CUTICULAR STUDIES OF THE REPRODUCTIVE ORGANS OF GLOSSOPTERIS. PART IV—*VENUSTOSTROBUS INDICUS* SP. NOV.

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ABSTRACT

A new species of *Venustostrobus*, *V. indicus* has been described in this paper. The female reproductive organ was preserved as carbonized compression under a long and narrow *Glossopteris* leaf to which it was attached. In order to study the fructification, three successive cellulose acetate pulls were taken. The first removed the leaf, the second removed the seeds, receptacle and a part of the protective bract, and the third pull removed the carbonized crust of only the bract. Cuticular structure of all these parts are described. *Venustostrobus indicus* is distinct from the other species, *Venustostrobus diademus*, in the leaf of *Glossopteris* to which it is attached and in the detailed structure of the bract, receptacle and the seeds. By taking out successive pulls it becomes clear that the bract and the seed bearing receptacle are two distinct and separate organs and that the receptacle occupies a position in between the leaf and the protective bract. Thus this study supports the interpretation we have given earlier to the multiovulate female reproductive organ of *Glossopteris*.

SOME Permian plants of the southern hemisphere possessing *Glossopteris* type of leaves bore multiovulate female reproductive organs. These were first described by Plumstead (1952, 1958) as *Scutum*, *Hirsutum* and *Cistella*. She interpreted them as cupules, one half of which was female and the other veined half as male. This interpretation of hers did not find favour with most of the palaeobotanists and these three types of fructifications remained an enigma. In 1974, Surange and Shaila Chandra (also see 1975) interpreted *Scutum* as a stalked, bilaterally symmetrical receptacle, covered with spirally arranged seeds and protected on one side by a veined protective bract. The receptacle and the protective bract were borne on a short, common peduncle, which in its turn is attached at the base or midrib of a *Glossopteris* type of leaf. They based their interpretation on the material from Handappa in Orissa preserved as impression and as partial cast. Later the authors collected carbonized compressions of the multiovulate fructifications from the Raniganj Coalfield, India and as the preservation was good, it was possible for them to carry out cuticular studies on the material. Based on the cuticular studies of the fructifications, they identified three new genera,viz., *Plumsteadiostrobus* (Cistella type), *Jambadostrobus* (Hirsutum type) and *Venustostrobus* (Scutum type) (Shaila Chandra & Surange, 1976). They obtained distinct cuticles of the receptacle, protective bract and different layers of seeds, thereby confirming their earlier interpretation of the multiovulate organs of *Glossopteris*. A new species of *Venustostrobus* fructification (Scutum type) attached on a new type of *Glossopteris* is described in the present paper. The leaf is lying on top of the fructification which enabled the authors to remove in successive cellulose pulls, the leaf, the protective bract and the receptacle, studded with seeds, separately for study. This again unmistakably proves the authors' morphological interpretation of the multiovulate organs of *Glossopteris*.

MATERIAL AND METHODS OF STUDY

We had only one specimen of Scutum type of female reproductive organ attached on a *Glossopteris* leaf. The leaf was a complete specimen of *Glossopteris*, from petiole to the apex, with what looked like a fructification attached to its midrib in the basal region. The fructification was, however, lying hidden under the leaf and showed only its broken but orbicular outline. This shape is characteristic of *Venustostrobus*, a Scutum type of female reproductive organ and we, therefore, identified it as *Venustostrobus*. The cuticular studies confirmed our initial observation.

We wanted to see whether it was possible to take out separate pulls of the leaf, receptacle (with seeds) and the protective bract. So we applied three successive cellulose acetate coats and then macerated them separately. A thin coat of cellulose acetate

was first applied to remove only the leaf organs. When the film was pulled out, it did remove the leaf completely but a little portion of the fructification also came out. The first pull was then macerated which mostly yielded leaf cuticles. The fructification thus exposed by removal of the leaf revealed outlines of small, round seed bodies in a mass, badly compressed. To this we applied a second coat of cellulose acetate which removed the seed mass partially together with the carbonized crust of the veined bract lying below. This second pull was macerated separately. A carbonized layer in one corner of the bract was still left on the shale which was removed by a thin film of cellulose acetate and this third pull was macerated for the bract cuticle. Thus the first pull gave only the cuticles of leaf, the second pull yielded small pieces of seed cuticles together with the cuticles of receptacle and the protective bract, all jumbled together. The third pull yielded only the cuticles of the protective bract. Incidently this also confirmed the position of the seed bearing receptacle which is between the leaf and the protective bract. After isolating leaf and bract cuticles in the first and third pull, it was easy to identify the receptacle cuticles in the second pull. The seed layers are distinct in appearance and, therefore, there was no difficulty in identifying them. All these preparations were stained by safranin, and we found that the cuticles of different organs, viz., receptacle, bract, seed integument, nucellus etc. displayed different shades of red. It helped in assigning cuticles to different organs. The three pulls are described separately below.

