Venation pattern in the sphenophyll *Trizygia speciosa* Royle from the Raniganj Formation

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There has been a running controversy about the independent taxonomic status of the genus *Trizygia* vis-a-vis *Spbenopbyllum*. The basic organisation of the foliage shoot in both the genera is apparently similar, except for the trizygoid leaf whorls in the former. The trizygoid leaf whorls are, however, not unknown in *Spbenopbyllum*. The two genera can not be compared at the level of anatomy of the axes or the organisation of the fertile shoot as this information is not available for *Trizygia*. The venation pattern in leaves of *Trizygia* has been analysed in detail with a view to compare it with that of *Spbenopbyllum*, when that information is forthcoming. The parameters chosen for analysis include length, width and area-index of leaves and number of dichotomies, ultimates and dichotomy levels.

Key-words-Sphenopsida, Trizygia, Venation pattern, Sphenophyllum, Raniganj Formation.

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साराँश

रानीगंज शैल-समुह से स्फीनोफिल टाइजीजिया स्पेसिओसा रॉयल में शिराविन्यास का स्वरूप

हरिकृष्ण माहेश्वरी, विनय कुमार सिंह एवं ऊषा बाजपेयी

स्फ़ीनोफ़िल्लम् की तुलना में ट्राइज़ीजिया प्रजाति की निरपेक्ष वर्गीकरणिक स्थिति विवादात्मक रही है।ट्राइज़ीजियामें केवल ट्राइज़ॉइगॉयडी पर्ण-चक़ों के अलावा उक्त दोनों प्रजातियों में पर्ण-समूह प्ररोह का विन्यास स्पष्टतः एक ही जैसा है। तथापि, स्फ़ीनोफ़िल्लम् ट्राइज़ाइगॉयडी पर्ण-चक़ अविदित नहीं है। अक्ष के शारीरीय लक्षणों अथवा अबन्ध्य प्ररोह के अंग-विन्यास के आधार पर इन दोनों प्रजातियों की तुलना नहीं की जा सकती क्योंकि ट्राइज़ीजिया के विषय में अभी तक यह जानकारी उपलब्ध नहीं है।स्फ़ीनोफ़िल्लम् से तुलना करने के लिए ट्राइज़ीजिया की पत्तियों के शिराविन्यास का विस्तृत विश्लेषण किया गया है। स्फ़ीनोफ़िल्लम् के विषय में अभी इस प्रकार की जानकारी नहीं है। प्रस्तुत विश्लेषण हेतु पत्तियों की लम्बाई, चौड़ाई एवं क्षेत्र-सूचक तथा द्विभाजनों की संख्या, अविभाज्य एवं द्विभाजन स्तरों का उपयोग किया गया है।

THE sphenophylls, important constituents of the Northern Hemisphere Upper Carboniferous floras, have a very distinctive foliage comprising a number of leaves, generally in multiples of 3, arranged in radially symmetrical whorls at each node of an articulate axis. The foliage shoots are referred to the genus *Sphenophyllum* Koenig 1825 (International Code of Botanical Nomenclature, 1982, p. 255, ascribes the genus to Brongniart, 1828). The sphenophyllalean foliage is also represented in the Permian sediments of Gondwana, but only as a minor component. The foliage shoots named as *Trizygia speciosa* Royle are different in having characteristic radially asymmetrical (trizygoid) whorls of 6 leaves at each node.

Trizygoid forms, however, do occur in the Northern Hemisphere coal floras and some of the species, e.g., *Sphenophyllum oblongifolium* (Germar & Kaulfuss 1831) Unger 1850 and *S. sinocoreanum* Yabe 1922 have been considered to be closely related to the Gondwana *Trizygia speciosa* (Asama, 1966). This fact coupled with apparent similarity in epidermal features of *Sphenophyllum* and *Trizygia* species led some authors to merge the two genera (McClelland, 1850; Pant & Mehra, 1963). However, Asama (1970) not only maintained separate identity of the two genera but established two more genera, viz., *Parasphenophyllum* and *Paratrizygia*. He feels that the straight or curved course of the veins has significance for generic delimitation.

In view of the apparent confusion about the taxonomic status of sphenophyll foliage genera we decided to investigate the venation pattern. The present study deals with the venation pattern in *Trizygia speciosa* Royle 1839.

