VOLUMINA JURASSICA, 2019, XVII: 1–16
DOI: 10.7306/VJ.17.1

Palaeofloras from the Kota Formation, India: palaeodiversity and ecological implications

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Key words: *Agathoxylon*, floral diversity, palaeoecology, Kota Formation, India.

Abstract. The Kota Formation of the Pranhita-Godavari Basin is well known for its fossil fauna and flora especially for its silicified woods. However, the palaeoflora and its palaeoclimatic significance within the formation are poorly known. In spite of the fact that the formation yields a rich fauna and flora chronostratigraphic problems still exist. The present study aims to analyze the palaeofloras from the Kota Formation to understand their diversity and palaeoecological significance. We also describe a new species *Agathoxylon kotaense* belonging to the conifer family Araucariaceae. Our study shows that the flora was dominated by conifers and that it is comparable to that of the ?Late Jurassic – Lower Cretaceous Gangapur Formation, Pranhita-Godavari Basin and that of the Rajmahal Formation of the Rajmahal hills. The growth ring pattern and leaf fossil assemblage suggest that the growth conditions were seasonal, but mostly stressed.

INTRODUCTION

Plant fossil assemblages are widespread, abundant and often diverse in the Mesozoic sequences of India, where they remain a valuable tool for understanding the diversity, and evolution of the Mesozoic ecosystems (Bose *et al*., 1990; Chinnappa *et al*., 2014, 2015; Chinnappa, Rajanikanth, 2016, 2017, 2018). A number of Mesozoic floras from Triassic and Cretaceous sequences have been described in India (Rajanikanth, Chinnappa, 2016 and reference therein). However, only limited palaeobotanical studies have been conducted on the Jurassic sequences in India (Mahabale, 1967; Biradar, Mahabale, 1978; Prabhakar, 1989; Sukh-Dev, Rajanikanth, 1988; Rajanikanth, Sukh Dev, 1989; Muralidhara Rao, 1991; Vijaya, Prasad, 2001; Bonde, 2010; Chinnappa, Rajanikanth, 2016; Rai *et al*., 2016). These studies were restricted to the description and listing of plant fossil assemblages. Consequently, little is known regarding the diversity and palaeoecology of the Jurassic floras of India. One of the main reasons for the lack of knowledge regarding the Jurassic floras of India is the lack of proper age control.

In India, the Jurassic sediments are distributed in the Kota Formation of Pranhita-Krishna-Godavari Basin, the Hartala Formation of South Rewa Basin, the Lathi Formation of Jaisalmer Basin, the Jhuran Formation of Kutch Basin and the Dubrajpur Formation of Rajmahal Basin (Fig. 1A, B). Among these formations, the Kota Formation has received great attention from various authors because of its rich palaeoflora (Mahabale, 1967; Biradar, Mahabale, 1978; Sukh-Dev, Rajanikanth, 1988; Prabhakar, 1989; Rajanikanth, Sukh Dev, 1989; Muralidhara Rao, 1991; Vijaya, Prasad, 2001; Chinnappa, Rajanikanth, 2016) and palaeofauna (Owen, 1952; Rao, Shah, 1959; Jain, 1973, 1974a, b, 1983; Tasch *et al*., 1973; Govindan, 1975; Jain *et al*., 1975; Yadagiri, Prasad, 1977; Misra, Satsangi, 1979; Yadagiri *et al*., 1979; Datta, 1981; Yadagiri, 1984, 1985, 1986; Yadagiri, Rao, 1987; Prasad, Manhas, 1997, 2001; 2002, 2007; Evans

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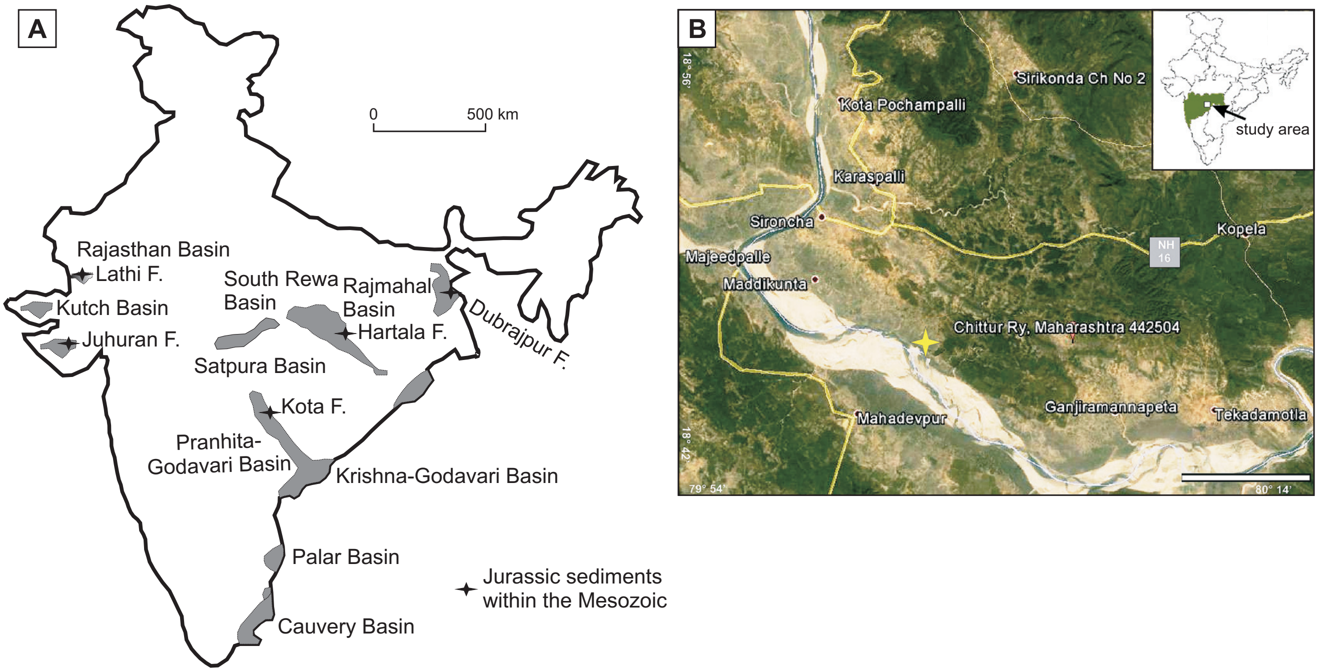

Fig. 1. A. Distribution of Mesozoic sedimentary basins in India, showing the Jurassic successions; **B.** Location map of Kota-Chittur area showing the fossil site

et al., 2002; Parmar *et al.*, 2013). The formation is named after the village of Kota, occurring on the eastern side of the Pranhita riverbank in the Chandrapur District, Maharashtra. In this study we report some leaf and wood fossils from the Kota Formation and we discuss the diversity and palaeoecology of the Kota flora. We have described the wood using a quantitative approach to fossil wood taxonomy. A quantitative approach is valuable because it allows the wood morphology to be described in a more precise way than by a qualitative description alone, and in addition it also enables the distinguishing of the the intra-sample and intra-taxon variability to be ascertained more exactly (Falcon-Lang, Cantrill, 2000, 2001).

