

## Auxin flow-mediated anatomical modifications in Indian Meso–Cenozoic plants

Ashalata D’Rozario, Illora Sen, Dipak Kumar Paruya, Anupam Guha, Vishal Verma, Sharmistha Paul, Tapas Kumar Gangopadhyay, Arindam Roy, Subhronil Mondal & Subir Bera

To cite this article: Ashalata D’Rozario, Illora Sen, Dipak Kumar Paruya, Anupam Guha, Vishal Verma, Sharmistha Paul, Tapas Kumar Gangopadhyay, Arindam Roy, Subhronil Mondal & Subir Bera (2019): Auxin flow-mediated anatomical modifications in Indian Meso–Cenozoic plants, Botany Letters, DOI: [10.1080/23818107.2019.1686064](https://doi.org/10.1080/23818107.2019.1686064)

To link to this article: <https://doi.org/10.1080/23818107.2019.1686064>



Published online: 04 Dec 2019.



Submit your article to this journal [↗](#)



View related articles [↗](#)



View Crossmark data [↗](#)

---

ARTICLE



## Auxin flow-mediated anatomical modifications in Indian Meso–Cenozoic plants

Ashalata D’Rozario<sup>a</sup>, Illora Sen<sup>a</sup>, Dipak Kumar Paruya<sup>a</sup>, Anupam Guha<sup>b</sup>, Vishal Verma<sup>c</sup>, Sharmistha Paul<sup>d</sup>, Tapas Kumar Gangopadhyay<sup>d</sup>, Arindam Roy<sup>e</sup>, Subhronil Mondal<sup>f</sup> and Subir Bera<sup>a</sup>

<sup>a</sup>Centre of Advanced Study, Palaeobotany –Palynology Laboratory, Department of Botany, University of Calcutta, Kolkata, India;

<sup>b</sup>Department of Botany, Women’s College, Agartala, India; <sup>c</sup>Bakaner Govt. High School, Dhar, India; <sup>d</sup>Department of Earth Sciences, IEST, Shibpur, Howrah, India; <sup>e</sup>Palaeontology Division, Geological Survey of India, Kolkata, India; <sup>f</sup>Department of Geology, University of Calcutta, Kolkata, India

### ABSTRACT

Polar transport of the phytohormone auxin is a well-known physiological phenomenon recorded in different extant plant groups including bryophytes and pteridophytes. Earlier, this phenomenon has been recorded in an Upper Devonian (375 million-year) arborescent progymnosperm, *Archaeopteris*. Since then further record of such occurrence of polar auxin flow is known especially from younger horizons. The present investigation records the evidence of such disrupted polar auxin flow in the form of auxin whirlpool in fossil woods of Tracheidoxyl, *Ailanthoxylon indicum* and *Calophylloxylon* sp. from the Middle Oxfordian (Jurassic) to Neogene (Mio-Pliocene) sediments of India.

### ARTICLE HISTORY

Received 2 August 2019  
Accepted 22 October 2019

### KEYWORDS

Polar auxin flow; tracheidoxyl; *Ailanthoxylon indicum*; *Calophylloxylon* sp.; Middle Oxfordian (Jurassic) to Neogene (Mio- Pliocene); India

### Introduction

Vascular tissue differentiation in living pteridophytes and seed plants is regulated by different phytohormones like auxin, gibberellin, cytokinin, and ethylene (Sachs 1969, 1981; Savidge and Wareing 1981; Uggla et al. 1996; Cooke et al. 2002). Auxin, however, is the only plant hormone to exhibit polar transport, which is found in almost all plants, including bryophytes and ferns (Cooke et al. 2002; Tomescu and Matsunaga 2019). In extant woody plants, auxin “whirlpools” arise wherever polar transport is disrupted by the presence of obstacles such as buds, knots and branches (Sachs and Cohen 1982; Hejnowicz and Kurczyn’ska 1987; Kramer 2006). As a result, the tracheary elements that differentiate in these regions form circular patterns. The vertical gradient of auxin from shoot to root (basipetal) affects various developmental processes like stem elongation, branching, apical dominance and others. Disruption of normal auxin transport often results in circular differentiation of tracheary elements above branch junctions (Lev-Yadun and Aloni 1990). Earlier, the presence of such similar circular patterns, indicating polar auxin transport has been detected in the fossil wood of a primitive progymnosperm of the Upper Devonian period (Rothwell and Lev-Yadun 2005). Since then further occurrences of polar auxin transport have been known (Rothwell et al. 2008; Sanders et al. 2011).