The foliage shoots of *T. speciosa* have slender articulate axes. Three pairs of leaves, different in size, arise at each node in zygomorphic but bilaterally symmetrical whorls. The maturation of foliage shoots is acropetal, that is, the larger or older whorls are towards the base and smaller or younger whorls are towards the apex. However, a definite basal or apical leaf whorl has not been reported so far. The longer diameter of the leaf whorls greatly varies and if the leaf size was taken to be a criterion for establishing species, more than a species will have to be chalked up.

MATERIAL AND METHODS

The specimens of T speciosa selected for analysis of the venation pattern were collected from the roof shale and intercalated shale of Nega Seam, Raniganj Formation, Raniganj Coalfield. After preliminary examination of several hundred specimens in field and laboratory, 99 better preserved leaf whorls were selected for study. The leaves were probably very delicate because more often than not their carbonified crust is found in oxidized state. Only those specimens were selected in which leaves were complete and veins were traceable from base to apex of the lamina.

The length, width and area-index of leaves, number of dichotomies, ultimates and dichotomy levels, nodal distances and angle of leaves were observed by wetting the specimens with liquid paraffin or xylol or with a mixture of both.

OBSERVATIONS

The leaves of the first or uppermost pair are inserted at an angle of 55°-85° at the node. The point of insertion is usually concealed and could be ascertained only after removing the overlying axis. The leaves of second or middle pair are inserted more or less at right angles, one each on either side of the axis whereas the leaves of the third or lowermost pair are pendulous and inserted on the exposed surface of the axis at an angle of 135° 155°

The first pair leaves are larger and are 0.7 to 2.9 cm long and 0.3 to 0.9 cm wide at the broadest point. The second or middle pair leaves are more or

less similar and are 0.7 to 2.9 cm long and 0.3 to 1 cm wide.

The third pair leaves are comparatively small, 0.4 to 2 cm long and 0.2 to 1 cm wide. The relationship between leaf length and width is plotted in Text-figures 1-3. It is apparent from the figures that the relationship between the two is quite consistent. The relationships between area-index (length × width) and length and between area-index (length × width) and width are also approximately the same (Text-figure 4) in leaves of all pairs. The lamina of leaves are entire and simple with rounded apices. The length of internodes increases basipetally in successive whorls and ranges from 0.5 to 2.5 cm in observed specimens.

Table 1 summarizes observations on 230 normal leaves (68 of first pairs, 77 of second pairs and 85 of third pairs) from 99 whorls. In 53 whorls, leaves of all the 3 pairs are satisfactorily preserved while in 46 whorls leaves of only one or the other pair are suitable for observation. Five abnormal leaves (3 leaves of first pair and 1 each of the second and third pair) were also studied.

The minimum total number of vein dichotomies is seven, which has been observed in smallest leaves of all the 3 pairs (Text-figure 5.1). In this case the dichotomy category is: 1 of I-order, 2 of II-order and 4 of III-order, totalling 7 dichotomies. The minimum number of ultimate veins (ultimates) is 8, all being III-order ultimates.

Leaves in which veins reach the fourth-level dichotomy normally should have a total of 15 dichotomies including 8 dichotomies of the IV-order. However, hardly any leaf has more than 6 dichotomies of the IV-order and hence the highest total number of dichotomies in such leaves is only 13. Rather some leaves have only 1 dichotomy of IV-order. In all cases, the two peripheral ultimates of III-order, one on each side, do not dichotomize, thus the maximum number of ultimates is fourteen (Text-figures 5.2-5.7)

The V-order dichotomy level is reached only when all the 6, IV-order dichotomies are present. Of



Text-figure 1—Relationship between length and width in the first pair leaves, each dot represents at least one leaf in this and other subsequent figures.



Text-figure 2—Relationship between length and width in the second pair leaves.



Text-figure 3—Relationship between length and width in the third pair leaves.

the 12 IV-order veins resulting from these dichotomies, only 1-10 vein further dichotomies and thus a maximum of 24 ultimates can be present in a leaf. Although the fifth-level dichotomy usually takes place in the central veins, it may occur in any of 12 IV-order veins (Text-figures 5.8-5.17).