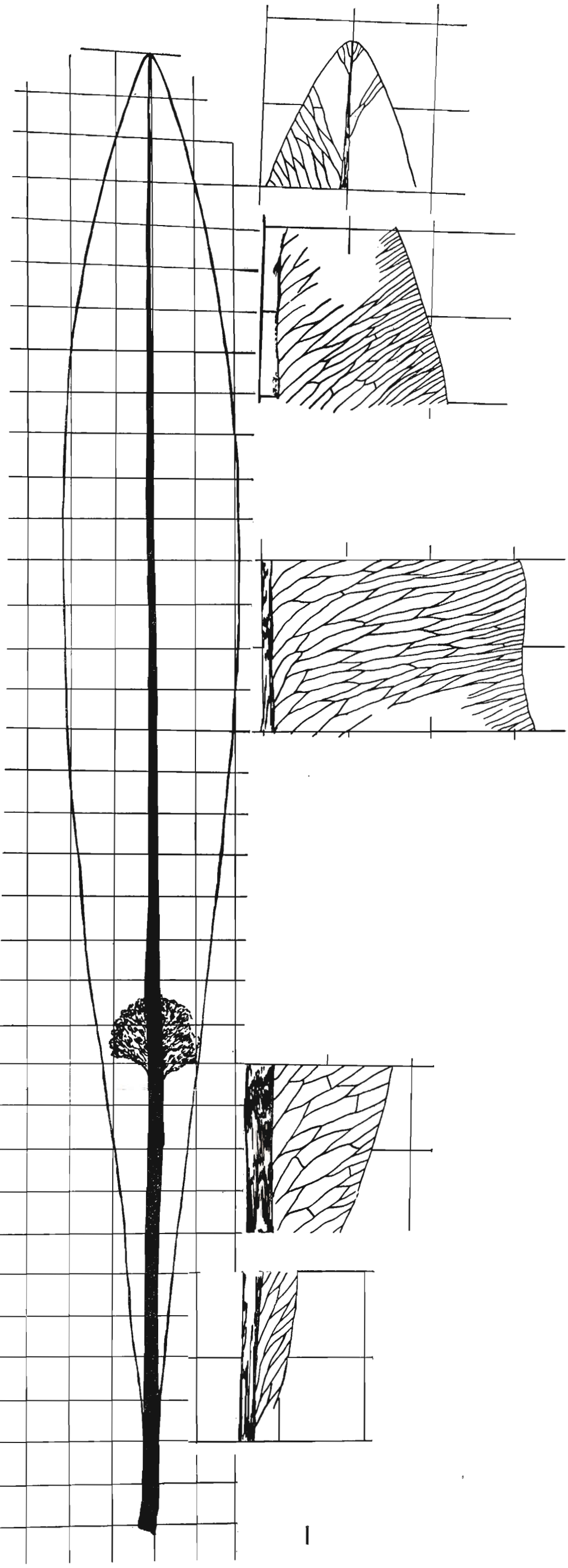
The First Pull — Fructification Bearing Leaf

The leaf is extremely long and very narrow (Text-fig. 1). It is 36 cm in length from the base of the petiole to the leaf apex, with a broad, prominent midrib, attenuating gradually and persisting right up to the apex. The petiole is about 3 cm long. The leaf attains its maximum width of 4 cm at about half way from the base, remains uniformly wide for about 8 cm and then converge rapidly to an acute apex (Pl. 1, figs. 1-4). The ratio between length and breadth of the leaf is approximately 8:1.

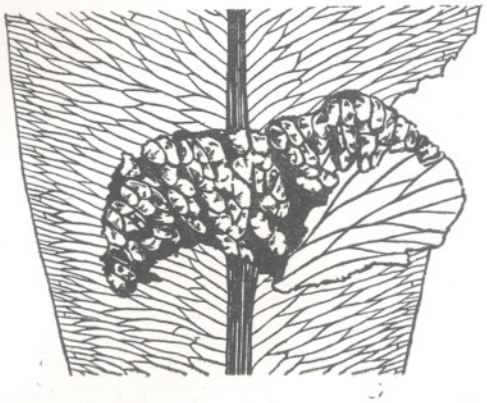
The lower side, the adaxial side of the leaf, is exposed to the view. The venation is clear but not prominent. The meshes are broad on either side of the midrib but become narrower towards the margin (Pl. 1, fig. 2). In Text-fig. 1, the leaf is drawn on 1 cm grid and the venation in 1 sq cm is exactly magnified four times and drawn on the right side, indicating the regions from where the venation is magnified. In the narrow part of the lamina in the basal as well as in the apical region, the veins arise at a more acute angle than in the middle region of the leaf (Pl. 1, figs. 1-4). They ascend straight to the margin, branching once. The arching of the secondary veins becomes more apparent as the lamina broadens. The veins also divides 2 to 3 times and the branches of adjoining veins unite to form pointed, hexagonal meshes (Pl. 1, fig. 3). In the broadest middle region of the leaf the veins arise from the midrib almost at right angles and they meet the margin almost in a straight line (Pl. 1, fig. 2). The venation in the middle region is quite different from that in the base and apex regions. The concentration of veins, their branching and fusion and their course from the midrib to the margin can be easily observed from Text-fig. 1.