GEOLOGICAL BACKGROUND AND AGE OF THE KOTA FORMATION

The geologic and stratigraphic information regarding the Kota Formation is available through the studies of Kutty (1969), King (1881), Rudra (1982), Bhandhyopadhyay and Rudra (1985), Raivarman *et al.* (1985), Kutty *et al.* (1987), Lakshminarayana (1994, 2002) and Sen Gupta (2003). The Kota Formation is divided into three members – the Lower, Middle and the Upper members, defined by Lakshminarayana (1994). The Lower Member is represented by sandstone, with pebbles of banded chert. The Middle member is composed of limestone. The Upper Member is characterized by the sandstone, siltstone and claystone (Tab. 1). The leafy fossils were collected from the claystones of the Upper Member while the woods were collected from the siltstones and fine grained sandstones of this member. The Kota Formation occurs between the Late Triassic Dharmaram Formation which is composed of coarse sandstone and red clays, and the Lower Cretaceous Gangapur/Chikiala Formation which is composed of coarse ferruginous sandstone, greywhite-pinkish mudstone and silty mudstone/shale. There is an unconformity between the Kota and Gangapur/Chikiala formations. The stratigraphic succession of the Pranhita-Godavari Basin is given in Table 1.

The precise age of the Kota Formation has been subject to numerous scientific debates. (Jain, 1973, 1983; Govindan, 1975; Kutty *et al.*, 1987; Rajanikanth *et al.*, 2000; Vijaya, Prasad, 2001; Prasad, Manhas, 2007). This is primarily because the sediments from the Kota Formation have not yielded any biostratigraphically significant index fossils (Parmer *et al.*, 2013). As no datable magmatic rocks occur in relation to the Kota Formation, radiometric data are also not available. Early Jurassic to Early Cretaceous ages have been suggested for the Kota Formation based on individual faunal and floral evidences. It was assigned a Jurassic age by King (1881) and more specifically, a Liassic (Early Jurassic) age by Krishnan (1968).

Table 1

Lithostratigraphic succession in the Pranhita-Godavari Basin (data after Kutty *et al.*, 1987; Lakshminarayana G., 1994, Sen Gupta 2003)

	Formation	Lithology	Age
Deccan Traps			
Upper Gondwana	Gangapur/Chikiala	Coarse ferruginous sandstone, greywhite-pinkish mudstone and silty mudstone/shale	Early Cretaceous
	--------------------------------unconformity--------------------------		
	Kota	Upper: Sandstone, siltstone and claystone Middle: Limestone Lower: Sandstone with pebbles of banded chert	?Late Jurassic – Early Cretaceous
	Dharmaram	Coarse sandstone and red clays	Late Late Triassic
	Maleri	Red clays, fine-medium sandstone and limestone	Early Late Triassic
	Bhimaram	Ferruginous/calcareous sandstone, minor red clays	Late Middle Triassic
	Yerrapalli	Red and violet clays with sandstone and limestone	Early Middle Triassic
Lower Gondwana	Kamthi	Upper: Coarse grained, ferruginous sandstone with quartz pebbles Middle: Siltstone Lower: Purple colored argillaceous sandstone interbedded with sandstone	Late Late Permian – ?Early Triassic
	--unconformity--------------------------------		
	Kundaram/Barren Measure (“Ironstone shale”/ “Infra Kamthi”)	White-light yellow feldspathic sandstone, ferruginous shale, ironstone and clay/ coal bands	Late Early Permian – Late Permian
	Barakar	Upper: Feldspathic sandstone, shale and carbonaceous shale Lower: Feldspathic sandstone, siltstone and coal laminae	Late Early Permian
	Talchir	Diamictite, rhythmite, tillite, greenish shale and sandstone	Early Early Permian
---unconformity---			
Proterozoic		Igneous and metamorphic rocks	Precambrian

Jain (1973, 1974b, 1983) suggested an Early Jurassic age based on semionotid fish taxa such as *Tetragonolepis olhdami* and *Paradapedium egertoni*, and the reptiles: *Campylognathoides indicus* and *Lepidotes deccanensis* (Tab. 2). Subsequently, Yadagiri, Prasad (1977) also favored an Early Jurassic age based on the pholidophorid fishes – *Pholodophorus indicus* and *P. kingi*. Feist *et al*. (1991) reported a charophyte taxon *Aclistochara* comparable to *A. jonesi* and *A. bransoni* known from the Late Jurassic and Early Cretaceous formations of USA and China (Peck, 1957; Liu, 1982). Despite this, Feist *et al*. (1991) followed the long established Early Jurassic age. Later, Bhattacharya *et al*. (1994) also reported another charophyte taxon, *Praechara symmetrica* and favored an Early Jurassic age.

Govindan (1975) suggested a Middle Jurassic age, based on the ostracod assemblage comprising *Darwinula* cf. *D. sarytirmensis*, as this species was originally known from the Middle Jurassic Mangyshlak Peninsula in Kazakhstan and Timiriasevia in Russia. Later, Misra, Satsangi (1979) also reported an ostracod assemblage comprising *Darwinula* cf. *D. sarytirmensis* and other taxa and they accepted the Middle Jurassic age as suggested by Govindan (1975). Nonetheless, the stratigraphic range of *Darwinula sarytirmensis* extends from Early to Late Jurassic (Hao *et al*., 1983; Meizhen, 1984; Kietzke, Lucas, 1995).

The fossil mammals from the Kota Formation are represented by the triconodont *Dyskritodon* and *Paikasigudodon*, and morgaucodontid *Indotherium* (Datta, 1981; Yadagiri, 1984, 1985; Prasad, Manhas, 1997, 2002). *Dyskritodon* is a significant stratigraphic index fossil known from the Early Cretaceous of Morocco (Sigogneua-Russel, 1995). More recently, Prasad and Manhas (2007) reported a docodont mammalian genus *Gondtherium* and suggested morphological similarities with the Late Jurassic *Haldanodan* of Portugal (Krusat, 1980). A Late Jurassic to Early Cretaceous age (Oxfordian to Barremian) for the Kota Formation also gained support from a palynological study by Vijaya and Prasad (2001). In this study we followed the age assignments of Vijaya and Prasad (2001) and Prasad and Manhas (2007).

