DOI: 10.1590/2317-4889201720160085

ARTICLE

# First record of Annonaceae wood for the Neogene of South America, Amazon Basin, Brazil

## *Primeiro registro de madeira de Annonaceae para o Neógeno da América do Sul, Bacia do Amazonas, Brasil*

**Emilio Alberto Amaral Soares[1], Adriana Cabral Kloster[2]*, Silvia Cristina Gnaedinger[2], Silvio Roberto Riker[3], Felipe José da Cruz Lima[3], Marcelo Batista Motta[3]**

**ABSTRACT:** The relief of the regions of Manaus and Itacoatiara, Central Amazon, is supported by Neogene siliciclastic rocks, bounded at the base and top by lateritic paleosols and covered by quaternary sedimentary deposits from the Solimões-Amazon river system. This unit is informally assigned to the Novo Remanso Formation, consists of usually reddish and ferruginized sandstones, conglomerates and pelites, with few identified fossil records, a fact that has hindered its stratigraphic position, and the paleoenvironmental reconstruction of the last phase of the Amazon Basin settling. This study describes, for the first time, the occurrence of fossil wood in outcroppings of the left bank of the Amazon River, where anatomical and morphological data has enabled its characterization to the species level. Thus, the data marks the record of the Annonaceae in South America, as well as the depositional processes related to incorporation of organic material in the sandy layer and the fossilization processes that allowed its preservation. In an unprecedented way, this study has described *Duguetiaxylon amazonicum nov. gen* and *sp*. and provided information on the anatomical and systematic character, as well as data on plant-insect interaction, and a better understanding of the family.

**KEYWORDS:** Annonaceae; *Duguetiaxylon*; Neogene Deposit; Amazon Basin.

**RESUMO:** *O relevo das regiões de Manaus e Itacoatiara, na Amazônia Central, é suportado por rochas siliciclásticas neogênicas, delimitadas na base e no topo por paleossolos lateríticos e cobertas por depósitos sedimentares quaternários do sistema fluvial Solimões-Amazonas. Essa unidade é informalmente atribuída à Formação Novo Remanso, constituída geralmente de arenitos avermelhados e ferruginizados, conglomerados e pelitos, com poucos registros fósseis identificados, fato que tem impedido sua posição estratigráfica e a reconstrução paleoambiental da última fase do assentamento da Bacia Amazônica. Este estudo descreve, pela primeira vez, a ocorrência de madeira fóssil em afloramentos da margem esquerda do Rio Amazonas, onde dados anatômicos e morfológicos possibilitaram sua caracterização ao nível da espécie. Assim, os dados marcam o registro de Annonaceae na América do Sul, bem como os processos deposicionais relacionados à incorporação de material orgânico na camada arenosa e os processos de fossilização que permitiram sua preservação. De modo sem precedentes, este estudo descreve Duguetiaxylon amazonicum nov. gen e sp. e fornece informações sobre as características anatômicas e sistemáticas, bem como dados sobre a interação planta-inseto e melhor compreensão da família.*

**PALAVRAS-CHAVE:** *Annonaceae; Duguetiaxylon; Depósito Neógeno; Bacia Amazônica.*

[1]Departamento de Geociências, Universidade Federal do Amazonas – UFAM, Manaus (AM), Brazil. E-mail: easoares@ufam.edu.br

[2]Centro de Ecología Aplicada del Litoral-Área de Paleontología-Consejo Nacional de Investigaciones Científicas y Técnicas (CECOAL-CONICET), Corrientes, Argentina. E-mails: klosterdri@gmail.com, scgnaed@hotmail.com

[3]Serviço Geológico do Brasil – CPRM, Manaus (AM), Brazil. E-mails: silvio.riker@cprm.gov.br, felipe.lima@cprm.gov.br, marcelo.motta@cprm.gov.br

*Corresponding author.

**Manuscript ID:** 20160085. **Received in:** 07/14/2016. **Approved in:** 01/11/2017.

## INTRODUCTION

The Amazon, Solimões and Acre sedimentary basins, respectively delimited by the structural arches of Iquitos, Purus and Gurupa, present expressive Paleogene-Neogene sedimentation. In the Solimões and Acre basins, this sedimentary record has been attributed to the Solimões Formation, which contains varied fossiliferous contents, such as mollusks (Vonhof *et al.* 1998), fishes (Richter 1984, 1989), chelonians (Bocquentin and Guilherme 1997), crocodiles (Souza Filho 1998), birds (Alvarenga and Guilherme 2003), mammals (Cozzuol *et al.* 2006), primates (Kay and Cozzuol 2006), ostracods (Ramos *et al.* 2001), palynomorphs (Latrubesse *et al.* 2007), sheets (Maury 1937) and fossil woods (Mussa *et al.* 2002; Kloster *et al.* 2013, 2015; Machado *et al.* 2012). As yet little studied, the Amazon basin's equivalent sedimentary record has been informally designated Novo Remanso Formation (Neogene), where few fossilized wood occurrences have been identified (Oliveira and Nogueira 2006, Soares 2007, Dino *et al.* 2012; Lima *et al.* 2013). However, neither systematic and/nor taphonomic study has been carried out aiming their classification and/or paleoenvironmental reconstitution.

The present study has carried out the analysis of a fossilized wood collected in the Novo Remanso Formation, on the left bank of the Amazon River, in the Amazon Basin (Fig. 1). The anatomical and morphological data of the cellular structures allowed relating the fossil sample to the Annonaceae family, thus being the first record reported in South America. The Annonaceae Juss. family is currently distributed in the Neotropics. For South America, there is an average of 40 genera and about 650 species with distribution centers in the Brazilian Amazon and Guianas (Ribeiro *et al.* 1999).

## GEOLOGICAL SETTING

The relief of the Central Amazon is supported by siliciclastic rocks from the Miocene unit — informally called Novo Remanso Formation — outcrops between the cities of Manaus and Itacoatiara. In the local stratigraphic context, this unit discordantly recovers the Cretaceous unit (Alter do Chão Formation), being delimited in the base, in the intermediate portion and on the top by lateritic paleosols and being partially covered by Quaternary fluvial deposits (Soares *et al.* 2010; Dino *et al.* 2012, Gonçalves Jr. *et al.* 2016) (Fig. 2).

The Alter do Chão Formation consists of sandstones, siltstones, mudstones and conglomerates (Caputo 1984, Soares *et al.* 2010, Dino *et al.* 2012), characteristic to a fluvial-lacustrine palaeoenvironment (Caputo *et al.* 1971; Cunha *et al.* 1994; Dino *et al.* 1999; Nogueira *et al.* 1999; Cunha *et al.* 2007, Mendes *et al.* 2012). In general, it displays silicified discontinuous-leaved variegated colors of red, yellow and white. Plant fossils are scarce in this formation, with angiosperm leaf debris standing out in sandstones of Serra da Paituna, municipality of Monte Alegre, Northwestern Pará state (Duarte 1987), in addition to fragmented, and much replaced fossilized woods, associated to paleosol levels in the vicinity of Manaus, Amazon (Vieira 1999; Nogueira *et al.* 1999; Horbe *et al.* 2006; Soares 2007), and amber — with spores and fungi included — in this Formation's voucher drillings (Dino *et al.* 1999; Pereira *et al.* 2006).

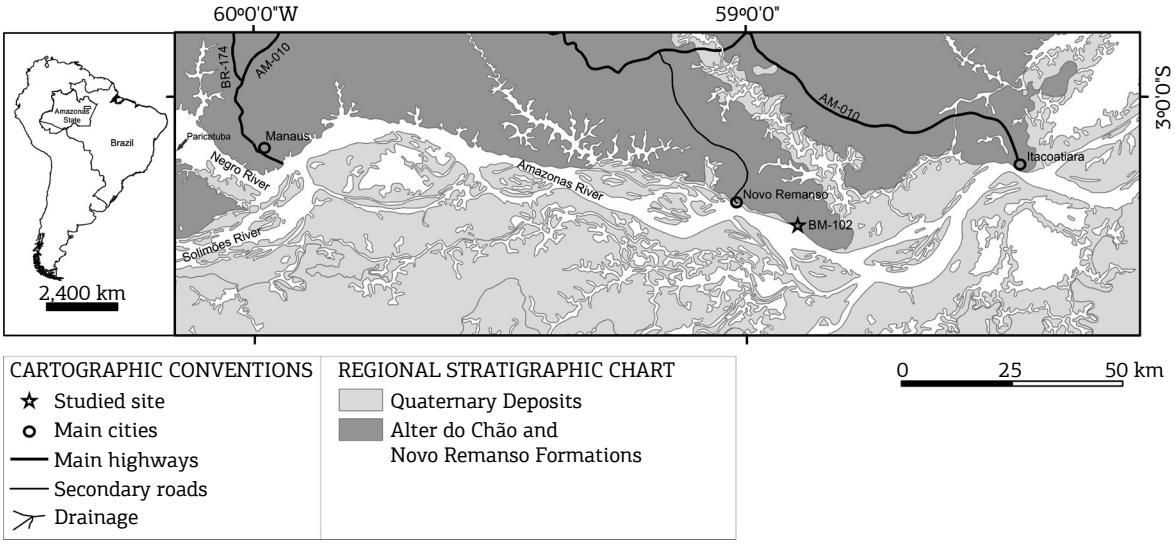


**Figure 1. Map of the location and access to the studied outcrop (Site BM-102), at the locality of Novo Remanso, on the left bank of the Amazon River (Modified from CPRM, 2006).**

