

THE STRUCTURE OF *VERTEBRARIA* *INDICA* ROYLE

by DIVYA DARSHAN PANT and R. SHANKER SINGH

ABSTRACT. Pulls of carbonised substance of Royle's type of *V. indica* and 250 other axes referable to the same species have been studied. The other specimens were collected from the Raniganj and Giridih coalfields (Permian; Upper Damuda Group, Gondwana System). They all show the same kinds of secondary xylem, large parenchyma, and phloem-like cells. The different kinds of pitting and their frequency in the tracheids, the frequency of uniseriate rays of different heights, their length, and the range of variation in xylem character, have been determined. It has been found that characters of xylem described for *V. raniganjensis* are within the range of *V. indica* and this species may be regarded as a synonym of *V. indica*. None of our several axes of *V. indica* shows any trace of pith.

ROYLE (1833) founded two species of *Vertebraria* from India (*V. indica* and *V. radiata*), that were later recognized as lateral and sectional views of the same fossil. By a strange coincidence McCoy (1847) and Dana (1849) made the same error in giving two names (*V. australis* and *Clasteria australis*) to laterally exposed and sectional views respectively of the same fossil. Arber (1905) and others have pointed out that all axes of this kind belong to a single species, *Vertebraria indica*, but Surange and Maheshwari (1962) have recognized two new species of the genus among compressions and Schopf (1965) has established a fourth species for a petrified axis, described earlier by Kraüsel. However, a review of the literature on *Vertebraria* gave us the impression that the characters of the various species of the genus were neither sufficiently known nor clearly demarcated.

MATERIAL AND METHODS

A large number of specimens of *Vertebraria* were collected from localities in the coalfields of Raniganj and Giridih. About 300 celloidin pulls of coaly material were prepared from 250 compressions. The pulls were mounted in Canada balsam and examined in ordinary transmitted light under a compound microscope and also under phase contrast and dark field illumination. Averages have been generally calculated from 300 random counts but where this was not possible, the smaller number of counts has been mentioned against the averages.

All figured specimens and slides of this paper form part of Divya Darshan Pant Collection of plant fossils, located in the Botany Department of the Allahabad University.

DESCRIPTION OF EXTERNAL FEATURES

Compressions of *Vertebraria* axes are either found lying almost vertical to the bedding plane and seen in sectional views or they lie horizontally in the layers of the Lower Gondwana rocks and are exposed in a lateral view (Pl. 124, Pl. 125, figs. 1-2; text-fig. 1A-C). Sectional views of *Vertebraria* axes show rays of carbon, all joined and radiating from a centre and separated from each other by rather wide bays of rock matrix. The

[Palaeontology, Vol. 11, Part 5, 1968, pp. 643-53, pls. 124-7.]

© 6055

U u

rays are simple and almost equal, their ends may be slightly flattened, occasionally the surface of a bay may be covered by a film of carbon which joins two adjacent rays (Pl. 125, fig. 1). The largest vertically preserved *Vertebraria* in our collection is 2.7 cm. in diameter. Lateral views of horizontally compressed *Vertebraria* axes are more common. The thickest specimen in our collection is 9 cm. wide. The axes show 2 to 4 series of rectangular areas with 1 to 3 intervening longitudinal furrows or ridges. As a rule the rectangular areas are of almost equal size but sometimes they may appear very unequal (text-fig. 1B). Branching axes are not uncommon. As described by Oldham (1897) the branching of these axes takes place in two ways. Either the branching axis divides into two or more almost equal branches or the axes produce thinner branches from their sides (text-fig. 1A-C). The branches may show similar rectangular areas but some of the thinner axes have a central longitudinal groove or ridge and only occasional obscure horizontal marks (Pl. 124, fig. 5). Some of these axes show attached roots (Pl. 124, fig. 3). An attached root is also seen in a vertically compressed axis (Pl. 125, fig. 1).

As suggested by Pant (1956) the preservation of horizontally compressed *Vertebraria* is not fundamentally different from that of vertically compressed axes, except that their xylem rays radiating dorsally and ventrally become shorter or narrower in the radial direction by undergoing greater radial compression, while the radial dimension of their horizontally placed rays remains practically uncompressed. Naturally such axes are usually exposed along the plane of easier splitting, i.e., along the wider horizontally placed rays and these appear as two series of typical rectangular areas on either side of a median ridge or furrow representing the central longitudinal core of *Vertebraria* and the transverse sides of the rectangles represent the upper and lower limits of the wide parenchymatous bays. Occasionally the rock is fractured along one of the dorsally or ventrally placed vertically compressed rays (Pant 1956, text-fig. 2A, where towards the top left a few narrower rectangular areas are those of a vertically compressed ray). Additional longitudinal rows of rectangular areas may be seen at a point where a *Vertebraria* branches (text-fig. 1B; Pl. 124, fig. 2). Many of our axes lie among leaves of *Glossopteris*, *Rhabdotaenia*, *Pteronilssonina*, and other specimens. In one of these a *Glossopteris* leaf at first sight appeared to be connected with a *Vertebraria* but a closer examination reveals that the apical end of the leaf was actually facing the axis.