The present investigation records the evidence of such disrupted polar auxin flow in the form of auxin

whirlpool in fossil woods of The Middle Oxfordian (Jurassic) to Neogene (Mio-Pliocene) sediments of India.

### Materials and methods

Materials of fossil woods of gymnosperm affinity found in close association with numerous ginkgophyte seeds (personal communication) were collected from the ferruginous Kantkote ammonite band, Maliband river (N 23° 29’ 46.7”, E 70° 29’ 40.8”) of Middle Oxfordian stage (Jurassic), Kutch, India. Angiosperm woods were collected from the Deccan Intertrappean beds (Palaeocene) of Madhya Pradesh, Ukala Road (N 22° 23’ 36.2”, E 75° 15’ 08.4”), India and The Neogene (Mio-Pliocene) sediments of Tripura, Melaghar (N 23° 28’ 60”, E 91° 19’ 60”) area of South Tripura.

The fossil woods were thin sectioned along transverse (T.S), tangential (T.L.S) and radial (R.L.S) planes using standard techniques employed for petrified materials (Haas and Rowe 1999). The sections were observed and studied under Leitz Laborlux D and Zeiss Axioskop 40 microscope and photographed using Zeiss Axioskop 2 microscope attached to a Leica DFC295 camera. Identification and affinities of the three wood specimens were determined by consulting reference works and databases (Metcalf and Chalk 1950, 1989; Metcalfe 1987; Illic 1987; IAWA Committee 1989; Cutler and Gregory 1998; INSIDEWOOD 2004-onwards) and comparing the

fossils with the wood slide collection housed in the herbarium and museum of the Department of Botany, University of Calcutta (CUH), India. Finally, the prepared slides were numbered and deposited in the repository of the CUH, India.

## Results

### Systematic description of the fossil woods

Order – Coniferales

Tracheidoxyl (Creber 1972)

Locality- ferruginous Kantkote ammonite band,  
Maliband river, District Kutch, Gujarat, India

Age – Jurassic (Middle Oxfordian)

### Description

Specimen number KUT 1. Transverse section (T.S.) of the fossil wood shows well-developed secondary xylem with annual rings (Figure 1(a)). The secondary xylem is composed of tracheids with moderately thick walls. Tracheids are rectangular to oval in cross-section, radial diameter 25–30 µm and tangential diameter 20–25 µm (Figure 1(a)). In transverse longitudinal section (T.L.S.) tracheids are conspicuous, but pits in radial walls of tracheids are poorly preserved. Rays consisting only of parenchyma cells, uniseriate, mostly 1–3 cells, rarely 4–6 cells in height (Figure 1(c)). Tangential walls unpitted or pits not preserved. Radial longitudinal section (R.L.S.) of the wood shows tracheids with one or two rows of more or less scattered bordered pits which are round and opposite (Figure 1(b)).

### Affinities

The present specimen is recovered as a portion of wood with poorly preserved tissues bearing tracheids and associated cells. As such, due to the absence of specific characteristic features, it cannot be assigned to any genus or family. It is placed under – tracheidoxyl (sensu Creber 1972) because the term tracheidoxyl is used to indicate those specimens containing only a detached portion of wood characteristically composed of tracheids with only a minor proportion of other tissues. The presence of growth rings, pycnoxylic wood with tracheids, indicates its resemblance to conifers.

Family – Simaroubaceae

Genus – *Ailanthoxylon* Prakash 1959

Species – *Ailanthoxylon indicum* Prakash 1959

Locality – Deccan Intertrappean beds, Ukala Road,  
District Dhar, Madhya Pradesh, India

Age – Palaeocene (Danian)

### Description

Specimen number DIn 1. Wood diffuse porous. Growth rings absent (Figure 2(a)). Vessels small to

medium, tangential diameter 70–130 µm, radial diameter 125–175 µm, 6–7 per sq. mm, solitary as well as in radial multiples of 2–3, circular to oval when solitary, tyloses not observed (Figure 2(a)). Vessel members 170–270 µm in height, truncate to oblique ends (Figure 2(d)), perforations simple, intervessel pit pairs 7–10 µm in diameter, alternate (Figure 2(d)). Parenchyma paratracheal, xylem rays 1–3 (mostly 2) seriate (Figure 2(b)), 7–8 per sq. mm, 3–14 cells, 65–230 µm in height, rays homogeneous, made up of procumbent cells (Figure 2(c)). Fibres thick-walled, non-septate (Figure 2(b, d)).

