

FURTHER OBSERVATIONS ON INDIAN LOWER GONDWANA SPHENOPHYLLALES

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ABSTRACT

New morphological details and the possible habit of *Trizygia speciosa* Royle are described along with two new forms of Sphenophyllales, *Paratrizygia rhodesii* (Rigby) n. comb. and *Parasphenophyllum crenulatum* sp. nov. from the Damuda Series of India.

INTRODUCTION

TRIZYGIA SPECIOSA Royle (1839) is the only Sphenophyllales known from the Indian Lower Gondwana succession. Recently, several specimens of *Trizygia speciosa* have been collected from the Raniganj Formation of Raniganj Coalfield. The study gives new information on the morphology and the possible habit of plants. The same is detailed here along with the record of two new forms of Sphenophyllales from the Lower Gondwana of India.

The specimens are preserved in the form of impressions or compressions. Observations on epidermal structures and other anatomical structures were possible by means of cellular pulls from compressions. For the identification of Sphenophyllales the nomenclature proposed by Asama (1970) has been followed.

All the figured specimens in this paper are preserved at the Museum of Birbal Sahni Institute of Palaeobotany, Lucknow.

DESCRIPTION

Trizygia Royle, 1839

Trizygia speciosa Royle, 1839

Pls. 1, 2, figs. 1-9; Text-figs. 1-6

Synonymy— See Maheshwari, 1968, p. 283.

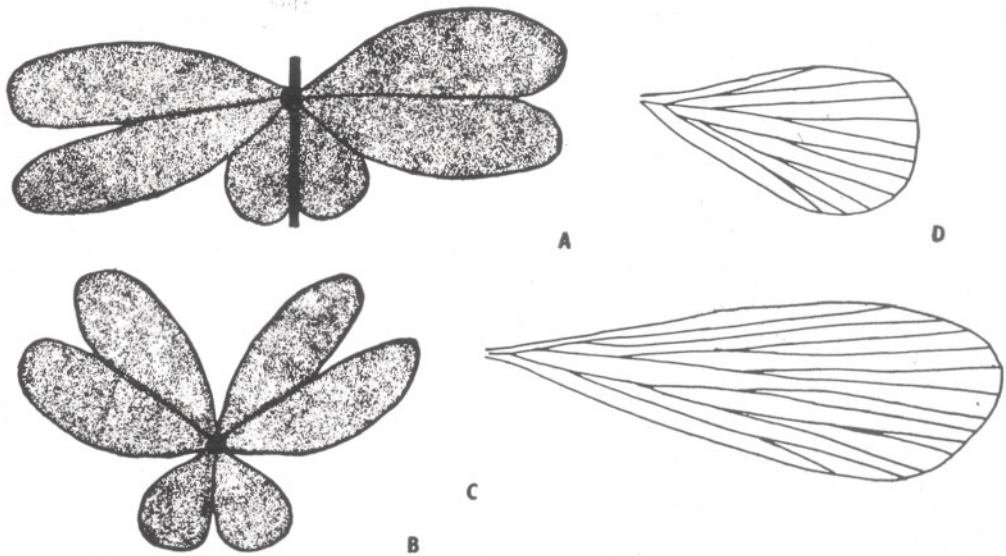
Two hundred specimens of *Trizygia speciosa* have been examined. All of them are either incomplete at the apical or basal ends, or both the ends.

The stems bearing the leaves are slender, unbranched, articulated with slightly swollen nodes (Pl. 1, fig. 1). The internodal region

has two distinct ridges, which do not alternate from one internode to the next, but are continuous. The internodal length of the stem varies from 0.4-2.2 cm and the width from 0.1-0.2 cm. The distance in between two nodes show progressive increase in length from apical to basal end. In cellulose pull of the stem, its substance generally appears to be black or dark brown, but at some places it is light brown and translucent. At such points the stem substance shows xylem elements with scalariform thickenings (Text-fig. 2A) or bordered pits (Text-fig. 2B). Bordered pits are in one row, occasionally in two rows, circular-oval in shape with circular pore. They are either contiguous or arranged separately. Bordered pits have also been reported earlier by Pant and Mehra, (1963), but it is not definite if this is of secondary wood. These elements are flanked on either side by surrounding fibres. The stem surface shows elongate-rectangular epidermal cells, which are placed end to end by their end walls.

Leaves are arranged in whorls on nodes (Pl. 1, fig. 1). Each whorl comprises six leaves. The six leaves are arranged in three distinct pairs (Text-fig. 1A), i.e. two bigger pairs and one small pair. Leaves are attached \pm at right angles to the axis by their cuneate base. Two bigger pairs of leaves occupy the lateral position while the third smaller pair occupies the central position in preserved condition.

