Revista Brasileira de Paleontologia, 25(4):303–321, Outubro/Dezembro 2022
A Journal of the Brazilian Society of Paleontology

doi:10.4072/rbp.2022.4.05

FIRST RECORD OF PLANT MACROFOSSIL FROM THE BOA VISTA FORMATION, TAKUTU BASIN, RORAIMA STATE, BRAZIL

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ABSTRACT – Clayey intraclasts containing leaves preserved as impressions and compressions were collected from the Takutu River channel in the State of Roraima, Brazil. In the present study, 23 leaf fragments are described (morphologically and anatomically) and their taxonomic identity is proposed. These fossiliferous intraclasts were suggested in previous studies as coming from the Boa Vista Formation (Upper Pleistocene–Holocene). With the aim of finding new evidence to support this correlation, X-ray diffractometry (XRD) and Laser induced-breakdown spectroscopy (LIBS) analysis were performed, comparing the fossiliferous sample with two outcrops from the Boa Vista Formation. The results evidenced the chemical and mineralogical similarity between the fossiliferous intraclasts and both outcrops, suggesting their correlation with the Boa Vista Formation. Taxonomically, the specimens were recognized as fossil representatives of Dilleniaceae Salisb., *Byrsonima* Rich. ex Kunth (Malpighiaceae), *Zanthoxylum* L. (Rutaceae), and other six morphotypes. These taxa represent typical elements of the savanna (*lavrados*) of Roraima. The anatomical-cutillary characters of the mummified leaves indicate the dominance of xeromorphic plants, similar to the predominant woody species in the "*lavrado*" today, thus suggesting the same climatic-environmental conditions.

Keywords: fossil leaves, leaf architecture, cuticular anatomy, angiosperm, Cenozoic.

RESUMO – Intraclastos argilosos contendo folhas preservadas como impressões e compressões foram coletados no canal do Rio Tacutu, Estado de Roraima, Brasil. No presente estudo, 23 fragmentos de folhas são descritos (morfológica e anatomicamente) e sua identidade taxonômica é proposta. Estes intraclastos fossilíferos foram sugeridos, em estudos prévios, como provenientes da Formação Boa Vista (Pleistoceno Superior–Holoceno). Com o objetivo de encontrar mais evidências para suportar essa correlação foram realizadas, neste estudo, análises com técnicas de Difração de Raio-X (DRX) e o *Laser-Induced Breakdown Spertroscopy* (LIBS) comparando as amostras fossilíferas com amostras de dois afloramentos da Formação Boa Vista. Os resultados das análises química e mineralógica evidenciaram similaridades entre as amostras fossilíferas e os dois afloramentos, reforçando a correlação desses intraclastos com a Formação Boa Vista. Taxonomicamente os espécimes foram reconhecidos como representantes de Dilleniaceae Salisb., *Byrsonima* Rich. ex Kunth (Malpighiaceae), *Zanthoxylum* L. (Rutaceae) e outros seis morfotipos. Estes táxons representam elementos típicos da savana (lavrados) de Roraima. Os caracteres anatômicos-cuticulares das folhas mumificadas indicam a dominância de plantas xerofíticas, similares às plantas lenhosas atuais típicas do "lavrado" sugerindo, portanto, as mesmas condições climáticas e ambientais.

Palavras-chave: folhas fósseis, arquitetura foliar, anatomia cuticular, angiospermas, Cenozoico.

INTRODUCTION

Studies related to paleobotany in the State of Roraima are limited to recent works, which results in a still incipient knowledge about the paleoflora of the region. Cruz (2019) recorded the occurrence of fossilized leaves, Santos (2015) described fossil woods and Santos *et al.* (2016) described the presence of coal formed during the Early Cretaceous. These studies were carried out with fossils recovered from the Serra do Tucano Formation.

The stratigraphic unit of the Cenozoic of the Takutu Basin with the highest phytofossilliferous potential is the Boa Vista Formation. Marques-de-Souza *et al.* (2018) published the record of two specimens of mummified fossil leaves, which were found *ex situ* on the banks of the Takutu River. Wankler & Marques-de-Souza (2018) suggested the Boa Vista Formation as the unit of origin of these fossils, based on the mineralogical and chemical similarity between the fossil samples and unconsolidated sediments from Boa Vista Formation. Oliveira (2020) described coal fragments recovered from the Boa Vista Formation, assigning them a Late Pleistocene–Holocene age on the basis of radiocarbonic and Optical Stimulated Luminescence (**OSL**) datings.

This work presents new records of plant macrofossils, discuss the taxonomy and anatomy of the fossil leaves, and gives more evidence to support the correlation of this fossiliferous material with the Boa Vista Formation.

MATERIAL AND METHODS

Geology of the study area

The study area is located in the Takutu Basin, which is distributed between Brazil (Roraima State), and the Federative Republic of Guyana (Figure 1). The Takutu Basin or, North Savannas Rift Valley as it is called in Guyana, is located in the central region of the Guiana Shield, north of the Amazon Craton (Costa & Falcão, 2011), and in the Maroni-Itacaiúnas belt (Tassinari & Macambira, 1999), formed during the Transamazonian Orogenic Cycle (2.1–1.8 Ga). It has an extension of about 300 km in length, 30–50 km in width, and its origin is related to the opening of the North and Central Atlantic Ocean (Burke, 1976), occurred at the end of the Jurassic and in the beginning of the Cretaceous, when old anisotropies of its framework were reactivated and resulted in the formation of faults of extensional character oriented NE-SW and NW-SE (Crawford *et al.*, 1985; Costa *et al.*, 1991; Vaz *et al.*, 2007).

The basin is composed by seven stratigraphic units that were deposited on the crystalline basement of the Surumu Group (Vaz *et al.*, 2007). These units are: (i) Apteri Formation (Upper Jurassic), with most of its rocks made up of basalts as result of successive flows, with some sedimentary rocks being found interspersed with basalt (Eiras & Kinoshita, 1990); (ii) Manari Formation (Upper Jurassic), formed by deposition of shales and siltstones (Crawford *et al.*, 1985); (iii) Pirara Formation (Upper Jurassic), formed by edge fanconglomerates, shales, siltstones, hyalites and lake carbonates; (iv) Takutu Formation, set up by sandstones, carbonates and shales with deposition of reddish layers; (v) Serra do Tucano Formation, composed of Lower Cretaceous sandstone layers (Vaz *et al.*, 2007); (vi) Boa Vista Formation (Upper Pleistocene–Holocene), formed by a thin, loose, light-colored sandy sedimentation, clayey cement, and interspersing pebbly layers (Barbosa & Andrade-Ramos, 1959); (vii) Areias Brancas Formation, which consists of the recent wind reworking of the deposits of the Boa Vista Formation (Vaz *et al.*, 2007).

Only two stratigraphic units of the Takutu Basin have macrofossils records: the Serra do Tucano Formation and the Boa Vista Formation. The latter, of Cenozoic age, crops out in the vicinity of the study area and was suggested as an unit of provenance for the fossils analyzed by Wankler & Marques-de-Souza (2018).

Boa Vista Formation

The first reference to the "Boa Vista Formation" as a lithostratigraphic unit was made by Andrade-Ramos (1956), who identified a sedimentary succession of unconsolidated gravel, clayey sand, and sandy clay (Reis *et al.*, 2002) filling a wide flat area in the center/east of the State of Roraima.

The Boa Vista Formation is considered a heterogeneous unit both spatially and vertically in terms of faciological composition. Recent studies describe it as a relatively shallow sedimentary unit, whose thickness changes according to the conformation of the basement, ranging from 15 to 120 m. It is constituted by two semi-consolidated sedimentary successions, the lower, composed of gravels with grains of varying sizes (between granule and boulder), and the upper one, composed of ferruginous sands slightly conglomeratic and silty-sandy deposits (Stern, 2019; Menezes *et al.*, 2020). According to Barbosa & Andrade-Ramos (1959) the Boa Vista Formation can be characterized as a set of layers of sand and, secondarily, laterite and mud, sometimes with intercalations of sandy to muddy layers, with gravel to pebbly levels, frequently with lateritic concretions. Carneiro *et al.* (1968) also identified the presence of gray clay and sandy clays in the unit.

According to Menezes *et al.* (2020), the deposition of the lower sedimentary succession would have been strongly controlled by the structuring of the Takutu hemigraben in its last tectonically active phase, transcurrent and compressive movements occurred in response to the interactions of the Caribbean and South American plates, inverting and uplifting the Mesozoic sedimentary units, which served as a source area for the sediments.