Cellulose pulls were taken in the basal, middle and apical regions of the leaf. All of them yielded tough cuticles of only the leaf but without cellular preservation. However, cells were found preserved at a few places which were differentiated into vein and mesh areas. Cuticle of one surface (Text-figs. 3A, 4B) possesses rectanguloid cells with straight cell walls. This surface perhaps does not possess stomata (Pl. 1, fig. 5). The cuticle of the other surface shows rectanguloid cells over the veins and short, oval to rectangular cells in the mesh areas (Text-figs. 3B, C, 4A). The cell walls are straight. The stomata are irregularly orientated in the mesh areas and show thickened guard cells. It was not possible to ascertain the number of subsidiary cells, but perhaps they are 5 to 6 in number. Both the surfaces are devoid of papillae or hair bases.

We tried to match this leaf of *Glossopteris* with those already described from India by various authors. But it did not fit in with any of the species already known from India. We are, however, not inclined to



TEXT-FIG. 1 — Leaf of *Glossopteris* bearing *Venustostrobus indicus* sp. nov. drawn on 1 cm grid. The fructification is lying below the leaf. The venation in 1 sq cm is magnified 4 times and drawn on the right side, opposite five different regions from where the venation is drawn. Note the angle, branching and fusing of the secondary veins × 1, veins × 4.



TEXT-FIG. 2 — The fructification as revealed when the leaf was removed by a cellulose pull. Note seeds on black mass (receptacle ?). A part of the protective bract is exposed on the right side, which was lying below the seed mass. Note the strong veins and large meshes of the bract as compared to the leaf meshes × 2½.

give it a new specific name as it will serve no purpose except to add one more name to the already confusing list of *Glossopteris* species. This leaf should only be known as the leaf of *Venustostrobus indicus*.

THE THIRD PULL — PROTECTIVE BRACT

We are describing the third pull earlier than the second as it yielded the cuticles of only the protective bract. A small part of the carbonized crust remained on the prominently veined protective bract which was removed and macerated. It yielded only three types of cuticles shown in Pl. 2, figs. 7-10 and Text-fig. 5A-E. The one which was rare (Text-fig. 5D; Pl. 2, fig. 8) possessed elongated, somewhat thick-walled cells, arranged end to end. The most prominent feature of this cuticle is the occurrence of a large number of circular, thickened hair bases over the cells. Elongated cells arranged end to end are generally found over the veins. We, therefore, ascribe these cells to those occurring over the thick veins of the protective bract (Text-fig. 2).

The two remaining cuticles obviously belonged to the two sides of the bract. One of them (Pl. 2, fig. 7; Text-fig. 5E) was thicker but the cell outlines were obscure. This cuticle does not take good stain. The cell walls are thick and straight. The cells are bigger in size and four to five sided (Text-fig. 5E). In some pieces stomata were observed. They are oval and thickened. Guard cells are not always visible, but when seen, they appear to be sunken and slightly thickened.

The cuticle of the other side of the bract consists of small, squarish, rectanguloid to elongated cells with a large number of circular, thickened hair bases (Pl. 2, figs. 9, 10; Text-fig. 5A, B, C, F). The cuticle pieces were very small and so the distribution of circular hair bases could not be studied. Elongated cells radiate from the hair bases and, together with the small squarish cells in between, present an odd, disturbed look to the cuticle. It appears that a large number of hairs were present on this surface (Pl. 2, fig. 10), one of them is enlarged in Text-fig. 5B. Stomatal opening is elongated with narrow ends with two guard cells in the centre (Text-fig. 5B, F). It has perhaps five subsidiary cells. This side with stomata and stiff hairs probably represents the outer surface of the protective bract.

THE SECOND PULL — RECEPTACLE, SEED-PARTS, AND PROTECTIVE BRACT

Removal of the leaf in the first pull exposed a mass with faint impressions of round seed bodies. Cellulose acetate was applied on this mass and when it was removed as a second pull, the mesh venation of the protective bract lying below was exposed. (Text-fig. 2). It clearly shows that on the top was the leaf, below it was the mass with round seed bodies and below the mass was the thick-veined protective bract.