A leaf whorl encircles completely round the node (Text-fig. 1B) and not one side of the node as Feistmantel (1879, p. 166) believed them to be. The whorls are spreading horizontally. During fossilization the lamina and the axis are so preserved that



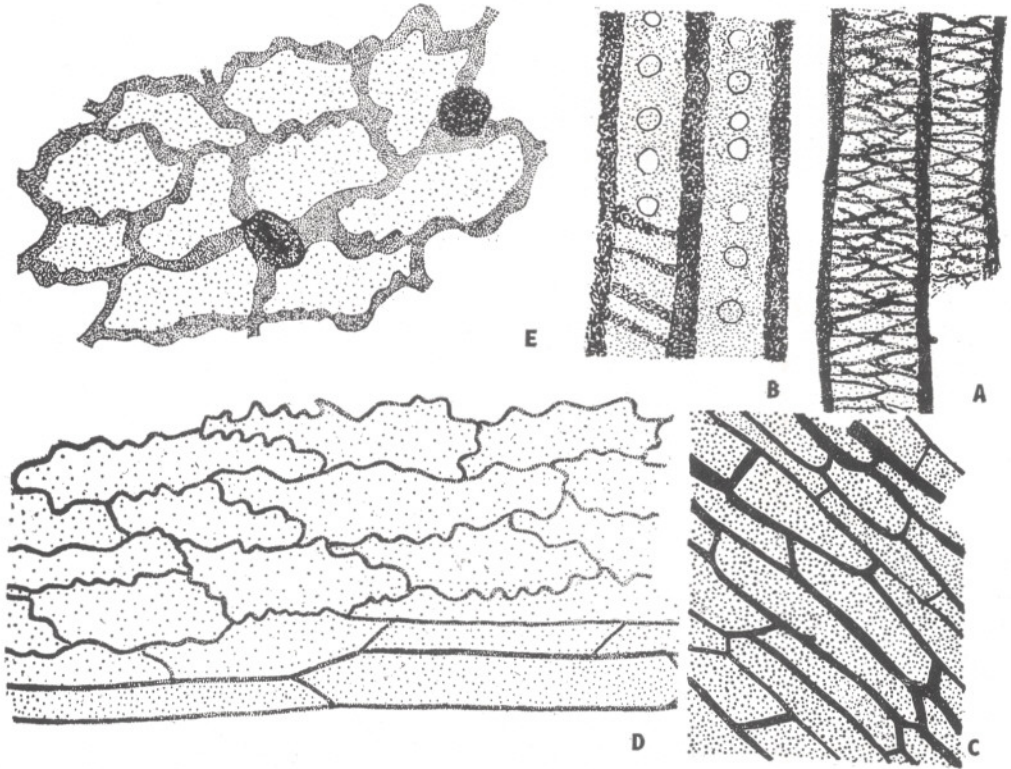
TEXT-FIG. 1. — A, leaf whorl laterally preserved $\times 1.5$. B, leaf whorl dorsi-ventrally preserved $\times 1.5$. C, venation in the lateral leaf $\times 3$. D, venation in the central small leaf $\times 3$.

the two bigger pairs of leaves are arranged on the lateral sides and the smaller pair in the centre. The lateral pairs of leaves are \pm double in size than the central pair. Lateral leaves are \pm asymmetrical in outline, whereas the central leaves are symmetrical. Leaves of the lateral pairs are elongate-ovate, apex obtuse, base cuneate and entire margin. The leaves of central pair are ovate, apex obtuse, base cuneate and entire margin. In all the leaves the inner margin are \pm straight, while the outer margin has a strong curvature. A progressive increase in the size of leaves is well marked, in each successive whorls from apical to basal end. Lateral leaves measure 0.5-2.6 cm in length while the central leaves measure 0.25-1.5 cm in length (see Table 1).

A single vein enters at the base of leaf (Text-fig. 1C, D), which dichotomises into two and then into four veins. The outer pair of veins divides only once before reaching to the margin. The inner pair subsequently dichotomises 1, 2 or 3 times. As a result of which 10-18 veinlets are at the apical margin of the lateral leaves and 10-12 veinlets in the central leaves. Veins

run \pm straight. The angle of divergence in between two veins is 5° . Interconnection in between the veins are absent and the interstitial fibres too.

