A *GLOSSOPTERIS* WITH WHORLED LEAVES

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AMONG the many valuable contributions to palaeobotany made by the late Prof. Birbal Sahni, his description of the cuticles of *Glossopteris angustifolia* Brongn. (SAHNI, 1923, p. 277, PL. 17) will always be remembered. Leaves of this type had been known for a century and had usually been regarded as ferns, but this work showed that they had characters now only known to exist in the leaves of seed-bearing plants.

The purpose of the present communication is to add one more fact to our knowledge of this same genus by describing the attachment of leaves, somewhat similar to those of *G. angustifolia*, to a slender stem in a verticillate manner. This is seen in a species from the Molteno beds of South Africa.

PREVIOUS OBSERVATIONS CONCERNING THE HABIT OF *GLOSSOPTERIS*

The habit of the plants bearing the leaves named *Glossopteris* has been debated for more than a hundred years. A century ago Dana (in WILKES, 1849, p. 716, PL. 12, FIG. 13 c) described and figured a number of fronds referred to *G. browniana* attached in a clump to a fragment of a stem. The figure shows a number of petioles radiating from a common level as though belonging to a whorl. Later the opinion was expressed by Zigno (BUNBURY, 1861, p. 327) that this species had a compound or digitate frond like that of *Sagenopteris*. There is, of course, considerable similarity between a leaf of *Glossopteris* and a leaflet of *Sagenopteris* in form and venation. It may well be due to parallel evolution, but it has led to considerable confusion. Thus Feistmantel (1881, p. 113) gave the name of *Sagenopteris longifolia* to a specimen showing about six leaves or leaflets attached at the same level to a common stalk, but he remarked that " a single leaflet might occasionally pass for a *Glossopteris angustifolia* Brongt. as regards general form and the secondary veins but the midrib in this latter is quite distinct throughout ". The stalk, which he figures but does not describe, is quite unlike the petiole of a *Sagenopteris* and the mode of attachment of the leaves is different. It seems highly probable that this specimen shows a whorl of *Glossopteris* leaves attached to a slender stem, for in the specimen of *G. angustifolia* figured by Sahni (1923, PL. 17, FIG. 1) the midrib appears to become very slender at some distance from the leaf apex. In the same work Feistmantel (1881, p. 113, PL. 41 A, FIGS. 3, 4) described another form as *Sagenopteris* (?) *polyphylla* founded on two specimens each showing seven stalked leaves arising from a common axis. The venation of these leaves resembles that of *Glossopteris retifera* Feist.

Etheridge (1894, p. 228) described another specimen from Australia which was believed to have come from the Newcastle Coal Measures, showing a small stem or caudex surmounted by a clump of closely packed fronds. All traces of organic matter had disappeared but the leaves were stated to resemble those of *Glossopteris clarkei* Feist. The stem was $\frac{3}{4}$ in. in width and appeared to be covered with transversely elongated leaf scars arranged alternately. Etheridge thought that his specimen resembled Feistmantel's *Sagenopteris longifolia*.

None of the above-mentioned examples showed stems of the *Vertebraria* type, long known to be commonly associated with *Glossopteris* leaves, but at the end of the century Zeiller (1896, pp. 356-362) described specimens from South Africa which seemed to show *Glossopteris* leaves attached to these stems. It now seems very uncertain that the specimens which he figured did show the organic connection between leaves and stems, and there can be little doubt that his interpretation of the structure of *Vertebraria* is incorrect. Walton and Wilson's important study of the structure of a *Vertebraria* stem from southern Rhodesia shows that this organ is entirely different from the structure envisaged by Zeiller. The paper by these authors (WALTON & WILSON, 1932, p. 201, TEXT-FIG. 1) includes a new figure of an interesting specimen from Vereeniging, South Africa, which had previously been figured by Seward (1910, p. 504, FIG. 339). This

shows a group of four leaves of *Glossopteris browniana* Bgt. at the end of a slightly tapering axis, about 1 cm. wide. There can be little doubt that the leaves were attached to the axis in a whorl, while the stem shows traces of other transverse nodes suggesting the production of a series of leaf whorls. There is no evidence that this stem had the *Vertebraria* structure.