Table 2

Showing the suggested age for the Kota Formation by various authors based on flora and fauna record

Author	Year	Studied fossil taxa	Suggested age
Bhattacharya *et al.*	1994	*Praechara symmetrica*	EJ
Datta	1981	*Kotatherium haldanei*	Jurassic
Datta & Das	2001	*Indozostrodon simpsoni*	EJ
Datta *et al.*	2000	*Indochelys spatulata*	Jurassic
Egerton	1851	*Lepidotes deccanensis*, *Tetragonolepis oldhami*	Jurassic
Evans *et al.*	2002	*Bharatagama rebbanensis*	EJ-MJ
Evans *et al.*	2001	*Godavarisaurus lateefi*, *Rebbanasaurus jaini*	EJ-MJ
Feist *et al.*	1991	*Aclistochara jonesi*, *A. bransoni*	EJ
Govindan	1975	*Darwinula* cf. *sarytirmensis*, ?*Limnocythere* sp., *Timiriasevia digitalis*	MJ
Jain	1973	*Paradapedium egertoni*	EJ
Jain	1974	*Campylognathoides indicus*, *Indocoelacanthus robustus*	EJ
Jain *et al.*	1975	*Barapasaurus tagoreii*	EJ
Misra & Satsangi	1979	*Clinocypris* sp., *Cypredea* sp., *Darwinula kingi*, *Darwinula* sp. 1 & 2, *Eucandona* sp., ?*Stenocypris* sp.	MJ
Owen	1852	?Teleosaurid crocodiles	EJ
Parmar *et al.*	2013	*Indobaatar zofiae*	EJ-MJ
Prasad & Manhas	2007	*Docodontidae dattai*, *Gondtherium*	LJ-EC
Prasad & Manhas	2002	*Dyskritodon indicus*, *Paikasigudodon yadagiri*	EJ-MJ
Prasad *et al.*	2004	*Lissodus indicus*, ?*Polyacrodus* sp.	MJ-LJ
Rao & Shah	1963	*Rhamphorhynchus* sp.	EJ
Vijaya & Prasad	2001	Pollen assemblage	LJ-EC
Yadagiri	1984	*Indotherium pranhitai*, *Trishulotherium kotaensis*	EJ
Yadagiri	1985	*Nakunodon paikasiensis*	EJ
Yadagiri	1986	*Paikasisaurus indicus, Lissodus indicus*	EJ
Yadagiri & Prasad	1977	*Pholidophorus kingii*, *P. indicus*	EJ
Yadagiri *et al.*	1979	*Kotasaurus yamanapalliensis*	EJ

MATERIALS AND METHODS

The fossil wood material studied here was collected from around the Kota and Chitur villages, Sironcha Taluk in Gadchiroli District of Maharastra State, India (Fig. 1A, B). The wood material prepared for this study was preserved as silicified surface material in a *nala* (Indian: small canal) section near Kota village. The leaves were preserved as fragmentary leafy impressions in a thin layer of mudstone in between two limestone layers of the Upper Member of the Kota Formation. No cuticles were recovered.

The preparation of the wood specimens was undertaken using conventional rock thin sections cut to varying thicknesses related to the unique preservation of each specimen. The sections were prepared in transverse (TS), radial longitudinal (RLS) and tangential longitudinal (TLS) planes. The sections were examined under an Olympus BH2 microscope with attached camera. The terminology used here mainly follows that of the the IAWA Committee (2004) and identification of the fossil taxa is mainly based on the key to identifying coniferous morpho genera by Philippe and Bamford (2008). The measurements were determined after measuring at least two dozen cells in each case as followed by most recent xylotomists (Falcon-Lang, Cantrill, 2000; Oh *et al.*, 2011; Chinnappa, Rajanikanth, 2016). The measurements represent minimum and maximum values with mean values in brackets. The slides (BSIP 16274a, 16274b, 16274c) are deposited at the repository of the Birbal Sahni Institute of Palaeosciences, Lucknow, India. The data for leaf fossils and spore-and pollen is obtained from the studies of Prabhakar (1989), Rajanikanth and Sukh-Dev (1989) and Vijaya and Prasad (2001).

The spore/pollen is assigned to family level following Ramanujam and Rajeshwar Rao (1979), and the pteridophytic fronds were assigned to family level after Harris (1961) and Barbacka and Bodor (2008). However, the taxonomic affinities at family level are not certain for many gymnosperm taxa; many of these taxa could be related to more than one family. Macro-and microfloral species diversity was analysed separately by considering the total number of taxa known in the flora. The taxonomic diversity of the flora is illustrated in pie diagrams as a simple percentage representation of each group (at taxon level), generated by using MS Excel. Similarly, the abundance of the various plant taxa was calculated by counting the number of samples of the given taxa.

RESULTS AND DISCUSSION

SYSTEMATIC PALAEOBOTANY

Family Araucariaceae Henkel & Hochstetter, 1865

Genus *Agathoxylon* Hartig *sensu* Rössler *et al*., 2004

Agathoxylon kotaense n. sp.

Pl. 1: 1–8.

Derivation of name. After the Kota Formation from where the specimens were collected.

Holotype. BSIP 16274.

Referred specimens. BSIP 16274a, 16274b, 16274c.

Location. Near village Kota, Sironcha Taluka in Gadchiroli District of Maharastra State, India.

Horizon and age. Kota Formation, ?Late Jurassic – Early Cretaceous.

Repository. Birbal Sahni Institute of Palaeosciences, Lucknow, India.

Description. In RLS, radial walls tracheid pitting is araucarian pitting on radial wall of tracheids *i.e.* with more than 90% of the pits contiguous, mostly deformed at contact; predominantly uniseriate, a few biseriate pits are also present (“IAWA 44”). Where pits are biseriate they are generally alternate (“IAWA 47”) to sub-oppositely arranged (Pl. 1: 5). Sanio rims absent. The radial wall tracheid pits are ranging in size approximately from 12– (16±1.76) –22 µm (vertical) by from 15– (17±1.76) –22 µm (horizontal). The shape of the tracheid pits is mostly circular. The crossfield pits are typically araucarioid (“IAWA 95”), 12–16 for each crossfield (“IAWA 100”; Pl. 1: 6–8). The crossfield pits are approximately 1.6 µm by 2.2 µm. Rays are abundant throughout.

In TLS rays are uniseriate and rarely biseriate (“IAWA 107”), 2– (4–8) –20 cells high (“IAWA 103”; Pl. 1: 3). The rays are barrel shaped and variable in size. The ray cells are ranging in size approximately from 27– (40) –53 µm (vertical) by 21– (32) –41 µm (horizontal). Tangential wall pits absent. Axial parenchyma is absent. No resin canals were observed.

In TS growth rings are indistinct (“IAWA 41”). The tracheids are more or less circular to hexagonal and intra-cellular spaces are present (“IAWA 53”; Pl. 1: 1, 2). They range in size approximately from 38– (67) –87 µm (vertical) by from 28– (59) –82 µm (horizontal). Tracheid walls are thin, 5– (6) –8 µm thick. No axial parenchyma and resin canals are observed. However, as the fossil wood material is poorly preserved it is difficult to unequivocally judge whether axial parenchyma is truly present or absent.

