

# Araucarian dominated fossil forest from the Jurassic Kota Formation, Pranhita-Godavari Basin, India

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The patterns of the Jurassic forest composition and productivity are analyzed using a comprehensive fossil wood database from Kota Formation (79° 57' 32" E; 18° 54' 50" N), Pranhita-Godavari Basin, India (n = 48). To ascertain forest composition, records were classified by botanical affinity on the basis of xylotomical features. The study confirms previous conjecture that araucarioid and podocarpoid conifers were dominant during the Mesozoic time, especially in humid tropical and paratropical biomes. The field observations of co-occurrence of various wood taxa suggest that podocarpoid conifers are most closely associated with araucarioids, while araucarioids and podocarpoids rarely co-occur with cupressoid and *Ginkgo* like wood. To ascertain forest productivity, mean tree-ring width data were obtained from direct measurements and literature reviews. Comparison with modern data shows that the Jurassic forest productivity was elevated in mid palaeolatitudes. The high araucarian percentage and the nature of growth ring pattern suggest the relatively warm and dry climate which is in concurring with Jurassic climatic models of Indian subcontinent.

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## INTRODUCTION

Continental Jurassic deposits of India are represented by the Kota Formation in the Pranhita-Godavari Basin and the Hartala Formation in the South Rewa Gondwana Basin, Lathi Formation of Jaisalmer Basin and Dubrajpur Formation of Rajmahal Hills (Fig. 1A). Among these Jurassic litho-units, the Kota Formation in the Pranhita-Godavari Basin received greater attention from the palaeontologists because of its rich fauna. Extensive investigations have been carried out on the rich vertebrate fauna of the Kota Formation (Prasad and Bajpai, 2016 and reference therein). The fauna include semionotid and pholidophorid fish taxa, ostracods, reptiles, sphenodontian taxa, triconodonts, morgaucodontids and docodont mammals.

Vegetation studies from the Kota Formation are scarce, only limited number of studies are known (Mahabale, 1967; Biradar and Mahabale, 1978; Rajanikanth and Sukh Dev, 1989; Muralidhara Rao, 1991; Chinnappa and Rajanikanth, 2016, 2018; Chinnappa *et al.*, 2019). The plant fossils such as leaves and spore-pollen are rare in the Kota, however, the formation is well known for the large number of silicified fossil wood logs (Chinnappa *et al.*, 2019). These woods include the members of Araucariaceae, Cupressaceae, Podocarpaceae, and Taxaceae. The fossil woods are considered to be an important component of the Mesozoic fossil flora and they are one of the major sources to understand the flora of the geological past (Philippe *et al.*, 2009; Jiang *et al.*, 2019). The fossil woods with well preserved anatomical characters

are particularly valuable in reconstructing composition and productivity of palaeo-forests, and palaeo-environments (Fritts, 1976; Creber and Chaloner, 1985; Peralta-Medina and Falcon-Lang, 2012; Brea *et al.*, 2015; Pujana *et al.*, 2015; Chinnappa and Rajanikanth, 2018).

The present study is aimed to understand the forest composition, productivity and palaeo-environments of the Jurassic Kota Formation. The study is based on the large collection of fossil wood made by the Rajanikanth in 1980s, and Rajanikanth and Chinnappa during 2013-2016 from the Kota Formation, Pranhita-Godavari Basin. The study also considered the previous fossil wood data from the Kota Formation (Mahabale, 1967; Biradar and Mahabale, 1978; Rajanikanth and Sukh Dev, 1989; Muralidhara Rao, 1991; Chinnappa and Rajanikanth, 2016, 2018; Chinnappa *et al.*, 2019).

## MATERIALS AND METHODS

To analyze the patterns of Jurassic forest composition, productivity and environments the Indian fossil wood records of the Jurassic time were considered. The data are extracted from the published literature (Mahabale, 1967; Biradar and Mahabale, 1978; Rajanikanth and Sukh Dev, 1989; Muralidhara Rao, 1991; Chinnappa and Rajanikanth, 2016, 2018; Chinnappa *et al.*, 2019) and from the authors' personal collection from in and around the Kota and Chitur villages, Sironcha Taluk in Gadchiroli District of Maharashtra State, India (Fig. 1B). Other types of fossil, e.g., leaves, reproductive