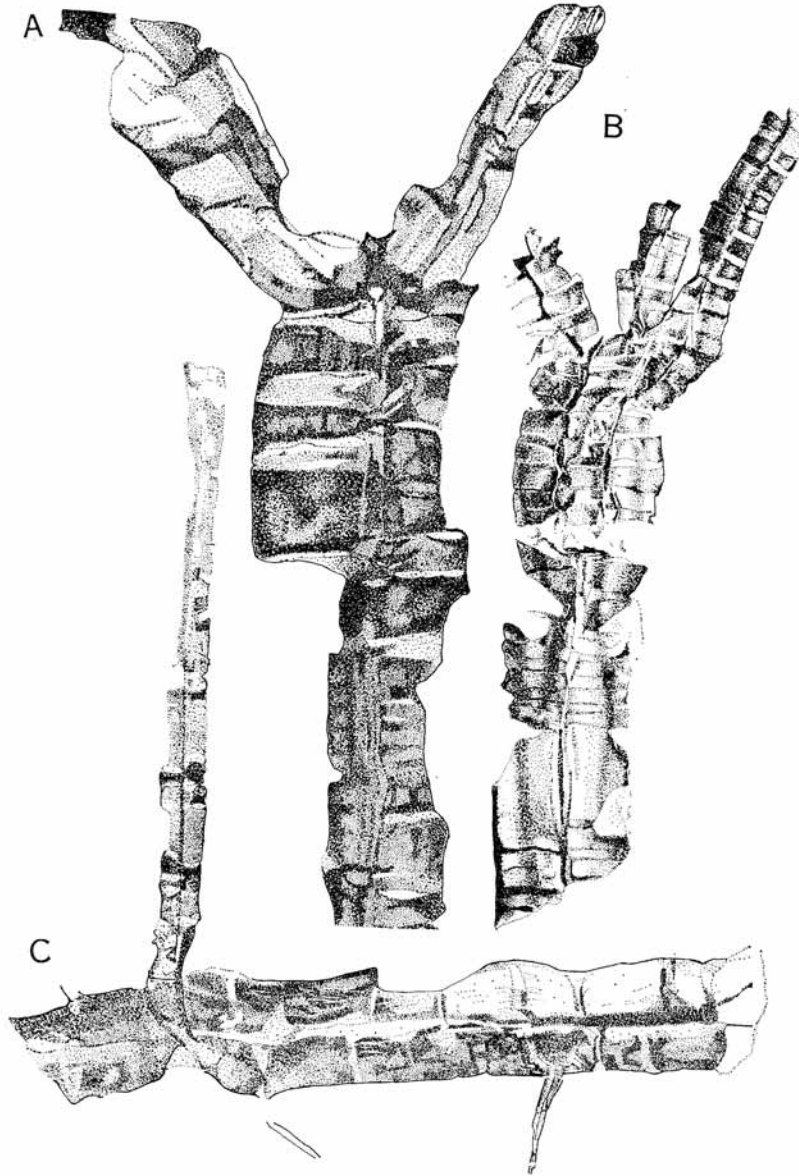
INTERNAL STRUCTURE

Horizontally compressed axes

Celloidin pulls of carbon from horizontally compressed axes and their branches with or without typical rectangular areas usually show the same kind of secondary xylem as

EXPLANATION OF PLATE 124

Figs. 1-5. *Vertebraria indica* Royle. 1, Forked axis, No. 1804, $\times \frac{6}{5}$. 2, Trifurcate axis showing wide rectangular areas in two series below and triseriate areas above; rectangular areas are not seen for some distance near the lower end; No. 1756, $\times \frac{2}{5}$. 3, Axis with elongated rectangular areas and a few thin branches (roots) with scalariform xylem (cf. *Lithorhiza tenuirama* Pant), No. 1805, $\times \frac{2}{5}$. 4, Fragment of a thick axis showing tetraseriate rectangular areas, No. 1808, $\times \frac{1}{2}$. 5, Axis with a median furrow but its rectangular areas are ill defined due to the presence of only a few rather obscure transverse marks, No. 3052, $\times \frac{1}{5}$.



TEXT-FIG. 1, A-C. *Vertebraria indica*. A, Axis forked into two almost equally thick branches, No. 1804, $\times 2$. B, Trifurcate axis showing short and wide rectangular areas above; rectangular areas not seen near the lower end (also Pl. 124, fig. 2), No. 1756, $\times \frac{1}{2}$. C, Axis showing thinner branch, No. 1789B, $\times 2$.

is seen in a radial section. Naturally, in compressed wood, such pulls also show the radial or tangential walls of the tracheids often overlapping each other. At a few places, the xylem is even seen in a tangential view or in a partially radial and partially tangential view (text-fig. 2H; Pl. 127, fig. 6).

Radial views of xylem. (a) Royle's type. A pull from Royle's type specimen No. V. 4189 in the British Museum (Natural History) shows the typical xylem of *Vertebraria* as if in a radial longitudinal section (Pl. 125, fig. 3). The tracheids have uniseriate to tri-seriate oval to circular pits placed far apart or contiguous. Biseriate and triseriate pits are usually opposite but alternately arranged pits have also been observed (text-fig. 3D, E). Rays are uniseriate and ray fields show pits usually without any border (text-fig. 3F). A few large parenchyma cells like those reported by Pant (1956) are mostly broken down.

(b) Specimens from Raniganj and Giridih coalfields. All our pulls of the carbon from horizontally preserved specimens of *Vertebraria* axes show well-preserved secondary xylem covering the entire surface of the rectangular areas (where carbon is preserved), from one side of the axis through the median ridge or furrow right up to the opposite side. On all our slides most of the xylem is seen as in a radial longitudinal section. A pith should have been visible in such radial views but no pull from the axes in our collection shows any trace of parenchyma cells in the centre, although ray parenchyma, phloem-like thin-walled cells and the typical large parenchyma cells of *Vertebraria* are usually well preserved. Instead, numerous pulls show undisturbed tracheids filling the central parts of the axes.