Rozo *et al.* (2005) informally denominated the term Novo Remanso Formation for the essentially sandy deposits, which discordantly cover the cretaceous unit of the homonymous locality, eastward from Manaus (Amazonas). In general, this unit exhibits around 10 to 20 m outcropping thickness; it is made up of sandstones with subordinated pelites and conglomerates, characteristic to a meandering fluvial paleoenvironment, bounded in both bottom and top by discontinuity surfaces, marked by lateritic crust and/or erosive contact (Soares 2007; Dino *et al.* 2012; Soares *et al.* 2015). Locally, records of fossilized plant fragments have been cited in some regional studies of this formation outcrops on the banks of the Negro (in Paricatuba, Oliveira and Nogueira 2006), Solimões (in Manacapuru, Dino *et al.* 2012) and Amazonas (in Novo Remanso, Lima *et al.* 2013, Kloster *et al.* 2013) rivers.

Based on palinological data, the age of Alter do Chão Formation was placed at Mid-Albian/Turonian (Daemon 1975) and Aptian-Cenomanian (Dino *et al.* 1999), and Novo Remanso Formation's at Middle Miocene (Dino *et al.* 2012; Soares *et al.* 2015).

Extensive deposits of pleistocene-holocene fluvial terraces constitute the alluvial plain of the Solimões-Amazonas system, partially covering the Miocene unit in canal and plain areas (Soares *et al.* 2010; Gonçalves Jr. *et al.* 2016).

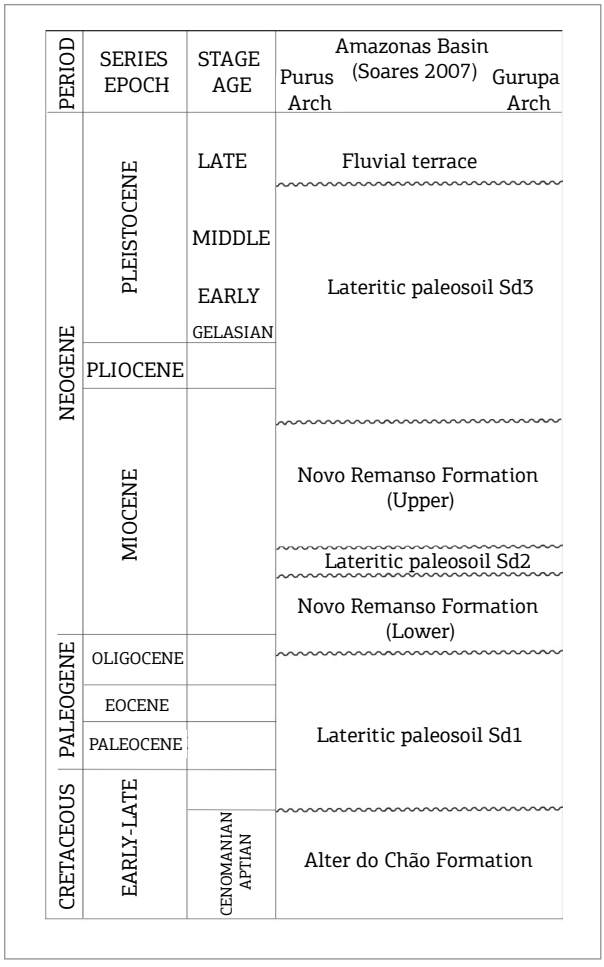


**Figure 2. Stratigraphic chart illustrating the column of Cretaceous, Paleogene and Neogene of the central portion of the Amazon Basin (Modified from Dino *et al.* 2012).**

## METHODOLOGY

The fossil wood was recovered from a Novo Remanso site (03º15'02,2"S and 58º55'49,3"W) on the Amazon River's left bank during the receding water period (September 2011 and December 2013) (Fig. 1). Litotypes, geological contacts and stratigraphic position of fossils are shown in photo mosaic and columnar section (Fig. 3).

A fragment of silicified wood with external inlays of ferruginous sandstone, showing very good cellular preservation, was analyzed. Petrographic thin sections of 30–40 µm thick were prepared from the wood fragments; three thin sections were made, orientated along three sections: transverse section (ST), tangential longitudinal section (TLS), and radial longitudinal section (RLS), at the Geological Survey of Brazil (CPRM) Lamination Laboratory (Manaus Regional Superintendence).

Wood and rock portions were pulverized and subjected to an x-ray diffraction analysis, using the PANalytical Brand, X'PERT PRO MPD (PW 3040/60) model, x-ray difractometer of the CPRM/Laboratory of mineral analysis (LAMIN) Difraction Laboratory.

The collected fossil wood sample lied at the CPRM/LAMIN Difraction Laboratory, under number BM-R-102B. These thin sections were thoroughly studied using a Leica DM500 microscope, with an attached EC2 (LM) camera, and some fragments were also observed using a Leitz M50 stereoscopic microscope. Observations were made using a Jeol5800 LV scanning electron microscope (SEM), at Universidad Nacional del Nordeste, Corrientes, Argentina.

For the various anatomical elements studied, at least 20 individual measurements were recorded, with means and minimum–maximum values determined according to Chattaway (1932). The diagnostic for Annonaceae anatomical characters were taken from Kribs (1935), Metcalfe and Chalk (1950), Détienne and Jacquet (1983), the IAWA recommendations for hardwood identification terminology (IAWA Committee, 1989), Carlquist (2001), the Inside Wood Database 2004 (Inside Wood 2004), and also from Gregorys's list (Gregory *et al.* 2009). Systematics follows the APG III (2009) classification.

## RESULTS

### Sedimentologic, stratigraphic and diagenetic data

The outcrop studied exhibits around 10 to 20 m outcropping thickness, divided into two portions in this study. The lower portion consists of whitish, reddish blended pinkish to brownish colored sandstone and pelite centimetric to metric interbedded layers, while the upper one is predominantly yellowish colored, clayey and massive, due to the intense pedogenesis (Fig. 3). It occurs discordantly on the cretaceous unit (Alter do Chão Formation), and is bounded in both bottom and top by lateritic ferruginous crusts, informally denominated here as S1 and S2 (Fig. 3). In general, crusts exhibit a massive and columnar aspect — at times seemingly fragmented —, up to 3 m thick and kilometric extension, covered by yellow latosol.

The layers of sandstones of the studied section exhibit massive aspect and/or cross-stratification with SE paleocurrent (Fig. 3, columnar section). They are mainly made up by quartz grains (monocrystalline and polycrystalline) and, more seldom, by rock fragments (sedimentary); they are fractured and exhibit weak to strong undulating extinction and corroded edges (Figs. 4A and A1). Grains are poorly sorted (fine to coarse granulometry), they range from angular to rounded, and display low to average sphericity. The grain arrangement defines an open framework, with point and floating contacts, cemented by goethite (containing amorphous portions), according to x-ray diffraction data (Figs. 4A, A1 and A2).

The basal — nearly 50 to 60 cm thick — Novo Remanso Formation's ferruginous sandstone layer, on the studied outcrop, lies discordantly on the ferruginous lateritic crust, developed from the overlying Alter do Chão Formation (Fig. 3, columnar section). There is concentration of fossilized woods in this layer, fragmented in varying sizes, arranged