Epidermal structure of leaves have earlier been reported by Pant and Mehra (1963) and Maheshwari (see Surange, 1964). Epidermal pulls of the leaves show sinuous outlines in which some walls appear faint, while others are darker. In fact, the cells arrangement as a whole indicates that in these pulls, the presence of two translucent layers of epidermis overlapping each other and both of them have sinuous-walled cells, alongwith the straight-walled rectangular cells of vein area. Epidermal cells are 70-140 μ in length and 15-40 μ in breadth. The cells of non-stomatiferous epidermis are longitudinally oriented and tend to be in series parallel to the veins (Text-fig. 2D). The walls are seemingly less sinuous. The cells of the other overlapping layer are irregularly arranged and their walls are deeply sinuous (Pl. 2, fig. 8; Text-fig. 2E). The cells measure 60-80 μ in size. The stomata are haplocheilic having thickened lateral lamellae, measuring 18-20 μ in length. The subsidiary cells are like

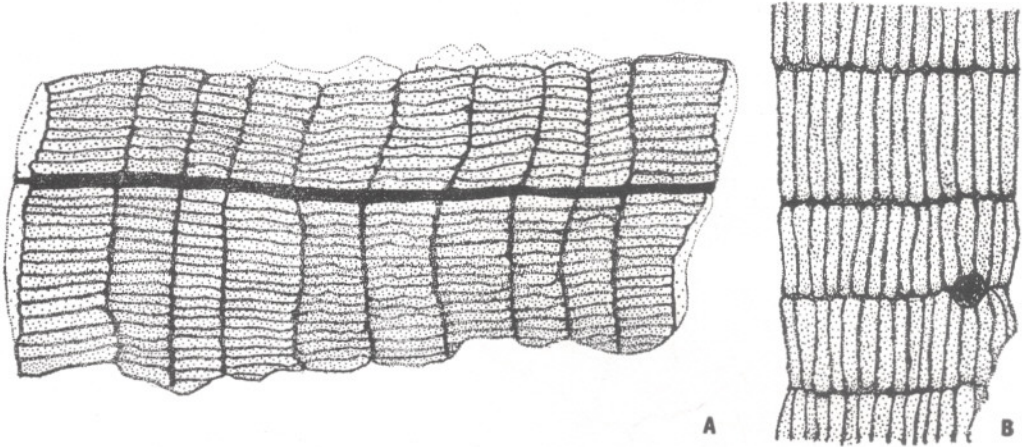


TEXT-FIG. 2. — A, tracheids of foliage shoot showing spiral thickenings $\times 500$. B, tracheids of foliage shoot showing single row of bordered pits $\times 500$. C, cells over the vein region near the basal portion of leaf $\times 400$. D, cells of the vein cells and the non-stomatiferous surface of leaf $\times 400$. E, cells of the stomatiferous surface $\times 400$.

ordinary epidermal cells and the polar subsidiary cells are not different from lateral ones. The basal most region of the leaf, i.e. ± 2 mm from point of attachment with stem show distinct cellular structure from the laminar portion of leaf. Cells in this portion (Pl. 2, fig. 7; Text-fig. 2C) on both the surfaces are thick-walled, rectangular, trapezoid, hexagonal in outline, margin straight and arranged end to end. Cells are $100-120 \mu$ long and $15-20 \mu$ broad. Cell wall $\pm 3 \mu$ thick.

A large number of leafless articulated axes are found along with these foliage shoots (Pl. 1, figs. 2, 4; Text-fig. 3A, B). The axes are preserved in form of impressions, compressions or casts. The axes are articulated and of varying length. The grooves

and ridges are continuous (Pl. 1, fig. 3). Occasionally, the axes are branched. The width of the axes vary from 2-4 cm. In some cases a distinct groove 1.5 to 2 mm broad is present in the middle (Pl. 1, fig. 4). The internodal length varies from 0.6 to 1.6 mm long. The nodal region of both the halves may either fall in one level or may be arranged at different levels (Pl. 1, figs. 2, 6). Branch scars are preserved on nodes. Branch scar is a rounded (Pl. 1, fig. 5; Text-fig. 3B) depression, measuring 1.5-2 mm in dimension. Occasionally, a carbonised crust of $\pm 4-5$ mm broad, is preserved on both the marginal side of stem. This carbonised crust, probably represents the cortical part of the axes. Usually the leafless articulated axes are found lying