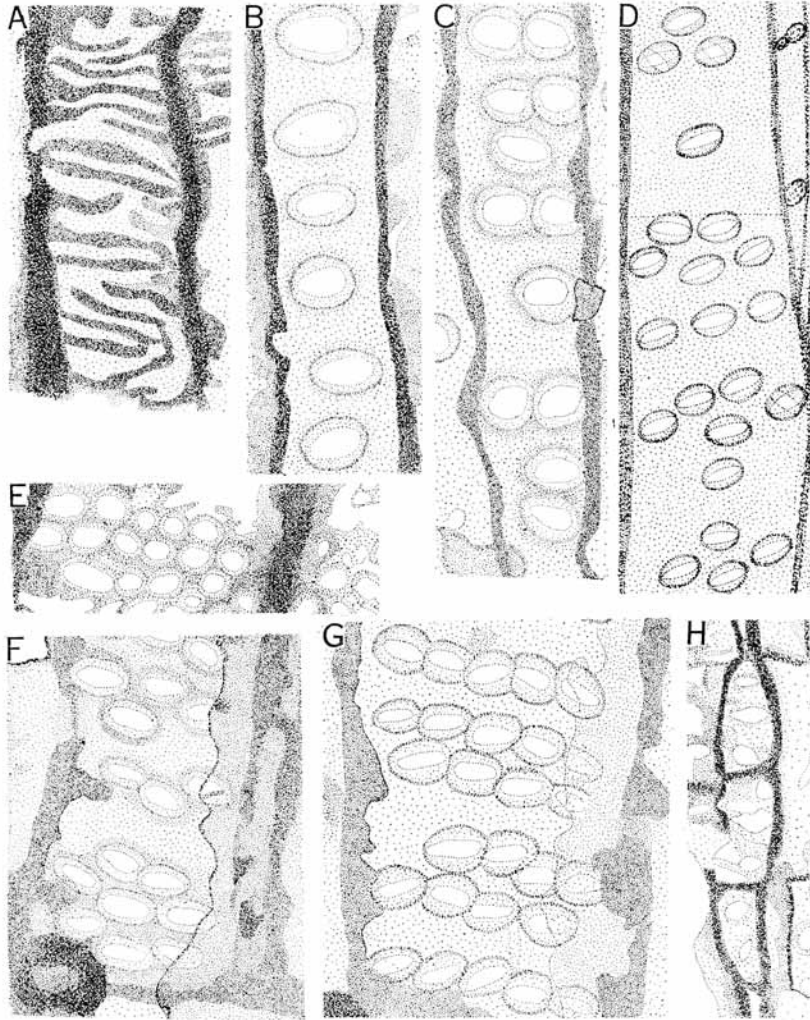
Primary xylem. Primary xylem tracheids consisting of scalariform, annular, or spiral elements were described from pulls of *Vertebraria* by Walton and Wilson (1932) and Pant (1956). Pant described them as occurring towards the periphery of the axes, where they could even have belonged to associated or attached roots.

Secondary xylem. The wood is mostly secondary and pycnoxylic. The tracheids are almost all of a uniform type without growth rings. The length of most tracheids is indeterminable in the pulls and this may suggest that they were usually longer than the size of our pulls. However, 60 complete tracheids have been observed; their length is 77–679 μ (average 250 μ , δ 105). As both ends of most tracheids are not seen, we presume that these sizes may represent the shorter elements in the xylem of *Vertebraria*. The width of the tracheids ranges from 10–56 μ (average width of tracheids is 31 μ , δ 20.5). The tracheidal walls are up to 4 μ thick. The ends of the tracheids taper gradually to a narrow point, the end walls being very oblique (Pl. 126, fig. 1). The tracheids over the rectangular areas on the surface of the axes are straight and vertical but in the region of the horizontal ridges or furrows they are slightly curved.

Arrangement of pits. The pits on radial walls are uniseriate, or multiseriate up to 5 series of pits (text-fig. 2 B, C, and G). A single tracheid with 6 seriate pits was also seen (text-fig. 2 E, Pl. 126, fig. 2).

EXPLANATION OF PLATE 125

Figs. 1–6, *Vertebraria indica* Royle. 1, Vertically compressed axis towards the top right-hand corner; part of transverse diaphragm (black) and an attached root also seen; No. 1375, \times 11. 2, Vertically compressed axis showing marks of peripheral tissues, No. 1810, \times 2. 3, Pull from Royle's holotype showing biseriate and triseriate pits and a two-cell high ray, V. 4189, \times 300. 4, Xylem of root attached to axis in Plate 124, fig. 3, showing scalariform tracheids, Slide No. 1805, \times 350. 5, Portions of tracheidal walls of axis showing crossed pit pores, Slide No. 1809 Ba, \times 500. 6, Tracheids showing uniseriate pits or mixed uniseriate and biseriate opposite pits, Slide No. 1808c, \times 800.



TEXT-FIG. 2, A-H. *Vertebraria indica*. A, Portion of tracheid showing scalariform pitting (also Pl. 127, fig. 4); Slide No. 586, $\times 1,000$. B, Part of tracheid with uniseriate non-contiguous pits; Slide No. 1784 Da, $\times 750$. C, Portion of tracheid showing uniseriate and biseriate pits; Slide No. 1784 Da, $\times 750$. D, Irregularly-pitted tracheid showing oval pit-pores, some with crossed pit-pores; Slide No. 1807A, $\times 1,000$. E, Portion of wide tracheid showing 6-seriate pits (also Pl. 126, fig. 2); Slide No. 1807A, $\times 750$. F, Portion of tracheid showing oval groups of pits with a central pit; Slide No. 1765 C2, $\times 750$. G, Tracheid showing tetraseriate and pentaseriate pits; Slide No. 1767C, $\times 750$. H, Uniseriate 3-cell-high ray in tangential view; Slide No. 1784 Da, $\times 450$.

The pits may be contiguous or far apart (text-fig. 2 b; Pl. 125, fig. 5) and the portions of the same radial wall may be pitted in some regions and unpitted for varying distances in other regions. Multiseriate pits may be opposite, araucarioid (i.e. with crowded alternate pits having hexagonal outlines) or irregularly arranged (Pl. 126, fig. 3). As a rule unpitted portions of the wall are seen in tracheids with irregular pits. Some of these may show circular or oval groups of 3 to 9 pits (text-fig. 2 d, f). The same tracheid may show different kinds of pitting in different regions i.e., uniseriate or multiseriate, opposite or alternate, contiguous or non-contiguous (text-fig. 2 c; Pl. 125, fig. 6; Pl. 126, fig. 3). A random count of 300 tracheids showed about 11% with uniseriate pits, 47% opposite multiseriate pits, 12% alternate crowded multiseriate pits of araucarioid type, 28% irregular pits, and 2% showed portions of walls without pits. Out of the 47% tracheids with opposite pits 19% are biseriate, 18% triseriate, 8% tetraseriate, and 2% pentaseriate.