Systematic affinities. Araucarian pitting on the 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 pits, which is characteristic of specimen BSIP 16274, is also found in the specimens of *Prototaxoxylon* Kräusel and Dolianiti (1958), and *Simplicioxylon* Andreanszky (1952). However, *Prototaxoxylon* is characterized by presence of spiral thickenings which are absent in the present specimen, therefore this material cannot be assigned to this xylotype. In *Simplicioxylon* the end wall of ray cells is at least locally strongly oblique, this is not the characteristic feature of specimen BSIP 16274.

Alternate and subopposite radial intertracheary pitting and cupressoid crossfield pitting is also characteristic of araucariaceous fossil wood and the wood of *Brachyoxylon* Hollick and Jeffrey (1909). However, *Brachyoxylon* includes woods with mixed radial pitting such that this fossil bears greater similarity to araucariaceous fossil woods than to those assigned to *Brachyoxylon*. Therefore this specimen has been assigned to the xylotype *Agathoxylon* erected for woods with araucarian radial wall pitting and araucarioid cross-field pits (Philippe, Bamford, 2008). No attempt has been made to place this specimen within an existing species since there are no other woods of this type yet reported from India and elsewhere. The fossil-genera for araucariaceous fossil wood are in need of revision (Bamford, Philippe, 2001).

Comparison. *Agathoxylon kotaense* n. sp. described in the present study closely resembles the wood of members of the modern Araucariaceae, in particular the genus *Araucaria* which grows across southern South America and northern Australasia (Greguss, 1955, 1972; Enright *et al*., 1995). *Agathoxylon* is found in Mesozoic rocks of high southern latitudes, being described from both Gondwanan and non Gondwanan countries (Philippe, 2011). The new species described in the present study is compared with the closely related Mesozoic species of *Agathoxylon* known to date, from various parts of the globe. But all the species known previously differ in one or other aspects (Tab. 3).

The new specimen is very similar to *Agathoxylon togeumense* described by Oh *et al.* (2011) from the Early Cretaceous of Korea, differing primarily in the absence of tangential wall pits and presence of tetra-seriate radial wall pits. It also corresponds closely to a specimen of *A. byeongpungense* described from the Early Cretaceous of Korea by Oh *et al.* (2011), differing only in the less abundance of triseriate tracheid pitting in *A. byeongpungense*. Another close match is with the specimen of *Agathoxylon agathiodes* (Krausel & Jain) Bose & Maheshwari *sensu* Chinnappa and

Table 3

Comparative table of *Agathoxylon* species reported from India and other parts of the globe

Age and Taxa name	Country	Growth rings	Axial Parenchyma	Xylem rays	Radial wall pits	Tangential wall pits	Crossfield Pits
TRIASSIC							
Agathoxylon dallonii (Boureau) Crisafulli & Herbst	Argentina	present	absent	1 seriate, 2–12 (5) cells	1–2 seriate, alternate contiguous	absent	1–2–[3]
A. africanum (Bamford) Kurzawe & Merlotti	Argentina	distinct	absent	1–[2] seriate, 2–15 cells	1–2 seriate, alternate contiguous	present	2–6
Agathoxylon sp. α (Sahni) Bose & Maheshwari	India	indistinct	……..	1 seriate, 1–20 cells	1–2 seriate, alternate	……..	2–5 or more
Agathoxylon sp. β (Sahni) Bose & Maheshwari	India	distinct	……..	1 seriate, 1–15 cells	2–3 seriate, alternate	……..	……..
JURASSIC							
A. pranhitensis Rajanikanth & Suhk-Dev	India	present	……..	1–[2] seriate, 1–52 cells	1–3 seriate, alternate–sub–opposite	……..	3–6
A. matildense Zamunar & Falaschi	Argentina	distinct	absent	1 seriate, 1–4 (2–3) cells	1 seriate, alternate contiguous	absent	4–5
A. liguaensis Torres & Philippe	Chile	distinct	absent	1 seriate, 1–56 (30) cells	1–2 seriate, alternate	present	4–5
A. arayaii Torres *et al.*	Antarctica	distinct	……..	1 seriate, 1–25 (8–10) cells	1–2–[3] seriate, alternate	present	2–6
A. saravanensis (Serra) Philippe *et al.*	Vietnam	indistinct	absent	1 seriate, 1–23 (3–11) cells	1 seriate, opposite	absent	2–12 (4–8)
A. kotaense n. sp.	India	indistinct	absent	1 seriate, 2–20 (4–8) cells	1–[2] seriate, sub-opposite	……..	12–16
Agathoxylon sp. Rajanikanth & Sukh-Dev	India	indistinct	……..	1–[2] seriate, 1–18 cells	1–[2] seriate, alternate	……..	2–5
Agathoxylon sp. Poole & Mirzaie	Iran	distinct	present	1–[2] seriate, 2–32 cells	1– (2) multi seriate, alternate to sub-opposite	present	up to 6
Agathoxylon sp. Ortega-Chávez *et al.*	Mexico	indistinct	absent	1 seriate, 2–21 (7) cells	[1]–2 seriate, alternate	……..	1–2–[3]
CRETACEOUS							
A. gondwanensis Kumarasamy	India	distinct	……..	1 seriate, 1–39 (11) cells	1–[2] seriate, alternate contiguous	present	1–3, (1)
A. mosurense Jeyasingh & Kumarasamy	India	indistinct	……..	1–[3] seriate, 1–27 (7) cells	1–2 seriate, alternate, contiguous	present	2–6
A. giftii Jeyasingh & Kumarasamy	India	distinct	……..	1 seriate, 2–29 (10) cells	1–[2] seriate, alternate, contiguous	absent	1 or 2, [5–7]
A. rajivii Jeyasingh & Kumarasamy	India	distinct	……..	1 seriate, 2–26 (12) cells	1–2 seriate, alternate, contiguous	absent	1–2, [3]
A. rajmahalense (Sahni) Bose & Maheshwari	India	indistinct	……..	1 seriate, 1–20 (6) cells	1–3 seriate, alternate	……..	……..
*A. amraparense (*Sah & Jain) Bose & Maheshwari	India	distinct	……..	1 seriate, 1–15 cells	1–3 seriate, alternate-sub-opposite	……..	2–4,
A. mandroense (Sah & Jain) Bose & Maheshwari	India	distinct	……..	1 seriate, 1–15 cells	1–3 seriate, alternate	……..	4–12
A. santalense (Sah & Jain) Bose & Maheshwari	India	distinct	……..	1– [2] seriate, 1–10 cells	1–[2] seriate, alternate	……..	2–6, (4)
A. bindrabunense (Sah & Jain) Bose & Maheshwari	India	indistinct	……..	1–[2] seriate, 1–45 cells	[1]–(2)–3 seriate, alternate	……..	4–12, (4–6)
A. agathiodes (Krausel & Jain) Bose & Maheshwari	India	indistinct	……..	1 seriate, 2–20 cells	1–2 [3] seriate, alternate	……..	2–8, (5–6)
A. jurassicum Bharadwaj	India	distinct	……..	1–[2] seriate, 1–11 cells	1–2 seriate, alternate	present	4–8
A. wynnei Borkar & Bande	India	indistinct	……..	Not available			
A. floresii Torres & Lemoigne	Antarctica	indistinct	present	1 seriate, 2–15 (4–7) cells	1 seriate, araucarioid	present	1–4
A. ohzuanum Nishida *et al.*	Chile	indistinct	present	1 seriate, 1–11 (1–7) cells	1–2 seriate, contiguous	present	1–4
A. pichasquense Torres & González	Chile	indistinct	absent	1 seriate, 1–11 (1–7) cells	1–2 seriate, contiguous,	present	5–10

Table 3 cont.