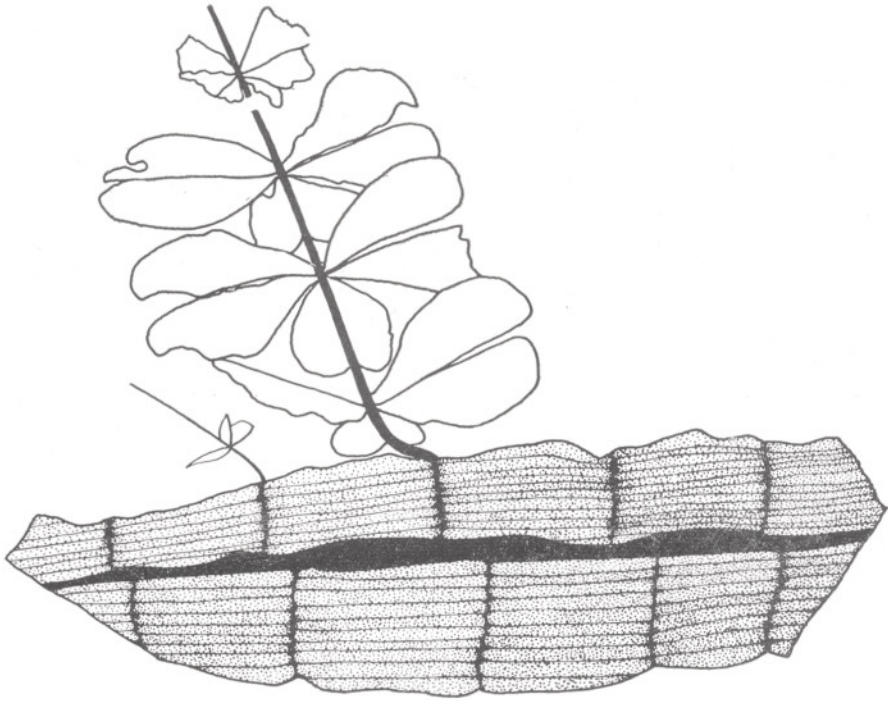
TEXT-FIG. 3. — A, leafless stem showing articulations and a distinct median groove \times Nat. size. B, stem showing branch scar \times Nat. size.

obliquely in the shales, but some specimens are transversely fractured showing three separate regions which can only be interpreted as the cortex, stele and pith. The pith appears to be hollow as no cellular structure is seen on examination of cellular pulls from that region. Cellular pulls taken from the stelar region show tracheids with bordered pits. Pits are arranged in 1-5 rows, bordered, circular-oval with a oval pore (Pl. 2, fig. 8). When pits are in more than one series, they are opposite to one another or arranged in groups of 2, 3 or 5 to 7 pits. Crossfield pits are simple and transversely oval in outline. The outer regions of the stem do not show any preservation of cellular structures.

Occasionally, the foliage shoots of *Trizygia speciosa* are found in close association to the leafless articulated axis suggesting a possible organic connection. The foliage shoots are arranged \pm at right angles only on one side of the axis. The figured specimen (Pl. 1, fig. 6; Text-fig. 4) shows a cast of leafless articulated axis measuring 9 cm long and 3.5 cm broad with a distinct median groove. The axis had distinct articulations which are continuous at nodes. On both the lateral margins of the axes the carbonised area of 5 mm broad are preserved. On one side, two leaf bearing axes emerge from two different nodal points (see Text-fig. 4). On one axis four leaf whorls are preserved on nodes, while on the

other axis only a whorl of a fragmentary leaf is preserved. The anatomical structure of the xylem, i.e. bordered pits from the leaf-bearing shoots are identical to those of leafless axes. This further supports that the leafless axes and the foliage shoots of *Trizygia* are parts of the same plant. The mode of preservation indicates that the leafless axes are rhizomatous structures and the foliage shoots are the aerial structures. Further record of better preserved specimen will throw more light on this problem.

Height of Plant — In this study an attempt has been made to reconstruct the possible height of the leaf-bearing shoots. The task was difficult, since all the specimens were incomplete. To complete this aspect of study, the size measurements of the leaves on different whorls and the length of the internodes have been taken from number of specimens representing different portions of the shoots (see Table 1). Two facts came out from this study that (i) a steady mathematical increase in the size of leaves and the internodal distance is marked from apical end to basal end and (ii) the different shoots representing the same level of aerial shoots show equality in their sizes, i.e. the size of the leaves and the internodal distance are nearly the same. Taking these facts into consideration, portions of aerial shoots representing different regions were placed below one after another on the basis of increase in the size of the leaves. By such



TEXT-FIG. 4— Leafless stem with two foliage bearing shoots arranged at the node $\times 1.5$.

