph on Indian species of *Lycopodium*. 
older decayed petioles and grown into them as described by Ogura in *Alsophila podophylla* HK and by Sahni in *Clepsydropsis australis* E. M. Osh. Whereas in the latter fern the roots were arrested in their growth by the living tissues of the leaf-base, in *P. Cottai* they seem to have overcome this resistance and gained entry into the pith, for in the longitudinally cut face of the Dresden specimen roots can be seen growing through the leaf-base towards the pith.

It is also possible that some of the intra-cortical roots strayed into the pith directly through the leaf gaps. The tissue was in a state of partial decay and the roots could bore their way in successfully, producing root hairs wherever decay had caused cavities in the pith.

As to how far these roots were able to draw nourishment from the pith with the help of these root hairs, it is difficult to estimate. But the large number of apparently healthy roots and root hairs would lead one to think that they must have served some purpose. It is possible that the partly decayed tissue provided some kind of food material or at least a meagre supply of water.

*Caulopteris Brownii* Renault.

A transverse section of a fern stem from the Göppert Collection at Breslau (Fig. 3) is probably a sister section to the one figured by Renault under the name *Caulopteris Brownii*.3

It agrees in several features with *P. Cottai* Corda and shows a well-developed sclerenchymatous layer on both sides of the stele. In the building up of the leaf-trace one of the meristeles bulges outwards as at *a* (Text-Fig. 1). This bulge becomes later on more pronounced as at *b* and gradually assumes the shape of an inverted flask (*c*). The leaf-trace is cut off at this stage and the meristeles of the stem assume gradually the positions as at *d* and *e*. The stage *f*, with the meristele margins turned inwards, seems to follow upon *e*, but no intermediate condition is seen in the section examined by me. All these stages are drawn from actual portions of the section figured here in Fig. 3. A large number of medullary and cortical roots are also seen, as in *P. Cottai*; the steles are diarch, but no root hairs are preserved.

A re-examination of this slide showed that there exists on both sides of the stele a layer of thin-walled, specially narrow cells (Figs. 4, 5 and 6). Often this layer is detached from the stele but still it remains as a separate continuous membrane (Fig. 5). The preservation is not very good; but when the section (originally rather thick) was ground thinner, it showed

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3 In the description of plates the fossil is labelled *Caulopteris Cottacena.*
TEXT-FIG. 1.
clearly the Casparian thickenings at certain places (Fig. 6). I therefore regard this layer as the endodermis.

Another interesting feature in this fern is the large number of secretory cells seen in the cortex and pith (Text-Fig. 2; Fig. 4).

Protopteris fibrosa Stenzel.

Protopteris fibrosa Stenzel is part of another tree-fern stem described by Stenzel, Goeppert and others from the Cretaceous deposits of Oppeln in Silesia. The internal anatomy has been fully worked out by Stenzel. The points open to criticism are the following.

Endodermis.—Stenzel and others who have described the species have failed to recognise the real endodermis. In Stenzel's very accurate sketches a layer of cells between the so-called "innere and äussere Gefässbündelscheide" has been labelled as the "Grenzschicht (Endodermis ?)". The actual endodermis (overlooked by Stenzel) is a layer of small, rather regularly arranged, thin-walled cells full of contents and having Casparian thickenings on their radial walls (Figs. 8, 9 and 10). There is, of course, an inner as well as an outer endodermis. At places the endodermis has become torn off the adjacent tissues; yet it remains intact as a separate continuous layer (Fig. 9).

Tangential Cells.—The layer indicated in Stenzel's sketches as the "Grenzschicht (Endodermis ?)" is a zone of cells tangentially elongated in transverse sections of the stem. This layer occupies the line of demarcation between the phloem and the pericycle and occurs on both sides of the stele. I have shown above that this layer has nothing to do with the endodermis but its real nature has not been possible to determine,
The cells have simple as well as bordered pits on their walls (Fig. 7). They cannot be a part of the phloem in view of their pitting, nor can they belong to the xylem as none of them show scalariform or other thickenings. They remind one of the tangential cells recorded by Ogura in a similar position in the stele in *Alsophila Ogurae* Hayata, *A. acaulis* Mak., *A. Bongardiana* Mett., *Cibotium Barometz* Sm., and *A. latebrosa* Pr. From their occurrence in the above ferns one is inclined to suspect that these tangential cells are a regular feature of the Cyatheaceae. But these cells in the modern Cyatheaceae are reported to occur between the sieve tubes and the protophloem and do not seem to bear any pits on their walls. If a homology could be established between these tangential cells of *Alsophila* and those of *P. fibrosa* the Cyatheaceous affinity of the latter would be further strengthened. I am tempted to suggest that these tangentially elongated cells in *P. fibrosa* are merely parenchymatous cells associated with the phloem and that the pits noticed on their walls are just the indispensable accompaniment of any thick-walled parenchyma. The pericycle seems to be many cells thick and the various tissues succeed one another in the following manner which is in conformity with the modern ferns:

| cortex | . . . | . . . |
| endodermis | . . . | . . . |
| pericycle | . . . | . . . |
| pitted parenchyma (tangential cells) | . . . | . . . |
| phloem | . . . | . . . |
| xylem | . . . | . . . |
| phloem | . . . | . . . |
| pitted parenchyma (tangential cells) | . . . | . . . |
| pericycle | . . . | . . . |
| endodermis | . . . | . . . |
| pith | . . . | . . . |

According to Stenzel

| cortex | . . . | . . . |
| äußere Gefässscheide. | . . . | . . . |
| Grenzschicht (endodermis ?). | . . . | . . . |
| innere Gefässbündelscheide. | . . . | . . . |
| xylem. | . . . | . . . |
| innere Gefässbündelscheide. | . . . | . . . |
| Grenzschicht (endodermis ?). | . . . | . . . |
| äußere Gefässscheide. | . . . | . . . |
| (overlooked by Stenzel). | . . . | . . . |

*Protopteris fibrosa* Stenz. resembles *P. Cottai* Corda in many respects but differs from it in having no medullary roots which are so abundant

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4 According to Ogura (Ogura, 1927, p. 147), Schütze (1906) who investigated the anatomy of the stem and petioles of many tree ferns has described on the outer side of the sieve tubes a layer of tubular elements with pointed ends, pitted walls and containing some albuminous substances. This layer is called by Schütze "false sieve tubes". In view of the fact that these tangentially elongated cells of *P. fibrosa* have also pitted walls and occupy a similar position in the stele, I think a comparison can be made with the layer of false sieve tubes as described by Schütze.
in the latter. The leaf-trace resembles that of \textit{P. Cottai} but the plicate base is not clear. The layer of prismatic cells seen in the position of the pericycle in \textit{P. Cottai} is entirely absent in \textit{P. fibrosa}. The fibrous bundles and the tangentially elongated cells near the phloem seen in \textit{P. fibrosa} are absent in \textit{P. Cottai}.

In spite of these differences the two ferns seem to be closely allied and may even belong to one and the same genus; they undoubtedly have common Cyatheaceous affinities.

Both \textit{P. Cottai} Corda and \textit{P. fibrosa} Stenzel differ in general from the recently described cyatheoid stem \textit{Dendropteridium cyatheoides} Bancroft in having inwardly directed meristelic margins and in the absence of sclerenchymatous sheaths round the meristeles as well as of cortical and medullary bundles.

\textit{Rhizodendron oppoliense} Goeppert.

\textit{Rhizodendron oppoliense} Goeppert is a silicified fern described by Stenzel from the cretaceous deposits of Oppeln. A thin transverse section prepared at Lucknow from the specimen figured by Stenzel shows a remarkable resemblance to \textit{P. fibrosa} Stenzel. The preservation is similar in both cases. The fibrous bundles seen in the pith and cortex of the latter fern occur in \textit{Rhizodendron oppoliense} also (Fig. 11). The row of tangentially elongated cells with pits on their walls are also seen here. The general disposition of the vascular tissues layer for layer in both seems to be alike. Stenzel was also struck by the close resemblance between these two ferns, which come from the same locality and formation. He mentions that one would easily mistake \textit{P. fibrosa} as the upper root-free part of \textit{R. oppoliense}. The differences between these two ferns, however, seem to be confined to the following points:

1. In \textit{R. oppoliense} there is a well-developed sclerenchymatous tissue surrounding the stele but at a little distance from it. This tissue is absent in \textit{P. fibrosa} Stenzel.

2. The sclerenchymatous tissue in \textit{R. oppoliense} is covered over by a thick felt of roots, a feature not seen in \textit{P. fibrosa}.

3. The leaf-trace in \textit{R. oppoliense} is made up of four or more strands whereas in \textit{P. fibrosa} the leaf-trace is a continuous band.