The deposition of the upper succession of the Boa Vista Formation took place after the end of the active phase and was structured from a low gradient alluvial plain, formed from the southern front of the Marari-Memória mountains. The landscape began to be exposed to weathering forming an intertwined fluvial system of distributary sandy bars, transporting the fine sediments that were deposited throughout the physiographic domain that today composes the Boa Vista Formation, resulting in the extensive pediplain that characterizes the central-northwest region of the State of

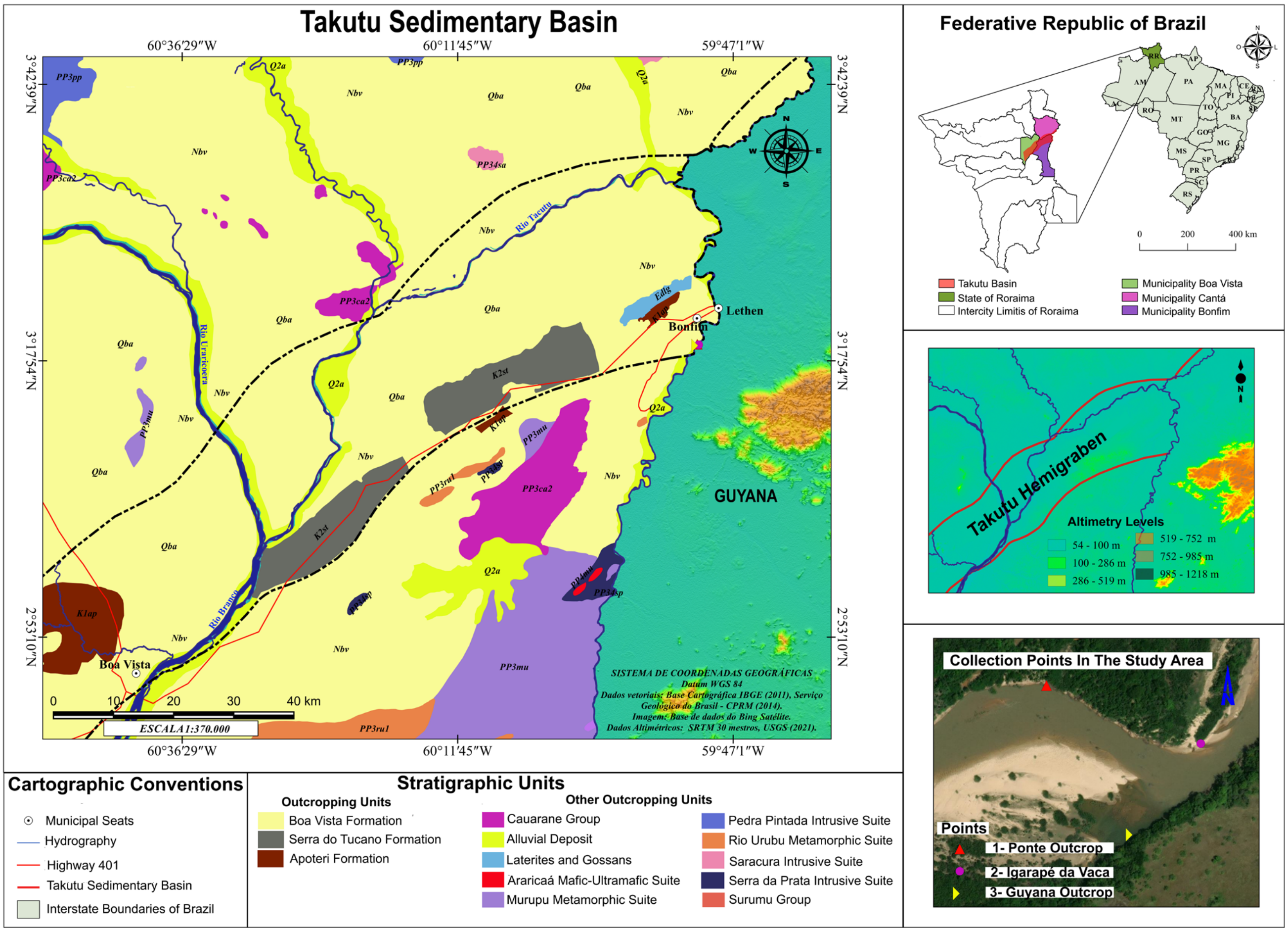

Figure 1. Location map of the Takutu Basin, with stratigraphic units and study area. Map prepared by Randielly Barbosa.

Roraima (Menezes *et al.*, 2020). The Optically Stimulated Luminescence dating of the upper unit of the Boa Vista Formation places the deposition of this unit in the Late Pleistocene–Holocene (Stern, 2019; Zular *et al.*, 2019; Oliveira, 2020).

Fossil material: origin and preservation

The fossil samples, deposited in a point bar of the Takutu river during the last flood cycle, were collected in a dry period (December to February). The plant fossils collected are into poorly consolidated light gray pelitic intraclasts containing medium and coarse sand. The nature of the sedimentary material, as well as the fragility of the preserved fossils (leaves), suggest that the initial deposition site and the final deposition site are not far.

Two outcrops located upstream of the intraclast collection site were chosen for comparative analysis due to textural similarities of the rocks with the fossiliferous samples, namely: Ponte Outcrop and Guyana Outcrop (Figure 1). Fossil prospecting studies were carried out in both outcrops. In the outcrop of Ponte, which corresponds to a fluvial terrace of the Takutu River, leaf impressions and mummified leaves were located, but, due to poor preservation, were not included in this study.

The collected plant fossils (n = 23) are preserved as impressions and compressions, in the latter case, mummified. They are deposited in the Scientific Collection of the Universidade Estadual de Roraima (**UERR**) and are listed in the Laboratory of Sample Processing and Collection of Rocks and Fossils under the acronym **CCU**.

Morphological analysis

The fossils were prepared following the classic methods in paleobotany (Dutra, 2002). For morphological analysis, the manuals of "Foliar Architecture" published by Hickey (1973), Ash *et al.* (1999) and Ellis *et al.* (2009) were considered.

At first the leaves were grouped by morphotypes. After this process, the samples were analyzed and described using the specimen description as proposed by Ellis *et al.* (2009). This process of analysis and description of the leaves was made with a Leica ES2 stereomicroscope, a Marberg digital caliper 300 mm-12" and the free software ImageJ.

The material was photographed with a Canon reflex 60D, 50 mm lens, and associated close-up filters. Drawings of the venation pattern were made from the photographs in the Inkscape program. The taxonomic identification of the material was made by consulting different virtual herbaria, such as Reflora Brasil (2020), New York Botanical Garden

(2017) and local herbaria Herbarium of the Universidade Federal de Roraima (**UFRR**) and the Herbarium of the Museu Integrado de Roraima (**MIRR**). For the initial approximation of botanical families, Flora Brasil (2020) was used, as well as Meneses *et al.* (2015) and Melo & Barbosa (2007) studies.

Anatomical Analysis

The analyses of the anatomical features were made from the observation and description of cuticles found in the samples. The "chemical maceration" technique was used to prepare the cuticles. It consists of a treatment with 20% hydrogen peroxide (H_2O_2), washing in distilled water, and fixing on a slide (technique detailed in Dutra, 2002). The slides were observed using a Nikon eclipse E200 optical microscope, with a Moticam 10 mp camera attached. Besides observing the macerated material, slides with unmacerated fragments were produced for observation under a fluorescence microscope (Olympus BX51 and BX61, with an Olympus DP71 camera).

Optical microscopy analyses were performed at the Laboratory of Sample Processing and Collection of Rocks and Fossils of the UERR, and the fluorescence microscopy analyses were performed at the Palynology Laboratory of the Universidade Federal do Rio Grande do Sul (**UFRGS**).

The identification of stomata followed Dilcher (1974) and Carpenter (2005), considering the following parameters: (i) contact cells, whether specialized or not; (ii) the presence or absence of lateral or polar subsidiary cells; (iii) the presence or absence of non-contact specialized cells; (iv) orientation of the walls of the contact cell.

For the description of trichomes were considered: (i) the presence of trichomes; (ii) shape; (iii) nature of the base; (iv) nature of the epidermal cells at the base o (v) number of cells; (vi) shape of the apex (Dilcher, 1974). Finally, for the description of the epidermis cells were considered: (i) shape and arrangement; (ii) wall pattern; (iii) type of cell wall undulation; (iv) presence and type of cellular ornamentation (Dilcher, 1974). In addition, the trichome frequency index (Dilcher, 1974) was performed, expressed by

$$(I) = [T \div (E + T)] \times 100$$

where "T" represents the number of trichomes per unit area and "E" the number of epidermal cells per unit area.

Chemical and mineralogical analysis

We used X-Ray Diffraction (**XRD**) and Laser-Induced Breakdown Spectroscopy (**LIBS**) to compare the nature of the fossils and the sedimentites cropping out nearby.

XRD was performed at the X-ray Laboratory of the Analytical Center of the Universidade Federal do Ceará (**UFC**). For this, the rock samples were macerated with the help of a mortar and ceramic pestle, sieved to 200 mesh and processed in the RIGAKU DMAXB equipment, using the powder method, through the following operational steps: Cu Kα radiation (30kV/40mA), 2θ reading, ranging from 3 to 50°, with a step of 0.02° every 0.5.