The second pull yielded a number of different types of cuticles (Text-figs. 6, 7). Three cuticles belonging to the veined bract as described above are also present in the slides and they could be easily eliminated. Brightly stained pieces of fibrous layers, obviously belonging to seeds, with bits of integument still sticking on to them are very common in the slides. Seed pieces, either with integument or translucent nucellar tissue attached to them are also very frequent (Pl. 2, figs. 12, 13). It is easy to recognize the seed tissues which look quite different from the cuticles of leafy organs. So the only remaining but

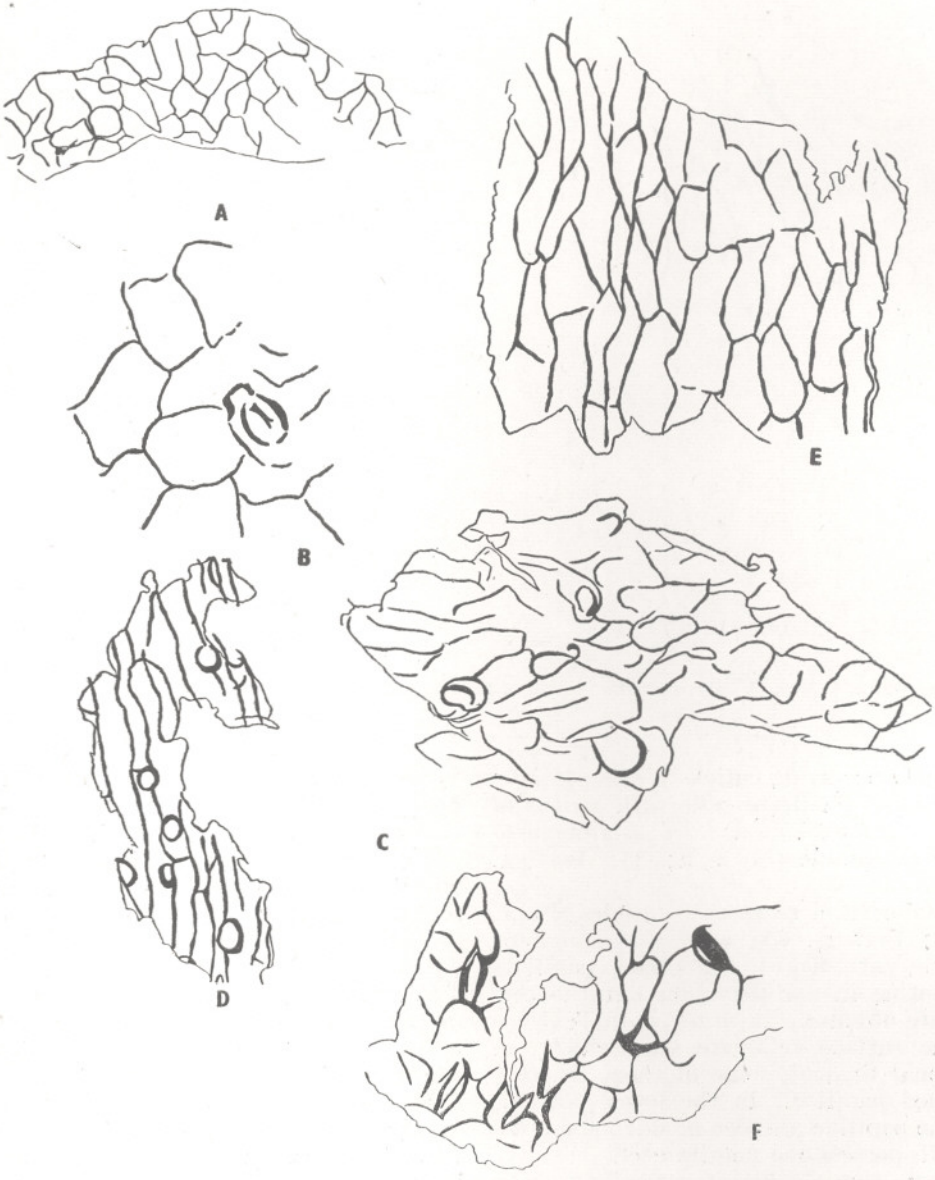
TEXT-FIG. 3 — Cells from the fructification bearing *Glossopteris* leaf. A, cells from the non-stomatiferous surface. Rectangular cells on the left are those over the veins. B & C, cells from the stomatiferous surface showing irregularly distributed stomata in the mesh area. Stomata magnified in A & C×175; B × 400.

TEXT-FIG. 4 — A, B, cells over the midrib of the leaf bearing *Venustostrobus indicus* × 175.

frequently occurring cuticle pieces consisted of thickened papillate cells with stripes of cuticular thickenings and we ascribe them to the receptacle (Pl. 2, fig. 11; Text-fig. 6A, B).