Age and Taxa name	Country	Growth rings	Axial Parenchyma	Xylem rays	Radial wall pits	Tangential wall pits	Crossfield Pits
A. parachoshiense Nishida & Nishida	Chile	distinct	absent	1 seriate, 1–4 cells	1–2 seriate, araucarioid	absent	2–4
A. novae-zeelandiae Stopes	New Zeland	……..	absent	1 seriate, 1–7 (3–4) cells	2 seriate, alternate	absent	5–6
A. kaiparaense (Edwards) Philippe *et al.*	New Zeland	distinct	absent	1–8 (2–3) seriate	1–2–[3] seriate, contiguous	absent	1–10
Dadoxylon (*A.*) *kellerense* Lucas & Lucey	Chile	distinct	……..	1 seriate, 1–11 (4–5) cells	1–3 seriate, araucaroid	absent	1–4
A. resinosum Torres & Biro-Bagoczky	Chile	distinct	……..	1 seriate, 1–40 cells	1–3 seriate, araucaroid	present	2–3
A. lemonii Tidweel & Thayn	US	distinct	present	1 seriate, 1–8 cells	1–2 seriate, alternate	present	1–4
A. pannonicum (Greguss) Barale *et al.*	Hungary	……..	……..	……..	araucarioid	……..	
A. ultimus Iamandei & Iamandei	Romania	indistinct	absent	1 seriate, 1–23 cells	1–2 seriate, contiguous	absent	1–7
A. nepalense (Barale *et al.*) Paudayal *et al.*	Nepal	indistinct	absent	1 seriate, 1–8 cells	1–[2] seriate, alternate, contiguous		1–5
A. togeumense Oh *et al.*	Korea	distinct	absent	1 seriate, 1–19 (2–5) cells	2–3–[4] seriate, alternate	present	4–22 (8–18)
A. kiiense (Ogura) Oh *et al.*	Korea	indistinct	absent	1 seriate, 1–19 (4) cells	1– 2–[3] seriate, alternate	absent	4–10 (6–9)
A. byeongpungense (Kim *et al.*) Oh *et al.*	Korea	indistinct	absent	1 seriate, 2–20 (8) cells	1– 2–[3] seriate, alternate contiguous	absent	7–15
D. (*A.*) *franconicum* Vogellehner		indistinct	absent	1 seriate, 1–40 (2–12) cells	1–4 seriate, alternate	……..	3–10
D. (*A.*) *japonicum* Shimakura	Japan	indistinct	absent	1 seriate, 1–24 (3–10) cells	1–3 seriate, opposite	present	5–14
D. (*A.*) *tankoense* Stopes & Fujii)	Japan	indistinct	absent	1 seriate, 1–15 cells	2–4 seriate, alternate	present	4–8
A. mineense Ogura	Japan	distinct	absent	1–[2] seriate, 1–29 (3–14) cells	1–2 seriate	……..	1–2
A. sidugawaense Shimakura	Japan	distinct	present	1 seriate, 1–14 (3–10) cells	1–2 seriate	present	1–3
A. chosiense Shimakura	Japan	indistinct	present	1 seriate, 1–3 cells	1–[2] seriate	present	1–4
A. biseriatum Nishida *et al.*	Japan	indistinct	absent	1–[2] seriate, 6–42 (2–10) cells	1–3 seriate	……..	2–3
A. jeholense Ogura	Japan	indistinct	absent	1 seriate, 10–20 cells	1–[2] seriate	……..	2
A. inuboense Nishida	Japan	indistinct	absent	1 seriate, 1–8 cells	1–2 seriate	……..	2–4 (3)
A. pseudochoshiense Nishida	Japan	indistinct	absent	1 seriate, 1–8 (2–3) cells	1 seriate	……..	2–5
A. laosense (Vosenin-Serra) Boura *et al.*	Vietnam	indistinct	absent	1–[2] seriate, 1–28 (2–15) cells	1–2 seriate, alternate	absent	3–8
Agathoxylon sp. A Ottone & Medina	Antarctica	distinct	absent	1–2 seriate, 1–25 (9) cells	1–2 seriate, araucaroid	absent	1–4
Agathoxylon sp. Falcon Lang & Cantrill	Antarctica	distinct	absent	1 seriate, 1–11 cells	1–2 seriate, alternate	absent	1–4
Agathoxylon sp. Torres	Antarctica	indistinct	absent	1 seriate, 2–10 cells	1–2 seriate, alternate	absent	2–3
Agathoxylon sp. Kustatscher *et al.*	Italy	indistinct	absent	1 seriate, 1–18 (1–7) cells	1–2 seriate, alternate	absent	2–5
Agathoxylon sp. Vera & Césari	Argentina	indistinct	present	1 seriate, 1–18 (6) cells	1–[2] seriate, alternate	absent	1–6 (3)
Agathoxylon sp. Pujana *et al.*	Argentina	distinct	absent	1 seriate, 1–5–[8] cells	1–[2] seriate, alternate, contiguous	absent	3–5
Agathoxylon sp. Philippe *et al.*	Argentina	distinct	absent	1 seriate, 1–15 cells	1–2 seriate	present	2–9
Agathoxylon sp. Nishida *et al.*	Chile	indistinct	……..	1 seriate, 2–11 cells	1–2 seriate	present	2–4
Agathoxylon sp. Esteban *et al.*	Iberian Peninsula	indistinct		1–[2] seriate, 1–12 cells	1–2 seriate, contiguous	present	1–2
Agathoxylon sp. Barale *et al.*	Lebanon	……..	present	……..	1 seriate	……..	8–10
MESOZOIC							
Araucaria araucana (Mol) C. Koch	Argentina	distinct	absent	1 seriate, 5–10 cells	1–2 seriate, alternate-sub-opposite	absent	2–4

Table 3 cont.