The samples for analysis in LIBS were processed in the Laboratory of Plasma and Atomic Spectroscopy (**LaPEA**), Physic Department, Universidade Federal de Roraima. After the procedure, the free software LTB Sophi was used to interpret the results.

RESULTS

Stratigraphic positioning of fossils

The results of the XRD analysis (Table 1) indicate that all the fossiliferous samples (CCU 033; 036; 013; 006; 025; 016; 015; 008; 010) are similar in mineralogy, as well as with the samples taken from the Outcrop of Ponte (CCU 055; 057) and Outcrop Guyana (CCU 056; 058). The LIBS results indicate also similarities synchronism between the fossiliferous samples and the two analyzed outcrops, as can be seen in Figure 2.

Quartz was the most abundant mineral, ranging from 32.7% to 41% of the sample composition. Kaolinite appeared in more variable amounts, ranging from 12% to 32.3%. These two minerals predominate in samples from the Boa Vista Formation being accompanied by hematite and goethite in small proportions (Carneiro-Filho, 1992; Meneses *et al.*, 2007). Although the presence of iron was indicated in LIBS, hematite and goethite were not detected in the XRD analysis, probably due to the low concentrations of these minerals in the samples.

The presence of Orthoclase (11% to 35%) and Plagioclase (14% to 38%) was also representative in the samples, and no differences were observed in the proportion of these minerals in the fossiliferous samples when compared with the samples from the outcrops of Ponte and Guyana (Table 1).

Both the Ponte Outcrop and the Guyana Outcrop are composed of light gray sands containing an important fraction of clay, which was evident in the mineralogical analysis presented. The outcrop of Ponte corresponds to a Quaternary fluvial terrace of the Takutu River, which strengthens the correlation of the fossiliferous material with the Boa Vista Formation.

SISTEMATIC PALEOBOTANY

Clade Core EUDICOTS APG IV, 2016
Clade SUPERROSIDES APG IV, 2016
Clade ROSIDES APG IV, 2016
Clade FABIDAE APG IV, 2016
Order MALPIGHIALES Juss. ex Bercht. & J. Presl
Family MALPIGHIACEAE Juss.

Byrsonima Rich. ex Kunth

Byrsonima sp.
(Figures 3–4)

Table 1. Mineralogical content of the control samples from the exposed levels of the Boa Vista Formation (CCU 058, 057, 056, 055), and from the fossiliferous samples (CCU 033, 036, 013, 006, 025, 032, 016, 015, 008, 010) recovered from the Takutu River.

Sample	Quartz (%)	Kaolinite(%)	Ortoclase (%)	Plagioclase (%)
	SiO_2	$Al_2Si_2O_5(OH)_4$	$KALSi_3O_8$	$(Na,Ca)Al(Si,Al)Si_2O_8$
CCU006	32.7	29.7	19.8	17.8
CCU008	39.6	16.8	22.8	20.8
CCU010	37	30	19	14
CCU013	18.2	18.2	26.3	37.4
CCU015	37	30	19	14
CCU016	34.3	16.2	11.1	38.4
CCU025	34.3	12.1	24.2	29.3
CCU032	34	18	19	29
CCU033	39	26	35	-
CCU036	41	24	35	-
CCU055	41	14	14	31
CCU056	34.3	32.3	18.2	14.1
CCU057	43	18	22	17
CCU058	37	17	12	34

Material. CCU 003 (Figure 4N); CCU 006a, b (Figure 4A); CCU 007 (Figure 4G); CCU 011 (Figure 4C); CCU 016 abA (Figure 3C); CCU 035 (Figure 4E).

Morphological description. Leaf organization simple, laminar size microphyll, L:W ratio 2:1, laminar shape elliptic/ovate(?) with medial symmetry. Margin entire with acute apex angle, straight apex shape, obtuse base angle and convex base shape. Primary venation pinnate with no naked basal veins, simple agrophic veins. Major secondaries are brochidodromous and, sometimes, eucamptodromous, with irregular spacing and variation of major secondary angle to midvein smoothly decreasing proximally, and excurrent attachment to midvein. Intersecondary proximal course parallel to major secondaries, length less than 50% of subjacent secondary, distal course parallel to major secondary and frequency less than 1 per intercostal area. Intercostal tertiary veins reticulate (Figure 3D, arrow) and, sometimes. percurrent mixed (Figure 3G, arrow) with obtuse angle to midvein and consistent vein angle variability. Epimedial terciaries opposite percurrent with admedial course perpendicular to the midvein and exmedial course parallel to intercostal tertiaries. Quaternary vein fabric alternate percurrent (Figure 4I). Quinternary vein fabric irregular reticulate. Areolation shows moderate development. Freely ending veinlets (FEVs) are usually dichotomous (Figure 4I). Marginal ultimate venation not preserved.

Anatomical description. anatomical data were obtained from the maceration of fossil cuticles of specimens CCU 007 (Figure 4G); CCU 011 (Figure 4C); CCU 016abA (Figure 3C) and CCU 035 (Figure 4E). The material has a rectangular epidermal cell shape, 27–98 µm in length, 17–78 µm in width, arrangement of tetragonal/random epidermal cells, primarily straight cell wall pattern (Figure 4J). Undulation assumes an "U" shape (Figure 3H) when present. Paracytic stomata on the abaxial surface (Figure 4M), and amphicyclocytic(?) on the adaxial surface. Trichomes present, with solitary occurrence, filamentous "V" and "T" shaped (Figures 3E and 4H). Nature of trichome bases with connection slightly modified, unmodified epidermal basal cells and unmodified base. Nature of trichomes of one to two cells, apex not conspicuous and/or branched once (Figure 3F). Trichomes 923–3030 µm in length and 203–7219 µm in width.

Comparison and discussion. After comparisons with specimens of the flora of the region (Flora do Brasil, 2020), a similarity with Malpighiaceae was observed, especially due to the presence of paracytic stomata and "T" and "Y" shaped trichomes (MetCalfe & Chalk, 1979). This family has 46 genera and 588 species occurring in Brazil. For Roraima, 17 genera and 47 species are recorded (Flora do Brasil, 2020). *Banisteriopsis* C.B.Rob. ex Small., *Blepharanda* Griseb., *Byrsonima* Rich. ex Kunth. and *Camarea* A. St-Hil. are recorded for Amazonian savannas, and *Banisteriopsis* C.B.Rob. ex Small., *Bronwenia* W.R.Anderson & C.C.Davis., *Bunchosia* Rich. ex Juss., *Byrsonima* Rich. ex Kunth., *Diplopterys* A.Juss., *Stigmaphyllon* A. Juss. and *Tetrapterys* Cav. occur in gallery and riparian forests.

Blepharanda has a rounded, obtuse and, sometimes, emarginate apex (Wilf *et al.*, 2021), course of tertiary vein angle acute with inconsistent variation and irregular reticulate quaternary venation. *Camarea* has a laminar size nanophyll, laminar shape elliptic-lanceolate (Menezes & Flores, 2013) and the spacing of the major secondaries decreasing

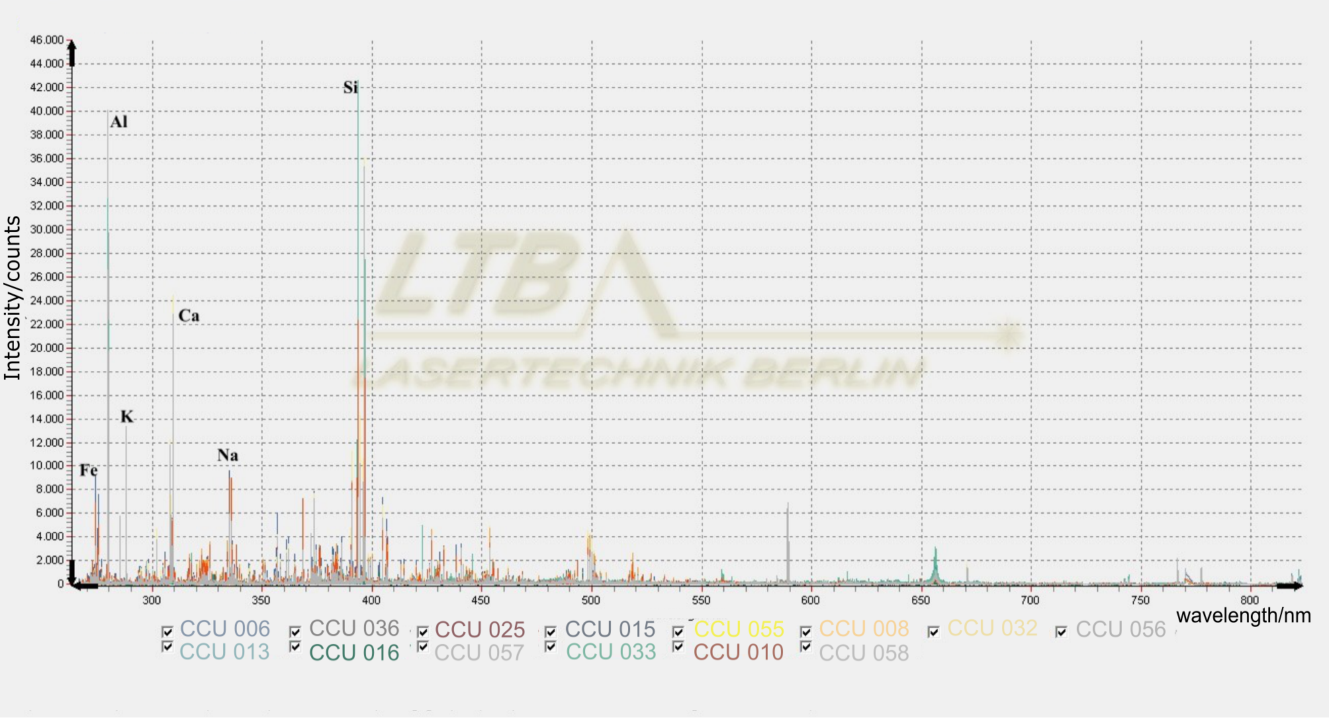

Figure 2. Result of Laser-Induced Breakdown Spectroscopy (**LIBS**) analysis on ten fossiliferous samples from the Takutu River and four control samples recovered from the Boa Vista Formation.

