NEW RECORD OF FABACEAE FOSSIL WOODS FROM THE SOLIMÕES FORMATION (MIOCENE), ACRE BASIN, AMAZON, BRAZIL

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ABSTRACT – Detailed descriptions are provided for specimens of a new genus and species of Mimosoideae and *Swartzioxylon naraense* Delteil-Desneux emended (Papilionoideae) from the Solimões Formation, Miocene, Acre Basin, Brazil. Anatomical characteristics of the woods show a resemblance with the extant genera *Zygia* P. Browne and *Swartzia* Schreb, respectively. These genera currently have a wide distribution in Brazil and throughout the Amazon region; their presence in the outcrops of the Solimões Formation supports the idea that these genera might have been important components and indicates their importance in the fossil record, both to establish its distribution and evolution from the past to present of Amazon flora.

Key words: wood anatomy, Mimosoideae, Papilionoideae, Neogene.

RESUMO – Descrições detalhadas são fornecidas para os espécimes de um novo gênero e espécie de Mimosoideae e *Swartzioxylon naraense* Delteil-Desneux emend. (Papilionoideae) da Formação Solimões, Mioceno, bacia do Acre, Brasil. Características anatômicas das madeiras mostram uma semelhança com os gêneros vivos *Zygia* P. Browne e *Swartzia* Schreb, respectivamente. Esses gêneros têm atualmente uma ampla distribuição no Brasil e em toda a região amazônica, sua presença nos afloramentos da Formação Solimões suporta a ideia de que poderiam ter sido importantes componentes e indica a sua importância no registro fóssil, tanto para estabelecer sua distribuição e evolução do passado ao presente da flora amazônica.

Palavras-chave: anatomia da madeira, Mimosoideae, Papilionoideae, Neógeno.

INTRODUCTION

Knowledge of Neogene floras is considered relevant to an understanding of the factors that modulated the origins of the extant floras, their patterns of evolution, and the distribution of communities as centers of biological diversity. Paleontological and geological studies performed on outcrops in the Amazonian rivers are very important for understanding and modeling Neogene environmental changes that occurred in the southwestern Amazon. In the Brazilian state of Acre, sedimentary rock from the Solimões Formation emerges alongside the Acre, Iaco, Envira, Purus, Tarauacá, and Juruá rivers (Adami-Rodrigues *et al.*, 2013).

Fossil wood records of the Solimões Formation are scarce. Mussa (1959) provided the first descriptions of fossil woods from the Juruá River, with Fabaceae family (*Zollernioxylon sommeri*, *Z. santosii*, *Z. tinocoi*), Lecythidaceae family (*Lecythioxylon milanezii*), and Sapindaceae family (*Sapindoxylon lamegoi*) being identified. Pons & De

Franceschi (2007) described and assigned fossil woods with affinities to the Anacardiaceae, Clusiaceae, Combretaceae, Humiriaceae, Lecythidaceae, Leguminosae, and Meliaceae families, but without anatomical description from the Pebas Formation, which emerges in western Peruvian Amazon in the Iquitos region. This was later designated as the Solimões Formation in Acre Basin by Hoorn & Wesselingh (2010). Machado *et al.* (2012) have described new records of fossil woods showing affinities with Fabaceae (*Zollernioxylon* sp.) and the families Lytracae and Myrtaceae from the Solimões Formation in the Acre Basin, and Kloster *et al.* (2013) have recorded a new sample of Fabaceae (*Zollernioxylon tinocoi*) from the same formation along the Juruá River.

Palynological data from the Amazon region suggest diverse and well-structured forest communities with pollen types belonging to taxa from all forest strata, including grasses, herbs, and understory and canopy taxa, as well as diverse types of climbing ferns and epiphytes (Jaramillo *et al.*, 2010). Approximately 30 plant families

have been identified for the Miocene, with a predominance of Arecaceae, Poaceae, Malvaceae, Euphorbiaceae, Malphiaceae, Humiraceae, and Melastomataceae (Hoorn, 1993, 1994; Latrubesse *et al.*, 2010).

This paper adds new information to records by providing the first descriptions of Miocene fossil woods of Fabaceae family with affinity to the subfamilies Mimosoideae and Papilionoideae from the Solimões Formation.

GEOLOGICAL SETTING

The fossil woods analyzed were recovered in the Acre Basin, at the Juruá River, from a locality called Estirão do Mississippi (Figure 1). The Acre Basin extends over an area of 150,000 km² between parallels 6°S and 9°S and meridians 72°30'W and 74°W (Cunha, 2007). It is geologically bounded to the east by the Iquitos Arch, to the north and northwest by the Marañón Basin, and to the south and southwest by the Ucayali Basin (Wanderley-Filho *et al.*, 2010).