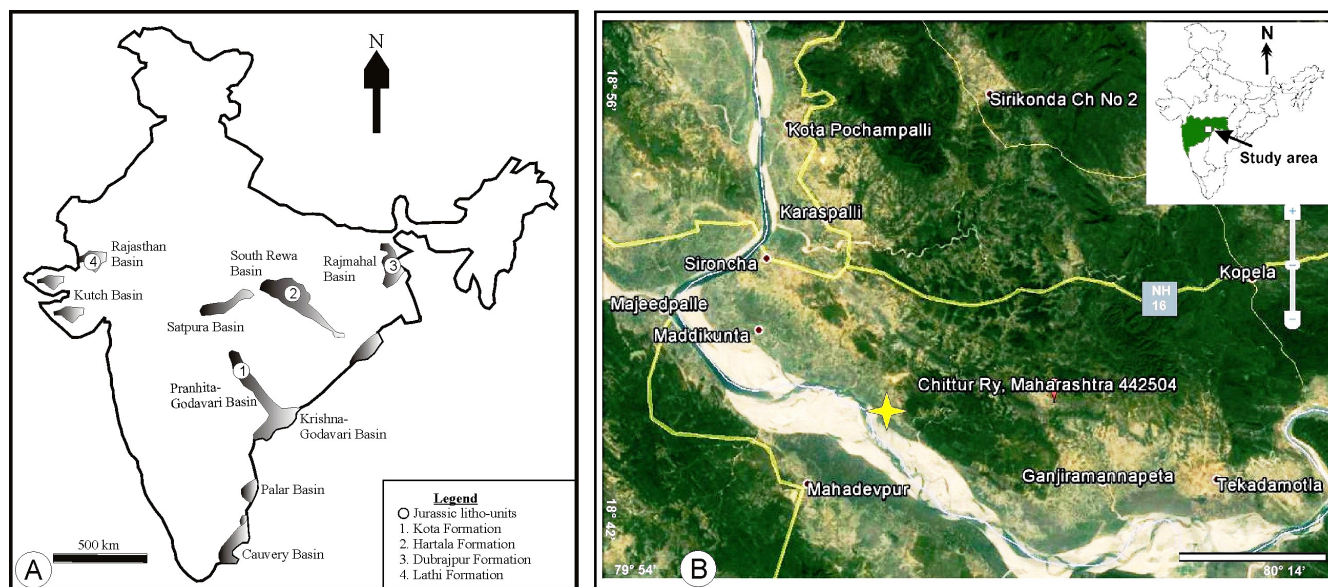


Fig. 1. A. Mesozoic sedimentary basins of India with Jurassic lithounits (marked with circle), B. Locality map showing the fossil sites (indicated by a star symbol) near the Chittur village.

structures, or pollen were not considered because only wood provides unequivocal evidence for canopy-forming trees (Peralta-Medina and Falcon-Lang, 2012). Each fossil wood record was assigned to the anatomical categories (araucarioid, podocarpoid, cupressoid and *Ginkgo* like wood) based on their xylotomy and wood character resemblance with the modern tree plants. In the Cretaceous Period, these four groups broadly reflect the extant families, Araucariaceae, Podocarpaceae, and the clade containing Sciadopityaceae, Cupressaceae, Cephalotaxaceae, and Taxaceae (Farjon, 2005), respectively. The cupressoid category also includes the extinct family Cheirolepidiaceae. The wood of *Ginkgo* type reflects Ginkgoaceae. The data are presented in the form of a simple pie diagram representing the percentage of the different wood taxa.

The preparation of the wood specimens was done by the conventional rock thin section, ground to varying thicknesses to account for the unique preservation characteristics of each specimen. The sections were prepared in transverse (TS), radial longitudinal (RLS) and tangential longitudinal (TLS) planes. The sections were examined under Olympus BH2 microscope with attached camera. The terminology used here strictly follows the IAWA Committee (2004) and identification of the fossil taxa is mainly based on the key to identify coniferous fossil genera by Philippe and Bamford (2008). The measurements were determined after measuring at least two dozens of cells in each case as followed by most recent xylotomists. The measurements represent minimum and maximum values with mean values in brackets. The specimens 36-8829-A, 36-8829-B, 36-8829-C are deposited at repository of Birbal Sahni Institute of Palaeosciences, Lucknow, India.

We analyzed mean tree ring data, nature of growth rings of about forty nine woods (these include woods with marked growth rings of the total sixty six woods) to understand the productivity and palaeoenvironments. The co-occurrence of plant groups were analyzed following the frequent association of taxa (fossil wood) in the field.