In majority of receptacle cuticles (Pl. 2, fig. 11; Text-fig. 6A) what is visible are the crescent shaped, thickened papillae, all pointing in one direction but the cell walls are obscure. In some, as in Text-fig. 6B, the surface cells are seen which are tetragonal to oval, some of them showing thickened papillae. In the lower portion, only the papillae are seen in side view. All the cells possess one papilla each. Text-fig. 6A shows two thickened cuticular stripes on either side of the papillate cells of the receptacle. Beneath the cuticular stripes, thickened papillae of the surface cells are sometimes visible. The cuticle of the receptacle appears to be unevenly thickened. Some of the pieces take bright red stain and appear to be somewhat thickened. Others are very light and even appear translucent. This gradation can be seen even in one piece of cuticle. As we have only very small pieces in the slides, it is not possible to visualize the surface cells of the entire receptacle. Although thickened stripes of cuticle are common, completely papillate surface cells are unkown in the receptacle cuticle of any of the glossopteroid fructifications described so far by us.

We do not have an entire seed for study in our single specimen, but the seed has straight-walled cells of the integument and the nucellus. This seed is thus distinct from the seeds of other genera of reproductive organs of *Glossopteris*, except *Venustostrobus*. It further confirms our identification of the fructification described here as *Venustostrobus indicus*. However, it is distinct from *V. diademus* described earlier by us (Shaila Chandra & Surange, *in press*). The seed has a long neck (Pl. 2, fig. 15; Text-fig. 7A, B) with narrow straight-walled cells, arranged end to end. The integument cells over the body of the seed are large, tetragonal, pentagonal or hexagonal (Pl. 2, fig. 12; Text-fig. 7A, B, C) and have straight cell walls. These are



TEXT-FIG. 5 — Cells from two sides of the protective bract. A, small square to rectangular cells with thickened circular hair bases from one side of the bract × 175. B, stoma enlarged from the surface shown in A × 400. C, circular hair bases prominent with cells radiating all round it × 175. D, cells over the veins of the protective bract, long cells arranged end to end, also possess thickened circular hair bases × 175. E & F, cells from the other side of the bract. E, shows large somewhat thickened cells with straight walls and stomata, although rare on this surface × 175.

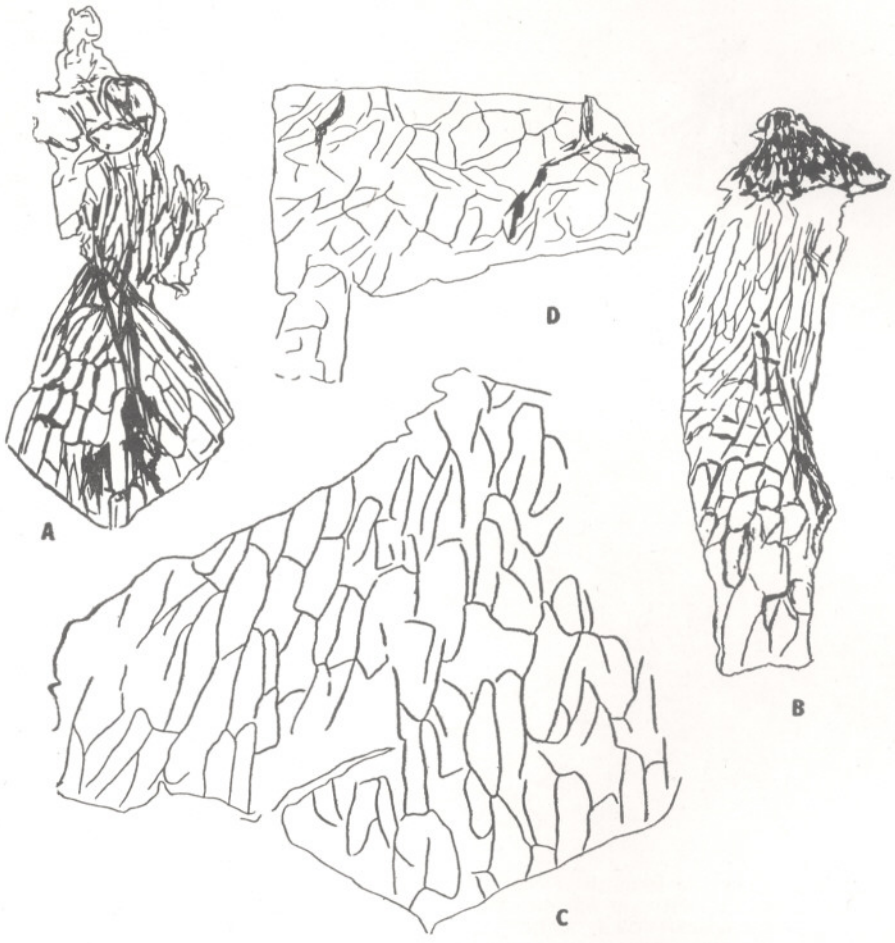
TEXT-FIG. 6 — A, cuticle from the receptacle surface. Cells obscure but crescent shaped papillae very prominent, generally pointing in one direction. Stripes of cuticular thickening are seen on right and left. Papillae are seen beneath them × 175. B, cell outlines of the receptacle surface seen in the upper part and the papillae are seen on the lower side × 175.