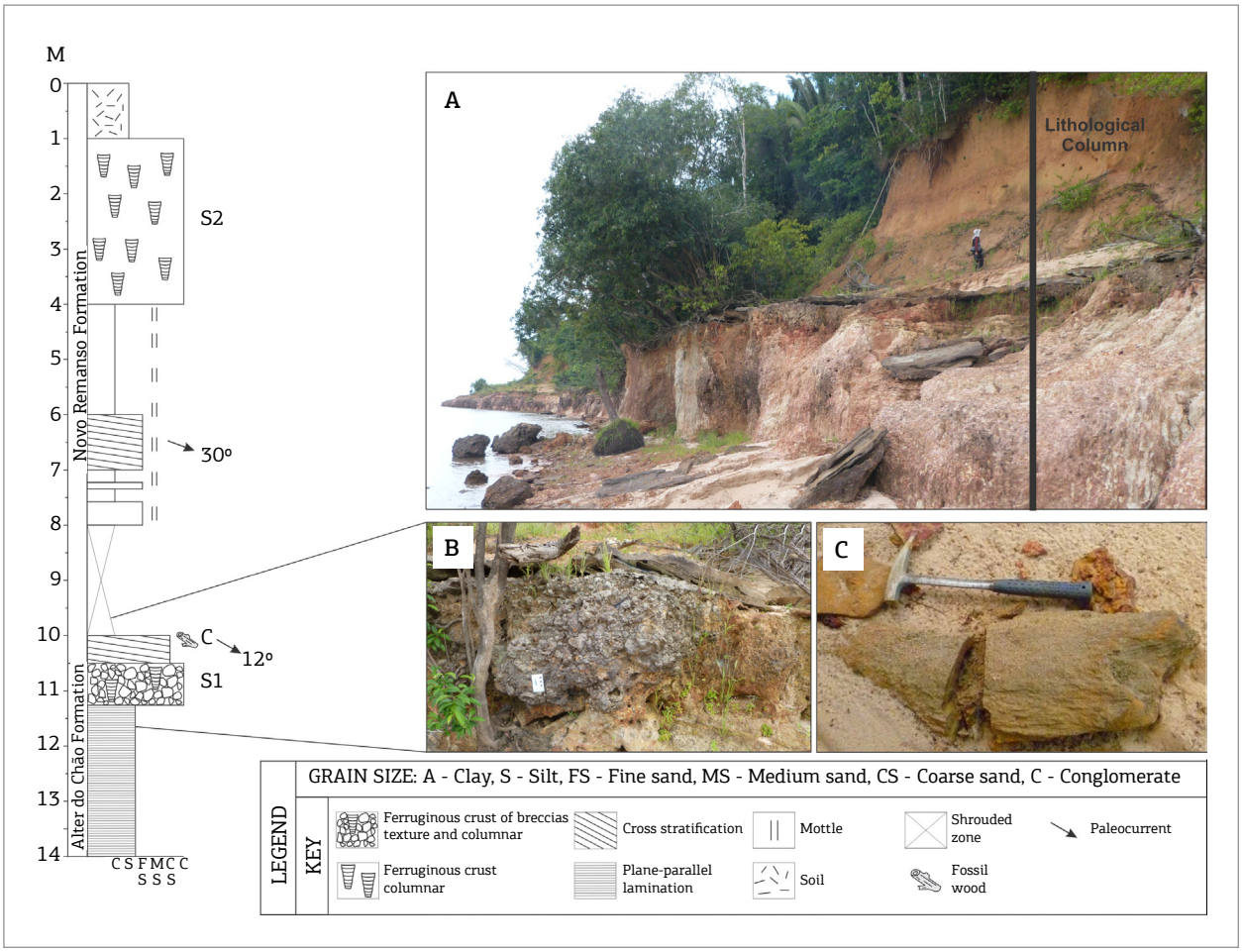


**Figure 3. (A) Panoramic and columnar view of the studied outcrop's (Point BM-102) showing a lareritic crust-marked discordant contact between cretaceous (base) and miocene (top) units. (B) Miocene unit's bottom highlighting the sandstone with fossilized remains layer overlying the lateristic crust. (C) Annonaceae fossil wood (sample BM-R-102B).**

horizontally and randomly. The wood's inner structure was replaced by goethite, according to the petrographic and diffraction data (Figs. 4B, B1 and B2).

This study only analyzed sample BM-R-102B, which is 70 cm length and is partially compressed, according to data from the elipsoidal cross-section, which exhibits up to 30 cm on its largest axis (Fig. 5A). Dispersed in the same layer, there are smaller plant fragments, up to 7 cm long and 0.3 to 0.5 cm wide, as well as two portions resembling fruits and/or seeds of rounded to ellipsoidal external contour (2.0 × 1.5 cm), which need future morphological studies for further classification (Figure 5B, B1)

## Systematic Palaeobotany

Order Magnoliales Bromhead

Family Annonaceae Jussieu

Genus ***Duguetiaxylon*** *gen. nov.*

**Type Specie** *Duguetiaxylon amazonicum sp. nov.* (this work)

**Generic Diagnosis**. Growth rings indistinct/not observed, diffuse porous, solitary and multiple vessels, numerous vessels per mm$^2$, simple perforation plates, small and alternate pits, vessel-ray pits similar to intervessel pits, simple fibers not septated, axial parenchyma apotracheal in lines, high and homogeneous tending to heterogeneous rays.

**Etymology.** *Nominis* derivations from the extant genus *Duguetia* Augustin Saint-Hilaire. Their specific epithet derivates from the Amazon region.

***Duguetiaxylon amazonicum*** *sp. nov.* (this work)

(Figs. 6 to 8)

**Holotype:** BM-R-102B

**Stratigraphic Horizon:** Novo Remanso Formation

**Specific Diagnosis:** Growth rings indistinct/not observed. Small vessels. Solitary and multiples of 2, 3 and 4 vessels. Density of 20 vessels per mm$^2$. Simple perforation plates. Vessel-ray pits, similar to intervessel ones. Intervessel pits minute, alternate. Parenchyma 1–2 seriate lines. Fibers not septated. High rays and commonly 4–10 seriate, homogeneous. Presence of oil/mucilage cells in rays.

## Description

The fossil sample presents 70 cm of length and 30 cm of diameter. Phloem is absent. Growth rings are indistinct/not observed, there are diffuse porous, vessels in diagonal/radial pattern, and solitary and multiple vessels of 2, 3 and 4 groups of vessels (Figs. 6A and 6B). Density of 20 vessels per mm$^2$, tangential diameter of vessels of 58 µm (45–115) (Figs. 7A, 8A and 8B), vessel's elements length of 144 µm (100–300), simple perforation plates (Figs. 6C and 7B), alternate and minute intervessel pits (2–4 µm) (Figs. 6C, 7B and 7C), vessel-ray pits similar to intervessel ones. Non-septate fibers with simple to minutely bordered pits (Fig. 6D). Axial apotracheal parenchyma reticulate of 1–2 cells wide, disjunctive parenchyma present as well (Figs. 6A, 6B, 6D, 7D, 7E, 8C

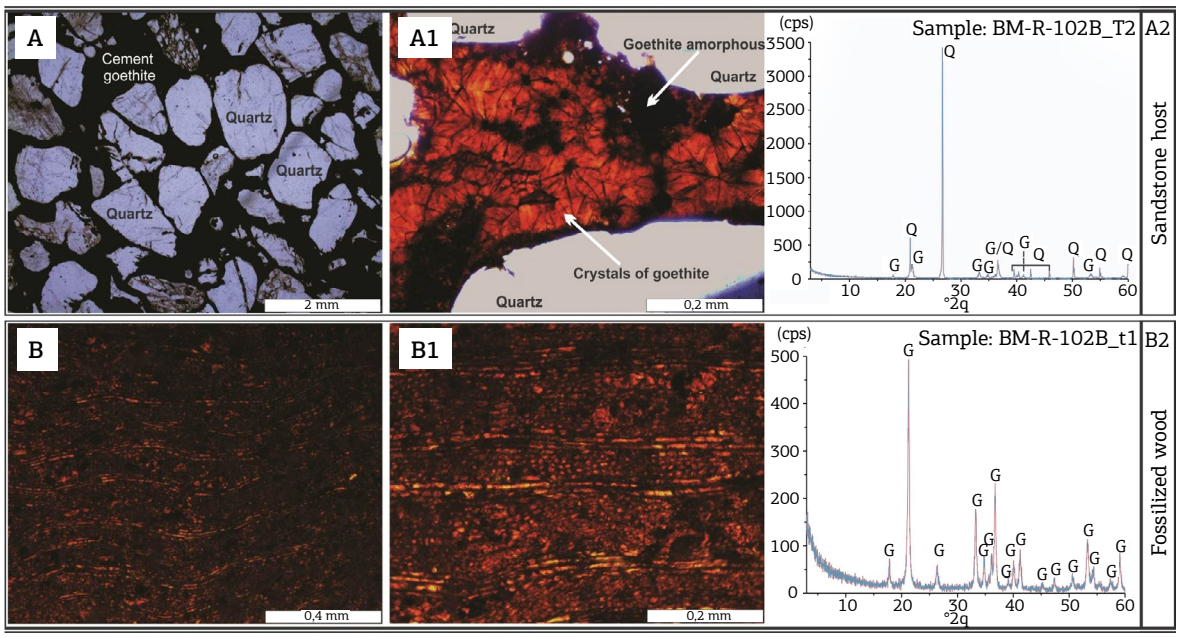


**Figure 4. (A) Shows fossiliferous sandstone layer photomicrograph highlighting the quartz grains (Qz) and rock fragments (Fr) loose packing, with goethite-enveloped point and floating contacts. (A1) Shows amorphous portions-associated goethite crystals, as illustrated in the diffractogram (A2). (B and B1) Show the plant tissue well preserved by the goethite replacement (as demonstrated in B2's diffractogram). Abbreviations: Q – quartz, G – Goethite.**

and 8D). Homogeneous rays, tending to heterogeneous 4 to 10 seriate — most (3–8 seriate) formed by procumbent cells (Figs. 6E, 6F and 7F). One upright cell, 8 rays per mm linear, 476–1,583 µm high and 55 µm wide and 46 cells high on average. Some rays > 1 mm (Figs. 6E, 6F and 7F). Oil/mucilage cells present in rays cells (Fig. 8E – black arrow). Prismatic crystals observed in axial parenchyma (Fig. 8E – red arrow). Storied structure not observed.