GLOSSOPTERIS IN THE MOLTENO BEDS OF SOUTH AFRICA

Leaves belonging to several species of *Glossopteris* are common in the beds of the Ecca series ; they occur less frequently in the Beaufort beds, and have been recorded by du Toit in the middle portion of the Molteno beds. Among the plants forming the rich and well-preserved flora from the waterfall in the valley of the Upper Umkomaas, du Toit found leaves which he named *G. browniana* and *G. conspicua* Feist. (DU TOIT, 1927, p. 364-367). He also discovered and described a beautiful specimen which he designated *Sagenopteris longicaulis* sp. nov. (1927, p. 325, TEXT-FIG. 4). This requires further consideration since it is probably an example of the same plant which will be described below. In his account of this form, du Toit states that the slab of black shale No. 8670 (South African Museum, Cape Town) carries the impressions of eight leaflets seemingly belonging to two verticils. The largest leaflet was 7 cm. long and 1·5 cm. wide, lanceolate in shape with an acute apex and a lamina which tapers gradually towards the base in an asymmetric manner; at the base of each leaflet there was a footstalk more than 1 cm. long which passes upwards into a midrib, prominent at the lower end but breaking up towards the apex into subparallel or gradually diverging veins with occasional cross connections. The secondary veins were coarse, given off very acutely from the midrib from which they gradually curved away, forked and anastomosed, producing a network very like that of *Glossopteris*. The specimen did not show the attachment of the leaflets to a stem or petiole, but from their converging arrangement it was assumed that they had formed parts of two leaves. In assigning the specimen to *Sagenopteris*, du Toit seems to have been influenced by the crenulate margin of some of the leaflets, the character of the midrib, and by the appearance of a slight thickening of the lamina along its crenulate margin. One of the leaflets showed a small lamina and a very long stalk, a remarkable feature for a compound leaf of the *Sagenopteris* type. The way in which the leaves or leaflets of the two groups cross each other was figured but not mentioned; it is very similar to the appearance of the specimen which will be described below. I examined this specimen when I was in Cape Town; it seemed to differ considerably from any specimen of *Sagenopteris* that I had seen, and its derivation from a member of the Caytoniales seemed unlikely.

New Evidence from the Molteno Black Shales — After examinning du Toit's collection in Cape Town I was able, through the kindness of Mr. J. W. B. MacLean, to spend some time in collecting at the waterfall locality in the valley of the Upper Umkomaas in Natal from which the specimens had been obtained. It seemed most important to ascertain if, in fact, the remains of plants referable to the Caytoniales did occur in the Triassic rocks of South Africa. The plant remains at this locality are singularly well preserved and often allow the preparation of good cuticle preparations. Many leaves and reproductive structures referable to the Pteridosperms (THOMAS, 1933, pp. 193-265) were discovered, but no trace of any structure belonging to the Caytoniales was found. My collection contains, however, about twenty examples of leaves referable to *Glossopteris* and a unique specimen, with its counterpart, which explains the nature of du Toit's supposed *Sagenopteris*.

This specimen, which is shown in the photographs in Plate 1, Fig. 1, shows two whorls of leaves of the *Glossopteris* type springing from a slender stem.[1] The attachment of the leaves of one whorl to the stem is clearly seen (PLATE 1, FIG. 1, lower part, and FIG. 2) but the specimen is fractured at the place where the leaves of the other whorl (the uppermost in PLATE 1, FIG. 1) join the stalk.

The stem from which the leaves sprang is 3 mm. wide throughout most of its length but its width increases to 4 mm. at the nodes. Its surface is generally smooth but traces of low longitudinal ridges are visible in places, as if due to the presence of lines of harder tissue in its internal structure ; it shows

1. In order to give a more correct representation of the specimen the whorl which was originally the lower one is shown in the upper part of the photograph.

nothing comparable to the *Vertebraria* structure. The length of the internode is 5·8 cm.