## SYSTEMATICS

### Genus *Agathoxylon* Hartig 1848

#### *Agathoxylon* sp.

*Referred specimen:* Specimen numbers BSIP. 36-8829-A, 36-8829-B, 36-8829-C

*Location:* Near Kota village (79° 57' 32" E; 18° 54' 50" N), Sironcha Taluk, Gadchiroli District, Maharashtra, India.

*Horizon and age:* Kota Formation, Middle Jurassic-Late Jurassic.

*Description:* In TS Growth rings are indistinct (Fig. 2.1-2), tracheids are thick-walled, with broad lumen, rounded, rounded-square and oval shape in transverse section. They range in size approximately from 28.3–(36)–45.4  $\mu$ m (vertical) by from 29.5–(35)–46.5  $\mu$ m (horizontal). Normal and traumatic resin canals are absent. Axial parenchyma is scanty, diffuse, sometimes with resin contents. The rays are separated from each other by 8-14 rows of tracheids; with an average of 9 rows.

In RLS, radial wall tracheid pitting is araucarian (Fig. 2.5-6) i.e., with more than 90% of the pits contiguous, mostly deformed at contact, while biseriate always clearly alternate, rarely sub-opposite; rare isolated pits are possible, especially in narrowest tracheids. Pits are circular, bordered with circular apertures with an average size of 3  $\mu$ m diameter. The radial wall tracheid pits are ranging in size approximately from 5–(6.6±1.26)–8.5  $\mu$ m (vertical) by from 6.7–(8±1.6)–9.2  $\mu$ m (horizontal). The shape of the tracheid pits is mostly circular and they are almost always touching or rarely are spaced more than one pit (Fig. 2.6). The cross-field pits are araucarian type, i.e. with numerous contiguous unordered cupressoid to taxodioid oculipores (Fig. 2.8). No ray tracheids observed. There are no bars of Sanio or spiral thickenings in the tracheids.

In TLS rays are mostly uniseriate and rarely partly biseriate (Fig. 2.3, 7), and range in height from 17.5 (75.7