### Affinities

The anatomical characters of the wood from Deccan Intertrappean beds of Madhya Pradesh mentioned earlier, such as mostly solitary, small to medium-sized vessels, paratracheal parenchyma, 1–3 (mostly 2) seriate, homogenous rays and thick-walled non-septate fibres indicate its close affinity with modern genus *Ailanthus* Desf. of the family Simaroubaceae (Pearson and Brown 1932; Metcalfe and Chalk 1950; Kribs 1959; INSIDEWOOD 2004-onwards).

Prakash (1959) reported the genus *Ailanthoxylon* for the fossil wood showing close resemblances with the modern genus *Ailanthus* Desf. The present fossil wood closely resembles *A. indicum* (Prakash 1959; Prakash et al. 1967; Mehrotra 1990), in the presence of solitary vessel with truncate to oblique ends, alternate pits in the vessels, paratracheal parenchyma and non-septate fibres, described from the Deccan Intertrappean beds of Madhya Pradesh, India and therefore, it is placed under the same species.

Family-Clusiaceae

Genus: *Calophylloxylon* Lakhanpal and Awasthi 1965

Species – *Calophylloxylon* sp.

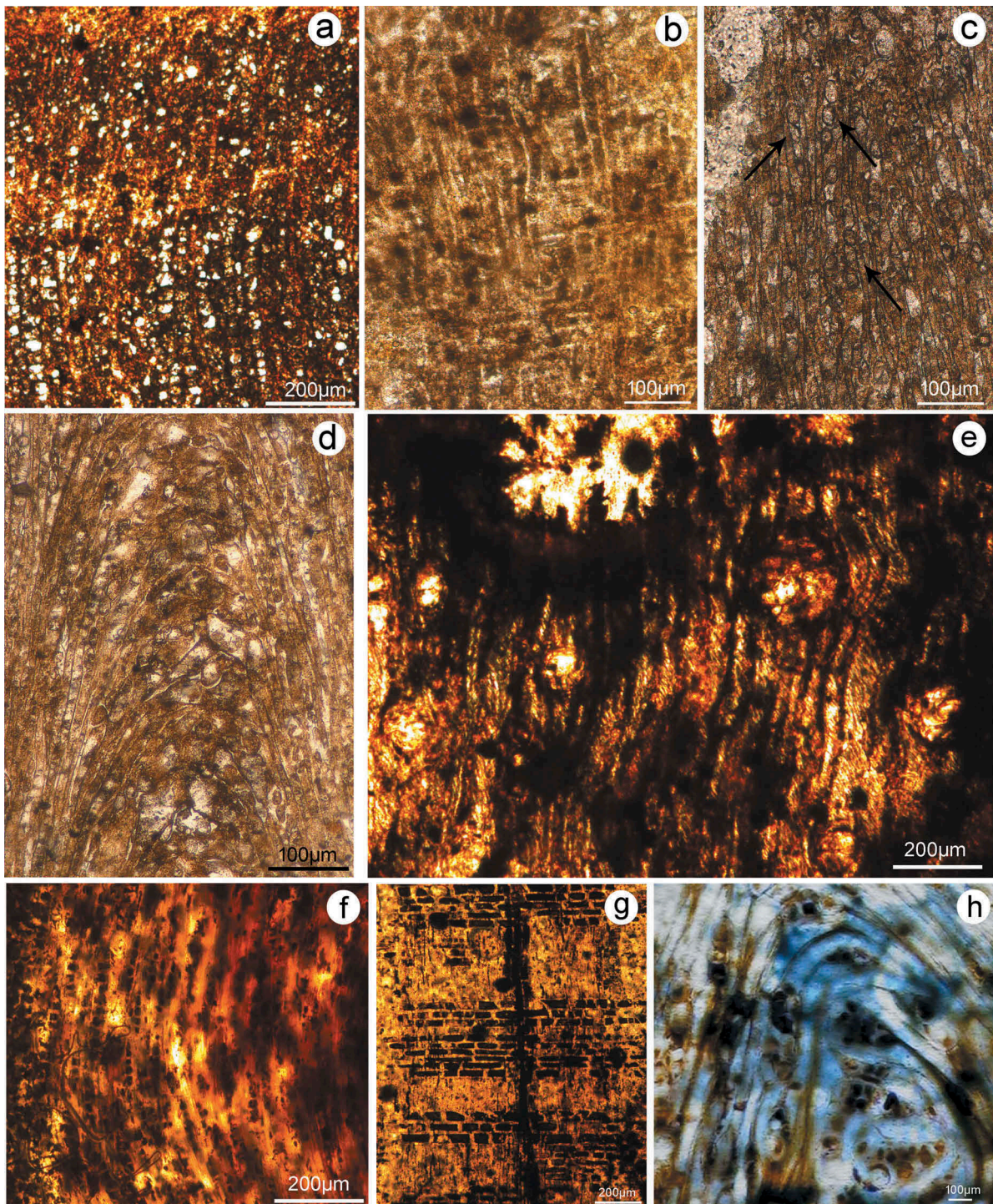
Locality – Melaghar, District West Tripura, Tripura,  
India