During the deposition the Acre Basin was affected by the late Hercynian and Andean orogenies (Cunha, 2007). This latter orogeny caused the uplift of the Andean Cordillera and deposition of the Solimões Formation as a typical foreland system (Wanderley-Filho *et al.*, 2010). This redirected the fluvial system (*e.g.* the Solimões and Amazon rivers) into the Atlantic Ocean (Hoorn *et al.*, 1995).

The lithotype sequence of the Solimões Formation consists of predominantly pelitic rock types, formed in a reducing environment and represented by greenish mudstones that range from light to dark and silty to sandy, and which are micaceous, locally calciferous and sometimes carbonaceous, or reddish with iron oxides, and highly fossiliferous (Maia *et al.*, 1977). There are also minor interbedded siltstones that have carbonate concretions either dispersed or in thin sheets, often microcrystalline (calcretes), as well as levels of lignite with pyrite that become thinner from the base to the top and transition to carbonaceous mudstone. These siltstones are light greenish gray to dark gray, sometimes clay, and the sandstones have an average particle size of medium to fine. Organic remains are common in this sequence. Also according to the cited author this formation presents some oxidized facies, with reddish, purplish, yellowish and whitish mudstones, siltstones, and sandstones, and with lignite and fossil contents in lesser amounts.

The outcrops that are the focus of the present study are located along riverbanks and represent exposure of sediments from the upper parts of the Solimões Formation. Data from fossil vertebrate assemblages and palynology of Late Miocene age for these deposits (Latrubesse *et al.*, 2010). The same authors reported an abundant and diverse vertebrate fauna from the intervals from the top of the interfluvial formation, dated to the Huayquerian and Montehermosian South American land mammal ages (Miocene-Pliocene).

In their review of the paleobiogeography of the Amazonian river system, Latrubesse *et al.* (2010) recorded that Miocene sedimentary rocks are associated with fossil of vertebrates, mollusk, and pollen. This support a scenario of continental

deposition, with the sedimentary environment probably formed by the combination of fluvial channels forming a large river system with floodplains, swamps, forests, and gallery forests, developed under a tropical to subtropical climate with a dry season. Palynological studies indicate the presence of more than 30 families of angiosperms, most of them still present in the modern landscape (*e.g.* Euphorbiaceae, Malvaceae, Rubiaceae and Amaranthaceae), while data from fossil vertebrate fauna suggest the presence of areas of open fields and various types of forests.

These lithological characteristics suggest a fluvial system, with interbedded floodplain deposits represented by plane-parallel siltstones and debris flow deposits represented by massive clast-supporting conglomerates (Simpson & Paula-Couto, 1981). The fossilized fragments of woods and turtle shells indicate that the depositional environment had moments of high energy, enabling the deposition of fossils and gravels. The banded iron carbonate concretions represent a post-depositional diagenetic process of palaeosol development in an arid climate. The character of the flattened and compressed woods indicates that the sedimentary basin received heavy sediment inputs, where a large volume of sediment was deposited in a short period of time.

MATERIAL AND METHODS

The fossil woods were collected from outcrops along the Juruá River in the State of Acre, more specifically in the locality known as Estirão do Mississippi, which gives its name to the stratigraphic sections adapted from Simpson & Paula-Couto (1981) (Figure 2). Fragments of silicified woods show a good cellular preservation. Petrographic thin sections with 30-40 µm thick were prepared from the wood fragments, orientated along three sections: transversal section (**TS**), tangential longitudinal section (**TLS**), and radial longitudinal section (**RLS**). These thin sections were studied in detail using a Leica DM500 microscope with an attached EC2 (LM) camera, and some fragments were also observed using a Leitz M50 stereoscopic microscope Leitz and a scanning electron microscope (**SEM**) observations using a Jeol5800 LV at the Universidad Nacional del Nordeste, Corrientes, Argentina.

For the various anatomical elements studied, at least 20 individual measurements were taken, with values recorded as means (minimum-maximum) following Chattaway (1932). The diagnostic anatomical characteristics for the Leguminosae were taken from IAWA Committee List of Microscopic Features for Hardwood Identification (1989), the Inside Wood Database (2004 and after - <http://insidewood.lib.ncsu.edu/search>), Kribs (1935), Metcalfe & Chalk (1950), Détienne & Jacquet (1983), Wheeler & Baas (1992), Carlquist (2001), Miller & Détienne (2001) and Evans *et al.* (2006). Gregory *et al.* (2009) list was also used for essential bibliographic information. The systematics follows the APG III (2009) classification.

The specimens studied have been deposited under the heading **LLP-CZS** in the Laboratory of Paleontology and Paleobotany of Universidade Federal do Acre, Campus Cruzeiro do Sul, Brazil.

