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Research paper

Fossil woods from the late middle Eocene Pondaung Formation, Myanmar

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ABSTRACT

Twelve species of fossil wood were identified from silicified specimens collected in the late middle Eocene Pondaung Formation, Myanmar. These species display affinities with modern Fabaceae, Moraceae, Combretaceae, Sapindaceae, Malvaceae, Dipterocarpaceae and Theaceae. They include five new species of the fossil genera *Ficoxylon* (*F. mogaungense* sp. nov.), *Sapindoxylon* (*S. burmense* sp. nov.), *Bombacoxylon* (*B. pondaungense* sp. nov.), *Shoreoxylon* (*S. panganense* sp. nov.) and *Schimoxylon* (*S. benderi* sp. nov.). This material represents the oldest record of fossil dipterocarps so far reported outside the Indian subcontinent. It reflects different ecotones of a dry dipterocarp forest, with coastal, riparian, and inland elements. The Burmese fossil assemblage further contrasts with the common idea that lowland rainforests were widespread in Southeast Asia during the Eocene. It suggests that the climate in the proto-Bengal Bay was more seasonal than previously thought. This confirms that early Dipterocarpaceae were adapted to seasonally dry climates, despite the modern prevalence of warm humid tropical species.

1. Introduction

The Cenozoic deposits of Myanmar have yielded an impressive amount of fossil land mammals and silicified wood (see eg. Theobald, 1873; Noetling, 1895; Pilgrim and Cotter, 1916; Chhibber, 1934; Bender, 1983; Gottwald, 1994; Jaeger et al., 1999; Privé-Gill et al., 2004; Beard et al., 2005; Chavasseau et al., 2010). Palaeobotanical studies have almost exclusively focused on the well-exposed Miocene–Pliocene Pegu and Irrawaddy deposits of the Central Myanmar Basin. Numerous fossil remains attributed to modern Araucariaceae, Anacardiaceae, Dipterocarpaceae, Fabaceae, Lythraceae, Lecythidaceae, Barringtoniaceae, Bombacaceae, Guttiferae, Sapindaceae, Sonneratiaceae, Sterculiaceae, Tetramelaceae, and Tiliaceae were recognized, suggesting the long-term persistence of seasonal, mixed-evergreen forests during the Neogene in Myanmar (Prakash, 1965, 1971; Prakash and Bande, 1980; Gottwald, 1994). Studies of older deposits are limited to the work of Privé-Gill et al. (2004) who identified two fossil species in the late middle Eocene Pondaung Formation, *Sonneratioxylon caseolarioides* Shete et Kulkarni and *Cynometroxylon holdenii* (Gupta) Prakash et Bande, typical of coastal, fluvial–deltaic swampy forests.

Recent discoveries of fossil primates in the Pondaung Formation have fueled interest in the Eocene Burmese deposits (Jaeger et al., 1999; Beard et al., 2009; Chaimanee et al., 2012). Indeed, the sites of the Pondaung Formation have yielded an abundant primate community, including anthropoids and adapiforms which are found in most fossiliferous localities (Ramdarshan et al., 2010). Achieving tighter constraints on the palaeoflora of these sites is a critical challenge, because it may highlight the environmental conditions that led to the first adaptive shifts of the primate evolutionary history. This paper gives an insight into the forested late middle Eocene environments in central Myanmar through the description and identification of twelve fossil wood taxa from the Pondaung Formation, collected during the last decade.

2. Palaeoenvironmental context

The Pondaung Formation is a thick continental sequence in the Central Myanmar Basin that can locally reach a thickness of more than 2000 m (Bender, 1983; Pivnik et al., 1998). Its upper member (upper 500 m of the section) comprises fossiliferous sandstones and alluvial mudstones characterized by a high density of palaeosols (Licht et al., 2014). It has yielded a large and diverse late middle Eocene (Bartonian) fossil fauna, including primates, creodontes, carnivorans, rodents, artiodactyles and perissodactyles (Tsubamoto et al., 2005). The palaeogeographical reconstructions by Morley (2009) and Hall (2012) proposed that central