Age – Neogene (Mio-Pliocene)

### Description

Specimen number TM26. Wood diffuse porous. Growth rings not distinct (Figure 1(e)). Vessels medium, almost solitary, round to oval in cross-section; 2–3 per sq. mm; tangential diameter 160–280 µm, radial diameter 140–240 µm; tyloses present (Figure 1(e)); intervessel pits not well-preserved. Vasicentric tracheids present, forming a sheath around the vessels (Figure 1(e)). Xylem rays fine, 1–2 seriate, closely spaced (Figure 1(f)); 15–45 µm broad; 2–12 cells in height and 30–165 µm in length; rays heterogenous, composed of procumbent and upright cells (Figure 1(e)); procumbent cells 12–30 µm in tangential height and 40–55 µm in radial length; upright cells 30–45 µm in radial length and 40–60 µm in tangential height. Parenchyma apotracheal, in continuous





**Figure 1.** (a) Transverse section (T.S.) of Tracheidoxyl wood showing the arrangement of tracheids and rays. (b) Radial longitudinal section (R.L.S.) of Tracheidoxyl wood showing the nature of ray cells. (c) Tangential longitudinal section (T.L.S.) of Tracheidoxyl wood showing uniseriate ray cells (arrow marked). (d) Auxin whirlpool in Tracheidoxyl wood. (e) Transverse section (T.S.) of *Calophylloxylon* sp. wood showing the arrangement of vessels and distribution of parenchyma cells. (f) Tangential longitudinal section (T.L.S.) of *Calophylloxylon* sp. showing xylem rays. (g) Radial longitudinal section (R.L.S.) of *Calophylloxylon* sp. showing ray histology. (h) Auxin whirlpool in *Calophylloxylon* sp.

slightly wavy concentric bands (Figure 1(e)), 2–3 cells wide, parenchyma cells thin-walled, 15–25 µm in diameter. Fibres arranged in distinct radial rows, moderately thick-walled, septate (Figure 1(f)).