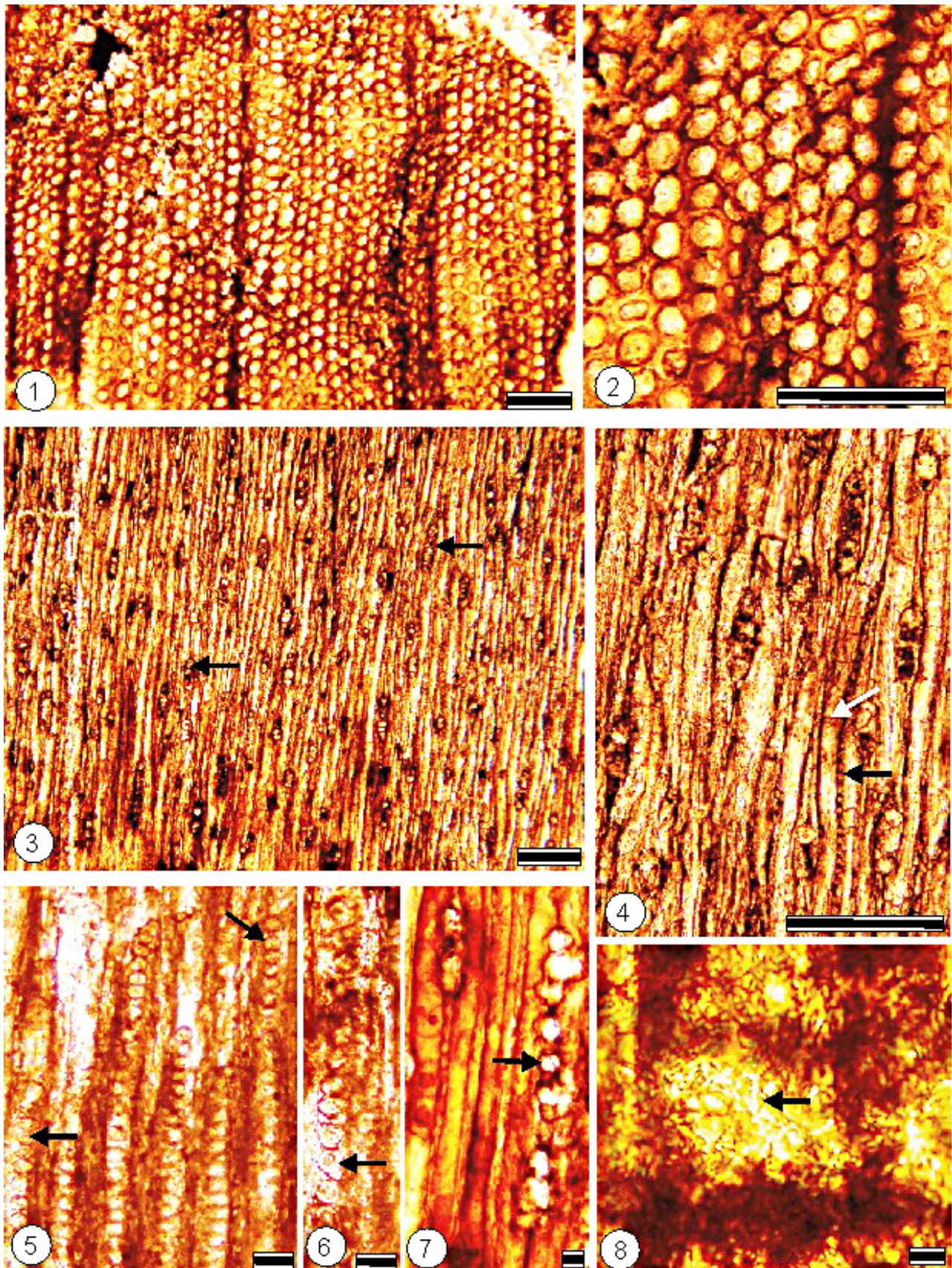
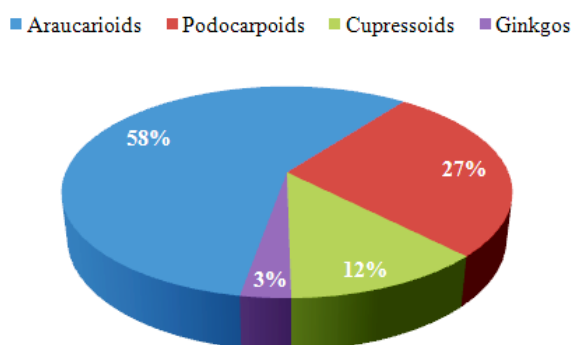


Fig. 2. BSIP 36-8829; 1-2, transverse section showing tracheid cells; 3, tangential section showing uni to partly biseriate rays (see arrows); 4, tangential section showing isolated nodular axial parenchyma with smooth end walls (see arrows); 5, 6, radial section showing uniseriate circular bordered pits (see arrows); 7, tangential section showing uniseriate rays 8. crossfield area with 8-10 araucarian type pits. Scale bar = 100  $\mu$ m.



**Fig. 3.** Percentage distribution of various wood taxa reported from the Kota Formation.

$\pm 2.65$ ) 175.2  $\mu\text{m}$  and the average ray height in number of cells is  $4 \pm 0.31$  (1–10). The rays are barrel to round shaped and variable in size (Fig. 4.4, 7). The ray cells are ranging in size approximately from 9.8– (18.5)–26.4  $\mu\text{m}$  (vertical) by 7.7–(16.4)–23.4  $\mu\text{m}$  (horizontal). Smooth, small and isolated nodular axial parenchyma is observed and the end wall of the axial parenchyma is smooth (Fig. 2.4). No tracheid pitting is observed in the tangential walls of the tracheids.