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Myanmar occupied during the middle Eocene a position similar to that of today. At that time, the Indo-Burman Ranges, which now separate central Myanmar from the Bengal Bay, had not emerged (Allen et al., 2008). The sedimentological study of the Pondaung Formation by Aung Naing Soe et al. 2002 distinguished large channel deposits, deltaic sequences, and finer-grained overbank deposits indicating a fluvial–deltaic environment opened towards the proto-Bengal Bay. Additional palaeoenvironmental information is scarce. Pondaung faunal assemblages and dietary studies are in agreement with a forested environment (Kay et al., 2004; Head et al., 2005; Tsubamoto et al., 2005; Ramdarshan et al., 2010). Ramdarshan et al. (2010) noted the absence of folivore species in the Pondaung primate fauna and suggested an environment similar to those of South American seasonal tropical forests, where young leaves emerge at the same time as fruits mature and constitute a secondary food source for primates. Growth arrest lines in mammalian fossil lower jaws indicate a seasonal, water-stressed climate (Jaeger et al., 2004). Palaeosols with carbonate nodules together with shrinking and swelling pedogenic features corroborate this observation, and are incompatible with the presence of dense ever-wet rainforests in the Pondaung floodplain (Licht et al., 2014).

3. Materials and methods

Seventy specimens of fossil wood from the upper member of the Pondaung Formation were collected in the Bahin and Mogaung townships, Magway district, Myanmar, during the 2001, 2002, and 2012 field trips of the French-Myanmar Paleontological Expedition (see Fig. 1 for localities). Specimens were found in-situ in channel lag deposits (Licht et al., 2014), or collected on the ground together with vertebrate remains. All samples are completely silicified. Sections of transverse, radial and tangential surfaces of the fossil woods were prepared following the standard techniques (Hass and Rowe, 1999) at the Muséum national d'Histoire naturelle (MNHN), Paris, France, and described following the IAWA Hardwood List (IAWA committee, 1989). Botanical affinities were determined using the Insidewood database (2004–2013) and literature on fossil and extant Asian woods (e.g., Metcalfe and Chalk, 1950; Brazier and Franklin, 1961; Gamble, 1972; Ilic, 1991; Gregory et al., 2009 and references therein). All microscopic slides, including one transverse, one longitudinal radial and one longitudinal tangential section per specimen (called L1/3, L2/3 and L3/3 respectively) and remains of the original specimens are deposited in the collection of the MNHN under the numbers MNHN.F.40098 to MNHN.F.40133.

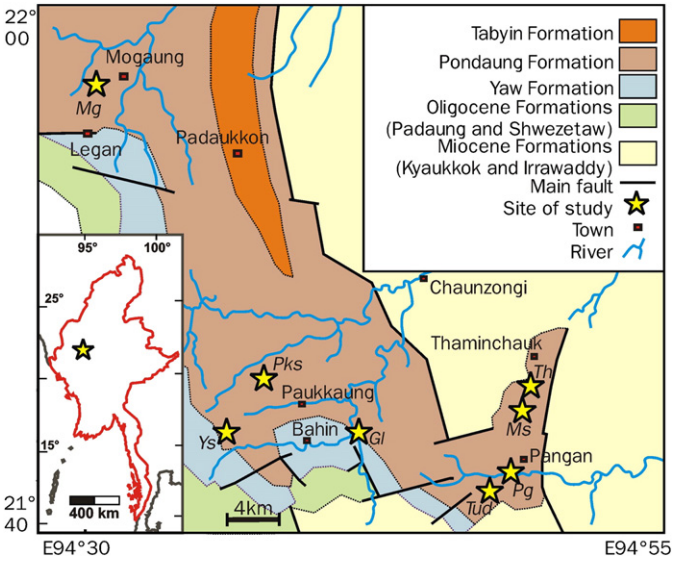

Fig. 1. Simplified geological map of the studied area (modified from Aung Naing Soe et al. 2002). The different localities are shown: Gl (Ganleh, N21°44′03.0″ E094°43′26.3″), Ms (Myong Se, N21°44′04.0″ E094°50′10.4″), Pg (Pangan, N21°42′31.0″ E094°49′21.6″), Pks (the PK1, 2, 3, 4 and 5 localities, N21°45′25.9″ E094°38′27.1″), Th (Thaminchauk, N21°45′41.0″ E094°50′29.4″), Tud (Than U Daw, N21°41′07.4″ E094°48′37.5″), Ys (Yarshe, N21°44′12.5″ E094°38′15.3″) and Mg (Mogaung, N21°54′40.0″ E094°32′30.0″).