The leaves of each whorl appear to have spread upwards and outwards from the stem; thus the whorl seen in the upper part of the photograph (FIG. 1) was probably produced below the whorl shown in the lower part of this figure. The latter (PLATE 1, FIG. 2) shows parts of seven leaves; four of them lie above the stem, two are seen on one side and one on the other. The other whorl shows parts of five leaves. Each leaf had a short petiole, about 1 cm. long and nearly 1·5 mm. wide. The counterpart shows the remains of the plant tissues (FIG. 2) and from this the original number of leaves in the whorl can be calculated. The petioles are contiguous at their base and are 1·2 mm. wide where they join the stem. The flattened stem is 4 mm. wide; if its diameter before compression was 3·7 mm. the circumference would allow for the production of nine leaves in each whorl. It may be noted that the positions of some of the leaves in the matrix show the same peculiarity as was illustrated in du Toit's figure of *Sagenopteris longicaulis*; one of the leaves of the earlier whorl lies above one and below the adjacent one of the leaves in the next whorl.

The individual leaves are lanceolate in shape with a bluntly acute apex. They are 10-12 cm. long and about 2 cm. broad at their widest part, which is generally about 6 cm. from the base. Their margins are sometimes entire and sometimes crenate, but the apparent undulation of the margin in some places is probably an artifact due to the lamina not being flat near the margin. In the lower part of the leaf the lamina tapers gradually towards the base where it becomes markedly asymmetric.

The large specimen shown in Plate 1, Fig. 1, shows in most parts only the moulds of the leaves and its counterpart (FIGS. 2, 3) contains remains of the plant tissues. Only the lower surfaces of the leaves are seen, but other examples of isolated leaves, probably belonging to the same species, show the upper surface. In the latter the midrib is represented by a shallow groove, while on the lower side it is seen to be a conspicuous raised rib, 1-1·2 mm. wide, gradually diminishing in size towards the apex. Near the centre of the leaf the midrib shows four or five minute longitudinal ridges and traces of elongated epidermal cells can sometimes be seen. About 1 cm. from the apex the longitudinal ridges may become more noticeable, and above this level the midrib becomes little thicker than a secondary vein. Eventually it divides up and looses its identity over the last 5 mm.

The secondary veins arise from the midrib at intervals of 3 or 4 mm. (PLATE 1, FIG. 3). From their place of origin they run forwards at a very acute angle and remain close to the midrib for a distance of some 2 mm., then turn outwards, fork and give rise to branches which curve round and run towards the margin forking two or three times. The ultimate branches form a regular parallel series making an angle of about 45° with the margin. Anastomosing branches are rather infrequent near the midrib but are more abundant near the margin, the meshes between the veins are thus elongated and curved. The cross connections are, however, considerably less numerous than in many other species of *Glossopteris*.

COMPARISON WITH OTHER FORMS

Du Toit (1927, p. 364) described two kinds of separate leaves from the waterfall locality which he referred to the genus *Glossopteris*. In one group the lamina was broad and had an oval-lanceolate form; he called these examples *G. conspicua* Feist. The other group showed a narrower lanceolate form in which the lamina was contracted more sharply at the base; it was named *G. browniana* Brongn. (pars). The midrib and the pattern of the secondary venation seem to be much alike in both groups, though in the narrower leaves the secondary veins are said to curve a little more and to be set much closer together than in the broader form. In my collection there are also broad and narrower leaves, some of the latter being similar to the attached leaves which have just been described, but I do not think that either of the specific names employed by du Toit are applicable to the specimen described in this paper. In the outline of the leaf, the midrib and the curvature of the secondary veins the present forms agree more closely with the figures given by Arber (1905, p. 68, FIG. 18) and Walkom (1922, p. 16, PL. 2, FIGS. 10-13) for *Glossopteris indica* Schimp., but show fewer anastomosing veins. The venation of *G. angustifolia* Brongn. is also somewhat similar, but this leaf seems to have had a different outline and its base is quite distinct.