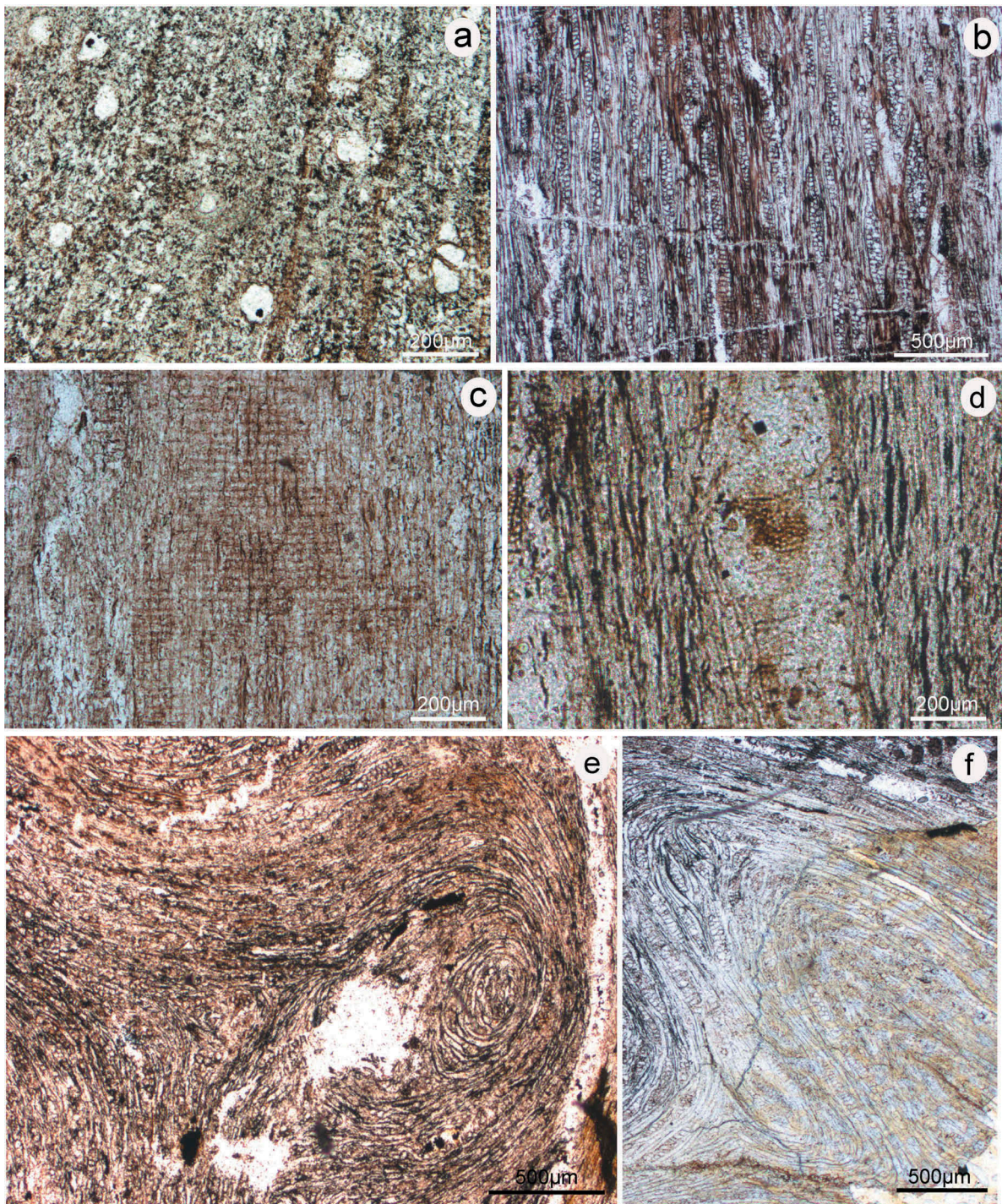
#### Affinities

The characteristic anatomical features observed in the wood from The Neogene (Mio-Pliocene) sediments of

Tripura, are almost exclusively with solitary vessels, 1–2 seriate rays, vascentric tracheids, which indicates its resemblance with *Calophyllum* of the family Clusiaceae. Lakhanpal and Awasthi (1965) instituted the genus *Calophylloxylon* for the fossil woods showing similarity with modern woods of *Calophyllum*.

However, due to poor preservation, the present fossil wood could not be assigned to any particular





**Figure 2.** (a) Transverse section (T.S.) of *Ailanthoxylon* sp. showing the arrangement of vessels and distribution of parenchyma cells. (b) Transverse longitudinal section (T.L.S.) of *Ailanthoxylon* sp. showing xylem rays. (c) Radial longitudinal section (R.L.S.) of *Ailanthoxylon* sp. showing ray histology. (d) Vessel enlarged showing the nature of pitting. (e, f) Auxin whirlpool in *Ailanthoxylon* sp.

species and hence described here as *Calophylloxylon* sp.

### Anatomical modifications due to disruption of auxin flow

Circular patterns were observed in the secondary wood of tracheidoxyl formed by the tracheids and rays, providing evidence of polar auxin flow and formation of auxin whirlpools (Figure 1(d)).

*Ailanthoxylon indicum* Prakash 1959 also revealed auxin whirlpools forming circular loops of vessels, fibres, parenchyma cells and rays, providing another evidence of polar auxin flow (Figure 2(e, f)).

The tangential section of the wood of *Calophylloxylon* sp. also clearly indicates the occurrence of a circular arrangement of tracheary elements such as vessels, xylem rays, fibres, parenchyma cells substantiating the presence of auxin whirlpool (Figure 1(h)).



Thus, all the three fossil woods from three different time intervals, Jurassic, Palaeocene and Neogene sediments showed identical circular patterns of auxin whirlpools in the secondary wood, thus providing evidence of polar auxin transport.

## Discussion

Vascular differentiation occurs along with an axial flow of auxin from leaves to roots and possibly other signals (Dengler 2001; Carlsbecker and Helariutta 2005; Reinhardt 2005; Tomescu and Groover 2019). Auxin flow thus determines the orientation of the vascular strands relative to the plant organs they serve. Thus, it can be suggested that vascular differentiation, particularly, xylem formation, can be used as an anatomical expression of auxin flow. Further, auxin can induce vessels and other associated tissues in the form of closed loops (Sachs and Cohen 1982; Sachs 2000).

In living woody seed plants, the axially elongated tracheary elements of the secondary xylem follow a uniformly straight or inclined course. But whirlpools are formed in the cambial zone upstream of the obstacles when the flow is disrupted (Sachs and Cohen 1982). These auxin whirlpools induce the differentiation of characteristic circular tissue patterns of tracheary elements above axillary buds of woody plants (Hejnowicz and Kurczynska 1987) and above branch junctions in the wood of conifers and woody dicotyledonous plants (Lev-Yadun and Aloni 1990).