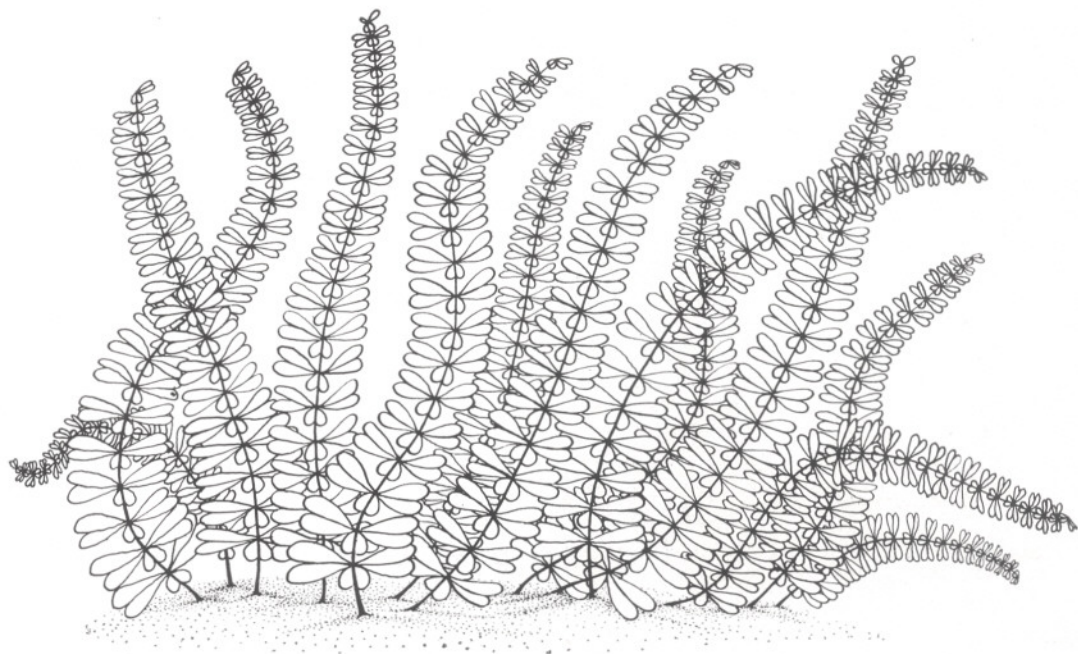
placement, it was possible to get an idea of the height of the plant. The plant, on the basis of such reconstruction, appears to be about 20 cm in height and has 16-22 whorls of leaves (Text-fig. 5).

Habit—*Trizygia speciosa* has been recorded from many parts of Gondwanaland. Most authors have considered that the leaves of *Trizygia* were borne on a plant with creeping habit. Both Seward (1941) and Plumstead (1966) have figured *Trizygia* plant as an insignificant creeper. Pant and Mehra (1963) have suggested that the shoots of *Trizygia speciosa* were probably strangling on the ground like those of *Galium* of Rubiaceae, because in fossil state the leaves are spread out in single plane. However, Rigby (1969) opined that the Gondwana species of *Sphenophyllum* should not have been borne on a plant that differed significantly from the plants suggested by the work of Darrah (1968). He further expressed that it is hard to reconcile the creeping habit with such a wide distribution. In our collection there are several examples which show a number of foliage shoots

preserved closely \pm parallel to one another. Near the basal point, the shoots are preserved fairly close suggesting that the plants were growing straight in tufts like modern grass. This is further supported by the size of plant and their mode of preservation that they were erect herbaceous plants (Text-fig. 5). If the plant was a creeper then it must have shown curves in the nature of stem, which is totally absent in all the recorded specimens.

DISCUSSION

The Indian forms were named by Royle (1839) as *Trizygia speciosa* due to the characteristic arrangement of the leaves on whorls. Subsequently McClelland (1850) opined that the leaves agree morphologically to *Sphenophyllum*, hence it should be transferred to it. This was followed by subsequent authors (see Maheshwari, 1968). However, Maheshwari (1968) preferred the form placing under the original name *Trizygia speciosa* Royle in accordance with the



TEXT-FIG. 5 — Reconstruction of *Trizygia speciosa* Royle.

views of Kräusel (1928) and Edwards (1955) that the northern form identified in *Glossopteris* flora are possibly different from similar looking elements occurring in Angara with which they have been identified. Asama (1970) has reclassified the members of Sphenophyllales on the basis of morphology. According to him the trizygoid attachment of leaves to the stems at nodes represents a distinct line of evolutionary series in Sphenophyllales. The leaves of trizygoids may either show straight or curved veins. *Trizygia* has been restricted by him for the forms with straight veins, while *Paratrizygia* has been used for the forms with curved veins. Following this view, the name *Trizygia* is used for the Indian forms.