proximally. *Stigmaphyllon* has a rounded apex and reflex base, decurrent attachment of the secondary venation into the midvein. Intersecondaries span more than 50% of the length of the subjacent secondary and have a reticulate or branched distal course. Epimedial tertiary fabric alternate percurrent. Reticulate quaternary vein fabric and quinternary vein fabric freely ramifying. Due to these characteristics, these three genera differ morphologically from the specimens under analysis.

Banisteriopsis, according to a study carried out by Araújo *et al.* (2020), in which they compared 42 species of this genus, only *B. adenopoda* (A. Juss) B. Gates has a quinternary venation. Furthermore, representatives of this genus have glands at the base of the petiole, in the basal and medial area of the leaf blade (Araújo *et al.*, 2010). *Diplopterys* represented by *Diplopterys pubipetala* (A. Juss) W.R. Anderson & C.C.Davis has glands on the abaxial surface of the leaf, along the margin, at the cusped apex and at the base of the blade (Possobom *et al.*, 2010). In this way, they differ from the specimens under analysis.

Bronwenia has only *Bronwenia cinerascens* (Benth.) W.R Anderson & C.C. Davis (Silva *et al.*, 2020) recorded in Roraima. This species differs from the fossil material because it has decurrent attachment of the secondary venation into the midvein, tertiary vein fabric sinuous percurrent with an acute angle and epimedial tertiary fabric alternate percurrent and irregular reticulate quaternary venation.

Tetrapterys has only *Tetrapterys discolor* (G. Mey.) DC and *Tetrapterys styloptera* A. Juss. registered in Roraima (Menezes & Flores, 2013). Both differ from the analyzed specimens by having the intercostal tertiary vein angle variability increasing proximally and reticulate epimedial tertiary fabric. *Bunchosia decussiflora* W.R. Anderson is the only species of this genus in the gallery and riparian forests of Roraima (Flora do Brasil, 2020) and differs from fossil record due her decurrent attachment of the secondary venation into the midvein, inconsistent intercostal tertiary vein angle variability and mixed percurrent tertiary epimedial venation.

About the morphoanatomy of the *Byrsonima*, the specimens under analysis have many similarities. *Byrsonima* is the largest genus in the Malpighiaceae family, comprising 150 species (Judd *et al*., 2009). In Roraima, it is represented by the species *B. chalcophylla* Nied., *B. chrysophylla* Kunth., *B. coccolobifolia* Kunth., *B. concinna* Benth., *B. coniophylla* A. Juss., *B. crassifolia* (L.) Kunth., *B. crispa* A. Juss., *B. delicatula* Sch.Rodr. & A.S.Flores., *B.eugeniifolia* Sandwith., *B. japurensis* A. Juss., *B. laevis* Nied., *B. punctulata* A. Juss., *B. schomburgkiana* Benth., *B. spicata* (Cav.) DC., *B. stipulacea* A. Juss. and *B.verbascifolia* (L.) DC.

Some of these species are considered dominant in the savannas of Roraima (Ferreira *et al*., 2015). Araújo *et al.* (2010) and Gavilanes *et al.* (2020), from morphological analysis performed on actual leaves of *Byrsonima*, described a camptodromous-brochidodromous/camptodromous-eucamptodromous venation pattern; primary venation pinnate with angles of the major secondary to midvein more acute at base than in the medial blade; similar to that observed in fossil specimens (Figures 3A; 4E). *B. crassifolia* and *B. verbascifolia* are the species that have the greatest similarities with the fossil material. Both studies register the

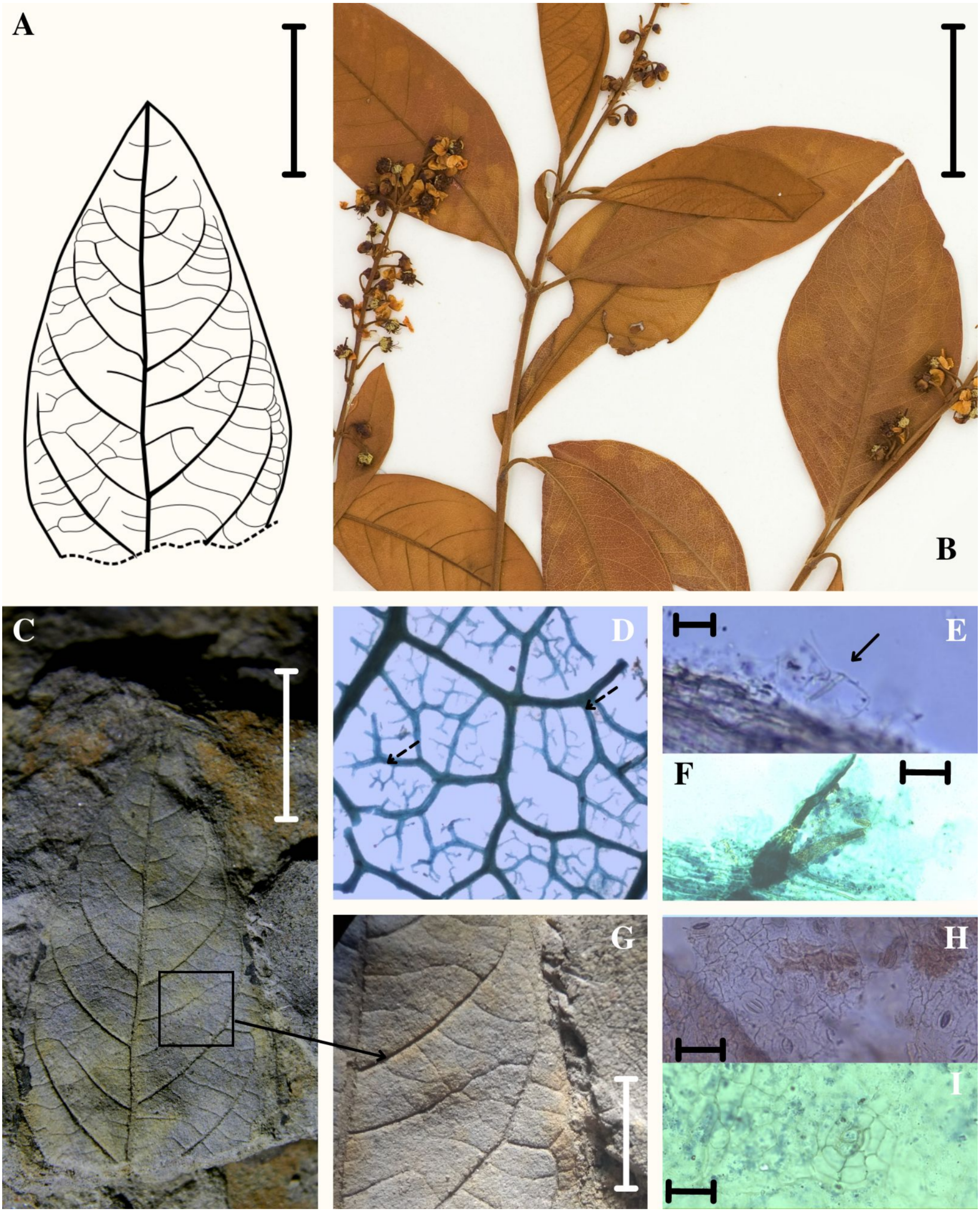

Figure 3. *Byrsonima*. **A**, illustration of primary, secondary and tertiary venations; **B**, *Byrsonima crassifolia* H.B.K exsicata, collectors: Lidio Coradin and Manoel dos R. Cordeiro (source: New York Botanical Garden – Herbarium); **C**, CCU 016; **D**, lower order venations with free endings veinlets (**FEVs**) (dashed arrows); **E**, Malpighiaceous trichome "T" (arrow); **F**, V-shaped trichome; **G**, detail of reticulated tertiary venation; **H**, paracytic stomata; **I**, amphicyclocytic stomata. Scale bars: A–C = 10 mm; E = 22.39 µm; F, I = 50 µm; G = 2 mm; H = 30.84 µm.