Age and Taxa name	Country	Growth rings	Axial Parenchyma	Xylem rays	Radial wall pits	Tangential wall pits	Crossfield Pits
Araucaria angustifolia (Bertol) Kuntze	Argentina	distinct	rare	1 seriate, 1–19 cells	2–[3] seriate, alternate	absent	1–12 (2–5)
A. colaniae Serra	Vietnam	indistinct	absent	1–[2] seriate, 1–13 (3–7) cells	1–2 seriate, opposite	absent	2–8 (4–6)
A. trungphanense (Vosenin-Serra1981) Boura *et al.*	Vietnam	absent	absent	1–[2] seriate, 1–39	1, rarely 2–3 seriate opposite	absent	1–7
A. huzinamiense Ogura	Japan	indistinct	absent	1–[2] seriate, 4–13 cells	2–3 seriate	……..	1
D. (*A.*) *orbiculatum* Vogellehner	Ethiopia	indistinct	absent	1 seriate, 1–27 (7–9) cells	1–4 seriate, alternate	……..	2–5
A. jimoense Zhang & Wang	China	distinct	absent	1 seriate, 2–25 (9) cells	1–[2] seriate, alternate	absent	3–18
D. (*A.*) *biradiatum* Vogellehner	Ethiopia	……..	……..	1 seriate, 1–53 (12–16) cells	1–4 seriate, alternate	……..	1–3
D. (*A.*) *mugherensis* Lemoigne & Beauchamp	Ethiopia	distinct	……..	1–3 seriate, 1–10 cells	1–[2] seriate, opposite	……..	6–16

Rajanikanth (2018) from the Early Cretaceous sediments of the Rajmahal Formation which differ primarily in the presence of an axial parenchyma and a lesser number of crossfield pits. The species newly described here also shows some similarities with *A. rajmahalense* (Sahni) Bose & Maheshwari *sensu* Chinnappa and Rajanikanth (2018) from the Early Cretaceous sediments of Rajmahal Formation differing only in the greater abundance of triseriate tracheid pitting in *A. rajmahalense*.

FLORAL COMPOSITION AND DIVERSITY

The Kota flora is preserved as woods, leaves and as spores- and pollen (Rao, Shah, 1963; Mahabale, 1967; Shah *et al.*, 1973; Biradar, Mahabale, 1978; Prabhakar, 1989; Sukh Dev, Rajanikanth, 1988; Rajanikanth, Sukh Dev, 1989; Vijaya, Prasad, 2001; Chinnappa, Rajanikanth, 2016). The leaves are comparatively less abundant. An analysis of the whole available data such as spore-and pollen, leaves and wood shows that the flora is composed of Pteridophytes and Gymnosperms (Tabs 4, 5). It resembles the flora from the Early Cretaceous Rajmahal and Gangapur formations in its composition. The leaf fossils reflect the preponderance of gymnosperms (44%) over pteridophytes (23%) (Fig. 2). The pteridophytes include *Cladophlebis* Brongniart, *Coniopteris* Brongniart, *Equisetum* Linnaeus, *Hausmannia* Dunker and *Sphenopteris* Sternberg (Rao, Shah, 1963; Shah *et al.*, 1973; Rajanikanth, Sukh Dev, 1989). The members of the gymnosperms are represented by bennettitaleans such as *Podozamites* (Brongniart) Braun, *Pterophyllum* Brongniart and *Ptilophyllum* Morris, the ginkgoleans include *Ginkgo* Linnaeus and the coniferaleans are constituted of *Araucarites* Presl, *Brachyphyllum* (Lindley & Hutton) Brongniart, *Ela-*

Table 4

List of the macro-floral elements known from the Kota Formation

Pteridophytes	Ginkgoales	Wood fossils (Coniferales)
Cladophlebis denticulata (Brongniart) Fontaine emend. Harris *C. indica* (Oldham & Morris) Sahni & Rao *C. reversa* Feistmantel *Cladophlebis* sp. *Coniopteris hymenophylloides* (Brongniart) Seward *Coniopteris* sp. *Equisetum rajmahalensis* (Oldham & Morris) Schimper *Hausmannia* cf. *buchii* Andreae *Sphenopteris* sp. **Bennettitales** *Podozamites* sp. *P. fissum* (Morris) Bose & Banerji *Ptilophyllum acutifolium* (Morris) Bose & Kasat *P. cutchense* (Morris) Bose & Kasat *Ptilophyllum* sp.	*Gingoites lobata* (Feistmantel) Seward **Coniferales** *Araucarites cuchensis* Feistmantel *Araucarites* sp. *Brachyphyllum* sp. *Elatocladus conferta* (Oldham & Morris) Halle *E. jabalpurensis* (Feistmantel) Seward *E. plana* (Feistmantel) Seward *Elatocladus* sp. *Pagiophyllum peregrinum* (Lindley & Hotton) Sahni *Pagiophyllum* sp. *Pagiophyllum* sp. cf. *peregrinum* (Lindley & Hotton) Sahni	*Agathoxylon kotaense* Chinnappa & Rajanikanth *A. pranhitaensis* (Rajanikanth & Sukh-Dev) Chinnappa & Rajanikanth *A. santalense* (Sah & Jain) Bose & Maheshwari *sensu* Chinnappa & Rajanikanth *Agathoxylon* sp. *Cupressinoxylon kotaense* Rajanikanth & Sukh-Dev *Ginkgoxylon dixii* Biradhar & Mahabale *P. chandrapurense* Rajanikanth & Sukh-Dev *P. krauselii* Rajanikanth & Sukh-Dev *P. rajmahalense* (Jain) Bose & Maheshwari *Podocarpoxylon* sp. *Prototaxoxylon liassicum* Muralidhar Rao *Taxaceoxylon sahnii* Rajanikanth & Sukh-Dev *Taxaceoxylon* sp.

Table 5

List of the micro-floral elements known from the Kota Formation

Bryophytes

Aequitriradites sp.
Cooksonites rajmahalensis Tripathi *et al*.
C. variabillis Pocock
Coptospora kutchensis Venkatachala
C. microgranulosa Venkatachala & Sharma
C. verrucosa Tripathi *et al*.
Foraminisporis tribulosus Playford & Dettmann
Triporoletes simplex (Cookson & Dettmann) Playford

Pteridophytes

Baculatisporites comaumensis (Cookson) Potonie
Biformaesporites baculosus Singh & Kumar
Ceratosporites equalis Cookson & Dettmann
cf. *Appendicisporites* sp.
cf. *Crybelosporites stylosus*
cf. *Dictyotosporites complex* Cookson & Dettmann
cf. *Kraeuselisporites linearis* (Cookson & Dettmann) Dettmann
Cicatricosisporites hughesii Dettmann
C. ludbrookii Dettmann
C. clavus (Balme) Dettmann
Concavissimisporites kutchensis Venkatachala
C. penolaensis Dettmann
C. subverrucosus Venkatachala
Contignisporites cooksoniae (Balme) Dettmann
C. multimuratus Dettmann
Crybelosporites punctatus Dettmann
Densoisporites mesozoicus Singh *et al*.
D. velatus (Weyland & Kreiger) Krasnova
D. harrisii Couper
Duplicisporites problematicus (Couper) Playford & Dettmann
Foveosporites canalis Balme
Impardecispora apiverrucata (Couper) Venkatachala *et al*.
I. indica Venkatachala
Ischyosporites crateris Balme
I. marburgensis de Jersey
Klukisporites venkatachalae Tripathi *et al*.
Leptolepidites major Couper
L. verrucatus Couper
Lycopodiacidites asperatus Dettmann
L. dettmannae Burger
Matonisporites phlebopteroides Couper
Microfoveolatosporites atbertonensis Cookson
Murospora florida (Balme) Pocock
Osmundacidites singhii Ramanujam & Srisailam
Regulatisporites sp.
Triletes tuberculiformis Cookson
Trilobosporites purverulentus (Verbitskaya) Dettmann