Epidermal structure of *Trizygia speciosa* has earlier been described by Pant and Mehra (1963) and Maheshwari (see Surange, 1964). According to Pant and Mehra (1963), the epidermal cells on both the laminar surfaces are sinuous, whereas Maheshwari observed (see Surange, 1964, p. 25) straight-walled cells on one surface and sinuous cells with stomata on the other surface. The present study confirms the observations of Pant and Mehra. The straight-walled epi-

dermal cells observed by Maheshwari must be the straight-walled cells preserved only at the basal portion of leaves.

A comparison of the epidermal structure of *Trizygia speciosa* from the known fossil articulates shows that the morphological structure of stomata in all of them is of advanced nature than *Trizygia speciosa*. The subsidiary cells in *Sphenophyllum majus* described by Abbott (1958, figs. 44, 45) and Remy (1962) and *S. thonii* described by Meyen (1970) are of specialized nature, i.e. they form more or less regular ring around the stomata. Similar ring is also seen in *Asterophyllites equisetiformis*, *Annularia mucronata* and *Annularia stellata* (Abbott, 1958). The subsidiary cells in *S. oblongifolium* (Germ. & Kaulf) Unger (see Meyen, 1970) are less specialized but the stomata are arranged in linear rows. The subsidiary cells of *Phyllothea angusta* Surange and Kulkarni (1968) show transverse thickenings on guard cells.

The leafless axes in their gross morphology, when ill preserved, show close resemblance with *Vertebraria indica* Royle due to presence of distinct nodes and internodes. However, the axis differs from *Vertebraria* in its

characteristic arthrophytic habit, i.e. parallel, continuous running ridges and grooves and the branch scars. Anatomically too, the axis differs from *Vertebraria*. The pit apertures in *Vertebraria* are vested, while in these axes they are circular. Recently Pant and Kidwai (1968) have described anatomical details of the tracheids from the leaf-bearing axis of *Phyllothea indica*. The pits compare in their bordered structure, but differs by crossed pit pores. Surange (1955) has described the rhizome of *Phyllothea* which in its organizational aspect agrees with the leafless axis of *Trizygia*. However, in the rhizome of *Phyllothea*, the characteristic ridges and grooves were absent.

***Paratrizygia* Asama, 1970**

Paratrizygia rhodesii (Rigby) n. comb.

Pl. 2, fig. 10

Synonymy:

1966 *Sphenophyllum rhodesii* Rigby, p. 126, pl. 33, figs. 30-32; text-fig. 2

Emended Diagnosis — Six leaves in a whorl arranged in a trizygoid pattern, two pairs bigger and one pair smaller, obtuse apex and rounded apex, venation dichotomous, arching towards the margin and straight in the middle.

Holotype — WA 23684 (Rigby, 1966).

Figured Specimen — 103/1216, Birbal Sahni Institute of Palaeobotany, Lucknow.

Horizon — Barakar Formation (Lower Gondwana).

Age — Lower Permian.

Description — A leaf whorl consisting of six leaves arranged around a central point. Two pairs of leaves are bigger in size than the third pair. The bigger pairs are obtuse in shape, broadly rounded, and emarginate apex, contracted base and non-petiolate. Leaves are almost as long as broad, measuring 10×8 mm. The smaller leaves are obtuse, broadly rounded apex, non-emarginate, contracted base and sessile. Leaves measure 8×5 mm. Venation repeatedly dichotomizing, arising from a single stouter vein that enters the leaf at base. All veins are curving towards the margin except those in the middle.

Comparison & Discussion — The specimen recorded from the Lower Nakari Seam of

South Karanpura Coalfield agrees morphologically to *Sphenophyllum rhodesii* Rigby (1966). However, the placement of these specimens under *Sphenophyllum* is wrong according to the new classification proposed by Asama (1970) for Sphenophyllales. The specimens morphologically agree to *Paratrizygia* Asama (1970) due to the trizygoid arrangement of leaves in whorl and arched veins towards the margin of leaves. Hence the Australian and Indian specimens are transferred to *Paratrizygia*.

***Parasphenophyllum* Asama, 1970**

Parasphenophyllum crenulatum sp. nov.