4. Results

Thirty-nine out of the seventy fossil wood samples were well preserved. Twelve species belonging to nine fossil genera were identified.

4.1. Fabaceae (Caesalpinioideae subfamily)

4.1.1. *Acrocarpoxylon siwalicus* Yadav, 1988

Specimen: MNHN.F.40109 (field number: TUDA; Than U Daw locality; Plate I, 1–3)

Description: Wood diffuse-porous with faint growth rings, marked by smaller fibres and marginal bands of axial parenchyma. Vessels solitary (30–60%) or in short radial multiples of 2 to 6 (Plate I, 1), 2–4 per mm^2, round to oval; tangential diameter 70–180 μm (average 145 μm); vessel elements 160–530 μm (average 390 μm) long. Simple perforation plates. Intervessel pits alternate, of rounded shape, 5 to 9 μm in diameter. Slightly larger vessel-ray pits (6 to 10 μm), polygonal or elongated. Fibres libriform, thin-walled, nonseptate, 4–10 μm wide. Rays equally 3- and 4-seriate (Plate I, 2); 7–9 rays per tangential mm, 150–500 μm high (average 350 μm); rays exclusively heterocellular, composed of procumbent cells, with 1–2 (sometimes up to 6) rows of upright marginal cells (Plate I, 3). Axial parenchyma paratracheal aliform confluent. Apotracheal parenchyma rare, diffuse, and also occurring as 2- to 6-seriate, tangential continuous marginal bands associated with growth ring boundaries. Parenchyma cells 80–200 μm high, 10–25 μm wide. Rhombic crystals abundant in the axial parenchyma, in crystalliferous strands (2–12 cells per strand).

Discussion: This fossil is characterized in having (1) diffuse-porous wood consisting of medium-sized vessels, solitary or in short radial multiples, (2) exclusively simple perforation plates, (3) paratracheal aliform confluent parenchyma, (4) diffuse apotracheal parenchyma, also forming rare 1- to 3-seriate continuous marginal bands, and (5) heterocellular, 3- to 4-seriate rays. These diagnostic features indicate affinities with modern Leguminosae woods, and closely resemble those of *Acrocarpoxylon siwalicus* Yadav from the Miocene of Assam (Yadav, 1988). The diagnosis of *A. siwalicus* by Yadav (1988) mentions a significantly higher density of vessels (12–14 per mm^2) that is inconsistent with the vessel density seen on the transverse sections figured in the same paper (2–4 vessels per mm^2). Comparisons of our material with the pictures of Yadav led us to attribute our specimen to the fossil species *A. siwalicus*; the diagnosis of the species thus should be emended in regard to the vessel density after a careful re-examination of the original thin sections. *A. siwalicus* shows strong similarities with the modern wood species *Acrocarpus fraxinifolius* Wight et Arnott (Yadav, 1988). *A. fraxinifolius* is a common deciduous tree in the semi-evergreen and moist deciduous tropical forests of Southeast Asia (Gamble, 1972). The presence of continuous, 2–6 marginal bands of parenchyma associated with growth ring boundaries in modern *A. fraxinifolius* indicates marked seasonality, and is suggestive of moist deciduous rather than semi-evergreen forests (De Franceschi et al., 2011).

4.1.2. *Acrocarpoxylon ungeri* Gottwald, 1994

Specimens: MNHN.F.40119 (field number: T10; Thaminchauk locality; Plate I, 4–6), MNHN.F.40121 (field number: PA1; Pangan locality)

Description: Wood diffuse-porous with faint growth rings marked by marginal bands of apotracheal parenchyma. Vessels solitary (30–60%) or in short radial multiples of 2–3 (Plate I, 4), 2–5 per mm^2 (average 4 per mm^2), round to oval; tangential diameter 75–200 μm (average 175 μm); vessel elements 40–490 μm (average