A few leaves show slight variation in venation pattern. Three first pairs leaves, with maximum fifthlevel dichotomy have unusual venation. One leaf with 14 dichotomies though has only 5, against the usual 6, IV-order dichotomies, yet it reaches the Vorder dichotomy level. In this leaf 2 out of the 10, IV-order veins have entered the fifth level of dichotomy without satisfying the condition that all the 6 potential III-order veins be present (Text-fig. 5.20). The second leaf has got all the possible 8, IV- order dichotomies, instead of the normal 6, and 6, Vorder dichotomies. Here all the 8, III-order veins, including the 2 peripheral ones dichotomize (Textfig. 5.22). The third leaf has 7, IV-order dichotomies, one more than the usual 6, and 8 V-order dichotomies. Here only one peripheral III-order vein has not dichotomized (Text-fig. 5.21). A second pair leaf with 12 dichotomies has 5, IV-order dichotomies, 4 in one half and only one in the other half of the lamina. Here all the 4, III-order veins including peripheral one in one half, have dichotomized (Text-fig. 5.18). A third pair leaf also shows fifth level dichotomy though only 5, IV-order dichotomies are present. Here one out of 10 IVorder veins has dichotomized (Text-fig. 5.19).



Text-figure 4-Relationship between area-index (length × width) and length (solid dots) or width (hollow dots) of leaves.

Maximum dichotomy level	Number of leaves	Length × width (mm)	Number of dichotomies and their order	Number of ultimates and their order
		FIRST	PAIR	
third	4	7-9 × 3-4	7 1 (I), 2 (II), 4 (III)	8 8 (111)
fourth	46	9-25 × 3-8	8-13 1 (1), 2 (H), 4 (III), 1-6 (IV)	9-14 7 (III), 2 (IV) to 2 (III), 12 (IV
fifth	18	14-29 × 5-9	14-23 1 (1), 2 (11), 4 (111), 6 (TV), 1-10 (V)	15-24 2 (111), 11 (IV), 2 (V) to 2 (111) 2 (IV), 20 (V)
		SECON	D PAIR	
third	4	7-9 × 3-4	7 1 (1), 2 (11), 4 (111)	8 8 (III)
fourth	44	9-25 × 3-9	9-14 1 (1), 2 (11), 4 (111), 2-6 (1V)	10-14 6 (III), 4 (IV) to 2 (III), 12 (IV
fifth	29	13-29 × 4-10	14-22 1 (1), 2 (11), 4 (111), 6 (1V), 1-9 (V)	15-23 2 (III), 11 (IV), 2 (V) to 2 (III), 3 (IV), 18 (V)
		THIRE) PAIR	
third	5	4-5 × 2-3	7 1 (I), 2 (II), 4 (III)	8 8 (111)
fourth	60	4-20 × 3-10	9-13 1 (I), 2 (II), 4 (III), 2-6 (IV)	10-14 6 (III), 4 (IV) to 2 (III), 12 (IV)
fifth	20	7-20 × 5-10	14-20 1 (I), 2 (II), 4 (III), 6 (IV), 1-7 (V)	15-21 2 (III), 11 (IV), 2 (V) to 2 (III), 5 (IV), 14 (V)

Table 1-Observed first, second and third pair leaves with maximum dichotomy levels, length × width-range, number of	
dichotomies and ultimates and their orders	

Numbers outside the parentheses indicate dichotomy or ultimate orders, respectively, mentioned in Roman numerals within the parentheses.

The relationships of total dichotomies to the length (Text-figs 6-8), to the width (Text-figs 9-11) and to the area-index (length × width, text-figures 12-14) in the leaves of all the pairs are more or less parallel. In Text-figures 6-11, the variation in dimensions of individual leaves having equal number of dichotomies is shown by the vertical lines. For example, the leaves having 13 dichotomies are 10 to 20 mm long in first pair (Text-fig. 6), 10 to 20 mm long in second pair (Text-fig. 7) and 5 to 14 mm long in the third pair (Text-fig. 8). For less than 10 or more than 15 dichotomies, the deviation in length range is small except in the third pairs where leaves having 17 dichotomies may be 10 to 19 mm in length. That is to say the greatest length variation is usually among the leaves having 11 to 15 dichotomies.