Pl. 2, figs. 11, 12

Diagnosis — Whorls comprising of six leaves of equal size; leaves spread out at right angles to the stem; triangular in outline, petiolate base, obcordate apex, apical margin undulate and lateral margin entire; a distinct median vein emerges at the base of leaf which dichotomises into two, each supplying one half of the leaf by repeated dichotomy, veins are arching in the lateral portion and straight in the middle portion, anastomoses absent.

Holotype — 10/1644, Birbal Sahni Institute of Palaeobotany.

Locality — Pit no. 7, Damodar Colliery, East Raniganj Coalfield, West Bengal.

Horizon — Raniganj Formation (Lower Gondwana).

Age — Upper Permian.

Description — Ten specimens are in collection, out of which only 2 are nearly complete. The detached whorls are composed of six leaves. Leaves are of equal size and 2.5-3.5 cm long and 2.2-2.5 cm broad. Leaves are isobilateral triangular in shape. They are broadest at the apex. At the apex, the median region of the leaves are deeply notched, while the marginal ends of the apex are acute. The apical margin has crenulations, while the lateral margins are entire. A single vein emerges at the base of leaf. Immediately after its entry into the lamina, it dichotomizes into two veins. Subsequently, the two veins dichotomize into 30-36 veinlets. Veins in the middle portion of leaf are straight while in the lateral portion they show strong outward curvature.

Comparison—The Lower Gondwana specimen is comparable to *Parasphenophyllum thonii* (Mahr) Asama, 1970 and *P. thonii* var. *minor* (Sterzel) Asama, 1970 which differ in their obovate shape. In *P. spinulosum* (Yabe & Oishi) Asama, 1970 the leaves have toothed margin. *P. neofimbriatum* (Halle) Asama, 1970 differs from *P. crenulatum* in its long elliptical-spathulate shape. *P. shansiense* Asama, 1970 is distinguished by its long obovate shape with rounded apex.

Lacey and Huard-Moine (1966, pl. 4, figs. 28-29; text-fig. 2) recorded a new genus *Benlightfootia mackii* from Wankie beds, Rhodesia. The specimens show bifid leaves occurring singly or in apparent clusters, i.e. in a few instances two, three, four or five leaves may be associated together, and their bases directed to a common point. Leaves are cordate in shape with deep apical notch; venation open, dichotomous arising from a single vein (or possibly two veins very close together) at the base of leaf, repeatedly forking to reach the margins and extremities of two lobes. The vascular system of the two halves of the leaf are completely separate from the base. This specimen shows close morphological similarity to *Parasphenophyllum crenulatum* sp. nov. described here. However, for the time being the Wankie specimens are kept separate in want of specimens showing the arrangement of leaf. Only future record will throw light on this problem.

REMARKS ON THE RECORDS OF SPHENOPHYLLALES FROM THE GLOSSOPTERIS FLORA OF THE SOUTHERN HEMISPHERE

There are a number of records of Sphenophyllales from the Glossopteris flora of

Southern hemisphere (Rigby, 1966; Walton, 1929; Huard-Moine, 1965; Lacey & Huard-Moine, 1966; Archangelsky, 1958). Most of the records from the different Gondwana continents have been referred to *Trizygia speciosa*. However, some records of Sphenophyllales from Wankie District, Rhodesia needs reconsideration in the light of work done by Asama (1970). *Sphenophyllum thonii* Mahr, 1868 recorded by Lacey and Huard-Moine (1966, p. 15, pl. 1, fig. 1) and *S. thonii* var. *minor* Sterzel reported by Walton (1929, pl. a, figs. 3, 4, 8) agree morphologically to each other but they differ considerably from the type specimen of the species. The Wankie specimens are considerably smaller than the European ones; the leaves are not laciniate and only two basal veins are present instead of four. From the illustrations it can be said that the Wankie forms are different from *S. thonii* Mahr and represent a new type.

The forms referred to *Sphenophyllum oblongifolium* (Germ. et Kaulf.) Unger by Walton (1929), Huard-Moine (1965) and Lacey and Huard-Moine (1966) are different from the European ones. The European forms are narrow, four lobed with indentations on the apical margins, while the Wankie specimens are broader and two lobed with only shallow indentations. Hence, it is felt that the Wankie specimens are distinct from the European ones and they should be placed separately under a new species.

Thus, we find that the Gondwana specimens earlier referred to Euramerian ones differ considerably. Hence, all the forms referred to European species from the Gondwanas need careful re-examination for their proper placement.