In view of the more complete information now available about the present form, it would seem desirable to use a distinct specific name for the specimens that have been described. The most appropriate specific name is the one given by du Toit to the specimen which came from the same locality, and which he called *Sagenopteris longicaulis*. I feel sure that his specimen belonged to the same species of plant as the form now described. Such differences as may be observed between the two specimens may well be due to a difference of position on the original plant. Du Toit's leaves were smaller, tapered more rapidly towards the base, and probably sprang from a shoot with shorter internodes.

The only real problem is the use of the generic name of *Glossopteris* for these specimens in view of the relatively few anastomosing branches among the secondary veins. But since all the leaves do show a considerable number of closed meshes, it would seem unnecessary to create a new genus. It has been shown above that there are many indications in the literature that the leaves of other species of *Glossopteris* were borne in whorls, though no specimen seems to have shown this habit so clearly as the present example.

CONCLUSIONS

The evidence that has slowly accumulated over a hundred years suggests that the leaves of *Glossopteris* were borne in whorls on relatively slender stems.

A specimen collected by the author from the black shales in the valley of the Upper Umkomass, Natal, South Africa, shows two whorls of leaves springing from a stem 3 mm. in diameter. There were probably nine leaves in each whorl.

The shape and venation of the leaves differ somewhat from that seen in other species and the specimen is named *Glossopteris longicaulis* (du Toit) comb. nov.

It is suggested that the forms from India and Natal, previously described by Feistmantel and du Toit as species of *Sagenopteris*, were really examples of *Glossopteris* with whorls of leaves.

The view that *Glossopteris* leaves sprang from stems of the *Vertebraria* type is regarded as unreliable, but such stems may have been of the nature of rhizomes bearing leafy shoots.

The specimen described and figured comes from the Middle Molteno beds and is of Triassic age.

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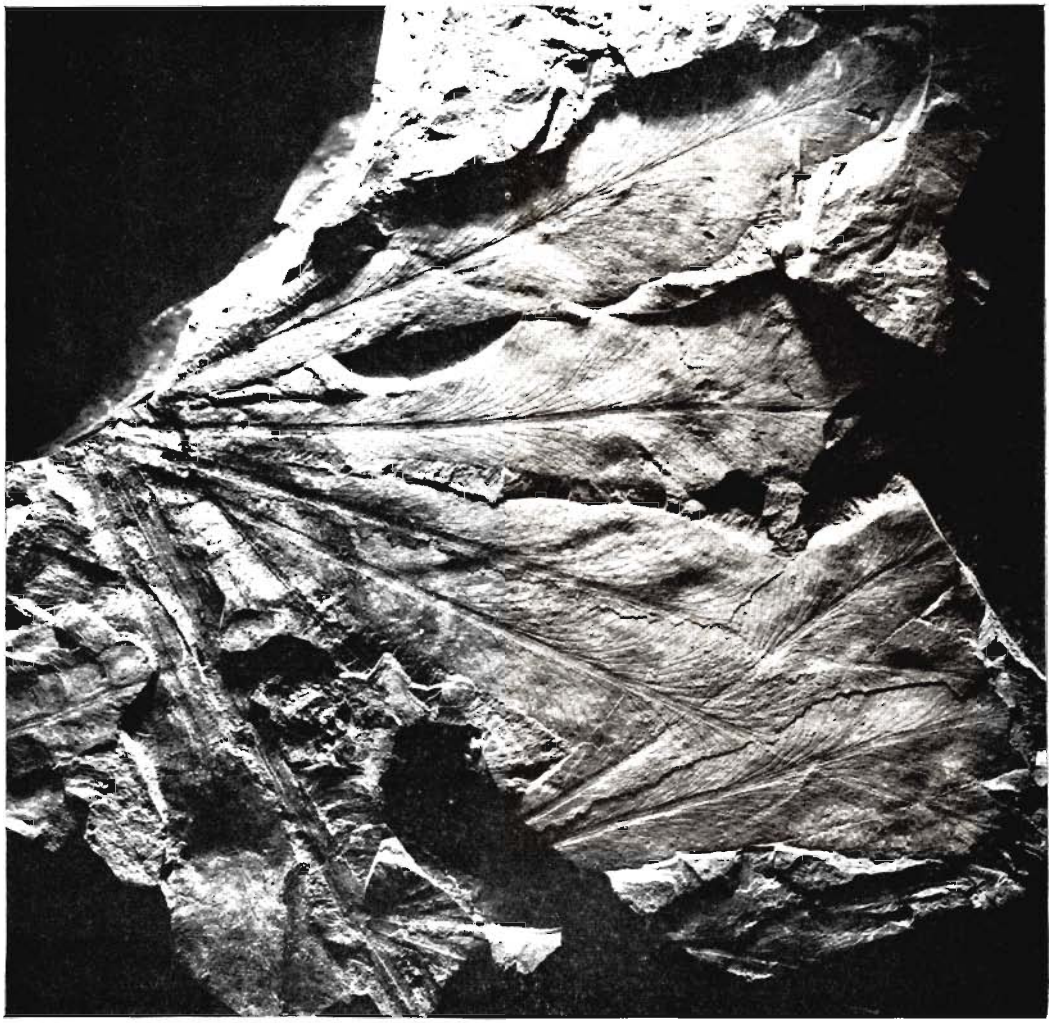
EXPLANATION OF PLATE 1