Gymnosperms

Araucariacites australis Cookson
A. cooksonii Singh *et al*.
A. ghuneriensis Singh *et al*.
Callialasporites dampieri (Balme) Sukh-Dev
C. segmentatus (Balme) Sukh-Dev
C. triletus Singh *et al*.
C. trillobatus (Balme) Sukh-Dev
C. turbatus (Balme) Schulz
Classopollis classoides Pocock & Jansonius
Microcachryidites antarcticus Cookson
M. mesozoica Pocock
Podocarpidites ornatus Pocock
P. tripakshii Rao

tocladus Halle and *Pagiophyllum* Heer (Rao, Shah, 1963; Shah *et al*., 1973; Rajanikanth, Sukh Dev, 1989) (Tab. 4).

Contrary to the macro-flora, the micro-flora exhibits the predominance of pteridophytes over the gymnosperms in terms of taxonomic diversity (Fig. 3). Nevertheless, in terms of abundance, the micro-flora is dominated by the *Araucariacites* and *Callialasporites* of Araucariaceae and Podocarpaceae respectively (Prabhakar, 1989; Vijaya, Prasad, 2001). These results also suggest a gymnosperm dominated flora. The peculiarity of the micro-flora is the occurrence of spores belonging to bryophytes such as *Aequitriradites*, *Cooksonites*, *Foraminisporis* and *Triporoletes* which have not been reported in the macro-floral record (Tab. 5).

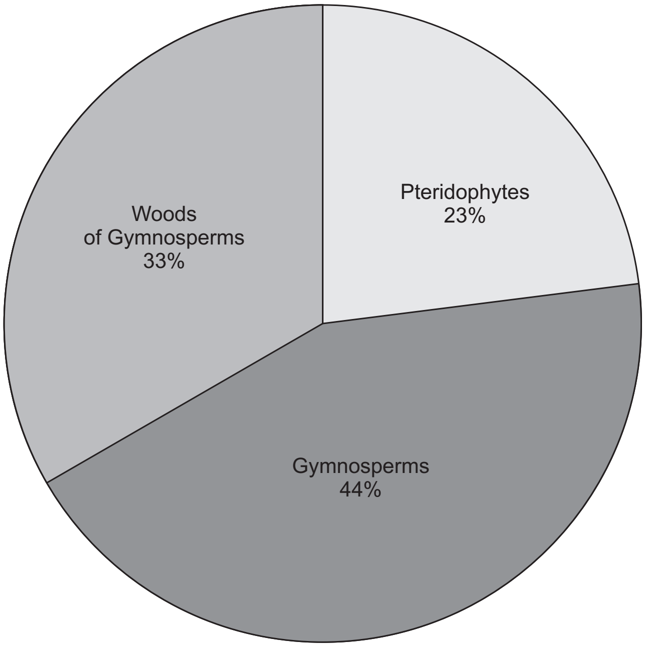

Fig. 2. Macro-floral diversity pattern of various taxonomic groups in the Kota-flora

The large sized fossil trunks of conifer affinity suggest that the flora is composed of woody vegetation. The fossil woods include the members of Araucariaceae (*Araucarioxylon*), Podocarpaceae (*Circoporoxylon* and *Podocarpoxylon*), Ginkgoaceae (*Ginkgoxylon*), Cuppressaceae (*Cupressinoxylon*) and Taxaceae (*Taxaceoxylon*) (Mahabale, 1967; Biradar, Mahabale, 1978; Rajanikanth, Sukh Dev, 1989; Chinnappa, Rajanikanth, 2016) (Tab. 4). Among these groups, the Araucariaceae and the Podocarpaceae are more abundant and taxonomically diversified and our results are in congruence with the reported leaf fossils and with the pollen and spores.

PALAEOECOLOGY

The fossil wood described here is characterised by the absence of distinct growth rings (D or E of Brison *et al*., 2001), which is feature of trees growing in non-seasonal

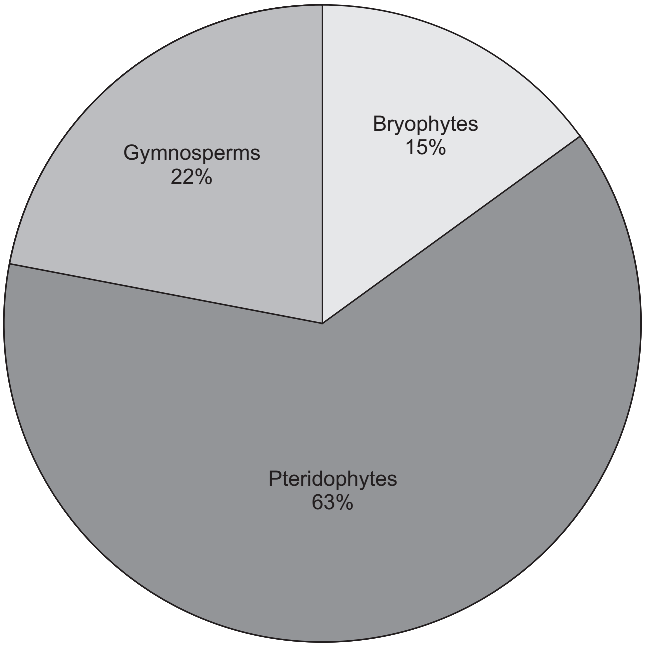

Fig. 3. Micro-floral diversity pattern of various taxonomic groups in the Kota-flora

conditions (Fritts, 1976; Creber, Chaloner, 1985; Francis, Poole, 2002; Yang *et al*., 2013). However, it is important to note that in spite of the wide latitudinal distribution of the genus *Agathoxylon*, this taxon never displays rings of the (A, B, C of Brison *et al*., 2001) super-type, even when other woods from the same locality do (Brison *et al*., 2001). Similar trends can also be evidenced in the living Araucariaceae with *Agathoxylon* (*Araucarioxylon*)-type wood. This wood type also never displays the A, B, or C types (Seitz, Kanninen, 1989), even when growing in clearly seasonal climates (Creber, Chaloner, 1985). The other fossil woods reported from the Kota Formation show growth rings (Chinnappa, Rajanikanth, 2018). However, these growth rings differ from the rings of temperate woods such as *Pinus sylvestris*; they have much more subtle, discontinuous ring boundaries defined only by very few (3–5) late wood cells, and possess ring increments of extremely narrow and irregular width (type D of Brison *et al*., 2001).