It has already been proposed that polar auxin flow was involved in the regulation of vascular differentiation in fossil plants (Stein 1993; Boyce and Knoll 2002; Rothwell and Lev-Yadun 2005). Evidence from extinct arborescent clades indicates that polar auxin transport initiated independently in several lines to regulate wood and root development (Rothwell et al. 2008; Hoffman and Tomescu 2013; Tomescu and Groover 2019).

Sachs and Cohen (1982) observed that in modern woods, the obstruction of basipetal auxin flow by branches leads to the development of a distinctive circular pattern of xylem cells in the wood above the branch. Rothwell and Lev-Yadun (2005) showed that the patterning of wood development in early trees belonging to the progymnosperms was under polar auxin transport (PAT) regulation. Circular patterns were also observed in permineralized progymnosperm fossil woods of Archaeopteridales in both the trunk (Rothwell and Lev-Yadun 2005) and the root (Meyer-Berthaud et al. 2013), indicating that similar developmental processes occurred.

Circular patterns of xylem cells were also observed in an arborescent lepidodendrid lycophyte stem as well as rhizomorphs (Rothwell et al. 2008), thus providing evidence that as in modern seed plants, PAT

proceeded from the shoot apex to root apex. Anatomical evidence seen in the isoetalean lycopside trees reveals that auxin transport occurred from the apex to the base of the aerial shoot system, then towards the apex of the rhizomorph, a shoot modified for rooting, thus mimicking the directional signal-regulating shoot and root systems in seed plants (Sanders et al. 2011). Comparative anatomical study to address hypothesized homology relationships between the rhizophore of *Selaginella* and rooting structures associated with branching points in early fossil lycophytes and zosterophylls (Matsunaga et al. 2017), revealed an anatomical fingerprint for a reversal of polar auxin transport associated with rhizophore development, basipetal polar auxin transport in shoots to acropetal in the rhizophore.

Based on anatomical evidence (Sanders et al. 2011), suggested that in the isoetalean lycopside trees auxin transport occurred from the apex to the base of the aerial shoot system, then towards the apex of the rhizomorph. Additionally, Tomescu and Matsunaga (2019) pointed out the implication of this information, stating that the direction of polar auxin transport transcends organ homology and is associated with the gravitropic response and rooting function of an organ, independent of its homology as in rhizomorphs and rhizophores.

In the most recent common ancestor of progymnosperms, horsetails and clubmosses, since wood had not yet evolved, it is likely that the secondary growth of these trees evolved separately but parallelly, with each clade independently forming a common PAT regulatory pathway (Rothwell et al. 2008; Hoffman and Tomescu 2013; Tomescu and Groover 2019). The records of similar auxin whirlpool as in *Archaeopteris* of the Upper Devonian age, is also found in tracheidoxyl (Creber 1972), of the Middle Oxfordian (Jurassic) age, *Ailanthoxylon indicum* from the Deccan Intertrappean beds (Palaeocene) and *Calophylloxylon* sp. from the Neogene, testify the existence of this natural physiological phenomenon as a regular process in woody vascular plants in the Upper Devonian, which continued through the Jurassic, Tertiary periods to the recent times. As auxin whirlpools are generally formed at the junction of branches, so it can be presumed that the fossil woods of the present study were of that portion where branching had occurred. Further data in this regard may throw light for interpreting the physiological basis for differentiation of the tracheary elements in the woody plants of the past.

This phenomenon reveals the potential of plant fossils to provide structural evidence of evolutionarily diagnostic physiological and developmental processes and for the use of various fossil evidences of different ages and developmental biologies to characterize evolutionary patterns in terms of genetic changes in growth regulation (Rothwell et al. 2014) and also

provides clear structural evidence of tissue disruptions due to polar auxin flow.

## Acknowledgments

UGC–CAS (Phase VII), Department of Botany, University of Calcutta, is thankfully acknowledged for necessary support.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Notes on contributors

**Ashalata D'Rozario** is a retired Associate Professor and researcher at the Department of Botany, University of Calcutta, India. She studied the literatures, worked out the specimen and carried out the anatomical and comparative study of fossil wood specimen of the gymnosperm wood and prepared the manuscript.

**Illora Sen** is an Assistant Professor at Department of Botany, Shri Shikshayatan College and researcher at the Department of Botany, University of Calcutta, India. She prepared the sample and carried out the anatomical and comparative study of fossil wood specimen of *Calophylloxyton sp.* and helped in writing the manuscript.

**Dipak Kumar Paruya** is an Assistant Teacher in Tiljala High School and researcher at the Department of Botany, University of Calcutta, India. He worked out the specimen and carried out the anatomical and comparative study of fossil wood specimen of *Ailanthoxyton indicum* and helped in the preparation of the manuscript.