Figure 1. A, Map showing the geographical location of the study area, along the Juruá River, in the Acre state, northwestern Amazon, Brazil. B, Photo of Estirão do Mississippi locality at Juruá River, Acre Basin. Map modified from Adami-Rodrigues *et al.* (2013), photo of Mississippi locality by A.C. Kloster. Scale bar = 1 m.

Figure 2. Stratigraphic profile of Estirão do Mississippi locality. Fossil woods were collected in the sandstone levels. Profile adapted from Simpson & Paula-Couto (1981).

The Fabaceae fossil. Herendeen *et al.* (1992) attributed the abundance of legumes in the Cenozoic fossil record, at least in part, to their ability to inhabit any environment, including disturbed areas such as streambeds and lake margins. The extensive diversification of the family into three subfamilies occurred during the Eocene (Herendeen *et al.*, 1992) and was accompanied by the “distribution” of dry climates in the tropics, creating groves in which each type of legume was common (Axelrod, 1992). The subsequent development of topographic complexity accompanied by formation of mountains and valleys was also conducive to occupation by legumes. Currently the Fabaceae is the third-largest family and they occupy almost environments. Africa and India have the most extensive fossil records for the Fabaceae, followed by the Americas and Europe (Gregory *et al.*, 2009). According to Jacobs (2004) the oldest legume yet discovered is a mid-Eocene sample from northern Tanzania, which was even suggested to be a center of origin for the subfamily Caesalpinioideae.

SYSTEMATIC PALEOBOTANY

EUDICOTS *sensu* APG III

Core EUDICOTS *sensu* APG III

FABIDS *sensu* APG III

FABALES Bromhead

Family FABACEAE Lindley. *nom. cons.* Leguminosae

Jussieu, *nom. cons. et nom. alt.*

Subfamily MIMOSOIDEAE De Candolle, 1825

Zygiaxylon gen. nov. Kloster & Gnaedinger

Type species. *Zygiaxylon amazonicum* sp. nov., by monotypy.

Etymology. Generic epithet refers to the extant genus *Zygia* Browne.

Diagnosis. Growth rings indistinct or absent. Diffuse porous wood without a clear pattern of distribution. Vessels commonly solitary or in radial multiples, some clusters, gum deposits presents. Simple perforation plates. Intervessel pits small, alternate, and vested. Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape throughout the ray cell. Axial parenchyma vasicentric, aliform to confluent, forming irregular wide bands, occasionally apotracheal parenchyma diffuse present. Simple fibers, non-septate. Rays are homogeneous, mostly 1-seriate or occasionally, 1-seriate partially 2-seriate, homocellular, formed by procumbent cells, not storied. Crystals in chambers present in the axial parenchyma.

Zygiaxylon amazonicum sp. nov. Kloster & Gnaedinger
(Figures 3-4A-B)

Holotype. LPP-CZS 0061.

Repository. Laboratory of Paleontology and Paleobotany of Universidade Federal do Acre, Campus Cruzeiro do Sul, Brazil.

Type locality. Estirão do Mississipi, Juruá River, State of Acre, Brazil.

Stratigraphic horizon. Solimões Formation, Acre Basin.

Etymology. Specific epithet refers to the Amazon region, where this fossil was recovered.

Diagnosis. The same to the genus by monotypy.

Description. This description is based on a specimen of silicified wood measuring 15 cm long and 10 cm in diameter. Pith, primary xylem, outer cortex, and secondary phloem are not preserved. The growth ring boundaries are indistinct or absent. The porosity is diffuse, without a clear pattern of distribution (Figure 3A). The vessels are more or less circular, solitary (62.5%) or in multiples of 2, 3, or 4-5 (19.64%, 12.5%, 5.35%, respectively), some clusters (Figure 3A). The mean vessel element tangential diameter is 195.2 μm (72-268 μm) and mean radial diameter is 142.9 μm (89-251 μm), mean vessels per mm^2 7 (5-8 per mm^2) (Figures 3A-B), mean vessel element length 354 μm (153-512 μm) (Figure 3C), gum/resin deposits present between vessels elements (Figures 3C,4A). Ground tissue fibers are circular to polygonal in outline, non-septate, with a mean diameter of 3.75 μm (3-7 μm) (Figure 3 B). Simple perforation plates with oblique end walls and intervessel pits alternate, small to medium and vested, mean 5 μm (3-7 μm) in diameter (Figures 3D,4B). Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape throughout the ray cell (Figure 3C). Axial paratracheal parenchyma vasicentric, aliform to confluent, forming irregular wide bands more than three cells wide, occasionally apotracheal parenchyma diffuse present, some crystals in chambers present (Figures 3A-B). Rays are homogeneous, mostly 1-seriate or occasionally 1-seriate partially 2-seriate (Figures 3E-F), mean height 291 μm (209-384 μm) and mean width 23.5 μm (19-28 μm), 15 (3-24) cells high, mean 15 rays per mm, composed by procumbent cells, not storied. Crystals in chambers present in the axial parenchyma (Figure 3G).