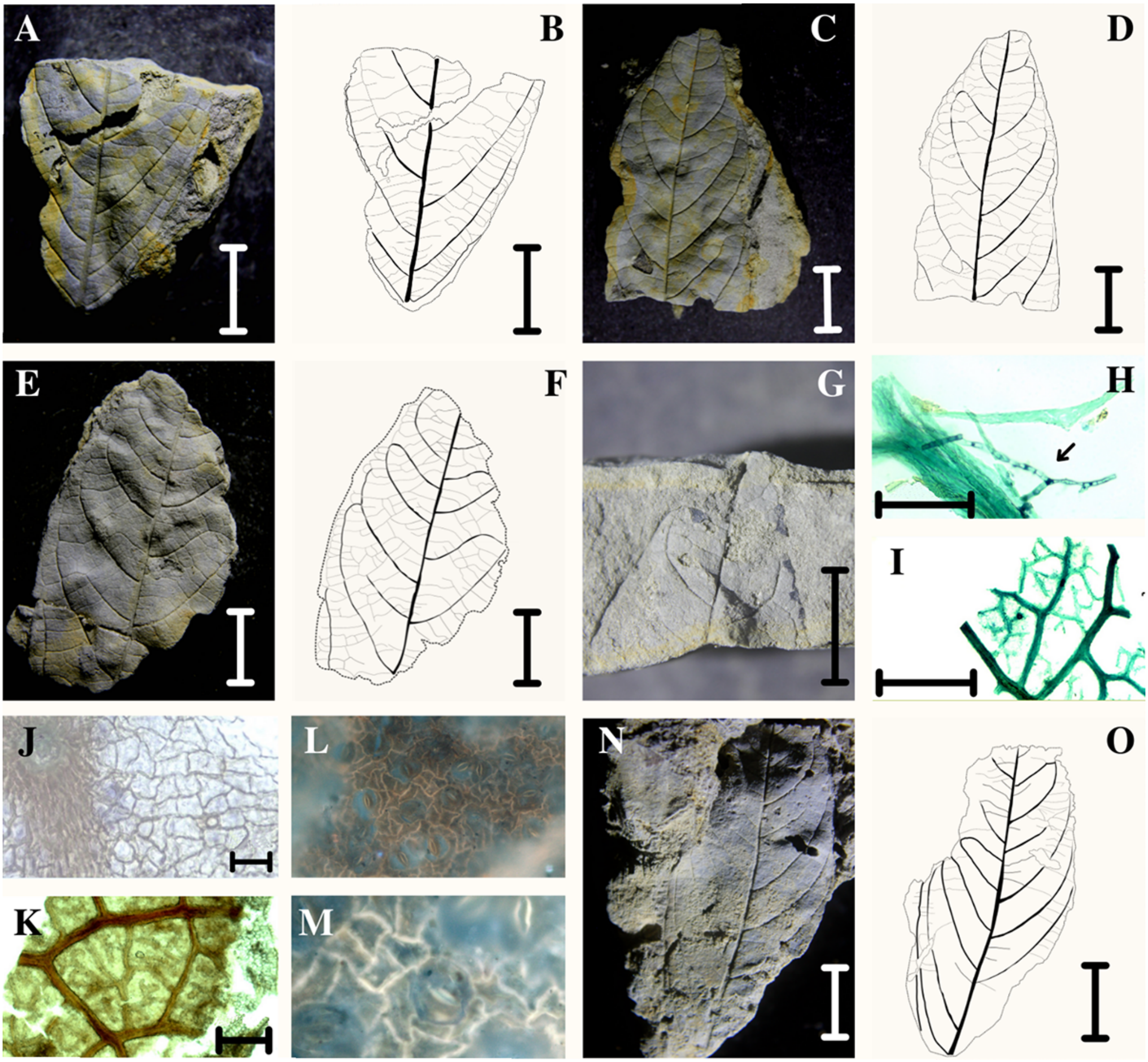

Figure 4. Fossil *Byrsonima* sp. (Malpighiaceae). **A**, CCU 006; **B**, illustration showing detail of the venation; **C**, CCU 011 and **D**, illustration showing detail of the venation; **E**, CCU 035; **F**, illustration detailing the venations in E; **G**, CCU 007; **H**, light microscope photograph showing a T-shaped trichome; **I**, quinternary vein fabric with free endings veinlets; **J**, epidermis; **K**, lower order venation; **L–M**, paracytic stomata; **N**, CCU 003 and **O**, illustration of N. Scale bars: A–G, N–O = 10 mm; H = 500 µm.; I = 5000 µm.; J = 50 µm.; K = 2500 µm.

presence of intersecondary veins and reticulate tertiary vein fabric in *B. crassifolia*, and a percurrent tertiary vein fabric in *B. verbascifolia* (Araújo *et al*., 2010). *B. crassifolia* has areolation with a good development and freely ending veinlets (FEVs) are usually dichotomous.

Anatomically, Ferreira *et al.* (2015) observed cells with thin walls, square and irregular shape on the adaxial face, and cells with rectangular to irregular shape on the abaxial face. The T-shaped, unicellular trichomes and paracytic stomata in *Byrsonima crassifolia* and *B. verbascifolia* (Araújo *et al*., 2010; Ferreira *et al*., 2015). *B. crassifolia*, however, has glands present in the proximal blade, which are not observed in the analyzed fossil material.

Given the above, it is understood that the analyzed fossils are very similar to *Byrsonima verbascifolia*. Nonetheless, given the fragmentary state of preservation, it was decided to include the material described here as fossil representatives of this genus, leaving the species undetermined.

Order SAPINDALES Juss. ex Bercht. & J. Presl
Family RUTACEAE Juss.

Zanthoxylum L.

Zanthoxylum sp.
(Figures 5A–J)

Material. CCU 005aA, CCU 005aB, CCU 024bA, CCU 024bB, CCU 024bE, CCU 024aA, CCU 024aB e CCU 034aA.
Morphological description. Laminar size microphyll, laminar shape elliptic/ovate(?) with medial symmetry, unlobed. Crenate margin with acute apex angle, emarginate apex shape and scattered dots on laminar surface. Primary venation pinnate with no naked basal veins and no agrophic veins. Major secondaries are eucamptodromous becoming brochidodromous distally, with spacing of major secondaries decreasing proximally, variation of major secondary angle to midvein inconsistent, and excurrent attachment to midvein. Intersecondary proximal course parallel to major secondaries, length more than 50% of subjacent secondary, and frequency usually one per intercostal area. Intercostal tertiary veins mixed percurrent.
Anatomical description. Anatomical data were obtained from fluorescence microscopy of specimens CCU 034Ab (Figures 5G–J) and CCU 005aB (Figure 5F). The material presents rectangular to slightly sinuous epidermal cells, measuring about 18–36 µm by 10–21 µm, with a tetragonal arrangement, predominantly hypostomatic with paracytic stomata (Figure 5G). Presence of glandular trichome (?).
Comparison and discussion. The fossils were compared with specimens of the current flora of the region and similarities with Rutaceae were observed. This family is characterized by the presence of scattered pellucid dots (secretory cavities containing ethereal oils) (Figures 5C, J) visible macroscopically (Pan, 2010; Flora do Brasil, 2020). Rutaceae has 50 genera and 238 species registered for Brazil. In Roraima only nine genera and 16 species (Flora do Brasil, 2020) are registered, although only *Conchocarpus* J.C.Mikan. and *Hortia* Vand. occurs in the Amazon savannas, and *Conchocarpus*, *Galipea* Aubl. and *Zanthoxylum* L. in gallery and riparian forest areas.

Conchocarpus differs by laminar size notophyll, untoothed margin, proximal course of intersecondaries veins are perpendicular to midvein with length less than 50% of subjacent secondary. Intersecondary frequency usually one per intercostal area and sinuous percurrent intercostal tertiary vein fabric. *Hortia* has untoothed margin, decurrent attachment of secondary vein to midvein and irregular intercostal tertiary vein fabric. *Galipea* has untoothed margin, decurrent attachment of secondary vein to midvein and intersecondary length less than 50% of subjacent secondary.