Shape and size of pits. The typical shape of bordered pits may be circular or oval (text-fig. 2 b). Oval pits in multiseriate tracheids are placed horizontally but where uniseriate they may be horizontal or oblique. The pit pores are generally oval but occasionally rounded. The two opposite pores of a pit pair are usually crossed (text-fig. 2 d; Pl. 125, fig. 5). In the tracheids of the thinner axes pit pores are wide with a very thin border.

In some regions of the pulls, the tracheids show large horizontally extended oval pits where a border is not discernible. Such pits may be uniseriate or multiseriate. Where uniseriate they almost look like scalariform thickenings (text-fig. 2A; Plate 125, fig. 4; Plate 127, fig. 4) and where multiseriate they often appear transitional between typical scalariform and pitted elements. Pant (1956) described such tracheids as in contact with large parenchyma cells.

The circular pits are 4–8.5 μ (average 5 μ , δ 0.5). The length of the oval pits is 8.5–26.5 μ (average length is 13 μ , δ 2.5) and the breadth is 4–10 μ (average breadth is 6 μ , δ 1). The length of the oval pits whose borders are not clear is 10–31 μ (average length is 21.5 μ , δ 1.5) and the breadth is 4–10 μ (average breadth is 7 μ , δ 1).

Secondary xylem rays. Only uniseriate secondary xylem rays have been observed. These are 1–13 cells high (Pl. 126, fig. 5; Pl. 127, fig. 1), but more commonly they are only 1–4 cells high:

Percentage of uniseriate rays of differing heights

Height of rays in number of cells	1	2	3	4	5	6	7	13
Percentage	33	29	17	10	6	2	2	1

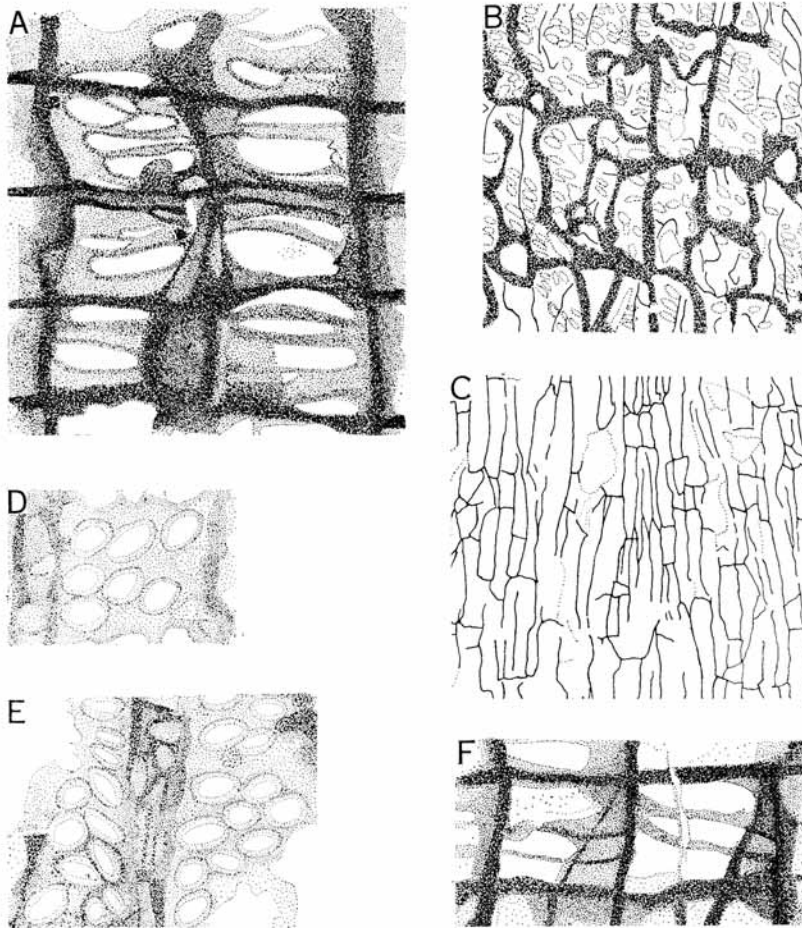
Frequency of rays per 10 mm.² is 4–18 averaging 9 (60 readings, δ 4). The rays are 1–48 cells long (average 11 cells, δ 4).

Crossfield pits. Crossfields of *V. indica* where clearly visible show 1–3 elongated oval pits (text-fig. 3A; Pl. 127, fig. 2). The oval pits are horizontally placed and seemingly simple. On the basis of our observations, we believe that the numerous bordered crossfield pits described by Walton and Wilson (1932) and by Surange and Maheshwari (1962) are pits of tracheidal wall, other than the common wall between a ray cell and a tracheid. In a compression, this wall may overlap a crossfield and then the pits can be mistaken for crossfield pits. The length of the crossfield pits ranges from 11–32 μ (average 18 μ , δ 2) and breadth from 4 to 14 μ (average 5 μ , δ 1).

Phloem like cells. Many pulls show thin elongated cells by the side of xylem which look like phloem (text-fig. 3 c; Pl. 127, fig. 3). The length of these cells is from 17 to 238 μ (average 61 μ , δ 17) and breadth 4–35 μ (average 10 μ , δ 3). The thickness of the walls of these cells is up to 3 μ .