Remarks. The presence of characters such as solitary and multiple vessels, simple perforation plates, alternate and vested intervessel pits, vessel-ray pits similar to intervessel pits in size and shape, confluent aliform or vasicentric axial parenchyma forming bands, and homogeneous rays suggest affinity with the Fabaceae family (Metcalfe & Chalk, 1950; Cozzo, 1951; Wheeler & Baas, 1992). The fossil woods described here have been compared with mostly Miocene fossil wood records. The fossil genera referred to Mimosoideae are: *Acacioxylon* Schenk, 1883, *Adenantheroxylon* Prakash & Tripathi, 1968, *Albizinium* Prakash, 1975, *Albizioxylon* Nikitin, 1935, *Dichrostachyoxyton* Müller-Stöll & Mädler, 1967, *Eucacioxylon* Müller-Stöll & Mädler, 1967, *Ingoxylon* Müller-Stöll & Mädler, 1967, *Menendoxylon* Lutz, 1979, *Metacacioxylon* Gros, 1981, *Mimosoxylon* Müller-Stöll & Mädler, 1967, *Mimosaceoxylon* Lakhanpal & Prakash, 1970, *Paraalbizioxylon* Gros, 1992 diagnosis emended by Martínez (2014), *Paracacioxylon* Müller-Stöll & Mädler, 1967, *Piptadenioxylon* Suguio & Mussa, 1978, *Tetrapleuroxylon* Müller-Stöll & Mädler, 1967, *Anadenantheroxylon* Brea *et al.*, 2001, diagnosis emended by Franco (2011) and *Microlobiusxylon* Franco & Brea, 2010 (Table 1). The fossil

Figure 3. *Zygiaxylon amazonicum* gen. et sp. nov. (LPP-CZS 0061 holotype). **A**, TS, general view. Diffuse porous, vessels, parenchyma and fibers distribution; **B**, TS, detail of parenchyma and fibers; **C**, RLS, vessel elements, gum deposits (arrow) and distribution of rays and parenchyma; **D**, TSL, vessel ray pits (arrow), similar to intervessel pits; **E**, TLS, rays homogeneous 1-seriate and 1-seriate partially 2-seriate composed by procumbent cells, not storied; **F**, TLS, detail of homogeneous rays, 1-seriate partially 2-seriate; **G**, RLS, chambered crystal (arrow) present in axial parenchyma cells. **Abbreviations:** see Material and Methods. Scale bars: A,C-D,G = 50 μ m; B = 10 μ m; E-F = 30 μ m.

sample was compared to the genus mentioned on (Table 1) and present more similarity in the group of diagnostically characters with: *Anadenantheroxylon*, *Microlobiusxylon* and *Piptadenioxylon* but differs by having different density of vessels by mm², and because the rays are low in *Microlobiusxylon* and 2-3 seriate in *Piptadenioxylon*, and differs of *Anadenantheroxylon* by having axial parenchyma completely vasicentric, aliform (rhomboid) and confluent, neither rays 1-3 seriates (Table 1).

In the subfamily Mimosoideae, the Ingeae tribe is the largest, and it includes about ten genera and 300 extant species. Following Evans *et al.* (2006) the *Inga* alliance can be divided into genera with septate fibers and those with non-septate fibers, although most of the genera have uniseriate rays that are nearly always homocellular. Generally, the elements are not storied, but sometimes the rays may appear to be partially storied. Calcium oxalate crystals are common and are found predominantly in chambered fibers, and to a

Table 1. Comparisons between fossil genera of Mimosoideae (adapted from Gros, 1992).