When considered as a whole the woods of the Kota Formation with their low percentage of latewood without thickening of the tracheidal walls, and the gradual transition of early-latewood suggest accentuated growing periods (Francis, Poole, 2002; Pires *et al*., 2011). These woods with interrupted growth rings indicate fluctuations in growing conditions over several growth periods. The false growth rings, which are common in most specimens, could reflect the palaeoclimatic and palaeoecological constrains (Pires *et al*., 2011). Although the false rings could be equally formed by the attack of bugs or floods, the former possibility can be suppressed based on the patterns of ring structure and the sedimentological factors. Therefore, severe droughts could be the controlling factor. Other plant fossils such as the abundant conifer leaves and pollen also present similar climatic inferences (Chinnappa, Rajanikanth, 2018). The resource constraints and the microenvironmental factors influenced the genesis of erratic growth rings as evidenced by the occurence of growth interruptions (Rajanikanth, Tewari, 2004; Chinnappa, Rajanikanth, 2016). The growth ring parameters suggest that the growth conditions were seasonal, but mostly stressed, and in some periods they induced an erratic full stoppage (Francis, Poole, 2002). These growth rings show closest similarity to the growth rings of modern tropical to subtropical conifers growing in the southern hemisphere.

The leaf fossil assemblage is characterized by the presence of conifers such as *Araucarites*, *Brachyphyllum*, *Pagiophyllum* and *Elatocladus*. These taxa with thick and leathery leaves also indicate that the plants were growing in subtropical environments with seasonal drought (Rajanikanth, Sukh-Dev, 1989). The palaeogeographic reconstruction of the Indian subcontinent during these time intervals is within the southern Subtropical Arid Belt (30–32°S), while the climatic conditions were very warm and dry (Chatterjee *et al*., 2013). Wood from warm subtropical climates usually shows weakly defined growth rings and growth interruptions, that cannot be traced, and the occurence of cupressoid conifers indicates a seasonally dry ecotone (Peralta-Medina, Falcon-Lang, 2012). These results are concurrent with the broad subtropical belt that existed in the Jurassic-Cretaceous interval (Chatterjee *et al*., 2013).

Acknowledgements. This work is undertaken as part of DST-NPDF project-2016/001442. One of the authors, Chinnappa Chopparapu thanks Department of Science and Technology for the financial support. The authors are thankful to R.C. Mehrotra, Director in charge of the Birbal Sahni Institute of Palaeosciences, Lucknow, India, for the encouragement and provision of infrastructural facilities. M. Philippe, Claude Bernard University Lyon, France, and Changhwan Oh, Chonbuk National University are greatly acknowledged for their constant support and encouragement. We are indeed greatly thankful to Mihai Emilian Popa, University of Bucharest, Romania and an anonymous reviewer for their constructive suggestions.

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PLATE 1

Agathoxylon kotaense n. sp., BSIP 16274

Fig. 1, 2. Transverse section showing indistinct growth ring and tracheid cells

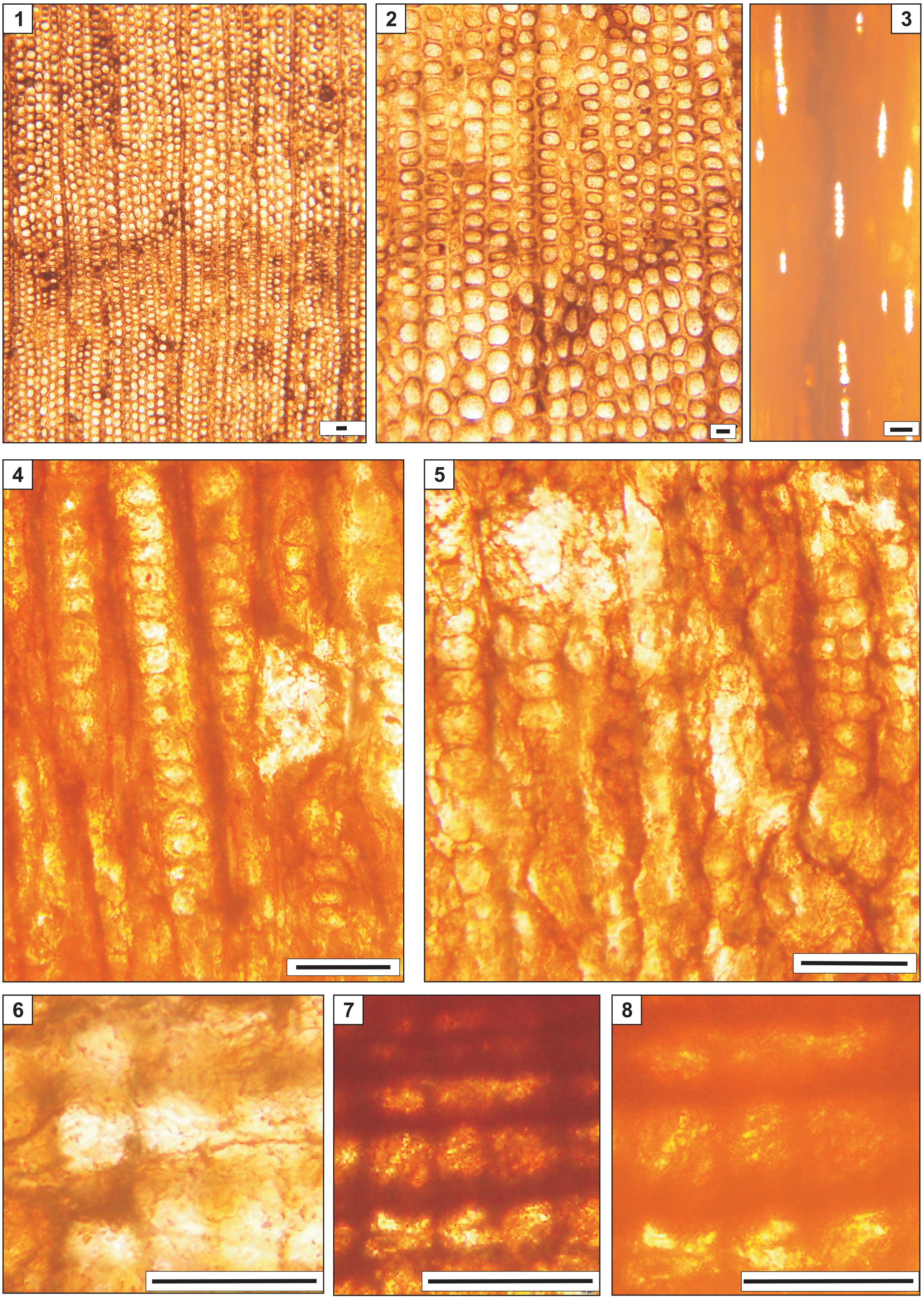
Fig. 3. Tangential section showing uniseriate ray cells

Fig. 4. Radial section showing uniseriate bordered pits

Fig. 5. Radial section showing biseriate bordered pits arranged in sub-oppositely

Fig. 6–8. Crossfield area with group of araucarioid pits

Scale bar 50 µm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