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EXPLANATION OF PLATES

PLATE 1

Trizygia speciosa Royle

1. A nearly complete specimen with 14 whorls of leaves. × Nat. size; No. 15/1644.
2. Leafless axes showing articulated stem with distinct nodes and internodes. × Nat. size; No. 97/1547.
3. A portion of leafless axes enlarged to show the continuity of ridges and grooves. × 3.
4. Leafless axes with a median groove, indicating region of pith. × Nat. size; No. 98/1547.
5. Leafless axes showing branch scar (B). × Nat. size; No. 6/1644.
6. Leafless axes with two shoots of *Trizygia speciosa*. The shoots are arranged at right angle from the leafless axes at two adjacent nodes. × Nat. size; No. 90/1547.

PLATE 2

Trizygia speciosa Royle

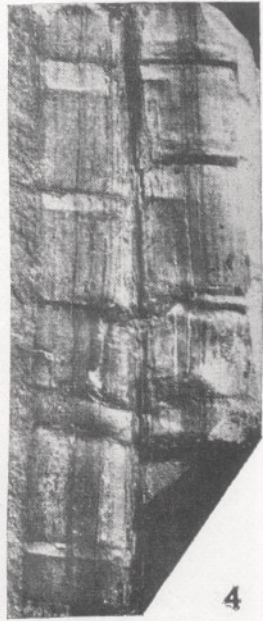
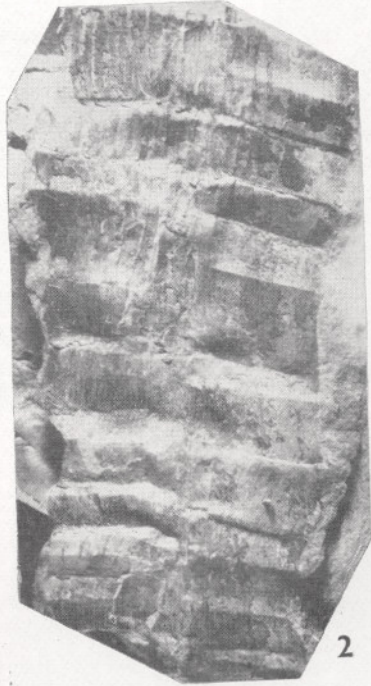
7. Epidermal structure from the basal-most region of the leaves. × 100.
8. Epidermal structure of stomatiferous surface. × 100.
9. Trachiedal structure in the cellular pulls taken from the surface of leafless axes. × 400.

Paratrizygia rhodesii n. comb.

10. A single whorl of six leaves: note the arching veins towards the margin of leaves. × 3; No. 103/1216.

Parasphenophyllum crenulatum sp. nov.

11. A single whorl of six leaves. × 1; No. 10/1644.
12. Two leaves enlarged to show venation. × 3.



B

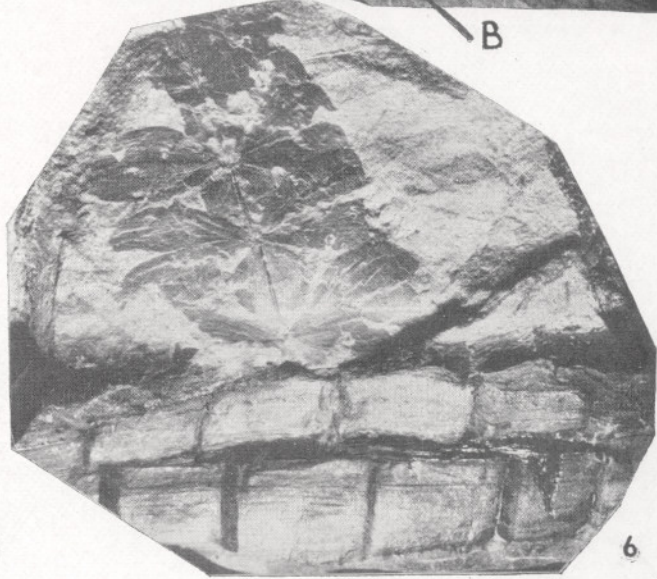
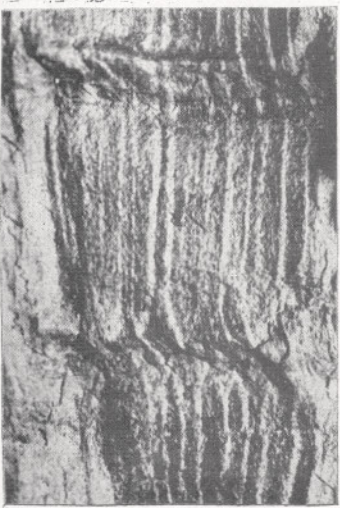


PLATE 1