Fossil genera	Vessels	Pits	Rays	Parenchyma	Fibers
<i>Acacioxylon</i> Schenk, 1883	most solitary	—	homogenous 1-3 seriate	paratracheal, uniseriate, apotracheal in bands	—
<i>Adenantheroxylon</i> Prakash & Tripathi, 1968	most solitary	—	homogenous 1-3 seriate	diffuse, vasicentric to aliform, confluent	non septate
<i>Albizzinium</i> Prakash, 1975	most solitary	medium	homogenous 1-seriate	diffuse, vasicentric to aliform, occasionally confluent	septate
<i>Albizzioxylon</i> Nikitin, 1935	solitary and groups	—	—	paratracheal	—
<i>Dichrostachyoxydon</i> Müller-Stöll & Mädél, 1967	solitary and small groups	medium	homogeneous and heterogeneous 1-10 seriate	vasicentric, aliform, and scarce confluent	non septate
<i>Euacacioxylon</i> Müller-Stöll & Mädél, 1967	solitary and small groups	medium	homogeneous 1-10 seriate	aliform to confluent in tangential bands	non septate
<i>Ingoxylon</i> Müller-Stöll & Mädél, 1967	solitary and small groups	medium	homogeneous 1-5 seriate	vasicentric to aliform, and occasionally confluent	septate
<i>Menendoxylon</i> Lutz, 1979	solitary and small groups	small to medium	homogeneous/ heterogeneous 1-3 seriate	vasicentric to aliform, and in short bands	non septate
<i>Metacacioxylon</i> Gros, 1981	solitary and small groups	medium	homogeneous 1-18 seriate	vasicentric to aliform, and oblique bands	non septate
<i>Mimosoxylon</i> Müller-Stöll & Mädél, 1967	solitary and small groups	small to medium	homogeneous 1-3 seriate	vasicentric and occasional aliform, and confluent	non septate
<i>Mimosaceoxylon</i> Lakhapal & Prakash, 1970	solitary and multiples	medium	homogeneous 1-9 seriate	paratracheal and diffuse	—
<i>Paraalbizzioxylon</i> Gros, 1992	solitary and small groups	small to medium	homogeneous 1-6 seriate	paratracheal, scarce to confluent and apotracheal present or absente	septate or non septate
<i>Paracacioxylon</i> Müller-Stöll & Mädél, 1967	solitary and small groups	medium	homogeneous 1-10 seriate	vasicentric, confluent and small bands	septate
<i>Piptadenioxylon</i> Suguio & Mussa, 1978	solitary and small groups	small	homogeneous 2-3 seriate	paratracheal, vasicentric and bands	non septate
<i>Tetrapleuroxylon</i> Müller-Stöll & Mädél, 1967	solitary and small groups	medium	homogeneous 1-5 seriate	vasicentric to aliform, and occasional confluent	non septate
<i>Anadenantheroxylon</i> Brea <i>et al.</i> , 2001	solitary and small groups	small	homogeneous 1-3 seriate	vasicentric complete, aliform (rhomboid form) and confluent	—
<i>Microlobiusxylon</i> Franco & Brea, 2010	solitary and small groups	small	homogeneous 1-2 seriate	vasicentric to aliform, confluent and banded	non septate
<i>Zygiaxylon amazonicum</i> (This work)	solitary and multiples	small to medium	1-seriate, occasional 1-seriate partially 2-seriate	Paratracheal vasicentric, aliform to confluent forming irregular wide bands of 4-10 cells high apotracheal diffuse present	non septate

lesser degree in chambered axial parenchyma cells. Gum deposits are very common and found in vessels, ray cells, axial parenchyma, and fibers. León (2008) also establishes the difference between genres of 31 species of Mimosoideae from Venezuela, taking characters as the presence or absence of septate fibers, parenchyma type and rays.

This specimen was compared with the extant species that now inhabit the Amazon region, whether endemic or not, and which present similar anatomical features: *Abarema jupunba* Willd, *Enterolobium maximum* Ducke, *Inga alba* Willd, and *Marmaroxylon racemosum* Killip, *Zygia longifolia* Willd and *Zygia cauliflora* Killip. The specimen is comparable to all of these genera in terms of its wood anatomy as density of vessels, tangential diameter of vessels, size and shape of intervessel pits, axial parenchyma type and distribution, fibers, rays, crystals and gum deposits. However, it seems to show closest affinity with *Zygia* based upon the types and distributions of its axial parenchyma and rays major uniseriate and occasionally uniseriate partially biseriate (see Table 2); the other genera feature 1-3 seriate rays series. The specimen presents more similarity in density of vessels by mm² and tangential diameter with *Z. cauliflora*, *Z. longifolia* and *Marmaroxylon racemosum*. Axial parenchyma and rays more similar to *Z. cauliflora* and *Z. longifolia*. Fibers more

similar with *Abarema jupunba*, *Z. cauliflora* and *Z. longifolia*. Presence of gum deposits are present in *Abarema jupunba*, *I. alba*, *Z. cauliflora* and *Z. longifolia* (Table 2).

Therefore, the sample described here presents characteristics that are especially similar to those of the extant neotropical and the absence of a fossil genus that shares all of the characteristics presented by the fossil in question, justifies the creation of the new genus *Zygiaxylon*, with the name reflecting its similarities with the extant genus *Zygia*.

Species from Ingeae tribe currently can be found in the forests of Africa, Asia, and Australia, as well as in Central America and throughout South America. In Brazil, their occurrence is recorded in all seven biomes, with the greatest center of diversity found in the Amazon region (Ducke, 1943). In the Brazilian Amazon the tribe is represented by 206 species in 14 genera. Studies on this group have determined that the species are limited to the rainforest areas, many of which are typically secondary forests on poorly drained or periodically flooded land areas (Pennington, 1997). As suggested by Herendeen *et al.* (1992), the Fabaceae show the ability to adapt to any environment. Early studies of extant legumes for the Brazilian Amazon were performed by Ducke (1925, 1930, 1943), with a large number of species having first been described in these sources.