The greatest width variation, like that of length occurs among the leaves having 11 to 15

dichotomies in all the pairs (Text-figs 9-11). For example, leaves with 13 dichotomies vary from 3 to 8 mm in width. The variation in width is very small in leaves with less than 11 or more than 17 dichotomies.

In terms of length, the maximum variation in dichotomy numbers occurs at 10 and 23 mm in the first pairs, 22 and 24 mm in the second pairs and 9 mm in the third pair leaves. In terms of width the maximum variation in number of dichotomies occurs at 8 mm in the first pairs, 4 mm in the second pairs and 3 mm in the third pair leaves.

The relationship between area-index (length \times width) and number of dichotomies is shown in Text-figures 12 to 14. The greatest area-index variation, like that for length and width, occurs among the leaves having 11 to 15 dichotomies. The leaves having 13 dichotomies vary in area-index from 30 to 185 in first, 30 to 126 in



Text-figure 5—Diagramatic representation of variation in leaf venation. Text-figure 5.1 represents the basic skeleton of venation in leaves of all pairs. Text-figures 5.2 to 5.17 illustrate the increasing number of dichotomies and dichotomy levels. Text-figures 5.18 to 5.22 represent unusual venation.





Text-figure 6—Relationship between length and number of dichotomies in leaves of first pair Vertical lines show length variation found in leaves having same number of dichotomies. Brackets indicate dichotomy levels in this and subsequent diagrams.

second, and 15 to 112 in the third pair leaves.

The frequency of leaves with different dichotomy numbers and dichotomy levels is shown in Text-figure 15. The data is plotted from leaves of 53 complete whorls. The majority of leaves in all the 3 pairs have 13 dichotomies. The frequency of leaves with 7 dichotomies increases from first to third pairs and frequency of leaves with higher number of dichotomies decreases from first to third pairs. The analysis of data indicates that although the leaves of the 3 pairs are dissimilar in dimensions yet have similar venation pattern.

Fifteen dichotomies are possible after the completion of fourth level dichotomy and 31 dichotomies after the fifth level dichotomy, i.e., 1 dichotomy of the I-order, 2 dichotomies of the II-order, 4 of the III-order, 8 of the IV-order and 16 of the V-order.

Of the five dichotomy levels, first to third (with total 7 dichotomies) are present in all the leaves, from smallest to largest. Except for a couple of leaves, only 6 out of the possible 8 dichotomies could be observed after the fourth dichotomy level (with 13 total dichotomies). Two outermost veins,

Text-figure 7—Relationship between length and number of dichotomies in leaves of second pair. Vertical lines show length variation found in leaves having same number of dichotomies.



Text-figure 8—Relationship between length and number of dichotomies in leaves of third pair. Vertical lines show length variation found in leaves having same number of dichotomies.



Text-figure 9—Relationship between width and number of dichotomies in leaves of first pair Vertical lines show width variation found in leaves having the same number of dichotomies.

one on either side, do not enter into fourth level dichotomy.

The highest number of dichotomies observed is 23 (with 10 dichotomies of fifth level dichotomy) and the lowest number of dichotomies observed is 7 (with third level dichotomy).

The number of dichotomies may either be equal in all the leaves of a whorl or may vary slightly. Out of the fiftythree complete whorls studied, all the leaves in twentytwo whorls have equal number of dichotomies (Table 2). For example, one of the smallest and youngest whorls in our study has only 7 dichotomies (8 ultimates) in all the leaves; none of the dichotomies entering the fourth level dichotomy. In another smaller whorl the second and third pair leaves have 7 dichotomies each (8 ultimates) whereas the first pair leaves have 9 dichotomies (10 ultimates). In the latter pair, 2 out of the 8 III-order veins, have entered the fourth level



Text-figure 10—Relationship between width and number of dichotomies in leaves of second pair. Vertical lines show width variation found in leaves having the same number of dichotomies.