the cells of the outer integument which is followed by darkly stained thick fibrous layer. The seed appears to possess a thick fibrous layer between the outer and the inner integument. The cells of the inner integument appear to be similar to those of the outer integument, only the cuticle is thinner and takes very little stain. There is also a still thinner tissue, almost transparent, showing faint outlines of small, tetragonal to pentagonal cells with straight, thin cell walls (Pl. 2, fig. 13). This we identify as nucellar tissue. We have not observed the pollen chamber, but some elongated cells of the micropylar end are seen with one type of two-winged pollen grains sticking on to it (Pl. 1, fig. 6).

COMPARISON

Because of its fan-like shape, we ascribe this fructification to *Venustostrobus* (Scutum type). Prominently veined, strong protective bract, possessing large number of stiff hairs as seen on the cuticle, further supports this identification.

We have described one species of *Venustostrobus*, *Venustostrobus diadenus*, attached on *Glossopteris ghusikensis* type of leaf. The species of *Venustostrobus* described here is new because firstly, it is attached on a different type of *Glossopteris* leaf and secondly, it differs from *V. diadenus* in many other characters. It is, therefore, named as *Venustostrobus indicus* sp. nov.



TEXT-FIG. 7 — Cuticles of seed of *Venustostrobus indicus*. A, micropylar end of the seed. Note the drawn outneck with two winged pollen grain trapped at the top. Neck cells long and straight-walled. Other integument cells are seen below the neck cells × 175. B, another cuticle showing the neck cells and the broad straight-walled integument cells × 175. C, large integument cells on the seed body × 175. D, small straight-walled, almost transluscent cells of the nucellus × 175.

The leaf of *V. diademus* is small with 5:1 length and breadth ratio and identified as *Glossopteris ghusikensis* type. The leaf of *V. indicus* is extremely long and narrow with 8:1 length and breadth ratio. This type of *Glossopteris* leaf has not been described so far by any one and, therefore, does not have any specific name. We have called it the leaf of *Venustostrobus indicus*.

The protective bract in both the species of *Venustostrobus* is strong and prominently veined. Even the cuticle is somewhat similar in the sense that one side shows large straight-walled cells which are not generally well-preserved, while the other side shows short cells with a large number of thickened, circular hair bases and also stomata. The receptacle cuticle is, however, quite distinct. The cuticle of *Venustostrobus diademus* receptacle has short surface cells with median papillae and large non-papillate cells with stomata. The cuticle of *Venustostrobus indicus* receptacle has surface cells with crescent shaped papillae and no stomata. Both have thickened

cuticular stripes on the receptacle surface, but perhaps they are more in *V. indicus*. Although we have not seen a complete seed of *V. indicus*, it appears to be longish with elongated micropylar end, lined by long, straight-walled cells. The seed of *V. diademus* is small, roundish with cells at the micropylar end slightly wavy. There is not much difference in integument cells and the seeds in both the species are filled with thick opaque tissue. The receptacle cells and the seeds of *Venustostrobus diademus* and *Venustostrobus indicus* sp. nov. thus appear to be quite distinet.

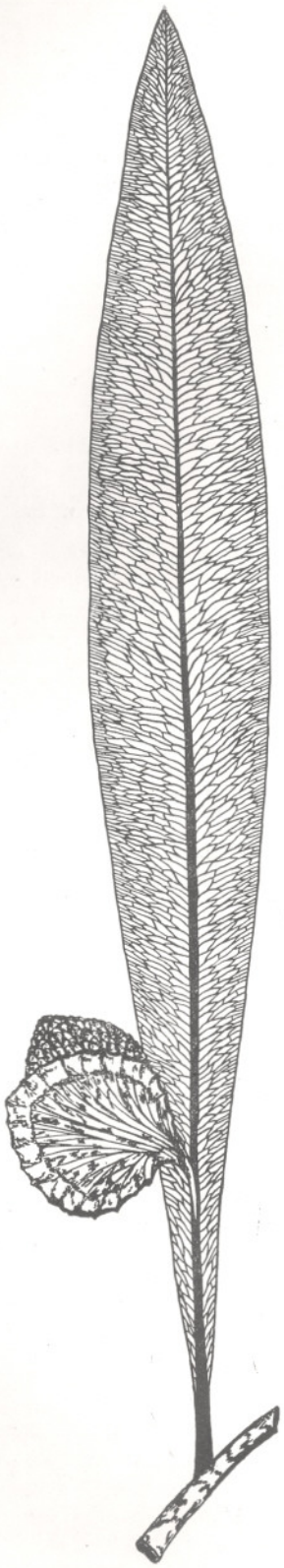
Venustostrobus indicus sp. nov.