## DISCUSSION

Anatomical features described in the fossil wood — such as short-length, vessel elements, simple perforation plates, axial apotracheal parenchyma reticulate, multiseriate and high rays — are distinctive characters of the Annonaceae family (Metcalf and Chalk 1950). Our sample was further compared to the fossil and extant genus essential bibliography of Prakash (1978), Détienne and Jacquet (1983), Wheeler and Manchester (2002), Inside Wood (2004 onwards), León (2007) and Gregory *et al.* (2009).

Therefore, the absence of a fossil genus that shares all the characteristics with the fossil wood studied here justifies the creation of a new fossil genus. Current *Duguetia* Augustin Saint-Hilaire presents most similarities with the fossil sample, since *Duguetia* is the genus with small vessel diameter and intravascular pits inside the family (Détienne and Jacquet 1983; Léon 2007).

### Comparison with fossil wood

According to Gregory *et al.* (2009), Annonaceae has only two fossil genera: the *Annonoxylon* Boureau and *Polyalthiaxylon*

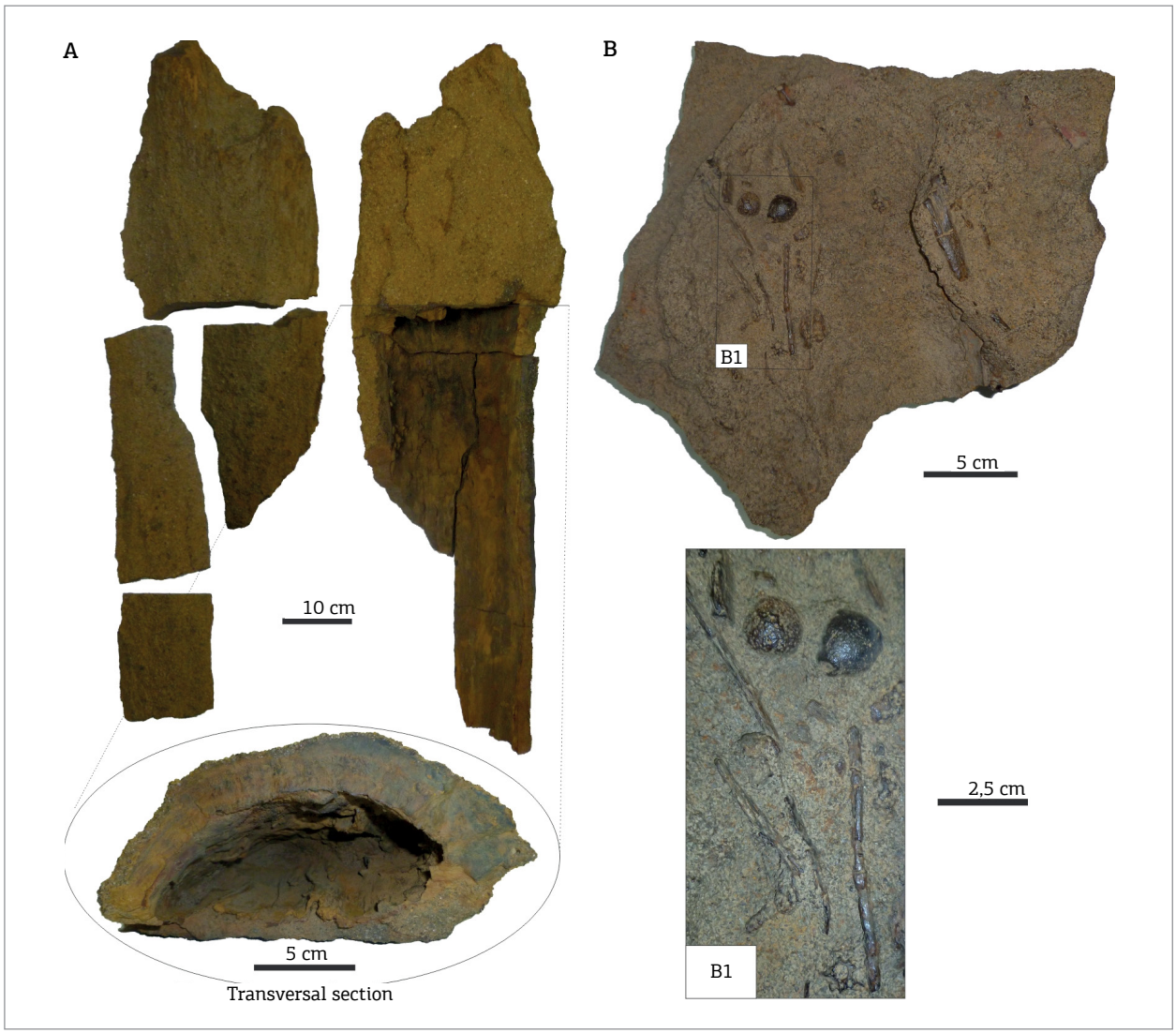


**Figure 5. (A) Fossil wood longitudinal and transverse view (sample BM-R-102B); (B) fossilized vegetal fragments fruits/seeds.**

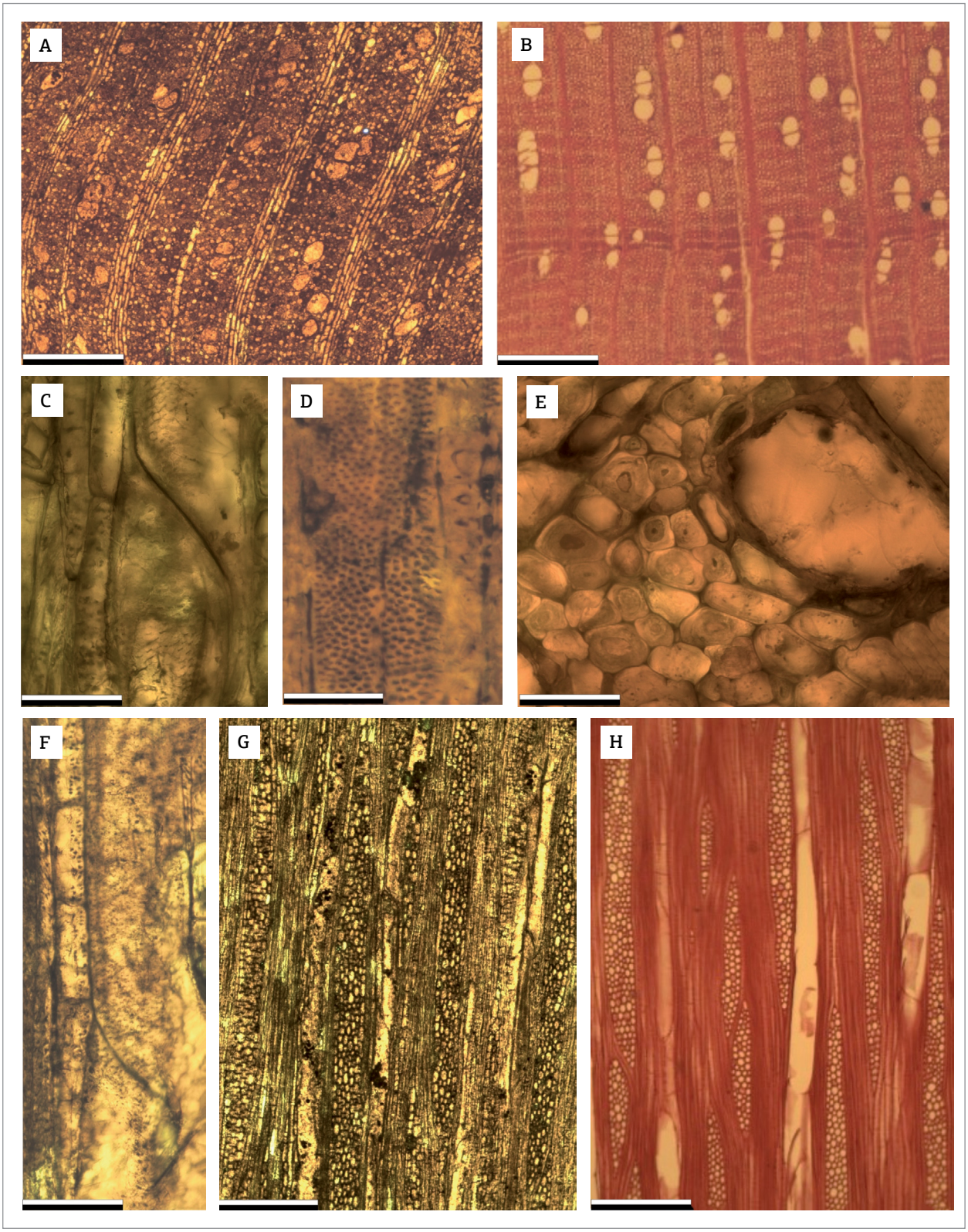


Figure 6. (A,B) Transversal section. Diffuse. porous vessels in diagonal/radial pattern, vessels solitary and multiple vessels of 2, 3 and 4. Density of vessels per mm$^2$, mean, vessel's tangential diameter 58 µm (A) fossil and (B) extant; (C) fossil (radial longitudinal section), simple perforation plate, intervessel pits alternate and minute (2–4 µm); (D) (transversal section) fibers with simple to minutely bordered pits and not septated; (E,F) (tangential longitudinal section) rays homogeneous tending to heterogeneous 4 to 10 seriate, most (3–8 seriate), formed by procumbent cells and, in some, one upright cell, some rays > 1 mm; (E) fossil and (F) extant. Scale bars A,B,G,H (200 µm); C,D (100 µm); E,F (50 µm).