Table 2. Comparisons between extant species of Mimosoideae.

Extant specie	Reference	Vessels	Intervascular pits	Axial parenchyma	Rays	Fibers	Crystal	Gum/ resin deposits
<i>Abarema jupunba</i> Willd	León, 2008	3-4 mm ² 135-255 µm	alternate minute to small vested	Paratracheal vasicentric, aliform to confluent in short wing. Occasionally apotracheal diffuse present on small islands	homogeneous 1-3 seriate 3-7 mm 170-460 µm height	non septated	—	present
<i>Enterolobium maximum</i> Ducke	Détienne & Jacquet, 1983	5 mm ² 170-240 µm	alternate medium vested	Paratracheal vasicentric, aliform to confluent in lozenge type 2-6 cells hight	homogeneous 1- 3 seriate 5-7 mm	some septated	present	—
<i>Inga alba</i> Willd	Miller & Détienne, 2001	1-3 mm ² 200-250 µm	alternate medium vested	Paratracheal vasicentric, aliform to confluent in lozenge type 2-6 cells hight	homogeneous 1- 3 seriate 7-10 mm	septated	present	present
<i>Marmaroxylon racemosum</i> Killip	Détienne & Jacquet, 1983	5 mm ² 160-200 µm	alternate small vested	Paratracheal vasicentric, aliform to confluent in lozenge type 2-6 cells hight	homogeneous 1- 3 seriate 5-7 mm	some septated	present	—
<i>Zygia cauliflora</i> Killip	Détienne & Jacquet, 1983	2-6 mm ² 110-170 µm	alternate small vested	Paratracheal vasicentric, aliform to confluent in lozenge type 2-4cells hight	homogeneous 10 mm uniseriate, occasional uniseriate partially biseriate	non septated	present	present
<i>Zygia longifolia</i> (Humb. & Bonpl. ex Willd.)	León, 2008	10-12 m ² 70-140 µm	alternate small to medium vested	Paratracheal vasicentric, aliform to confluent in wide bands; apotracheal diffuse present	homogeneous uniseriate, occasional uniseriate partially biseriate 6-12 mm 90-310 µm height	non septated	present	present
<i>Zygiaxylon amazonicum</i> (This work)	this work	5-8 mm ² (89-251) 195 µm	alternate small to medium vested	Paratracheal vasicentric, aliform to confluent forming irregular wide bands of 4-10 cells hight; apotracheal diffuse present	homogeneous uniseriate, occasional uniseriate partially biseriate 10 mm 209-384 µm height	non septated	present	present

Subfamily PAPILIONOIDEAE De Candole, 1825

Swartzioxylon Delteil-Desneux, 1980 emend.
Kloster & Gnaedinger

Type species. *Swartzioxylon naraense* Delteil-Desneux, 1980.

Emended diagnosis. Growth rings indistinct to absent. Diffuse porous. Vessels commonly solitary or in radial multiples; small vessels with scarce clustering. Simple perforation plates oblique or horizontal. Intervessel pits alternate, small and vestured; vessel-ray pits with distinct borders, similar to intervessel in size and shape throughout the ray cell. Simple fibers very thin-walled. Axial parenchyma vasicentric to aliform and in scarce bands. Rays homogeneous, numerous and storied. Chambered crystals present in the axial parenchyma.

Remarks. Generic diagnosis was emended to include the small size and vesturing of intervessel pits, description of vessel-ray pits, scarce clustering, classification of the ray cells, and arrangement of axial parenchyma.

Swartzioxylon naraense Delteil-Desneux, 1980 emend.
Kloster & Gnaedinger
(Figures 4C-D,5)

Specific diagnosis. Growth rings indistinct or absent; diffuse porous and low density of vessels; vessels commonly solitary or in radial multiples; very small vessels; scarce clustering; simple perforation plates oblique or horizontal. Intervascular pits alternate, small and vestured. Vessel-ray pits with distinct borders, similar to intervessel in size and shape throughout the ray cell. Simple fibers very thin-walled. Axial parenchyma vasicentric, aliform, confluent and in scarce bands. Rays homogeneous, 1-2 seriate, 9-14 per mm linear and very low, storied. Chambered crystals present on axial parenchyma.

Material studied. LPP-CZS 0069.

Repository. Laboratory of Paleontology and Paleobotany of Universidade Federal do Acre, Campus Cruzeiro do Sul, Brazil.