Zanthoxylum has laminar shape elliptic/obovate, acuminate apex shape, round to cuneate base shape, crenate margin, and scattered dots on laminar surface (Porter, 1972; Melo & Zickel, 2004). The material is morpho anatomically similar to *Zanthoxylum caribaeum* Lam (Wilf *et al*., 2021; New York Botanical Garden, 2017). The species has glabrous and compound leaves (Melo & Zickel, 2004), which possibly explains the large number of overlapping leaves in the fossil material sample (Figure 5A). Oil dots are observed macroscopically both in fossil material and in *Z. caribaeum.* Anatomical studies have shown that the oil glands are scattered in the mesophyll, and the secretions are drop shaped (Hartley, 1966; Andrade *et al*., 2020). The presence of glandular trichomes in epidermal depressions, as well as the secretory cavities (Andrade *et al*., 2020) recorded in *Z. caribaeum* seem to resemble the structures observed in the fossils studied (Figures 5G, H, J). However, the fragmented state of the leaf epidermis of the analyzed fossils did not allows a more precise analysis of the anatomical characters, which raises doubts about the species determination. Thus, we chose to include these fossil leaves in *Zanthoxylum*, leaving the species undetermined.

Order DILLENIALES DC. ex Bercht. & J. Presl.
Family DILLENIACEAE Salisb.

Incertae sedis
(Figures 6A–F)

Material. CCU 008.
Morphological description. Laminar size microphyll, unlobed, margin entire and possibly erose. Primary venation pinnate with simple agrophic veins. Major secondaries brochidodromous (?) and excurrent attachment to midvein. Intersecondary absent. Intercostal tertiary veins sinuous percurrent with obtuse angle to midvein and inconsistent vein angle variability. Epimedial tertiary alternate percurrent with admedial course perpendicular to the midvein and exmedial course basiflexed. Quaternary vein fabric opposite percurrent. Reticulate quinternary vein fabric. Areolation shows good development and freely ending veinlets (FEVs) absent.
Anatomical description. The specimen has stellate trichomes usually positioned on the venation of the abaxial surface (Figure 6C), a solitary occurrence with a pin-like connection(?). It was not possible to observe other characteristics related to the nature of the trichome base. Trichome support with one basal cell, trichome apex branched more than once. Trichomes lacking ornamentation. Presence of idioblast in the cuticle epidermis (Figure 6F arrow). Stomata present on the abaxial face of indeterminate architecture. The cells on the adaxial face are isodiametric in shape, 12.88–26.73µm in length and 7.73–14.73µm in width, with a pentagonal arrangement of cells (Figure 6F) and a straight cell wall pattern. It was not possible to observe the epidermis cells of the abaxial face.
Comparison and discussion. The fossil material was compared with local flora species and similarities with representatives of the Dilleniaceae were noted. In Brazil, six genera of Dilleniaceae are known (Fraga & Stehmann, 2010) and five are registered in Roraima (Flora do Brasil, 2020): *Curatella* Loefl.; *Davila* Vand.; *Doliocarpus* Rol.; *Pinzona* Mart. & Zucc.; and *Tetracera* L. *Pinzona* has no recorded occurrence in Amazonian savannas. *Doliocarpus* differs from the fossil material because it has unicellular, simple, thin and pointed trichomes (Dickison, 1970).

Morphoanatomically, *Tetracera*, *Curatella* and *Davilla* are similar to the studied material, which, as it is fragmented, does not allow a more secure specific approach. *Tetracera*, has primary venation pinnate, major secondaries eucamptodromous proximally and brochidodromous distally (Gonzáles, 2016) or craspedodromous, intercostal tertiary veins mixed percurrent.

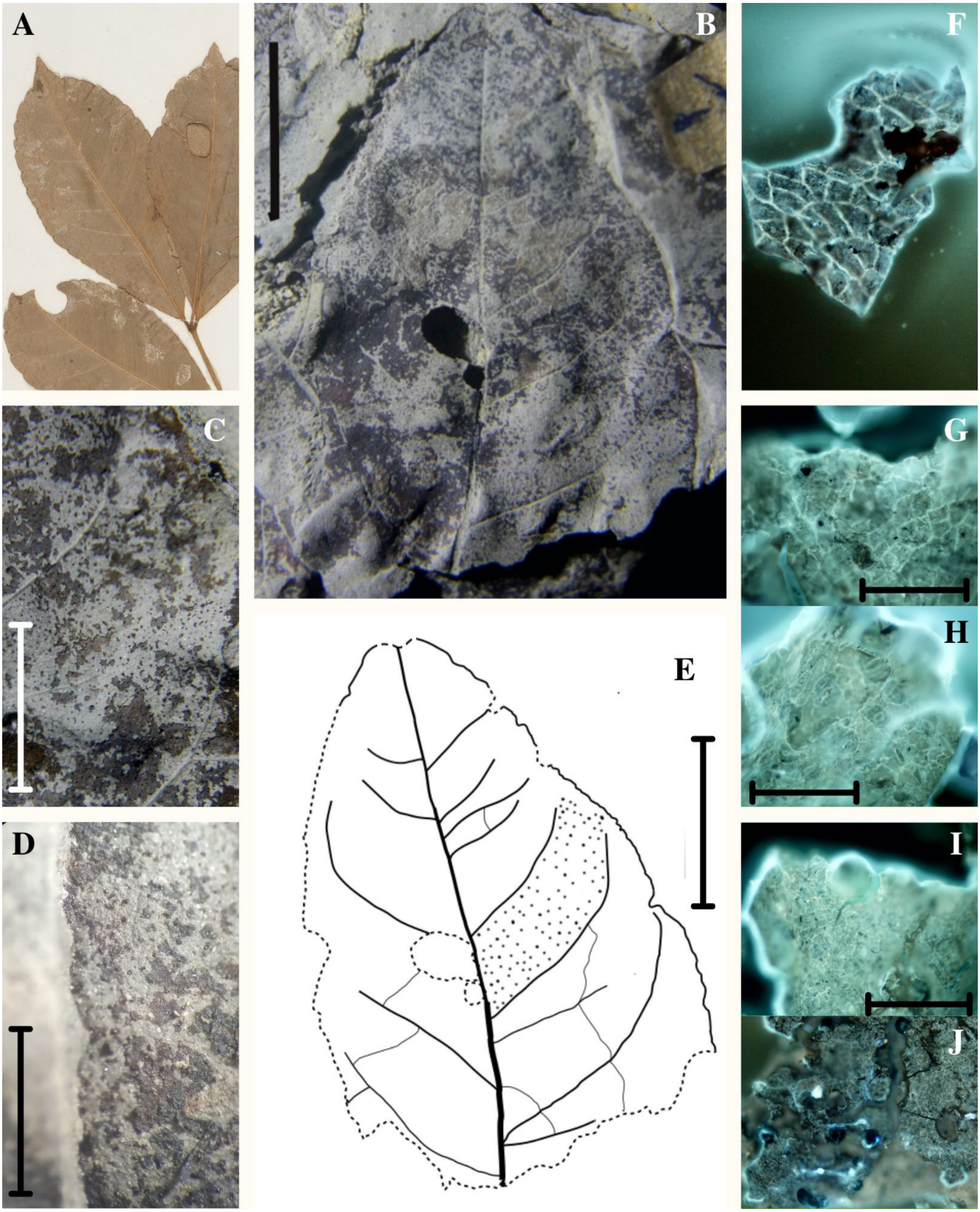

Figura 5. *Zanthoxylum* (Rutaceae). **A**, exsicata of *Zanthoxylum caribaeum* Lamarck, collectors: G.T Prance, J.R. Stevarnd, J.F. Ramos e L.G. Farias (source: New York Botanical Garden – Herbarium); **B**, fossil (CCU 005aA); **C**, detail of scattered dots; **D**, detail of crenate margin (CCU 005bB); **E**, illustration; **F**, epidermis cells; **G**, paracytic stomata; **H**, paracytic stomata; **I**, secretion oil drop; **J**, oil gland cavity. B–E = 10 mm; G–I = 50 µm.