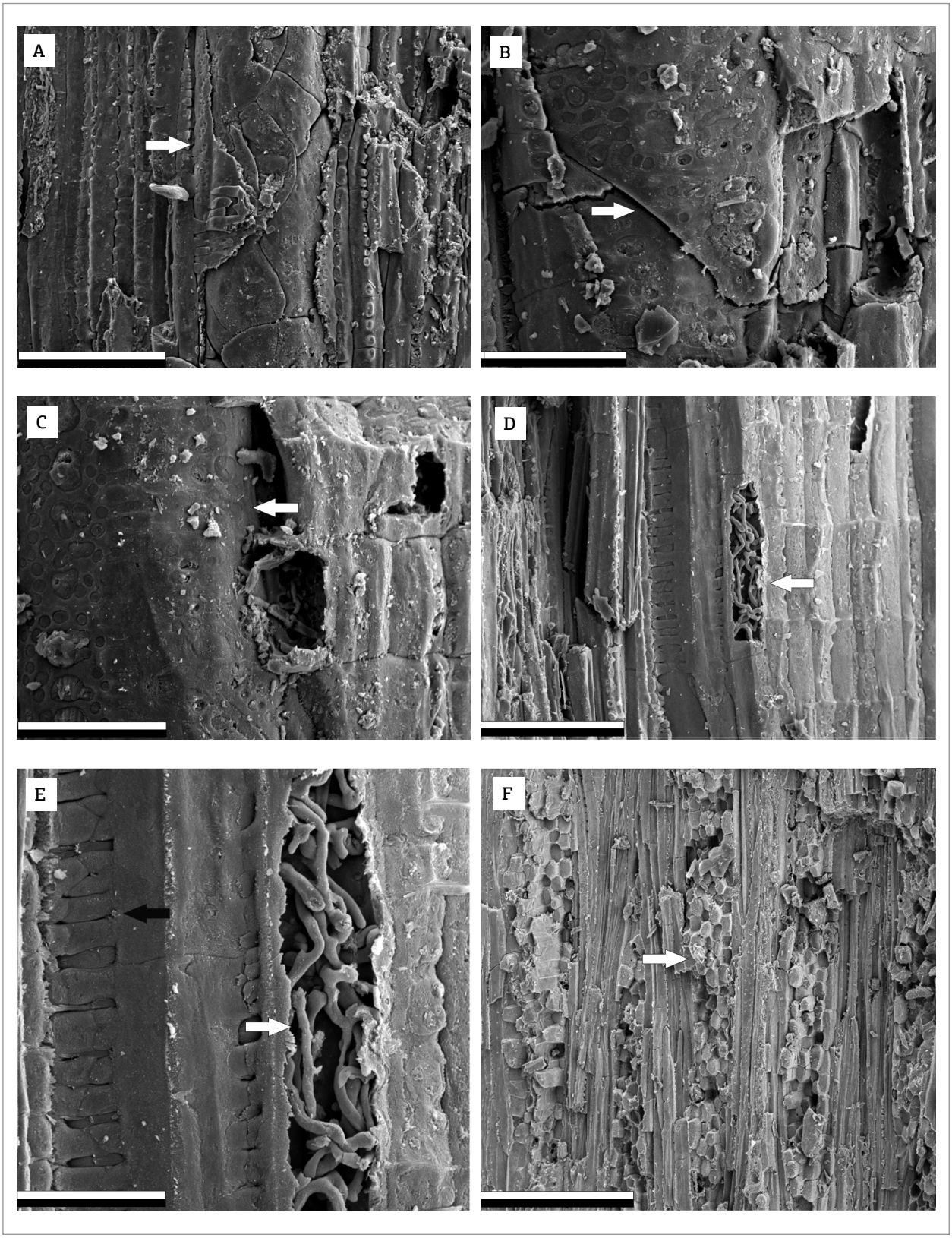


Figure 7. Scanning electron microscope. (A to E) (radial longitudinal section). (A) Arrow indicating a vessel element. Scale bar (50 µm); (B) arrow indicating a simple perforation plate; (B,C) intervessel pits. Scales bar (25 µm); (D) general view of parenchyma cells and presence of fungus (arrow). Scale bar (50 µm); (E) detail of cell containing fungus (white arrow), and the indicating disjunctive parenchyma (black arrow). Scale bar (15 µm); (F) (Tangential Longitudinal Section) arrow indicating a ray. Scale bar (100 µm).

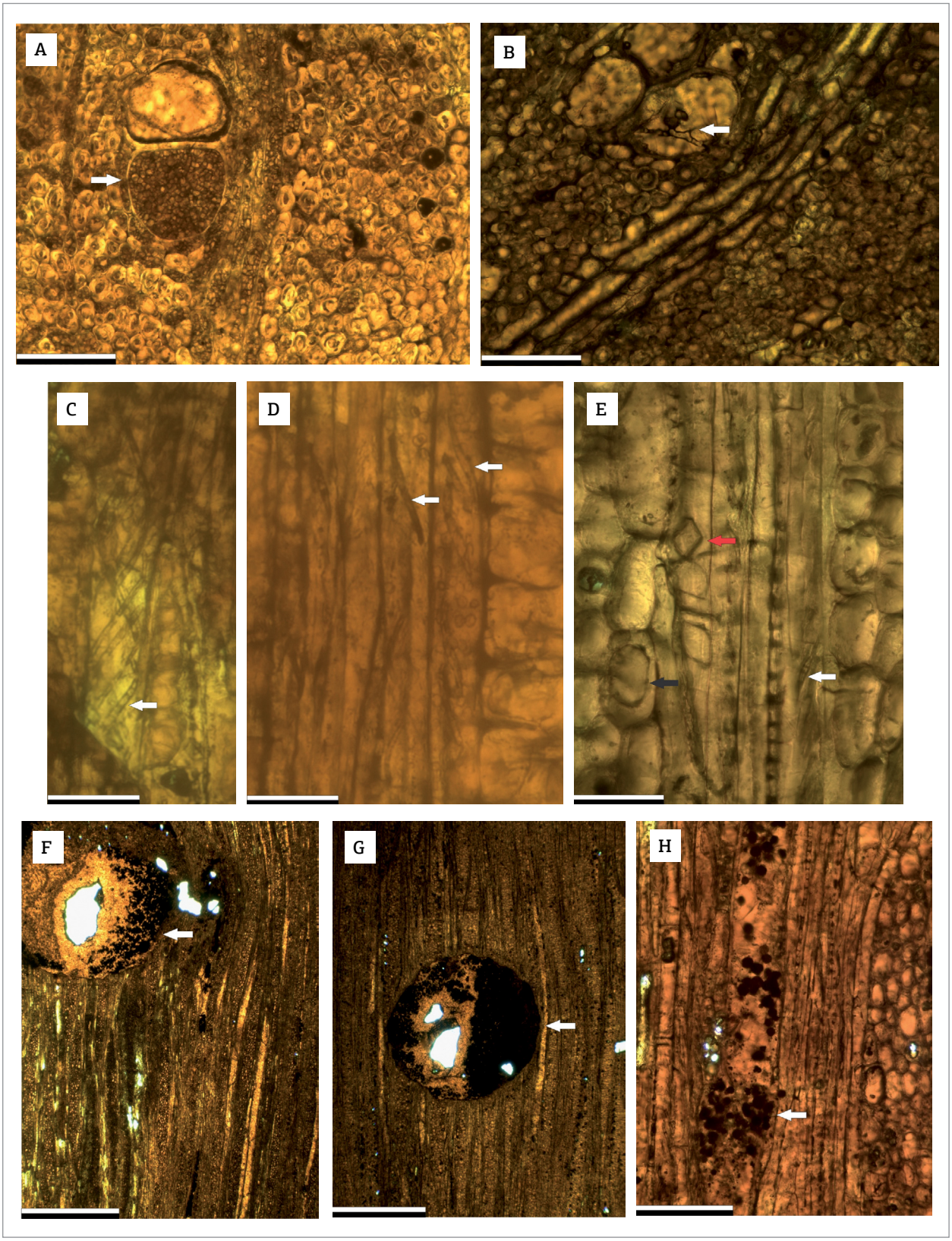


Figure 8. Fungi and insect-plant interactions. (A to E) Fungi. (A,B) (transversal section) hyphae are observed in the parenchyma cells and vessels; (C,D) (longitudinal radial section) arrow indicating hyphae fungi; (E) (longitudinal tangential section). cavities forming T-branches or L-branching are caused by the thin penetration of hyphae (white arrow), oil/mucilage cells found in rays (black arrow) and Prismatic crystals observed in axial parenchyma (red arrow); (F,G) (longitudinal tangential section) galleries caused by insects; (H) (longitudinal radial section) damage caused by insect. Scales bar: A,B (50 µm); C,D (25 µm); E (50 µm); F,G (200 µm) and H (100 µm).