Stratigraphic horizon. Solimões Formation, Acre Basin.

Type locality. Estirão do Mississippi, Juruá River, State of Acre, Brazil.

Figure 4. SEM. **A-B**, *Zygiaxylum amazonicum* gen. et sp. nov. (LPP-CZS 0061 holotype); **A**, TS, gum deposits between vessels (arrow); **B**, RLS, detail of small and vestured intervessel pits (arrow). **C-D**, *Swartzioxylon naraense* (LPP-CZS 0069 holotype), RLS, detail of small and vestured intervessel pits (arrows). **Abbreviations:** see Material and Methods. Scale bars: A = 30 μ m; B-D = 5 μ m.

Description. This description is based in one piece of silicified wood measuring 20 cm long and 15 cm in diameter. Pith, primary xylem, outer cortex, and secondary phloem are not preserved. Growth ring indistinct or absent. Diffuse porous with diagonal and/or radial patterning (Figure 5A). The vessels are more or less circular, solitary (55%) or in multiples of 2, 3, or 4 (30%, 9%, 6%, respectively), and rarely in clusters (Figures 5A-C). Mean vessel tangential diameter of 87.4 μm (31.5-137 μm), mean vessel element length 198.8 μm (100-269 μm) (Figure 5D). Mean vessels per mm^2 22 (17-27 per mm^2) (Figure 5A), simple perforation plates with transverse or oblique end walls and intervessel pits alternate, small and vestured, mean 6 μm (5-8 μm) (Figures 4C-D,5E). Vessel-ray pits with distinct borders, similar to intervessel pits in size and shape throughout the ray cell (Figure 5F). Ground tissue fibers are circular to polygonal in outline, non-septate, with a mean diameter of 5.5 μm (4.5-6.7 μm) (Figure 5C). Axial paratracheal parenchyma vasicentric,

aliform to confluent (Figures 5A-C). Rays are 1-seriate and 2-seriate with mean height of 25 μm (15-32 μm) and mean width of 6.8 μm (5-10 μm), 6 (2-10) cells high, mean of 12 rays per mm , homogeneous Kribs type III, composed entirely of procumbent ray cells. All elements storied (Figures 5G-H). Chambered crystals present in axial parenchyma (Figure 5I).

Remarks. The subfamily Papilionoideae is represented by characteristics including vessels solitary and in radial multiples of 2 or 3; simple perforation plates; alternate intervessel pits; and very small, vestured vessel-ray pits similar to intervessel pits. Axial parenchyma is usually abundant, confluent and banded, with chambered crystals present in most genera. Rays are mostly 1 to 3 seriate, homocellular, and composed of procumbent cells, with non-septate fibers and rays storing (Metcalf & Chalk, 1950; Cozzo, 1951; Wheeler & Baas 1992). In the present work more comparisons were made, with *Dalbergioxylon antiquum* Ramanujam, 1960 and *Dalbergioxylon dicorynioides* Müller-

Figure 5. *Swartzioxylon naraense* (LPP-CZS 0069). **A-B**, TS, general view, diffuse porous, vessels solitaires and multiples and parenchyma distribution; **C**, TS, detail of a solitary vessel, axial parenchyma and fibers; **D**, RLS, vessel elements and simple perforation plates (arrow); **E**, RLS, detail of a vessel and intervessel pits small, alternate and vestured (arrow); **F**, RLS, vessel-ray pits, similar to intervessel pits (arrow); **G-H**, TLS, rays homogeneous, 1-seriate, 1-seriate partially 2-seriate and 2-seriate, parenchyma and rays storied; **I**, TLS, chambered crystals; present in axial parenchyma (arrows). **Abbreviations:** see Material and Methods. Scale bars: A-D, 50 μm ; E-I = 30 μm .

Stoll & Mädél, 1967 differing from *Swartzioxylon naraense* by having fewer vessels per mm² and rays 1 to 3 seriate and higher. When compared with *Andiroxylon cinnamomeus* Martinez-Cabrera, *S. naraense* differs because the former has heterogeneous rays, and it differs from *Pterocarpoxylon arcotense* Ramanujam (1960) by having more vessels per mm² and lower rays. *Swartzioxylon naraense* was also compared with the extant genera *Pterocarpus* Jacquet and *Cynometra* L. and the fossil taxa *Pterocarpoxylon arambourgii* Boureau, *P. tibestiense* Boureau, *Caesalpinioxylon tchadense* Koeninger, and *Paratrachilioxylon* Koeninger (Table 3). Because of the great similarity between the sample of Solimões Formation and *S. naraense* it was decided to include the sample in the specie previously described and an emend have been made to the description by Delteil-Desneux (1980).