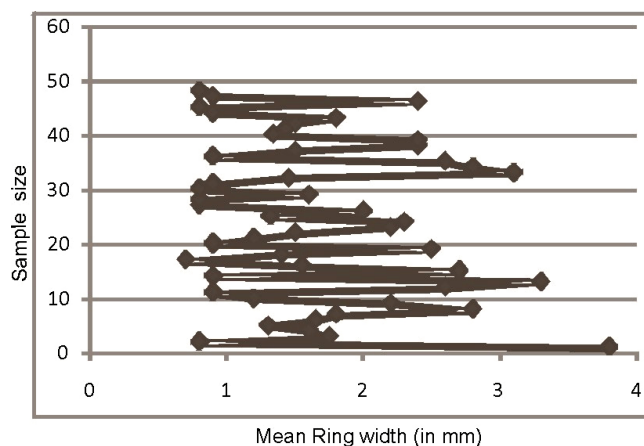
### Systematic affinities

Araucarian pitting on radial wall of tracheids (i.e., with more than 90% of the pits contiguous, mostly deformed at contact, while biseriate or pluriseriate always clearly alternate, rarely subopposite; rare isolated pits are possible, especially in narrowest tracheids; Sanio rims absent) with araucarian cross-field is a diagnostic features of the *Agathoxylon* woods. Similar combination of characters is also found in the other genera such as *Prototaxoxylon* Kräusel and Dolianiti (1958), and *Simplicioxylon* Andreanszky (1952). However, presence of spiral thickenings in *Prototaxoxylon* and an oblique end wall of ray cells in *Simplicioxylon* help in distinguishing these two genera from the *Agathoxylon*. Alternate and subopposite radial intertracheary pitting and cupressoid crossfield pitting is also characteristic of araucariaceous fossil wood and wood of *Brachyoxylon* Hollick and Jeffrey (1909). However, *Brachyoxylon* includes woods with mixed radial pitting.

The present wood is characterised by araucarian radial pitting and cross-field, but no spiral thickenings and an oblique end wall of ray cells, thus the specimens show greater similarity to araucariaceous woods than to those assigned to *Prototaxoxylon*, *Simplicioxylon* and *Brachyoxylon*. Consequently, the specimens are assigned to the xylotype *Agathoxylon* (Philippe and Bamford, 2008).

### Comments and Comparison

*Agathoxylon* wood type is one of the most extensively described taxa among all the fossil conifer wood. As many as 428 species have been described to date and they range in age from Carboniferous to Cenozoic (Philippe, 2011). Most anatomical features used up to now to distinguish species among this group are environmentally and also genetically controlled. The seriation of radial pits and the number of cross-field pits are *pro parte* functions of tracheid width, itself a function of water availability. The ray height is, *pro parte* similarly, a function of the distance to the pith, and thus of trunk diameter. According to Philippe (2011), now that the



**Fig. 4.** Jurassic forest productivity based on the mean ring width data.

documented variability is more complete, there is apparently no reason anymore to distinguish species within this group of woods. Therefore, we are not attempting to erect new species although character combinations of wood suggest a new specific status and eventually, we preferred to assign the wood under *Agathoxylon* sp.

The present wood can readily compared with *Agathoxylon kotaense* Chinnappa *et al.* (2019) known from the Jurassic Kota Formation, India and *A. bindrabanense* (Sah and Jain) Chinnappa and Rajanikanth (2018) reported from the Early Cretaceous Rajmahal sediments in the number of cross field pits. However, the present wood differs from them in height of the xylem rays (2-20 in the *A. kotaense* and 1-45 in *A. bindrabanense* but only 1-10 in the present wood). The wood described here can also be comparable with *A. dallonii* (Boureau) Crisafulli and Herbst (2010) reported from the Triassic of Argentina, in the xylem ray cell height (1-12 with average of 5), however, the number of cross field pits in *A. dallonii* are very less (1-2, rarely 3). *Araucarioxylon termieri* (Attimis) Gnaedinger and Herbst (2009) shares the characters like presence of circular pits in the radial walls of the tracheids, and the seriation and distribution of pits in the radial tracheid walls, the number of pits in the cross-fields, and the ray height. However, the wood described here differs from them in having nodular axial parenchyma.

### Forest composition and productivity

The analysis of the available wood data shows that araucarioids and podocarpoid conifers were the most abundant (85 %) among all (Figure 3). The wood type placed under the araucarioids comprises *Agathoxylon*, *Araucarioxylon* and *Dadoxylon*, and the podocarpoid comprise *Circoporoxylon*, *Mesembrioxylon*, *Podocarpoxyton*, and *Protopodocarpoxyton*. Of the two conifer families, the former occupies (58 %) and latter is (27%). Other wood types such as cupressoid conifers comprise *Cupressinoxylon*, *Prototaxodioxylon*, *Taxaceoxylon*, *Protaxodioxylon* are rare (12%) components of the forest. Finally, Ginkgo like wood is least represented (3%). Although fossil leaf studies from the Kota Formation are not abundant, they show the presence of conifers (Podocarpaceae and Araucariaceae) dominated leaves (Rajanikanth and Sukh-Dev, 1989). Pollen analyses also have an abundance of Araucariaceae and Podocarpaceae

but indicate the predominance of Araucariaceae (Vijaya and Prasad, 2001). Therefore, the taxa found on the fossil woods are consistent with previous palynological and fossil leaf studies.