Number of whorls	Number of dichotomies in first pair leaves	Number of dichotomies in second pair leaves	Number of dichotomies in third pair leaves
1	7	7	7
1	9	7	7
1	8	9	7
1	10	10	7
1	10	11	7
1	12	13	10
1	7	7	11
3	11	11	11
1	12	12	12
6	13	12	12
2	13	13	12
1	15	15	12
1	11	10	13
1	11	13	13
15	13	13	13
1	13	14	13
1	15	13	13
1	15	14	13
2	15	15	13
1	15	15	14
1	15	14	15
1	15	15	15
1	16	15	15
1	21	15	15
1	19	17	15
1	14	14	17
1	17	17	17
1	20	22	17
1	22	17	18
1	22	22	19

Table 2-Observed complete whorls (identical or unidentical) with number of dichotomies in leaves of all the 3 pairs

Total whorls studied = 53

dichotomy resulting into 2 dichotomies and 4 ultimates of the IV-order; 6 III-order ultimates have remained unbranched further.

-There are three whorls that show third pair leaves with 7 dichotomies (8 ultimates) but their first and second pair leaves have entered the fourth level dichotomy resulting in 8 to 11 dichotomies (9) to 12 ultimates, respectively). One to 4, III-order veins enter the fourth level dichotomy to produce 1 to 4 dichotomies (2 to 8 ultimates respectively) leaving 7 to 4 III-order ultimates respectively, unforked. In a rather rare condition, the third pair leaves have more dichotomies than those of the other two pairs. One such unusual whorl shows its first and second pair leaves with 7 dichotomies (of up to third level dichotomy) but its third pair leaves have unusually entered the fourth level dichotomy to produce 4 dichotomies resulting 8, IV-order ultimates, leaving 4 III-order ultimates, 2 each on either side on the periphery.



Text-figure 11—Relationship between width and number of dichotomies in leaves of third pair Vertical lines show width variation found in leaves having the same number of dichotomies.

In leaves with total 11 dichotomies, 4 out of 8, III-order veins, two in either half of lamina, enter the fourth level dichotomy. Thus the leaves have 4, III-order and 8, IV-order ultimates. If the total number of dichotomies is 12, then 5, III-order veins enter the fourth level dichotomy, thus producing 3, III-order and 10, IV-order ultimates. In leaves with 13 dichotomies, all III-order veins, except 2, one on either side, divide to produce 12, IV-order ultimates, remaining two being of III-order.

All the leaves that have a total of 14 or more dichotomies, one or more veins enter the fifth level dichotomy. There is no definite trend as to leaves of which pair will first enter the higher level dichotomy.

A total of 17 complete whorls, show fifth level dichotomy. All the leaves in 11 whorls show V-order dichotomy but one such whorl has first pair leaves with 7, IV-order dichotomies, one more than the usual 6. In 4 whorls the third pair leaves do not attain fifth level dichotomy. One whorl has only first pair leaves with V-order dichotomy while still another whorl has only second pair leaves with fifth level dichotomy. Another group of 20 whorls also shows V-order dichotomies but in these whorls one or the other leaf pair is not well-preserved.

DISCUSSION

Although more than one vein may usually be seen entering the base of the leaf yet the fact is that the venation in all the leaves of *Trizygia speciosa* results from a single vein (frequently distinct in younger and smaller leaves) which arises from a single trace at the point of leaf attachment. The initial vein after the first dichotomy results into two basic I-order veins, one for the left and other for the right half of the lamina. These two costae (veins)



Text-figure 12—Relationship between area-index (length × width) and number of dichotomies in leaves of first pair Vertical lines show variation in area-index in leaves having the same number of dichotomies.

form the basis of venation. Each dichotomizes two to four times and produces usually similar venation pattern in its respective half.

Further dichotomy of two basic I-order veins results into 4, II-order veins. The two successive dichotomies, first and second, occur so close to the point of attachment that 2-4 veins are apparently seen entering the lamina base. The 4, II-order veins further dichotomize. Thus a total of 7 dichotomies results into 8 ultimates, the minimum for a leaf. These 8, III-order veins may terminate as ultimates in younger and smaller leaves or a maximum of 6 may further divide. The two III-order peripheral veins, one in either half, normally do not dichotomize.



Text-figure 13—Relationship between area-index (length × width) and number of dichotomies in leaves of second pair. Vertical lines show area-index variation in leaves having the same number of dichotomies.