Currently both of these tribes are well represented in Amazonian rainforest. With approximately 68 species, the genus *Swartzia* Schreber is the most extensively represented member of subfamily Papilionoideae (Ribeiro *et al.*, 1999). However, *Swartzia* was previously considered as belonging to subfamily Caesalpinioideae, and discussion of this group's position has continued up until the present time. Both of the tribes mentioned are very well distributed throughout the Amazon region as trees, shrubs, and lianas.

For the Neogene record in the Americas, Mussa (1959) described the morphogenus *Zollernioxylon* Mussa from the Solimões Formation and assigned three new fossil species.

Boureau & Salard (1962) described a fossil wood assigned to *Ficoxylon cretaceum* Schenk, and Suguio & Mussa, 1978 described two new fossil species: *Piptadenioxylon chimeloi* and *Myrocarpoxyton sanpaulense*. From the department of Sucre in Colombia, Pons (1980) described a new Pliocene morphogenus *Crudioxylon*. Selmeier (2004) described *Crudioxylon brasilense* from Cenozoic sediments collected in the Parnaíba Basin in the Brazilian State of Maranhão, although without establishing greater accuracy in terms of age. Finally, Pons & De Franceschi (2007) briefly mention two Miocene woods from the Pebas Formation in Peru, one with affinity to *Andira* Jussieu or *Hymenolobium* Benthham and the other to the Ingeae tribe, although they do not provide anatomical descriptions.

The South American fossil wood record was recently reviewed in a paper by Pujana *et al.* (2011), who state that the best represented subfamily is the Mimosoideae, followed by the Papilionoideae and Caesalpinioideae. Most recently from this region a new record of *Zollernioxylon* sp. from the Solimões Formation was published by Machado *et al.* (2012), as well as a new record of *Zollernioxylon tinocoi* by Kloster *et al.* (2013) from the Solimões Formation in the Acre Basin.

FINAL CONSIDERATIONS

The specimens described here provide new evidence regarding the past distribution of the Papilionoideae and Mimosoideae subfamilies, which appears to be similar to

Table 3. Fossil wood species compared with *Swartzioxylon naraense*.

Species Age/Country	Vessels	Intervessel Pits	Parenchyma	Fibres	Rays	Storied	Crystals
<i>Dalbergioxylon antiquum</i> Ramanujam, 1960 Miocene/India	190 - 275 µm 6 - 12 mm ²	small alternate	abundant aliform - confluent and apotracheal	non septate	8-14 per mm 1-3 seriates, most 3-seriate heterogeneous	+	—
<i>Pterocarpoxylon arcotense</i> Ramanujam, 1960 Miocene/ India	165 - 215 µm 10 - 15 mm ²	very small alternate vestured	abundant, aliform- confluent and apotracheal	non septate	12-18 per mm 1-2 seriate, Most 1-seriate homogeneous	+	—
<i>Dalbergioxylon dicorynioides</i> Müller-Stöll & Mädél, 1967 Oligocene/Egypt	< 350 µm 5 - 20 mm ²	very small alternate	aliform confluent banded	non septate	4-12 mm 1-3 seriate homogeneous	+	—
<i>Andiroxylon cinnamomeus</i> Martinez-Cabrera, 2006 Miocene/Mexico	100 - 200 µm 5 - 20 mm ²	small alternate	aliform confluent banded	non septate	4-12 mm 1-3 seriate Heterogeneous	+	—
<i>Swartzioxylon naraense</i> Delteil-Desneux, 1980 Tertiary/Tunisia	100 µm 68 - 100 µm 27 vessels mm ²	—	vasicentric confluent	non septate	12 mm 1-2 seriate homogeneous	+	crystals in chambered
<i>Swartzioxylon naraense</i> Miocene/Brazil (this work)	85 µm 31 - 137 µm 22 vessels mm ²	small alternate vestured	vasicentric aliform to confluent	non septate	12 mm 1-2 seriate homogeneous	+	crystals in chambered

that of the extant genera in the Ingeae and Swartzieae tribes. *Zygiaxylon* gen. nov. and *Swartzioxylon* may have been important components of the flora during the Miocene in this region of the Amazon, and thus the presence of these genera contributes to our existing knowledge of the South America paleofloras. The fact that in the Miocene the temperature in the Brazilian Amazon was warmer and more humid may explain an increasing diversity in the flora.

The anatomy of these fossil woods shows characteristics similar to those of fossil specimens found in the Americas, Africa, and India. However, our current knowledge is still very fragmented and not yet sufficient to clearly show the biogeographic patterns and processes involved in the origin and differentiation of the Amazon flora. The taxa discussed in this work probably inhabited the upland forests and floodplains in Amazonia during the Miocene. Adami-Rodrigues *et al.* (2013) support the interpretation of a fluvial environment with periodic flooding, reinforcing the theory that the Fabaceae can inhabit a diversity of environments.

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