Bande, most species from Africa, Asia and Europe, and only one record from North America, *Annonoxylon bonesii* (Wheeler and Manchester 2002). The sample studied here is compared to the eight fossil species of the Annonaceae family (Table 1), the sample differs from *Annonoxylon striatum* (Boureau 1950) by having major density of vessels by mm$^2$, higher rays, less axial parenchyma and the presence of oil cells. It differs from *Annonoxylon edegense* (Boureau 1954) by having smaller diameter of vessels, less density of vessels by mm$^2$ and axial parenchyma. It differs from *Annonoxylon bonesii* (Wheeler and Manchester 2002) by having smaller diameter of vessels, higher density of vessels by mm$^2$, rays with a major number of wide cells and the presence of crystal and oil cells. It differs from *Polyalthioxylon parapaniense* (Bande 1973), *Polyalthioxylon platymitroides* (Kramer 1974) and *Polyalthioxylon oldhavenense* by having smaller diameter of vessels, less parenchyma cells and the presence of crystal and oil cells. It differs from *Polyalthioxylon stelechocarpoides* (Kramer 1974) and *Polyalthioxylon indicum* (Prakash 1978) by having different diameter of vessels by mm$^2$, smaller intervessel pits than *P. indicum* and the presence of crystals in ray cells (Table 1).

## Comparisons with extant wood

Among modern species, the fossil wood described and denominated as *Duguetiaxylon amazonicum* strongly resembles the extant genus *Duguetia* Augustin Saint-Hilaire, and can be distinguished from others genera of Annonaceae by the presence of small vessels diameter (Figs. 6A and 6B), the small size of intervasculary pits (Figs. 6C, 6D, 7B and 7C), the high and multiseriate rays (Figs. 6G and 6H) and the presence of oil and crystal in ray cells (Fig. 8E) (Détienne and Jacquet, 1983; León 2007). Léon (2007), in his paper about the wood anatomy of 26 species of Annonaceae from Venezuela, exposed a high xylem homogeneity, which makes difficult the differentiation between genera and species. Oil cells were found in only two species of *Xylopia* and *Duguetia*, while *Oxandra* and *Duguetia* are characterized by smaller diameters of vessels. Both rays' height and the length of their fibers and vessel elements also characters as rays, fiber lenth and vessels elements can show trends where genders can be differentiated (Table 2). Over all the characteristics presented by the fossil sample, the most similar extant genus is *Duguetia*, especially by the diameter of vessels, the small diameter of intervessel pits and the presence of oil cells in rays.

Table 1. Comparison between fossil woods

| Specie | Diameter of vessels (µm) | Vessels/ mm² | Pits | Rays high (µm) | Rays width cells | Axial parenchy – ma cells | Crystal | Oil cells in rays |
|---|---|---|---|---|---|---|---|---|
| **Annonoxylon. striatum* Boureau 1950, Sahara | 50 – 100 | 5 | nd | > 350 | 4 – 10 | 3 | + | – |
| **Annonoxylon edengense* Boureau 1954, Sahara | > 200 | 5 | nd | > 1 mm | 4 – 10 | 3 | + | + |
| *Annonoxylon bonesii* Wheller & Manchester 2002, USA | 155 | 4 – 13 | 4 – 6 | 250 – 1750 | 1 – 6 (3 – 4) | 1 – 2 | – | – |
| **Polyalthioxylon parapaniense* Bande 1973, India | 50 – 200 | 5 – 20 | nd | > 1 mm | 4 – 10 | 3 | – | + |
| **Polyalthioxylon Platymitroides* Kramer 1974, Borneo | 50 – 200 | 5 – 20 | nd | > 1 mm | 4 – 10 | 3 | – | – |
| **Polyalthioxylon stelechocarpoides* Kramer 1974, West Java | 50 – 100 | 2 – 40 | nd | > 1mm | 4 – 10 | 3 | – | + |
| *Polyalthioxylon indicum* Prakash 1978, India | 60 – 195 | 4 – 11 | 4 – 6 | 132 – 2.475 | 6 – 10 | 2 | – | + |
| **Polyalthioxylon oldhavenense* Crawley 2001, Britain | 50 – 200 | 20 – 40 | nd | > 1 mm | 4 – 10 | 3 | – | – |
| *Duguetiaxylon amazonicum* (This work) Brazil | 45 – 115 | 20 | 2 – 4 | 500 – 1538 | 4 – 8 | 1 – 2 | + | + |

*InsideWood. 2004 – onwards; – = absent; + = presente; nd = no data

## Palaeoecological inferences: organic evidence of fungi and insect-plant interactions

In the studied sample, evidence of fungal decay and hyphae of fungi, as well as related galleries insect activities are registered — Plates II (Fig. 7) and III (Fig. 8). The axial alignment of tracheids, vessels and fibers, and the radial arrangement of the xylem ray parenchyma facilitate access into the wood and allow a widespread distribution of hyphae within the xylem (Rayde and Boddy 1988 *apud* Schwarze 2007). The colonization of wood by hyphae is observed in the parenchyma cells and vessels (Figs. 7D, 7E, 8A and 8B). The hyphae are septate, with simple branches and random arrangement within cellular elements (Figs. 7D, 7E and 8B). It is possible to observe the formation of the secondary wall cavities in the fibers. These cavities have the form of T-branches or L-branching and are a result of the thin penetration of the hyphae (Schwarze 2007) (Figs. 8C to 8E). The structures of the cavities and the formation of multiple L-branching colonization, associated with hyphae, are typical of a soft rot, more precisely basidiomycete (Schwarze 2007, Schwarze *et al.* 2004).

Furthermore, the presence of circular-shaped galleries of about 1.3 mm in diameter, caused by insects which are likely to be the first ones to enter the wood, facilitates the invasion by fungi or vice versa (Schweingruber *et al.* 2006; Schweingruber 2007) (Figs. 8F to 8H).

This interaction occurs in current ecosystems, enabling us to infer an active plant/insect interaction, and the presence of fungi in Miocene as well confirms Novo Remanso Formation to have had hot and humid weather (typically tropical).

## Novo Remanso Formation depositional paleoenvironment

Sedimentary facies (channel bottom, fluvial bars and crevasse splay deposits), described for the Novo Remanso Formation, by Dino *et al.* (2012) and Soares *et al.* (2015), are representative of the meandering fluvial paleoenvironment which implanted itself on the Amazon Basin in the Miocene. The characterization of this continental paleoenvironment is corroborated by the presence of algae (such as *Botryococcus*) indicating a fresh to brackish water environment, as well as the lack of elements of marine microphytoplankton, in which there was a predominance of paleovegetation of palm trees (*Mauritia*, *Grimsdalea*), (Grimineae, Bombacacae) and aquatic elements (*Deltoidospora*, *Botryococcus*).

Under this context, the presence of fragments of fossil plants on top and inside the sandy spit bars of this Miocene fluvial system is an indicative of alternating periods of subaerial exposure and sedimentation of the bar, which may be related to seasonal variations (receding and rising water levels of the Amazonian rivers, respectively), and persist up to now in Amazon. Furthermore, the fragmentation of the fossil plants along the studied layer indicates them to have been reworked and inserted into the fluvial bars during deposition, generating an autochthonous accumulation. However, the evidence of insect-plant interaction described in the studied sample shows plants to have been exposed to insect biotic activity prior to their burial.

The open framework of the studied sandstone layer is indicative of an incipient mechanical compactation, which characterizes a shallow diagenesis (eodiagenesis). This datum is consistent with the stratigraphic positioning of Novo Remanso Formation, which represents the Amazon Basin's sedimentary cover, and indicates this unit not to have undergone deep burial.