EXPLANATION OF PLATE 126

Figs. 1–5. *Vertebraria indica* Royle. 1, Xylem showing tapering ends of two tracheids and longitudinal walls of others with multiseriate pits, Slide No. 1807A, \times 800. 2, Portion of wide tracheid (on the right side) showing six-seriate pits, Slide No. 1807A, \times 800. 3, Xylem showing triseriate pits, opposite in some regions but alternate and araucarioid in other parts, Slide No. 1754c, \times 350. 4, Pull from thinner axis with obscure rectangular areas showing typical *Vertebraria* type of xylem, Slide No. 1784 Db, \times 140. 5, Xylem showing a 7-cell-high ray, Slide No. 1807A, \times 200.



TEXT-FIG. 3. A-F. *Vertebraria indica*. A, Portion of xylem showing simple, horizontally elongated, oval pits in cross-fields; Slide No. 1809 Ba, $\times 600$. B, Pull showing xylem with simple pits overlapped by broad parenchyma cells, which tend to be in radial series; Slide No. 586, $\times 150$. C, Pull showing thin-walled phloem like cells; Slide No. 1767A, $\times 150$. D, Portion of tracheid from holotype showing triseriate opposite pits; V. 4189, $\times 750$. E, Pull from holotype showing tracheid with uniseriate, biseriate, and irregularly arranged pits; V. 4189, $\times 750$. F, Xylem showing horizontally elongated, simple oval pits in crossfield; Holotype, V. 4189, $\times 750$.

Large parenchyma cells. In addition, sheets of large rectangular to polygonal parenchyma cells were seen overlying xylem almost in all preparations. Very often the cells tend to arrange in radial rows (text-fig. 3 b; Pl. 127, fig. 5). The length of these cells is 21–228 μ (average 79 μ , δ 49) and breadth 21–84 μ (average 34 μ , δ 17).

Tangential views of xylem. In portions of the pulls where the xylem appears in a partially or wholly tangential view, the xylem rays are seen and they are invariably uniseriate (text-fig. 2H). Where the rays are obliquely compressed, presenting a combination of tangential and radial views, the ray field pits appear to be simple and horizontally oval. The tangential walls of the tracheids are devoid of pits and their surface presents a uniformly granular texture (Pl. 127, fig. 6). The xylem of axes with obscure areas is essentially similar, showing identical pitting, uniseriate rays, crossfield pits, phloem-like cells and large parenchyma cells.

Vertically preserved axes

Xylem and other cells from vertically preserved axes are also indistinguishable from those of horizontally compressed *Vertebraria* except for the presence of short tracheids with tapering or truncated ends over the transverse side of the rectangular areas.

COMPARISON AND DISCUSSION

Surange and Maheshwari (1962) described a new species *V. raniganjensis*, with xylem differing specifically from that of *V. indica* as described by Walton and Wilson (1932), Pant (1956), and Sen (1958). Surange and Maheshwari (1962) assumed that Royle's type specimen of *V. indica*, No. V. 4189 in British Museum (Natural History) was without carbon. However, since one of us (D. D. P.) had examined Royle's type of *V. indica* and seen carbon in it, we obtained through the courtesy of Dr. Pettitt a small pull from Royle's type. Therefrom, we have been able to confirm that it shows exactly the same kind of xylem as has been described by Walton and Wilson (1932), Pant (1956), Sen (1958), and by us here from other specimens assignable to *V. indica*. This xylem is also similar to that of Surange and Maheshwari's *V. raniganjensis*.

Surange and Maheshwari described the following peculiarities of the xylem of *V. raniganjensis*:

- (a) The pits are 'often' six seriate.
- (b) The pits are 'more than often' arranged irregularly and in groups of 2 to 9 which are sometimes of stellate shape.
- (c) 'Xylem rays if not common are also not scarce as in *V. indica*'. They are usually 1–5 cells high, rarely up to 8 cells high.
- (d) Crossfield pits are 7–9 in number, bordered and with an oval pore and some fields show no pits.
- (e) Absence of large parenchyma cells.

They did not, however, mention the frequency of tracheids with six seriate or irregularly arranged pits or of the xylem rays. The frequent occurrence of irregularly pitted

EXPLANATION OF PLATE 127

Figs. 1–6. *Vertebraria indica* Royle. 1, Xylem showing 13-cell-high ray, Slide No. 1777b, \times 150. 2, Xylem showing horizontally elongated, simple oval pits in crossfields, Slide No. 1809 Ba, \times 800. 3, Pull showing thin-walled phloem-like cells, Slide No. 1767A, \times 300. 4, Portion of tracheid showing scalariform pits, Slide No. 586, \times 350. 5, Pull showing broad parenchyma cells, tending to be in radial series, Slide No. 1781c, \times 40. 6, Portion of xylem showing unpitted tangential walls, Slide No. 1789c, \times 230.

elements of xylem and the occurrence of six seriate tracheids (even though rare) in axes whose xylem is otherwise exactly like that of *V. indica* suggests that such tracheids may not be used to distinguish another species. The frequency of rays in *V. indica* is rather variable. Calculated on the basis of figures and photographs given by Walton and Wilson (1932), Pant (1956), and Surange and Maheshwari (1962), the frequency of rays in the axes described by these authors is within the range determined for *V. indica*. As mentioned above we believe that there is an error in the description of crossfield pits by Walton and Wilson and by Surange and Maheshwari. The only remaining difference is the absence of large parenchyma cells in *V. raniganjensis* and their presence in *V. indica*; however, the negative evidence of the absence of such cells in a pull may be misleading for even in two pulls of the same axis, such cells are often seen to be preserved in some regions and not in other portions. We have also re-examined Pant's original pulls of *V. indica* from Mhukuru coalfield, Tanganyika, and they show the same kind of the xylem as the type. Accordingly we are convinced that axes described as *V. raniganjensis* and *V. indica* belong to the same 'species'.