Endodermis. In Stenzel's description or diagrams an endodermis is not indicated. Gothan has, however, noticed the presence of an endodermis in a specimen of \textit{R. oppoliense} from Oppeln, fragments of which I have also examined. According to him there is a layer of cells radially elongated and two cells thick next outside the phloem. He considers this layer as
sclerenchymatous and locates the endodermis on its outer side. I do not however find this palisade like sclerenchymatous layer in the specimen of *R. oppoliense* Goeppert figured by Stenzel. I venture to suggest that the layer labelled by Gothan as sclerenchyma may be the pericycle comparable to that mentioned in *Protopteris Cottai* Corda (see above). The endodermis in the specimen of *R. oppoliense* Goeppert which I have examined, is not well preserved all through; still it can be made out at particular places where even the Casparian strips may be seen. The position of this layer agrees with that of the endodermis in *P. fibrosa* Stenzel.

My grateful thanks are due to Dr. B. Sahni for suggesting this piece of work and for his ready and valuable guidance. I am also indebted to him for the photograph of *P. Cottai* Corda (Fig. 1). I must also express my gratitude to the authorities of the Breslau, Berlin and Dresden museums who very kindly lent the type specimens and slides for re-examination.

**Summary and Conclusions.**

A re-examination of the type specimens and slides of some silicified fern stems from the Cretaceous of Germany revealed the following new points.

1. *P. Cottai* Corda.  
   (a) The basal loop of the leaf-trace is plicate; this feature strengthens the Cyatheaceous affinity of the plant already suspected on other grounds.
   
   (b) The layer called by Corda "innere Bastscheide" occurs on both sides of the stele in a position corresponding to that of a pericycle and is here interpreted as such.
   
   (c) An attempt has been made to explain the manner in which the large number of roots found their way into the pith.

2. *Caulopteris Brownii* Renault. The presence of an endodermis showing Casparian thickenings at places is demonstrated and the building up of the leaf-trace elucidated.

3. The structure of *Rhizodendron oppoliense* Goeppert and *Protopteris fibrosa* Stenzel has been compared in detail and found to agree very closely except for a few differences which are enumerated in the text.
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EXPLANATION OF FIGURES.

PLATE XXXIII.

Fig. 1.—*Protopteris Cottai* Corda. Part of type-specimen showing leaf scars (a, magnified in Fig. 2). (Dresden Museum). Nat. size.

Fig. 2.—*P. Cottai* Corda. The leaf-trace a of Fig. 1. × 8.

Fig. 3.—*Caulopteris Brownii* Renault. Transverse section of stem. Nat. size.

Fig. 4.—*C. Brownii* Ren. Part of the stele showing end. endodermis; s.e. secretory sac; per. pericycle; ph. phloem; scl. sclerenchyma; and xy. xylem. × 100.

Fig. 5.—*C. Brownii* Ren. Part of the stele showing end. endodermis remaining as a separate layer though detached from the other tissues. × 70.

Fig. 6.—*C. Brownii* Ren. Photomicrograph of part of the stele showing esp. Casparian thickening; end. endodermis; per. pericycle; ph. phloem; and xy. xylem. × 250.

PLATE XXXIV.

Fig. 7.—*Protopteris fibrosa* Stenzel. One of the tangentially elongated cells magnified to show pitting. × 465.

Fig. 8.—*P. fibrosa* Stenzel. Photomicrograph of stem stele showing end. endodermis; per. pericycle; esp. Casparian thickening; ph. phloem; and tan. tangentially elongated cells. (Breslau, Geol. Inst.) × 350.

Fig. 9.—*P. fibrosa* Stenzel. Transverse section of stem stele showing end. endodermis; f.b. fibrous bundle. × 13.

Fig. 10.—*P. fibrosa* Stenzel. Transverse section of stem stele showing cort. cortex; end. endodermis; per. pericycle; ("äußere Gefäßbündelscheide" of Stenzel); ph. phloem ("innere Gefäßbündelscheide" of Stenzel); tan. tangentially elongated cells ("Grenzschicht" of Stenzel); and xy. xylem. × 50.

Fig. 11.—*Rhizodendron oppoliense* Goeppert. Photograph of the stem section of the type-specimen showing f.b. fibrous bundles. × 10.
Fig. 1. × 1.

Fig. 2. × 8.

Fig. 3. × 1.

Fig. 4. × 100.

Fig. 5. × 70.

Fig. 6. × 250.