**Anupam Guha** is an assistant professor at Department of Botany, Women's College, Agartala, **Vishal Verma**, teacher at Bakaner Govt. High School, Dhar District, M.P., **Sharmistha Paul**, Department of Earth Sciences, IEST, Shibpur, Howrah, **Tapas Kumar Gangopadhyay** Department of Earth Sciences, IEST, Shibpur, Howrah collected the fossil woods and helped in writing the manuscript.

**Arindam Roy** (GSI, Kolkata) and **Subhronil Mondal** (Department of Geology, University of Calcutta, India) collected the fossil gymnosperm wood and gave relevant stratigraphic information of the fossil sample.

**Subir Bera** is a researcher and Professor at the Department of Botany, University of Calcutta, India. He guided the entire course of this research, scrutinized and refined the manuscript as a corresponding author.

## References

- Boyce, CK, AH Knoll. 2002. Evolution of developmental potential and the multiple independent origins of leaves in Paleozoic vascular plants. *Paleobiology*. 28:70–100. doi:10.1666/0094-8373(2002)028<0070:EODPAT>2.0.CO;2.
- Carlsbecker, A, Y Helariutta. 2005. Phloem and xylem specification: pieces of the puzzle emerge. *Curr Opin Plant Biol*. 8:512–517. doi:10.1016/j.pbi.2005.07.001.
- Cooke, TJ, DB Poli, AE Sztein, JD Cohen. 2002. Evolutionary patterns in auxin action. *Plant Mol Biol*. 49:319–338. doi:10.1023/A:1015242627321.
- Creber, GT. 1972. Gymnospermous wood from the Kimmeridgian of East Sutherland and from the Sandringham sands of Norfolk. *Palaeontology*. 15 (4):655–661.
- Cutler, YDF, M Gregory. 1998. Anatomy of Dicotyledons. Volume IV. Saxifragiales. Oxford: Clarendon Press; p. 324.
- Dengler, NG. 2001. Regulation of vascular development. *J Plant Growth Regul*. 20:1–13. doi:10.1007/s003440010008.
- Haas, H, NP Rowe. 1999. Thin Sections and Wafering. In T P Jones, N P Rowe, editors. *Fossil plants and spores: modern techniques*. London: Geological Society; p. 76–81.
- Hejnowicz, Z, EU Kurczynska. 1987. Occurrence of circular vessels above axillary buds in stems of woody plants. *Acta Societe Botanica Polonica*. 56:415–419. doi:10.5586/asbp.1987.039.
- Hoffman, LA, AMF Tomescu. 2013. An early origin of secondary growth: *Franhueberia gerriennei* gen. et sp. nov. from the Lower Devonian of Gaspé (Quebec, Canada). *Am J Bot*. 100:754–763. doi:10.3732/ajb.1300024.
- IAWA Committee. 1989. List of microscopic features for Hardwood Identification. *IAWA Bull*. 10:218–358.
- Illic, J. 1987. The CSIRO family key for hardwood identification. Leiden: E.J. Brill.
- INSIDewood. 2004-onwards. [Accessed 2015 Nov 11]. Published on the internet (<http://insidewood.lib.ncsu.edu/search>).
- Kramer, EM. 2006. Wood grain pattern formation: a brief review. *J Plant Growth Regul*. 25:290–301. doi:10.1007/s00344-006-0065-y.
- Kribs, DA. 1959. Commercial foreign woods on the American market. Pennsylvania: Pennsylvania State University.
- Lakhanpal, RN, N Awasthi. 1965. Fossil wood of *Calophyllum* from the tertiary of South India. *Palaeobotanist*. 13(3):328–336.
- Lev-Yadun, S, R Aloni. 1990. Vascular differentiation in branch junctions of trees: circular patterns and functional significance. *Trees*. 4:49–54. doi:10.1007/BF00226240.
- Matsunaga, KKS, NP Cullen, AMF Tomescu. 2017. Vascularization of the *Selaginella* rhizophore: anatomical fingerprints of polar auxin transport with implications for the deep fossil record. *New Phytol*. 216(2):419–428. doi:10.1111/nph.14478.
- Mehrotra, RC. 1990. Further observations on some fossil woods from the Deccan Intertrappean beds of Central India. *Phytomorphology*. 40(1 & 2):169–174.
- Metcalf, CR. 1987. Anatomy of Dicotyledons Volume III Magnoliales, Illiciales and Laurales. 2nd ed. Oxford: Oxford University Press; p. 240.
- Metcalf, CR, L Chalk. 1950. Anatomy of dicotyledons. Vol. 1&2, Clarendon Press: Oxford. p. 1500. doi:10.1016/0006-2944(75)90147-7.
- Metcalf, CR, L Chalk. 1989. Anatomy of Dicotyledons: II. Wood structure and conclusion of the general introduction. 2nd ed. Oxford: Oxford University Press; p. 330.
- Meyer-Berthaud, B, AL Decombeix, X Ermacora. 2013. Archaeopterid root anatomy and architecture: new information from permineralized specimens of Famennian age from Anti-Atlas (Morocco). *Int J Plant Sci*. 174:364–381. doi:10.1086/668685.
- Pearson, RS, HP Brown. 1932. Commercial timbers of India. Vol. 1&2. Calcutta: Government of India, Central Publishing Branch Calcutta. doi:10.1016/0006-2944(75)90147-7.