The maximum dichotomy level found in leaves of all pairs is 3 to 5 and that of dichotomies is 7 to 23 (8 to 24 ultimates, respectively). No leaf of any pair has been observed possessing less than 7 dichotomies (8 ultimates) with the maximum third dichotomy level or more than 23 dichotomies (24 ultimates) with the maximum third dichotomy level or more than 23 dichotomies (24 ultimates) with the maximum fifth dichotomy level.

The leaves advance into the fourth dichotomy level mostly in larger and older leaves. The first leaves of a whorl are usually the first to enter the next higher dichotomy level. The leaves with fourth dichotomy level may have 8 to 13 dichotomies and 9 to 14 ultimates, respectively. At this level all the 6, III-order potential veins are satisfied by the IV-order



Text-figure 14—Relationship between area-index (length × width) and number of dichotomies in leaves of third pair. Vertical lines show variation in area-index in leaves having the same number of dichotomies.

dichotomies, except in a few cases where the leaf has produced one V-order dichotomy after satisfying all but one potential III-order vein by the IV-order dichotomies.

The leaves advance into fifth dichotomy level, generally after filling all the 6, IV-order dichotomies. The leaves possessing fifth level of maximum dichotomy, the highest level in the present study and found in leaves of all the pairs, may have 14 to 23 dichotomies (15 to 24 ultimates, respectively). The highest number of dichotomies in first pair leaves is 23 (10, V-order dichotomies) observed in a single leaf, in second pair leaves 22 (9, V-order dichotomies) observed in third pair leaves 20 (7, V-order dichotomies) observed in a single leaf.

Asama (1966) proposed two types of evolutionary series in Sphenophyllum, (1) Sphenophyllum oblongifolium series, changing in order of S. oblongifolium \rightarrow S. speciosum \rightarrow S. sincoreanum and (2) Sphenophyllum thonii series, changing in order of S. shansiense \rightarrow S. Thonii \rightarrow S. thonii var. minor. According to him in the former, trizygoid series represented in Cathaysian and Gondwana floras, the size of the leaf segment



Number of dichotomies

Text-figure 15—Comparative frequency of leaves with different number of dichotomies. Broken line with dot, solid line and broken line represent leaves of first, second and third pairs respectively.

increases with the lapse of time whereas it decreases in the latter, non-trizygoid series. For establishing the *T. oblongifolia* series, Asama (1966) selected 3 specimens of *T. speciosa* from the Barakar Formation and 10 specimens from the Raniganj Formation all figured by Feistmantel (1880). The specimens selected from Barakar were smaller than those of Raniganj. However, it does not necessarily mean that there were apparent size differences between Barakar and Raniganj forms. Feistmantel had also pointed that the differences in size between Barakar and Raniganj specimens can not be taken as distinguishing and constant characters.

It is noteworthy that, so far, branching or apical or basal regions have not been observed in *T. speciosa* from the Gondwana. The specimens from the Raniganj Formation show small as well as large leaf whorls, obviously belonging to apical and basal parts respectively, of different specimens.

Although a very simple open dichotomous venation is present in sphenophyllalean leaves, a detailed analysis of venation pattern was not attempted so far. We were encouraged to undertake this investigation following interesting results from similar investigation on venation pattern in petals of certain dicotyledonous flowers. Our study shows significant and strong correlation between leaf length and number of dichotomies, leaf width and number of dichotomies, area-index of leaves and frequency of dichotomies. Sphenophyllales is a large group comprising a number of species distributed in southern and northern palaeofloristic zones from Lower Carboniferous to Upper Permian or Lower Triassic and hence one may expect a considerable variation in venation pattern. Detailed analyses of venation pattern in other species of the group may indicate affinities between northern and southern members of the group. The botanical affinities of Trizygia speciosa are certainly with the Arthrophyta, notwithstanding the alleged connection between Trizygia speciosa Royle foliage shoot and Vertebraria indica Royle, a gymnospermic root axis (Maithy, 1976). It is just one of the million examples of overlap of a fossil by another. This fact was overlooked in the excitement of a new discovery and to justify his observation Maithy (1976, p. 273, 274) even found morphographical and anatomical differences between Vertebraria and the axis reported by him (1976, pl. 1, figs 2, 4, 5, 6; pl. 2, fig. 9), where none existed.

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