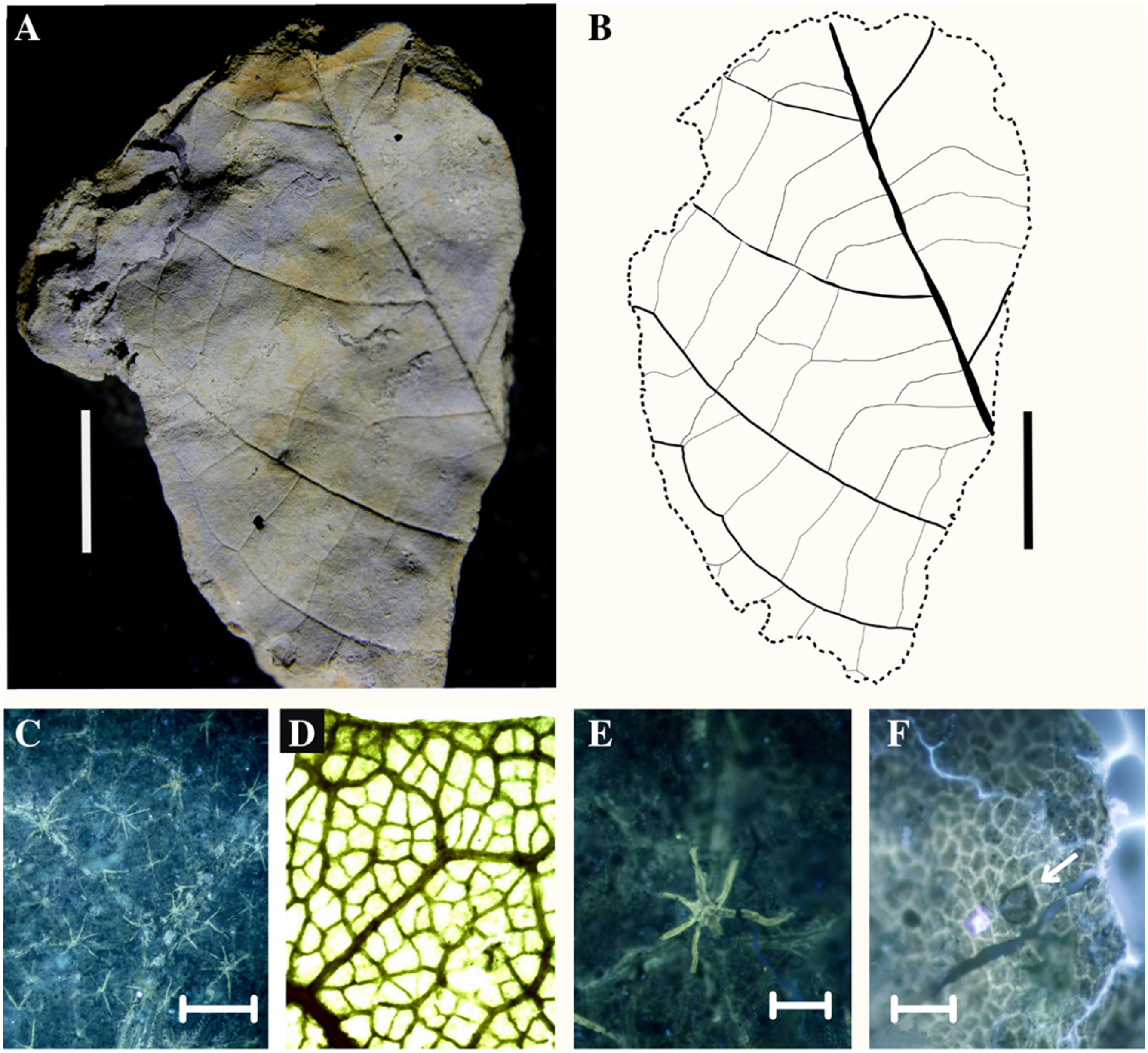

Figure 6. Dilleniaceae *incertae sedis* (specimen CCU 008). **A**, incomplete fossil; **B**, illustration of CCU 008 venation details; **C**, fluorescence microscopy of stellate trichomes on the leaf blade over the venations (10x); **D**, optical microscopy showing the quaternary and quinternary venations (10x); **E**, detail of stellate trichome, fluorescence microscopy (20x); **F**, isodiametric epidermal cells, and idioblast (arrow). A–B = 10 mm; C = 63 µm; E–F = 50 µm.

Anatomical details of *Tetracera willdenowiana* Steud., species that occurs in Roraima, were not found in the literature. However, studies of other representatives of the genus (Fraga & Aymard, 2007) describe the presence of simple and stellate trichomes on the adaxial and abaxial face, respectively.

Curatella is a monospecific genus, and *Curatella americana* L. is quite frequent in the Amazonian savannas of the State of Roraima (Morais & Carvalho, 2015; Melo & Barbosa, 2007). According to Filho (2021), *C. americana* has primary venation pinnate, major secondaries craspedodromous with uniform spacing and uniform secondary angles. Major secondarie angles to midvein range about 70° and follow practically straight until they reach the edge of the leaf blade. In anatomical analysis performed by Ferreira *et al.* (2015) and by Filho (2021), structures such as stellate-type multicellular trichomes were described, often located on the abaxial surface and sometimes on the adaxial surface. Paracytic stomata of the abaxial surface. The epidermis cells are thin, presenting a rectangular to rounded shape, and they are similar on both sides.

Davilla has primary venation pinnate, major secondaries eucamptodromous proximally and brochidodromous distally. Major secondaries angle to midvein range about 60–65° and are curvilinear until they reach the edge of the leaf blade. Although Dickison (1970) suggested that representatives of this genus have simple trichomes, Jácome *et al.* (2009)

recorded the presence of stellate trichomes on the abaxial face of *Davilla rugosa* Poir. There is no morphological pattern for the shape of the epidermis cells in *Davilla*, which may have sinuous walls on both sides, as in the case of *Davilla rugosa* (Jácome *et al*., 2009), or cells with sinuous walls on the abaxial and straight on the adaxial surface, as described by Soares *et al.* (2005) for *Davilla elliptica* A. St.-Hil.

Although the presence of stellate trichomes is better defined for *Curatella*, as well as straight-walled cells, the fossil material described here presents curvilinear secondary veins as those observed in *Davilla* and *Tetracera*, differing from the pattern found in *Curatella*. On the other hand, it does not present simple trichomes, as recorded in *Tetracera*. Thus, as it is a single specimen, it is considered plausible to maintain the determination of the material only at the family level recording the presence of representatives of Dilleniaceae in the Late Pleistocene–Holocene (Boa Vista Formation) of the Takutu Basin.

Angiosperm *Incertae sedis*

Morphotype 1
(Figures 7A–E, G)

Material. CCU 027aA.

Morphological description. Laminar size microphyll (?), laminar shape ovate (?) and symmetrical, unlobed, margin entire. Primary venation pinnate. Major secondaries eucamptodromous with intramarginal secondary perimarginal veins and excurrent attachment to midvein. Intersecondary proximal course parallel to major secondaries with length less than 50% of subjacent secondary and frequency less than 1 per intercostal area. Intercostal tertiary vein fabric mixed percurrent with acute angle.

Anatomical description. Isodiametric cells of the epidermis of the adaxial surface (Figure 7E) with a tetragonal arrangement. Rectangular cells of the abaxial surface (Figure 7C). Straight cell wall. Hypostomatic, with paracytic stomata (Figure 7C) densely arranged on the abaxial surface. Guard cells above the epidermis (?) (Figure 7C). Filamentous and glandular trichomes present on the abaxial surface (Figures 7 D, F), solitary occurrence. Trichome index 19.31%. Trichome base with pin-like connection, unmodified epidermal basal cells and thickened base. Two-celled trichome. Nature of trichome basal cells one cell, trichome apex one cell, trichome 12–66 µm in length and 3–9 µm in width.

Remark. The material represents a single incomplete leaf specimen, with a set of features that is insufficient for a taxonomic classification.

Morphotype 2
(Figures 7G–I)

Material. CCU 015b (Figures 7H-I); CCU 036cbA (Figure 7G).

Material description. It's probably a leaflet with marginal lamina attachment. Laminar size nanophyll, laminar shape elliptic, symmetrical, unlobed, margin entire, obtuse base angle and rounded base. Primary venation pinnate with no naked basal veins and agrophic veins absent. Major secondary craspedodromous with irregular spacing, uniform secondary angle and excurrent attachment to midvein. Intersecondary present. Reticulate intercostal tertiary vein (Figure 7I).

Remarks. This is a very incomplete material, in this case, leaflets belonging to a composite leaf, which do not have enough characteristics to allow their taxonomic classification here. Representatives of the Fabaceae that occur in Roraima have morphological similarities with the material analyzed here, however the available information is insufficient for identification.

Morphotype 3
(Figures 8A–B)

Material. CCU 016 abB; CCU 017 aB (Figures 8A–B).

Morphological description. Leaf probably with marginal lamina attachment, unlobed, margin entire, obtuse (?) base angle, and rounded base. Primary venation pinnate with no naked basal veins and agrophic veins absent. Major secondaries brochidodromous. Minor secondary course simple brochidodromous, major secondaries spacing irregular, and variation of angle to midvein inconsistent. Excurrent attachment of major secondary to midvein. Intersecondary proximal course parallel to major secondaries, length less than 50% of subjacent secondaries and frequency less than 1 per intercostal area. Intercostal tertiary veins mixed percurrent with acute angle. Reticulate quaternary vein fabric (Figure 8B) and reticulate (?) quinternary vein fabric.

Remarks. The material corresponds to very incomplete specimens of leaves, which implies little morphological information, which prevents its classification until a more complete material is obtained in future.

Morphotype 4
(Figures 8C–I)

Material. CCU 009.

Morphological description. Leaf with marginal lamina attachment, laminar size microphyll, laminar shape elliptic (?), unlobed, and margin entire. Primary venation pinnate with no naked basal veins and agrophic veins absent. Major secondaries eucamptodromous with spacing abruptly increasing proximally and variation of angle to midvein inconsistent. Excurrent attachment of major secondary to midvein. Intercostal tertiary veins mixed percurrent with acute angle and inconsistent angle variability. Irregular reticulate quaternary vein fabric. Quinternary vein fabric not preserved (Figure 8D).