It appears that the cementation of goethite was precocious, preventing the advance of the mechanical compaction and also filling up gigantic and secondary pores (in some grain boundaries), formed by intra-stratified dissolution. These data indicate this unit to have undergone some changes on its framework's composition by the time it was

Table 2. Comparison between extant genera of Annonaceae. Adapted from Léon (2007).

| Genus of Annonaceae | Diameter of vessels (µm) | Vessels (mm²) | Pits (µm) | Rays high (µm) | Rays width cells | Oil cells in rays |
|---|---|---|---|---|---|---|
| *Annona* | 50 – 100 | 8 – 16 | ≥ 5 | 300 – 1300 | 1 – 9 | - |
| *Bocageopsis* | 100 – 200 | 5 – 8 | ≤ 5 | 700 – 1400 | 3 – 10 | - |
| *Duguetia* | 60 – 100 | 15 – 20 | ≤ 5 | 300 – 1600 | 3 – 8 | + |
| *Guatteria* | 100 – 200 | 3 – 5 | ≥ 5 | 300 – 2400 | 3 – 14 | - |
| *Oxandra* | 50 – 100 | 15 | ≥ 5 | 58 – 384 | 3 – 6 | - |
| *Porcelia* | 100 – 200 | 11 – 15 | ≥ 5 | 570 – 1200 | 1 – 3 | - |
| *Rollinia* | 100 – 200 | 4 – 8 | ≥ 5 | 300 – 1000 | 2 – 6 | - |
| *Unonopsis* | 100 – 200 | 9 – 10 | ≥ 5 | 700 – 1700 | 5 – 10 | - |
| *Xylopia* | 100 – 200 | 5 – 12 | ≤ 5 | 200 – 1200 | 1 – 8 | + |

- = absent; + = presente

subjected to the eodiagenesis field. This field is marked by an abundant presence of iron (goethite), which may have been originated while the just-deposited sediment was still in contact with the environment, according to the process suggested by Carvalho *et al.* (2010).

## CONCLUSIONS

This study describes a new fossil wood occurrence in the Amazon Basin's Neogene unit, informally called Novo Remanso Formation. The sample was collected in an outcrop on the left bank of the Amazon River and, despite the absence of a precise stratigraphic positioning for the studied fossiliferous layer, it can be associated to the other occurrences in outcrops in the same formation, identified on the banks of the Negro (Paricatuba Town) and Solimões (Manacapuru Town) rivers.

The present study has analyzed a sample of a fossil wood and their anatomical characteristics — such as short length vessel elements, simple perforation plates, apotracheal reticulate axial parenchyma, multiseriate and high rays — have enabled it to be related to the Annonaceae family. This discovery becomes relevant, since it is the first record of this species in South America and may contribute to new paleofloristic studies in the Americas.

The preserved fungus inside the parenchyma cells and vessels, along with the presence of insect galleries, support the hypothesis of a hot and humid climate in Central Amazon during the Novo Remanso Formation's deposition in the Miocene, and therefore consistent with the paleoclimatic data obtained from the regional palynological studies conducted on this Formation by Dino *et al.* (2012) and Soares *et al.* (2015).

The fossil plants random arrangement and fragmentation degree in the studied sandy bar, as well as the described plant-insect interaction data, are indicative of — prior to deposition — subaerial exposure and reworking, for generating the autochthonous deposit.

The studied open sandstone layer framework may be related to the early development of ferruginous cement (goethite) between the grains, which prevented physical compaction advancement in a shallow silting zone (Eodiagenesis stage). This is consistent with the stratigraphic positioning of Novo Remanso Formation, which discordantly overlays the cretaceous unit and makes up most of the Central Amazon's relief.

The Novo Remanso Formation fossil wood study, despite its being a punctual analysis, has demonstrated its value as a paleoenvironmental indicator for the Amazon's Neogene.

## ACKNOWLEDGEMENTS

The authors are grateful to the xylotheque of the National Research Institute of Amazonia (INPA) for allowing them to photograph, as well as undertake comparative studies between the fossil and its extant.

They also thank the Serviço Geológico do Brasil (CPRM) for the analyses performed and fieldwork financial support through the Manaus Metropolitan Region's Geology and Mineral Resources Project (2011).

We would also like to thank Rodolfo Dino, geologist, for his generous suggestions and criticism.

## REFERENCES

Alvarenga H.M.F., Guilherme E. 2003. The Anhingas (Aves: Anhingidae) from the upper Tertiary (Miocene Pliocene) of Southwestern Amazonia. *Journal of Vertebrate Paleontology,* **23**(3):614-621.

APG. 2009. An update of the Angiosperm Phylogeny Group classification for the ordersand families of flowering plants: APG III. *Botanical Journal of the Linnean Society,* **161**:106-121.

Bande M.B. 1973. A petrified dicotyledonous wood from the Deccan Intertrappean beds of Mandla district. *The Botanique*, **4**(1):41-48.

Bocquentin J., Guilherme. E. 1997. A cintura pélvica do quelônio Stupendemys (Podocnemididae, Podocnemidinae) proveniente do Mioceno Superiorplioceno, do Estado do Acre, Brasil. *Acta Geologica Leopoldensia*, **20**(45):47-50.

Boureau E. 1950. Étude paléoxylogique du Sahara (XII): Sur un Annonoxylon striatum n. gen., n. sp., des couches post-éocénes du Sud-Ouest de l'Adrar Tiguirirt (Sahara Soudanais). *Bulletin Society Geology,* France. serie. **5**(20):393-397.

Boureau E. 1954. Étude paléoxylologique du Sahara (XX). Sur un Annonoxylon edengense n. sp., des couches post-eocénes du Sud-Ouest de l'Adrar Tiguirirt (Sahara Soudanais). *Bulletin Museu Natural History,* 2è Sér. **26**:286-291.

Caputo M.V., Rodrigues R., Vasconcelos D.N.N. 1971. Litoestratigrafia da Bacia do Amazonas. *Relatório interno Petrobras.* (641-A) p. 99.

Caputo M.V. 1984. *Stratigraphy, tectonics, paleoclimatology and paleogeography of northern basins of Brazil.* PhD Thesis, University of California, Santa Barbara, 583 p.

Carlquist S. 2001. *Comparative Wood Anatomy. Systematic, Ecological, and Evolutionary Aspects of Dicotyledon Wood.* Springer Series in Wood Science. Springer, p. 448.

Carvalho R.R., Neumann V.H., Fambrini G.L., Vieira M.M., Rocha D.E.G.A. 2010. Origem e proveniência da seqüência siliciclástica inferior da Bacia do Jatobá. *Estudos Geológicos*, **20**(2):113-127.

Chattaway M. 1932. Proposed standards for numerical values used in describing woods. *Tropical Woods*. **29**:20-28.

CPRM. 2006. *Carta Geológica do Brasil ao Milionésimo*. Geologia e Recursos Minerais do Estado do Amazonas, Programa Geologia do Brasil. Brasília: Ministério de Minas e Energia/CPRM/Serviço Geológico do Brasil. p. 125.

Cunha P.R.C., Gonzaga F.G., Coutinho L.F.C., Feijó F.J. 1994. Bacia do Amazonas. *Boletim de Geociências da Petrobras*, **8**(1):47-55.

Cunha P.R.C., Melo J.H.G., Silva O.B. 2007. Bacia do Amazonas. *Boletim de Geociências da Petrobras*, **15**(2):227-251.

Cozzuol M.A., Goin F., Reyes M., Ranzi A. 2006. The oldest species of Didelphis (Mammalia, Marsupialia, Didelphidae), from the late Miocene of Amazonia. *Journal of Mammalogy*, **87**(4):663-667.

Daemon R.F. 1975. Contribuição à datação da Formação Alter do Chão, Bacia do Amazonas. *Revista Brasileira de Geociência*, **5**(2):58-84.

Détienne P., Jacquet P. 1983. *Atlas of the woods of the Amazon and of adjoining regions* (Atlas des bois de l'Amazanie et des regions voisines). Nogent-surmarne Cedex, France. Centre de Guyane, CTFT, Centre Technique Forestier Tropical. p. 640.

Dino R., Silva O.B., Abrahão D. 1999. Caracterização palinológica e estratigráfica de estratos cretáceos da Formação Alter do Chão, Bacia do Amazonas. *In: 5.º Simpósio sobre o cretáceo do Brasil*. Rio Claro, UNESP, p. 557-565.

Dino R., Soares E.A., Antonioli L., Riccomini C., Nogueira A.C. 2012. Palynostratigraphy and sedimentary facies of miocene fluvial deposits of the Amazonas Basin, Brazil. *Journal of South American Earth Sciences*, **34**:61-80.

Duarte L. 1987. Restos foliares de Angiospermas da Serra de Paituna, PA. 10.º *Congresso Brasileiro de Paleontologia*, **2**:859-877.

Gonçalves Júnior E.S., Soares E.A., Tatumi S.H., Mittani J.C.R. 2016. Pleistocene-Holocene sedimentation of Solimões-Amazon fluvial system between the tributaries Negro and Madeira, Central Amazon. *Brazilian Journal of Geology*, **46**(2):167-180.