The field observations of co-occurrence of various wood taxa suggest that podocarpoid conifers are most closely associated with araucarioids, while araucarioids and podocarpoids rarely co-occur with cupressoid and *Ginkgo* like wood. The analysis of fossil woods at global scale by Peralta-Medina and Falcon-Lang (2012) also showed the similar co-occurrence pattern of plant groups during the Mesozoic Period. Forest productivity analysis (Fig. 4) shows that annual tree growth rate was elevated compared to the present (mean  $1.68 \pm 0.78$ ; cf. modern mean  $1.18 \pm 0.51$  at mid latitudes), but not significantly.

### Palaeoecology and environments

The woods collected from the Jurassic Kota Formation are found in coarse fluvial settings. The woods include members of *Agathoxylon*, *Podocarpoxylon*, *Cupressinoxylon* and *Taxaceoxylon*. This association of araucarian dominant vegetation along with associated groups of plant families probably indicates riparian vegetation (Chinnappa and Rajanikanth, 2017). Large size trunks are hints of such possibility (Philippe *et al.*, 2003). This interpretation is supported by the sedimentological association of large assemblage of fossil woods near the fossil site (Boggs, 2006). There, large sized trunks in great number are found to be associated with the overbank sand deposits along the stream margins. Extant podocarpeans and araucarians primarily inhabit rainforest or wet montane environments and indicate the presence of rain forest vegetation (Hill and Brodribb, 1999; Kershaw and Wagstaff, 2001).

The growth rings presented in the wood from the Jurassic Kota Formation are characterised by the low percentage of latewood without thickening of the tracheidal walls, and the transition from early to latewood is in general abrupt to less gradual. This suggests that the growth conditions were interpreted to have manifested as accentuated growing periods (Francis and Poole, 2002). Fossil woods show uneven sequences of growth rings, indicating fluctuations in growing conditions over several growth periods (Pires *et al.*, 2011). The false growth rings which are a common characteristic in most of the specimens suggests an ecological constraints that were responsible for an early near cessation of cambial growth and a renewal of growth within the same growing period (Pires *et al.*, 2011). Resource constraints and possible microenvironmental factors resulted in erratic growth ring features as evidenced by the presence of growth interruptions (Chinnappa and Rajanikanth 2018). The growth ring parameters presented here are indicative of seasonality but

often stressed and in some periods it presented an erratic full stoppage. The growth rings can be comparable to the growth rings of modern tropical to subtropical conifers growing in the southern hemisphere.

The palaeo- latitudinal position of the Indian subcontinent during the Jurassic was southern Subtropical Arid Belt (30°-32°S) and the climatic conditions were very warm and dry (Chatterjee *et al.*, 2013). The weakly defined growth rings and growth interruptions are characteristics of growth under warm subtropical climates and association of cupressoid conifers indicative of seasonally dry ecotone (Rajanikanth and Sukh-Dev, 1989; Peralta-Medina and Falcon-Lang, 2012). These results are concurring with the broad subtropical belt that existed in the Jurassic. The Araucariaceae appear to be one group of plants that evolved after the major extinction phase at the end of the Permian, prompted by arid conditions throughout much of Gondwana (Hill *et al.*, 2000). The group increased in abundance and diversity during the Jurassic. It is likely that rising sea levels through the Jurassic corresponded to both increased precipitation and temperature that facilitated the development of forest vegetation. The relatively warm and dry climates were also suggested by the high araucarian pollen percentages through this period (McLoughlin and Hill, 1996).

### CONCLUSIONS

Patterns of Jurassic forest composition and productivity collated here are based on a nearly complete compilation of fossil wood, synthesizing from the data available in the previous studies and authors' personal collections. The analysis of about 48 woods from the Jurassic sediments suggests that the vegetation is primarily dominated by araucarians. The studies from the other Gondwanan regions also suggest that the araucarians were the dominant components of the Jurassic and Cretaceous vegetation (Kershaw and Wagstaff, 2001; Kunzmann, 2007). The forest composition and productivity during the Jurassic times is comparatively richer than the present, which are mostly consistent with the global Jurassic productivity (Beerling and Woodward, 2001). The high araucarian percentage and the nature of growth ring pattern suggest the relatively warm and dry climates which concur with Jurassic climatic models of Indian subcontinent.

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