Surange and Maheshwari (1962) described another new species, *V. myelonis*, which differed from *V. indica* in having a pith in the centre of the axes but no parenchymatous tissue was recorded in the 'pith' region. None of our pulls from the Raniganj and Giridih coalfields shows any trace of a parenchymatous pith although the xylem and parenchyma cells are usually well preserved. Surange and Maheshwari based their species on a single specimen which does show a narrow space (pith) in the centre between the two lateral series of rectangular areas, but they did not describe any parenchyma from this region and the space possibly represents the width of the solid central part of the xylem because we have actually observed solid xylem in this region in numerous specimens and also in the centre of vertically preserved axes. In the absence of any positive evidence of a pith it would be simpler, if this species too is regarded as a synonym of *V. indica*.

MORPHOLOGY OF *VERTEBRARIA*

Structural features

Oldham believed that *Vertebraria* had a solid central core joined to a peripheral bark by a series of radiating longitudinal septa which could be branched (Oldham 1897, pl. 4, fig. 2), and according to his description eight of these septa could usually be seen in a sectional view in vertically preserved axes. He thought that the longitudinal septa were joined at intervals by transverse partitions so that the axes of *Vertebraria* were visualized as having a ring of air chambers around a central solid core. In his view the transverse partitions are responsible for the septate appearance in horizontal preservation. Zeiller (1896) thought that *Vertebraria* axes had an externally ridged form with transverse septa between the longitudinal ridges as in the rhizomes of the living fern *Struthiopteris*.

Both Oldham and Zeiller agreed in regarding the rectangular areas as representing empty spaces (internal or external). Walton and Wilson (1932), however, suggested that the axes of *Vertebraria* had a rayed stele practically without a pith; each carbonaceous ray in a vertically preserved *Vertebraria* was formed by compression of compact secondary xylem having uniseriate parenchymatous rays between its tracheids. These rays of xylem were joined with adjacent xylem rays on either side; rock-filled spaces

(bays) between the carbonaceous rays were not empty but originally occupied by a soft tissue. Pant (1956) agreed with Walton and Wilson on the basis of his study of a *Stigmaria* with rays similarly preserved, and he described large parenchyma cells which occupied the bays.

An interpretation of the features of *Vertebraria* which is similar to that given earlier by Oldham has recently been given by Plumstead (1962), but she agrees with Walton and Wilson (1932) in believing that the chambers were filled with a soft tissue. However, her reconstruction visualizes a solid 'central column communicating by means of large oval cavities with the rest of the axis', and also a woody bark. Recently, Schopf (1965) has generally confirmed the reconstructions of the structural features of *Vertebraria* suggested by Walton and Wilson (1932).

Our investigation of the extensive new material of *Vertebraria* is fully consistent with the views of Walton and Wilson (1932). Pulls from rays of carbon in vertically preserved axes show the same kind of xylem as the surface of the rectangular areas in horizontally compressed axes. Celloidin pulls of carbon from rectangular areas of horizontally preserved axes show tracheids which tend to be short, wide, and curved near the transverse portions but elsewhere the tracheids run uniformly in the longitudinal direction. We have also confirmed that the transverse connections joining adjacent carbonaceous rays are also formed by xylem. As already described by Pant (1956) xylem and phloem over rectangular areas is often overlapped by large parenchyma cells, which are clearly the remnants of a soft tissue which originally filled the bays. The absence of rectangular areas in thinner branches of *Vertebraria* leads us to the conclusion that the parenchymatous bays may have been formed after secondary growth as in the axes of some modern lianas like *Aristolochia*. This may also explain the regular seriated arrangement of the large parenchyma cells.

Stem or root

Vertebraria has been generally recognized as the stem or rhizome of *Glossopteris* after Zeiller (1896) and Oldham (1897) described axes showing apparent attachment of *Glossopteris* leaves, and an axis described by Dolianiti (1954) seemingly confirms this. On the contrary *Glossopteris* bearing axes of *Glossopteris* described by Etheridge (1894), Seward (1910), and Walton and Wilson (1932), do not show any *Vertebraria* features. An explanation for this inconsistency has been offered by Arber (1905) and Pant (1956, 1962) who suggest that the features of *Vertebraria* are only those of its vascular cylinder and accordingly axes where the peripheral tissues are intact would appear different. Walton and Wilson (1932), and Thomas (1952) have, however, doubted the attachment of *Glossopteris* leaves on *Vertebraria* axes.

On the basis of his study of some roots called *Lithorhiza tenuirama*, Pant (1958) suggested by implication that *Vertebraria* could be a root, and pointed out that the roots of *L. tenuirama* could sometimes be found attached to axes of *Vertebraria* and sometimes to axes which combined the features of roots as well as those of a *Vertebraria*. Such axes are somewhat thicker than undoubted roots but thinner than axes showing typical *Vertebraria* features. Roots arise from them endogenously. Unlike roots they show large parenchyma cells characteristic of *Vertebraria* but they entirely lack its rectangular areas. Lately, Schopf (1965) has strongly supported the root nature of *Vertebraria* on the basis of a petrified axis. In this connection he emphasizes the lack of leaf traces or

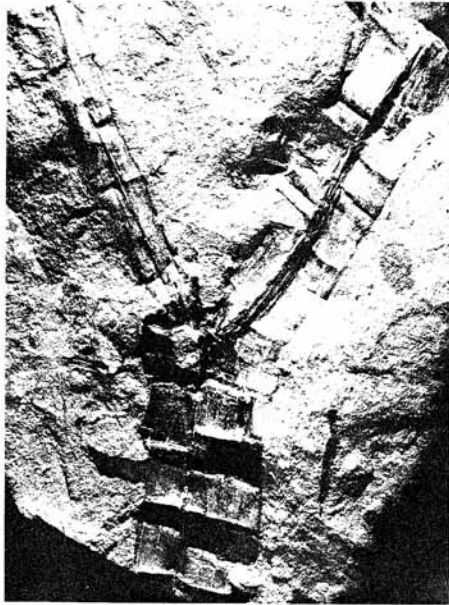
nodes by *Vertebraria* axes and also the endogenous insertion of its roots (but adventitious roots in stems are also endogenous). However, *Vertebraria* axes are sometimes dichotomised or trichotomised like stems or adventitiously branched roots, although Pant (1958) has also described some similarly forked roots. Pant (1967) has recently described a number of axes lacking rectangular areas of *Vertebraria* type but showing attached leaves of *Glossopteris* and this may also serve as a negative evidence favouring the root character. An investigation of the structural features of *Glossopteris* bearing stems which appear to differ from *Vertebraria* axes may help in solving the problem.