Gregory M., Poole I., Wheeler E.A. 2009. Fossil dicot wood names – annotated list with full bibliography. *IAWA Journal Supplement* 6. p. 220.

Horbe A.M.C., Vieira L.C., Nogueira A.C.R. 2006. Geoquímica de camadas vermelhas bioturbadas da Formação Alter do Chão, Cretáceo da Bacia do Amazonas. *Revista Brasileira de Geociências*. **36** (3):396-402.

IAWA Committee. 1989. IAWA List of Microscopic Features for Hardwood Identification. *IAWA Bulletin n.s*, **10**(3):219-332

InsideWood 2004 – onwards. Published on the Internet. http://insidewood.lib.ncsu.nedu/search [consulted August, 2013].

Kay R.F., Cozzuol M.A. 2006. New platyrrhine monkeys from the Solimões Formation (late Miocene, Acre State, Brazil). *Journal of Human Evolution*, **50**:673-686.

Kloster A., Soares E.A.A., Riker S.R., Lima F.J.C., Motta M.B., Gnaedinger S. 2013. Primeiro registro de lenho fóssil de Annonaceae na Formação Novo Remanso, Mioceno da Bacia do Amazonas, Brasil. Paleontologia em destaque. *In:* XXIII Congresso Brasileiro de Paleontologia. *Boletim informativo da Sociedade Brasileira de Paleontologia*. Edição especial. p. 173.

Kloster A., Gnaedinger S., Adami-Rodrigues K., Urban C. 2015. New Record of Fabaceae fossil woods from the Solimões Formation (Miocene), Acre Basin, Amazon, Brazil. ***Revista*** *Brasileira de Paleontologia*, **18**(3):391-402.

Kramer K. 1974. Die Tertiären Hölzer Südost-Asiens (Unter Ausschluss Der Dipterocarpaceae). 1. Teil. *Palaeontographica* Abt. B **144**:45-181.

Kribs D.A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. *Botanical Gazette*, **96**:547-557.

Latrubesse E.M., Silva S.A.F., Cozzuol M., Absy M.L. 2007. Late Miocene continental sedimentation in southwestern Amazonia and its regional significance: biotic and geological evidence. *Journal of South American Earth Sciences*, **23**:61-80.

León H.W.J. 2007. Anatomía xilemática de 26 especies de la familia Annonaceae en Venezuela. *Revista Forestal Venezolana*, **51**(2):165-177.

Lima C.B.C., Salazar C.A, Soares E.A.A., Barbosa V.P. 2013. Análise petrográfica e paleontológica da formação Novo Remanso, região do Baixo Rio Negro, Amazônia Central. *Simpósio de Geologia da Amazônia*, **13**:25-28.

Machado L.G., Scheel-Ybert R., Bolzon R.T., Carvalho M.A., Carvalho I.S. 2012. Lenhos fósseis do Neógeno da Bacia do Acre, Formação Solimões. Contexto paleoambiental. *Revista Brasileira de Geociências*, **42**:67-80.

Mendes A.C., Truckenbrod W., Nogueira A.C.R. 2012. Análise faciológica da Formação Alter do Chão (Cretáceo, Bacia do Amazonas), próximo à cidade de Óbidos, Pará, Brasil. *Revista Brasileira de Geociências*, **42**(1):39-57.

Maury C.J. 1937. Argilas fossilíferas do Plioceno do Território do Acre. *Boletim do Serviço Geológico e Mineralógico do Brasil*, **77**:1-29.

Metcalfe C.R., Chalk L. 1950. *Anatomy of the Dicotyledons*. Clarendon Press. Oxford. I. p. 731.

Mussa D., Bernardes-De-Oliveira M.E., Mune S.E., De Siqueira E., Castro-Fernandes M.C. de, Carmo D.A. 2002. Lenho de Dicotiledônea da Formação Solimões, Neógeno da Bacia do Acre, Brasil. *Paleontologia em Destaque*, **40**:16-17.

Nogueira A.C.R., Vieira L.C., Suguio K. 1999. Paleossolos da Formação Alter do Chão, Cretáceo-Terciário da Bacia do Amazonas, regiões de Presidente Figueiredo e Manaus. 5.º *Simpósio sobre o cretáceo do Brasil*. Rio Claro, UNESP, p. 261-266.

Oliveira S.B.S.G., Nogueira A.C.R. 2006. Lenhos fósseis de Paricatuba-Amazonas. SBG, IX Simpósio de Geologia da Amazônia. *Resumos Expandidos* (CD-ROM), Belém.

Pereira R., Carvalho M.A., Mendonça Filho J.G., Azevedo D.A., Carvalho I.S. 2006. Ocorrência de esporos de fungos preservados em âmbar cretácico da Bacia do Amazonas, Formação Alter do Chão. ***7.º*** *Simpósio do Cretáceo do Brasil e 1.º Simpósio do Terciário do Brasil*. Serra Negra. p 101.

Prakash U. 1978. Fossil woods from the Lower Siwalik beds of Uttar Pradesh, India. *Paleobotanist*, **25**:376-392.

Ramos M.I.F., Silveira R.R., Coimbra J.C. 2001. Ostracodes mixoalinos do Mioceno da Formação Solimões, Bacia do Solimões, Amazonas, Brasil. SBP, Congresso Brasileiro de Paleontologia, Rio Branco, *Boletim de Resumos*, **17**:86.

Ribeiro J.E.L.S., Hopkins M.J.G., Vicentini A., Sothers C.A., Costa M.A.S., Brito J.M., Souza M.A.D., Martins L.H.P., Lohman L.G., Assunção P.A.C.L., Pereira E.C., Silva C.F., Mesquita M.R., Procópio L.C. 1999. *Flora da Reserva Ducke: Guia de Identificação das Plantas vasculares de uma Floresta de terra-Firme na Amazônia Central*. Manaus: INPA/DFID, p. 816.

Richter M.1984. Dental histology of a Characoid fi sh from the Plio-Pleistocene of Acre, Brazil. *Zoologica Scripta*, **13**(1):69-79.

Richter M. 1989. Acregoliathidae (Osteichthyes, Teleostei), a new family of fi shes from the Cenozoic of Acre State, Brasil. *Zoologia Scripta*, **2**(18):311-319.

Rozo J.M.G., Nogueira A.C.R., Horbe A.M.C., Carvalho A.S. 2005. Depósitos neógenos da Bacia do Amazonas. *In:* Horbe A.M.C. Souza V.S. (eds.) Contribuições à Geologia da Amazônia. *SBG-NO*, **4**:201-207.

Schwarze F.W.M.R. 2007. Wood decay under the microscope. *Fungal Biology Reviews*, **1**:133-170.

Schwarze F.W.M.R., Engels J., Mattheck C. 2004. *Fungal Strategies of Wood Decay in Trees*, second edition. Springer-Verlag, New York. p. 185.

Schweingruber F.H. Börner A., Schulze E.-D. 2006. *Atlas of Woody Plant Stems.* Evolution, Structure, and Environmental Modifications. Springer-Verlag, Berlin. p. 229.

Schweingruber F.H. 2007. *Wood structure and environment.* Springer, Berlin. p. 279.

Soares E.A.A. 2007. *Depósitos pleistocenos da região de confluência dos rios Negro e Solimões, porção oeste da Bacia do Amazonas.* PhD thesis, Instituto de Geociências, Universidade de São Paulo, São Paulo, 205 p.

Souza Filho J.P. 1998. *Novas formas fósseis de Crocodylia (Alligatoridae e Gavialidae) da Formação Solimões, Cenozóico do Estado do Acre-Brasil, representadas por materiais cranianos e mandibulares.* Dissertação de Mestrado, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, 194 p.

Soares E.A.A., Tatumi S.H., Riccomini C. 2010. OSL age determinations of pleistocene fluvial deposits in central Amazonia. *Academia Brasileira de Ciências*, **82**(3):14-19.

Soares E.A.A., Dino R., Soares D.P., Antonioli L., Silva M.A.L. 2015. New sedimentological and palynological data from outcropping miocene strata in the central portion of the amazon basin. *Brazilain Journal of Geology*, **45**(3):337-357.

Vieira L.C. 1999. *Depósitos fluviais da Formação Alter do Chão, Cretáceo-Terciário da Bacia do Amazonas, Ponta Negra, Manaus.* MS Dissertation, Instituto de Ciências Exatas, Universidade Federal do Amazonas, Manaus, 53 p.

Vonhof H.B., Wesselingh F.P., Ganssen G.M. 1998. Reconstruction of the Miocene western Amazonian aquatic system using molluscan isotopic signatures. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **141**:85-93.

Wheeler E.A., Manchester S.R. 2002. Woods of the Middle Eocene Nut Beds flora, Clarno Formation, Oregon, USA. *IAWA Journal supplement*, **3**:188.

Available at www.sbgeo.org.br