Diagnosis — Female fructification of Scutum type attached on midrib of a very long and narrow leaf, leaf petiolate, length and breadth ratio 8:1, veins at right angles to the midrib in middle region, meshes broad on either side of midrib, long and narrow near margin; reproductive organ orbicular or fan shaped; protective bract possesses strong veins forming short, broad meshes, one side bract cuticle with short square to elongated cells with stomata and large number of thickened circular hair bases, the cells of other cuticle large, straight-walled, often obscure; receptacle cuticle consisting of papillate cells, papillae crescent shaped and characteristic, receptacle surface covered with short thickened cuticular stripes, thickeniug of receptacle cuticle uneven; seed integument possesses large tetragonal to pentagonal, straight-walled cells; drawn out micropylar end, cells long, narrow and straight-walled; nucellar cells thin, straight walled; thick, opaque tissue between two layers of integument.

Holotype — B.S.I.P. no. 35281.

Horizon — Raniganj Stage.

Locality — Raniganj Coalfield.



TEXT-FIG. 8

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TEXT-FIG. 8 — A diagrammatic reconstruction of *Venustostrobus indicus* attached on the midrib of a long and narrow *Glossopteris* type of leaf. Seed bearing receptacle is situated between the leaf and the strongly veined, tough, protective bract × *Ca* 1.

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EXPLANATION OF PLATES

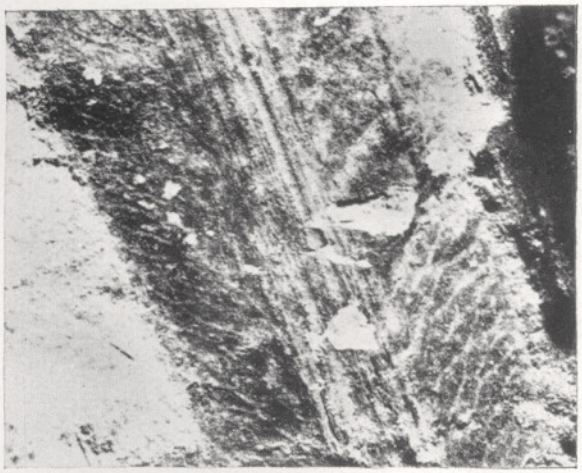
PLATE 1

Venustostrobus indicus sp. nov.

1. Lower portion of *Glossopteris* leaf on which *Venustostrobus indicus* fructification was attached. × 4.
2. Venation in the middle portion of the same leaf. × 4.
3. Basal part of the leaf showing outline of the fructification lying underneath it. × 4.
4. Apical part of the leaf. × 4.
5. Leaf cuticle showing outlines of few cells on the non-stomatiferous surface. × 200.
6. Drawn out neck of the seed. Note hexagonal cells, arranged end to end and two winged pollen grains on the top. × 200.

PLATE 2

7. Cuticle from one surface of the protective bract. × 200.
8. Cuticle from the other surface of the protective bract. Note elongated and rectangular cells. × 200.
9. Elongated cells over the veins of protective bract. Note thickened circular hair bases. × 200.
10. Three stomata from the surface of the protective bract cuticle shown in fig. 8. × 200.
11. Surface cells from the receptacle. Note crescent-shaped papillae. × 200.
12. Cells of the outer integument of the seed. × 200.
13. Cells of the nucellus. × 200.
14. Elongated cells on the drawn out neck of the seed. Note shorter cells of the integument at the base of the neck and the body of the seed. × 200.



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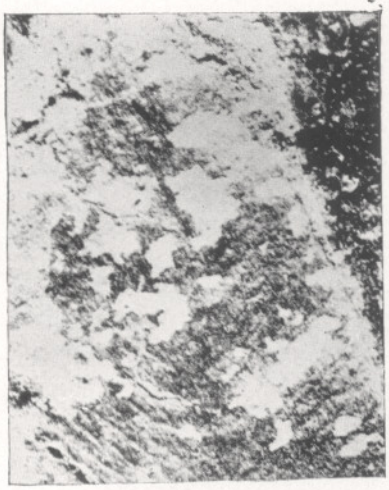

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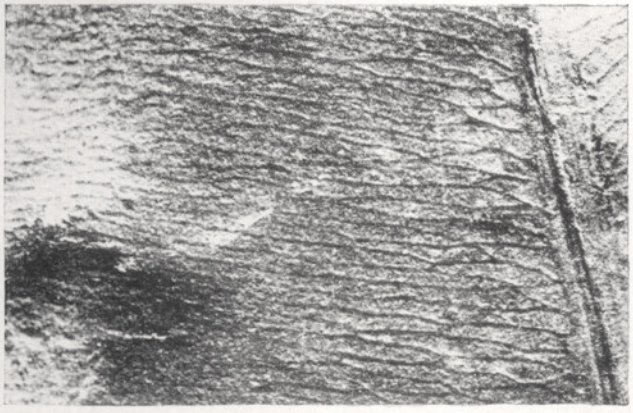