Acknowledgements. We are grateful to Dr. J. M. Pettitt of the British Museum (Natural History), London, for sending us a pull from Royle's type specimen and to Drs. D. D. Nautiyal, G. K. Srivastava, B. K. Varma, and Mr. K. B. Singh for help in the collection of *Vertebraria* axes and Dr. (Miss) P. F. Kidwai for help in taking some enlargements. We thank the State Council of Scientific and Industrial Research, Uttar Pradesh, for financial assistance.

REFERENCES

- ARBER, E. A. N. 1905. *Catalogue of the fossil plants of the Glossopteris flora in the Department of Geology, British Museum (Natural History)*. London.
- DANA, J. D. 1849. *Wilkes' United States exploring expedition, during the years 1838-1842 under the Command of Charles Wilkes, U.S.N. 10, Geology*, New York.
- DOLIANITI, E. 1954. A Flora do gondwana inferior em Santa Catarina, IV O genero *Vertebraria*. *Div. Geol. Min. Notas Prel. E. Estudos*, **81**, 1-5.
- ETHERIDGE, R. JUN. 1894. On the mode of attachment of the leaves or fronds to the caudex in *Glossopteris*. *Proc. Linn. Soc. N.S.W.*, Ser 2, **9**, 228-58.
- MCCOY, F. 1847. On the fossil botany and zoology of the rocks associated with the coal of Australia. *Ann. Mag. Nat. History*, **20** (132), art 15, 145-57; **20** (134), art 28, 298-312.
- OLDHAM, R. D. 1897. On a plant of *Glossopteris* with part of the rhizome attached, and on the structure of *Vertebraria*. *Rec. Geol. Surv. India*, **30** (1), 45-50.
- PANT, D. D. 1956. On the two compressed Palaeozoic axes: *Stigmaria ficoides* in *Gymnostrobos* condition and *Vertebraria indica*. *Ann. Bot. N.S.* **20** (79), 419-29.
- 1958. Structure of some roots and spores from the Lower Gondwana (Permo-Carboniferous) of East Africa. *Vijnana Parishad Anushandhan Patrika*, **1** (4), 231-44.
- 1962. Some recent contributions towards our knowledge of the *Glossopteris* flora. *Proceedings of the Summer School of Botany, Darjeeling*, 302-10.
- 1967 (In press). On stem and attachment of *Glossopteris* leaves. *Phytomorphology*, **17**.
- PLUMSTEAD, E. P. 1962. Fossil flora of Antarctica. *Trans-Antarctic Expedition (London), Rept. 9, Geology*, pt 2, 154 p.
- ROYLE, J. F. 1833. *Illustrations of the botany and other branches of natural history of the Himalayan mountains, and of the flora of Cashmere*. London.
- SCHOPF, J. M. 1965. Anatomy of the axis in *Vertebraria*. *Geol. and Paleont. of the Antarctic. Antarctic Research Series*, **6**, 217-28.
- SEN, J. 1958. Further studies on the structure of *Vertebraria*. *Bot. Not.* **3**, (2), 436-48.
- SEWARD, A. C. 1910. *Fossil plants*, vol. 2. Cambridge.
- SURANGE, K. R. and MAHESHWARI, H. K. 1962. Studies in the *Glossopteris* flora of India-11. Some observations on *Vertebraria* from the Lower Gondwanas of India. *Palaeobotanist* **9**, (1, 2), 61-7.
- THOMAS, H. H. 1952. A *Glossopteris* with whorled leaves. *Ibid.* **1**, 435-8.
- WALTON, J. and WILSON, J. A. R. 1932. On the structure of *Vertebraria*. *Proc. Roy. Soc. Edinburgh*, **52**, pt. 2, 200-7.
- ZEILLER, R. 1896. Étude sur quelques plantes fossiles, en particulier *Vertebraria* et *Glossopteris*, des environs de Johannesburg (Transvaal). *Bull. Soc. Geol. France*, Paris, ser. 3, **24**, 349-78.

DIVYA DARSHAN PANT
R. SHANKER SINGH
Department of Botany,
The University, Allahabad, India