1. *Glossopteris longicaulis* (du Toit) Thomas from the valley of the Upper Umkomaas, Natal, South Africa. The stem bearing the two whorls of leaves is seen on the left side of the photograph. × 7/5.

2. Counterpart of the specimen shown in Fig. 1. Shows the attachment of one whorl of leaves, to the stem. × 5/2.

3. Portion of the counterpart with parts of leaves. Shows the midribs and secondary veins on the lower side of the leaves. × 5/2.



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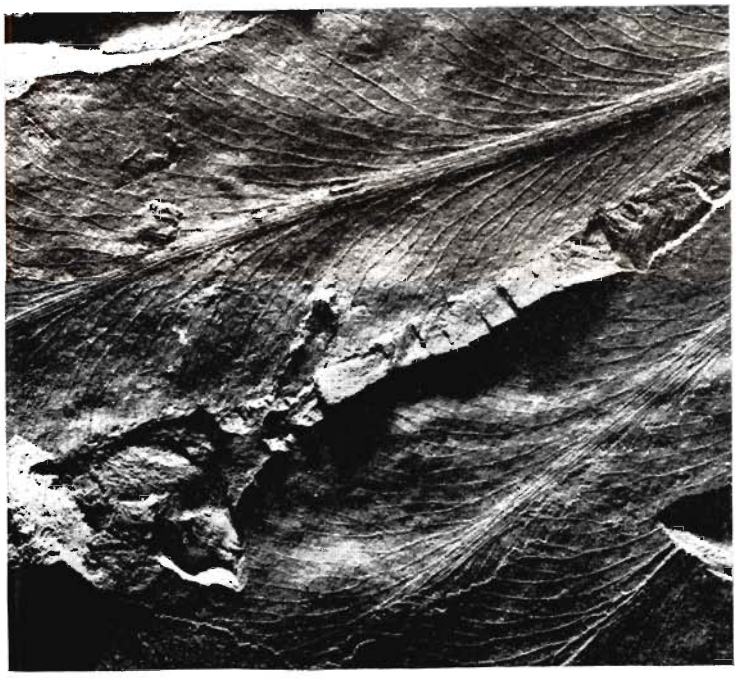

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