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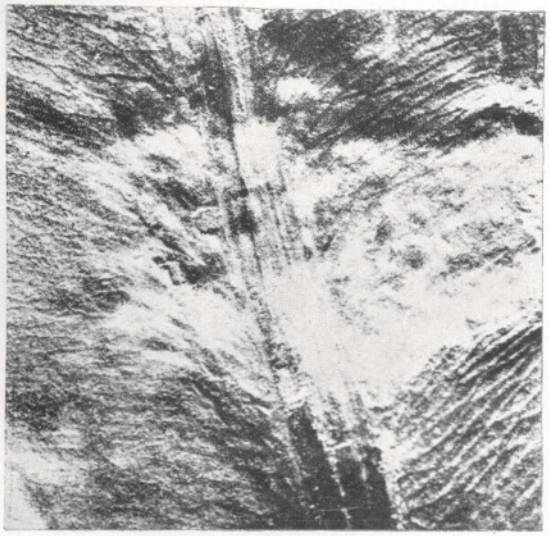

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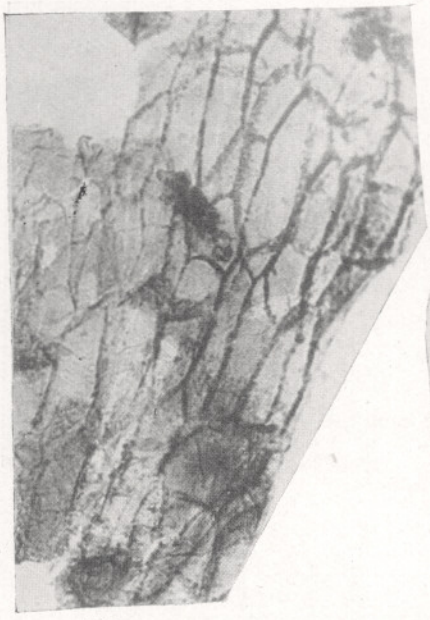

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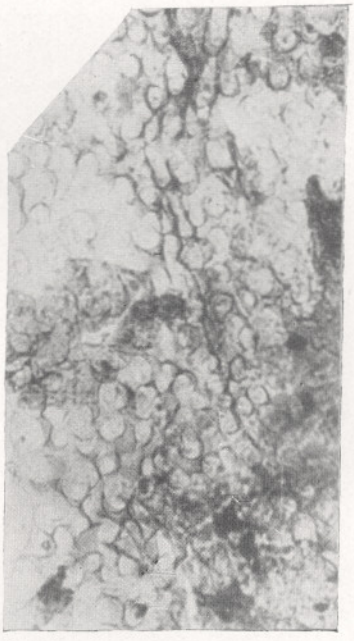

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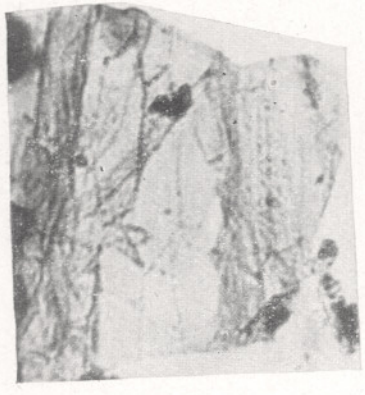

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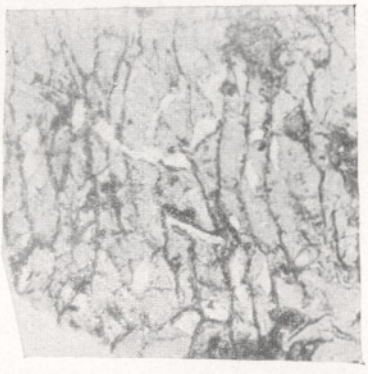

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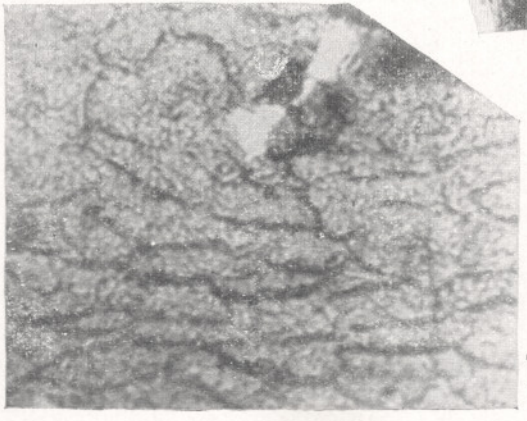

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