- Prakash, U. 1959. Studies in the Deccan Intertrappean flora –4. Two silicified woods from Madhya Pradesh. *Palaeobotanist*. 7:12–20.
- Prakash, U, JK Verma, R Dayal. 1967. Revision of the genus *Gondwanoxylon* Saksena with critical remarks on the fossil woods of *Ailanthoxylon* Prakash. *Palaeobotanist*. 15:294–307.
- Reinhardt, D. 2005. Phyllotaxis - a new chapter in an old tale about beauty and magic numbers. *Curr Opin Plant Biol*. 8:487–493. doi:10.1016/j.pbi.2005.07.012.
- Rothwell, GW, S Lev-Yadun. 2005. Evidence of polar auxin flow in 375 million-year-old fossil wood. *Am J Bot*. 92 (6):903–906. doi:10.3732/ajb.92.6.903.
- Rothwell, GW, H Sanders, SE Wyatt, S Lev-Yadun. 2008. A fossil record for growth regulation: the role of auxin in wood evolution. *Ann Missouri Bot Garden*. 95:121–134. doi:10.3417/2006208.
- Rothwell, GW, AMF Tomescu. 2018. Structural fingerprints of development at the intersection of evo-devo and the fossil record. In L Nuño de la Rosa, G B Müller, editors. *Evolutionary developmental biology*. Cham: Springer International Publishing AG; p. 1–30. doi:10.1007/978-3-319-33038-9\_169-1.
- Rothwell, GW, SE Wyatt, AMF Tomescu. 2014. Plant evolution at the interface of paleontology and developmental biology: an organism-centered paradigm. *Am J Bot*. 101 (6):899–913. doi:10.3732/ajb.1300451.
- Sachs, T. 1969. Polarity and the induction of organized vascular tissues. *Ann Bot*. 33:263–275. doi:10.1093/oxfordjournals.aob.a084281.
- Sachs, T. 1981. The control of the patterned differentiation of vascular tissues. *Adv Bot Res*. 9:151–262.
- Sachs, T. 2000. “Integrating Cellular and Organismic Aspects of Vascular differentiation.”. *Plant Cell Physiol*. 41(6):649–656. doi:10.1093/pcp/41.6.649.
- Sachs, T, D Cohen. 1982. Circular vessels and the control of vascular differentiation in plants. *Differentiation*. 21:22–26. doi:10.1111/j.1432-0436.1982.tb01189.x.
- Sanders, H, GW Rothwell, SE Wyatt. 2011. Parallel evolution of auxin regulation in rooting systems. *Plant Syst Evol*. 291:221–225. doi:10.1007/s00606-010-0383-1.
- Savidge, RA, PF Wareing. 1981. Plant-growth regulators and the differentiation of vascular elements. In J R Barnett, editor. *Xylem cell development*. Tunbridge Wells (UK): Castle House Publications; p. 192–235.
- Stein, W. 1993. Modeling the evolution of stelar architecture in vascular plants. *Int J Plant Sci*. 154:229–263. doi:10.1086/297106.
- Tomescu, AMF, AT Groover. 2019. Mosaic modularity: an updated perspective and research agenda for the evolution of vascular cambial growth. *New Phytol*. 222:1719–1735. doi:10.1111/nph.15640.
- Tomescu, AMF, KKS Matsunaga. 2019. Polar auxin transport and plant sporophyte body plans. In: *Reference module in life sciences*. Elsevier; p. 1–12. doi:10.1016/B978-0-12-809633-8.20905-9. ISBN: 978-0-12-809633-8.
- Uggla, C, T Moritz, G Sandberg, B Sundberg. 1996. “Auxin as a positional signal in pattern formation in plants.” *Proceedings of the National Academy of Sciences, USA* 93: 9282–9286. doi: 10.1073/pnas.93.17.9282.