1



2



3

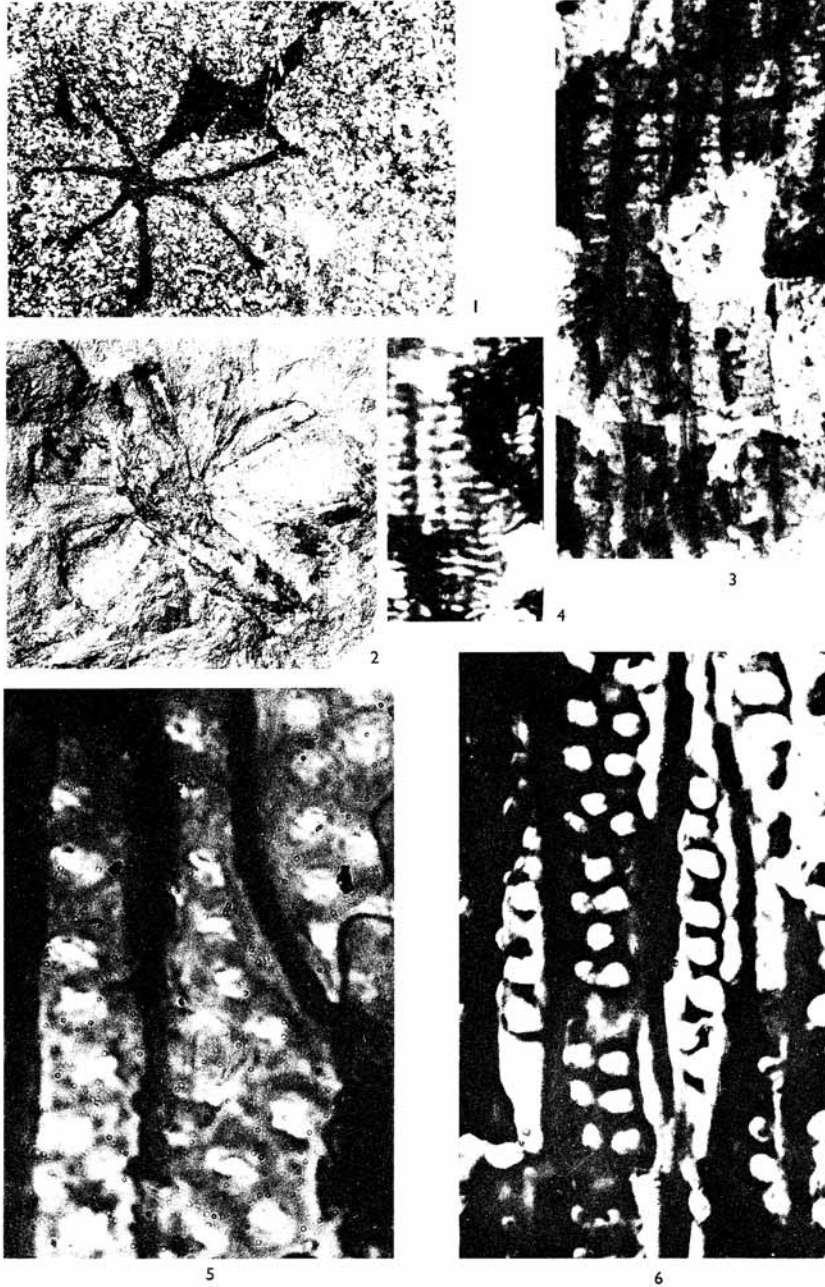


4



5

PANT and SINGH, Permian *Vertebraria*



PANT and SINGH, Permian *Vertebraria*



1



4



2

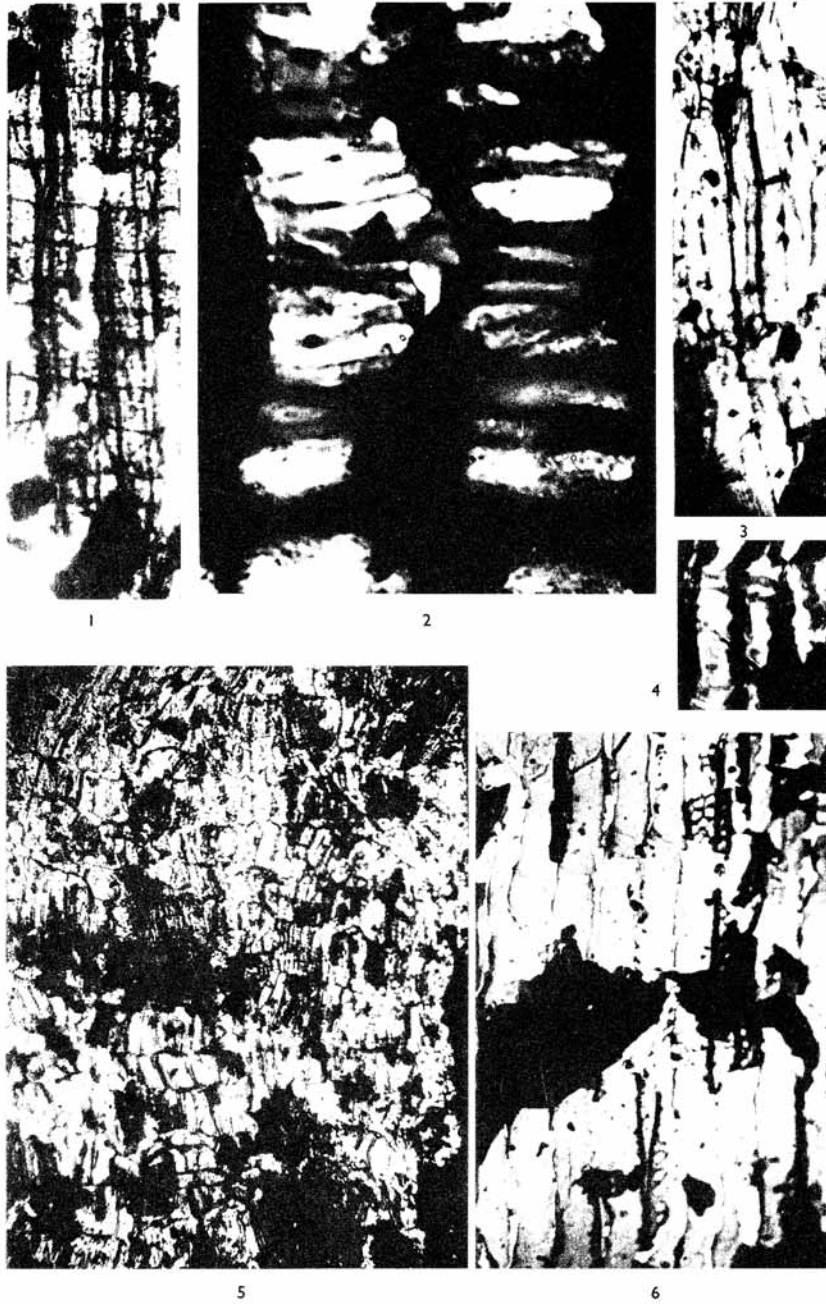


5



3

PANT and SINGH, Permian *Vertebraria*



PANT and SINGH, Permian *Vertebraria*