Anatomical description. Isodiametric epidermal cells (Figure 8F), with a tetragonal arrangement on the adaxial face, and random arrangement on the abaxial face (Figure 8E). Straight cell wall (Figure 8E). Epicuticular-type surface ornamentation. Amphistomatic with paracytic stomata (Figure 8G). Trichome occurring in the upper epidermis, peltate

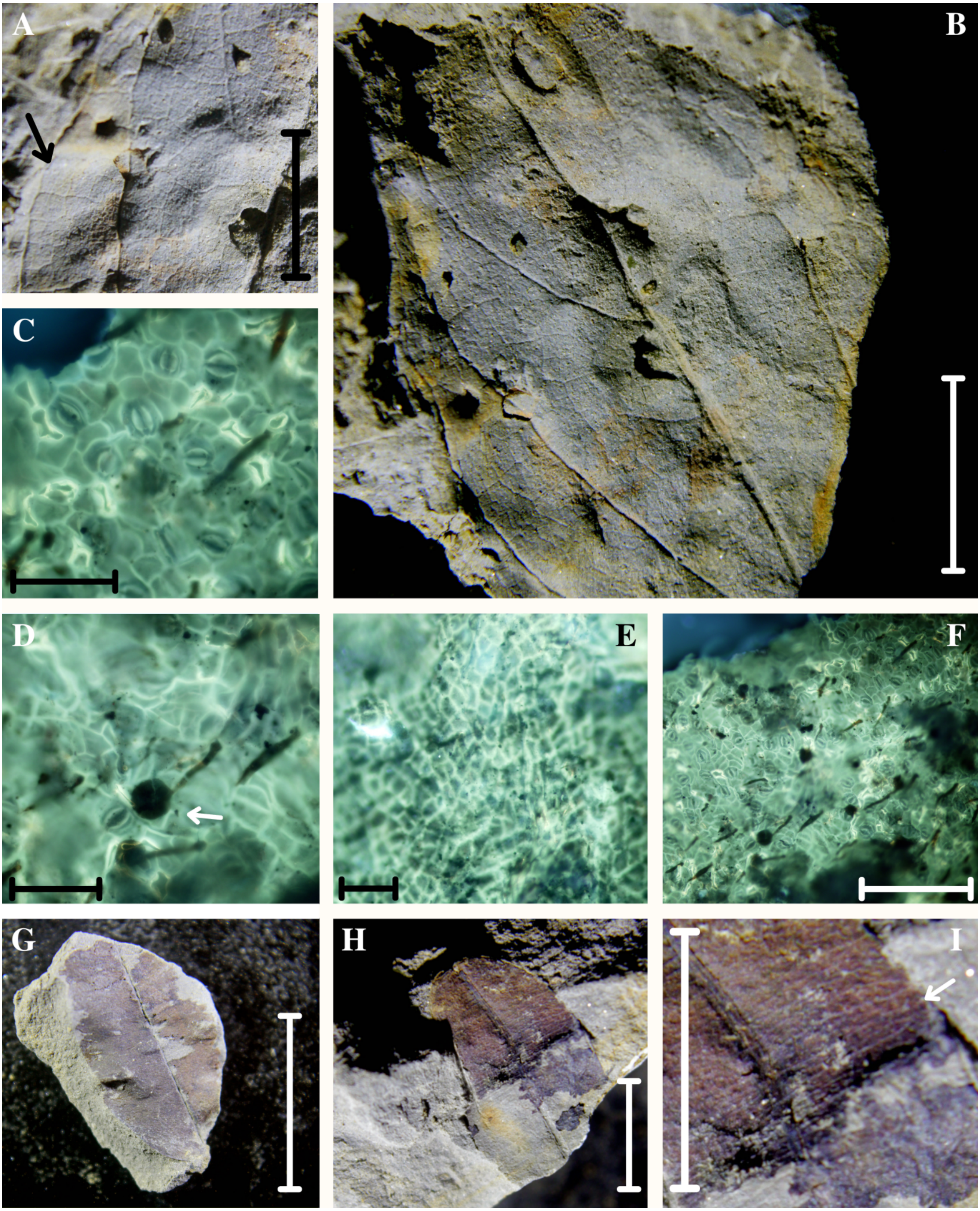

Figure 7. Morphotypes 1 and 2. **A–F**, Morphotype 1 (specimen CCU 027). **A**, detail showing the venations (arrow); **B**, CCU 027; **C**, fluorescence microscopy of the abaxial epidermis (20x); **D**, tector trichome, fluorescence microscopy (arrow) (40x); **E**, adaxial epidermis (20x); **F**, paracytic stomata (40x). **G–I**, Morphotype 2 (specimens CCU 036; CCU 015). **G**, CCU 036; **H**, CCU 015; **I**, venations details (white arrow) of CCU 015. A–B, G–I = 10 mm; C, D–E = 50 µm; F = 100 µm.

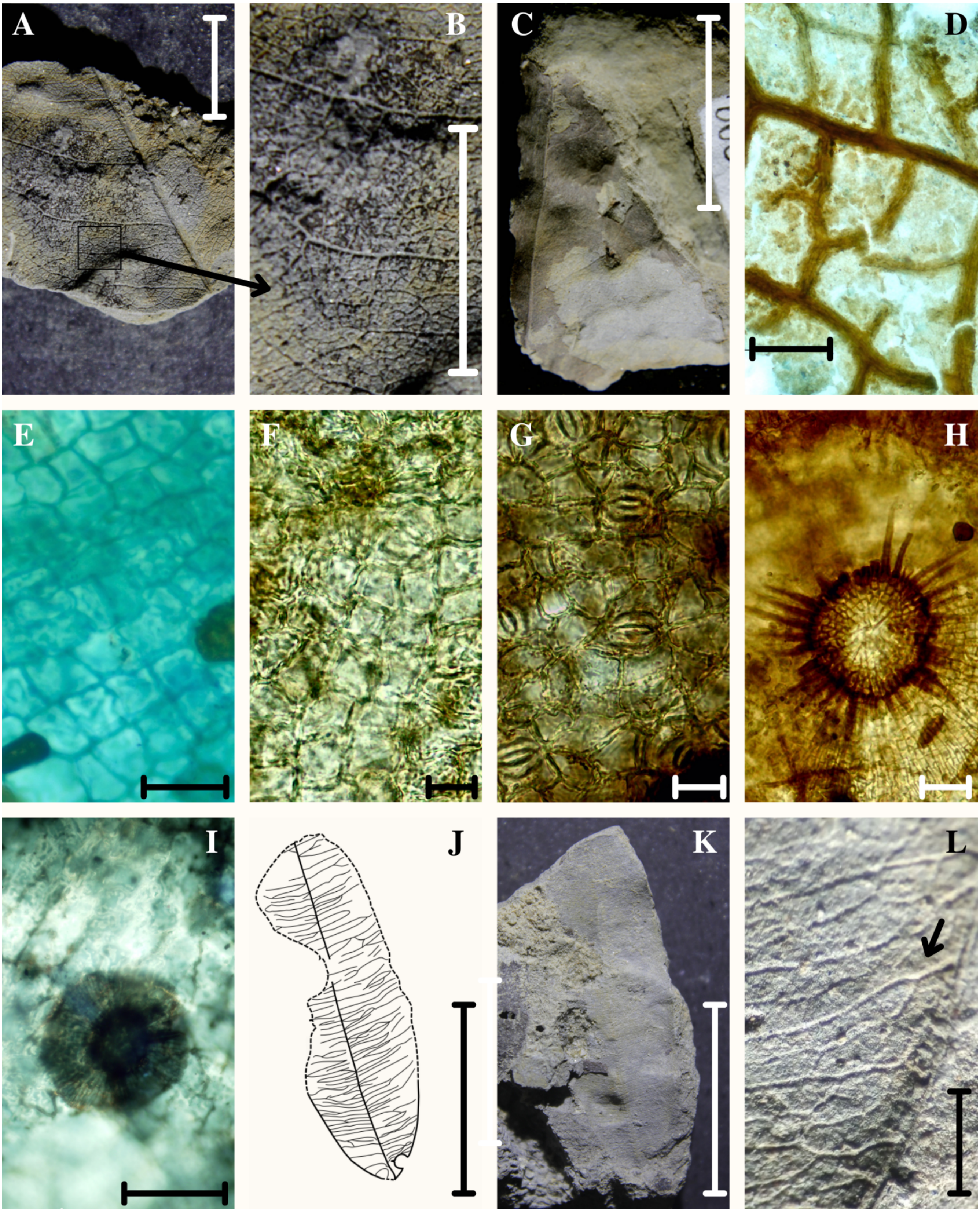

Figure 8. Morphotypes 3, 4 and 5. **A–B**, Morphotype 3 (specimen CCU017ab). **A**, CCU 017ab; **B**, detail of venations CCU 017ab; **C–I**, Morphotype 4 (specimen CCU 009). **C**, CCU 009; **D**, fourth-order venations (4x); **E**, adaxial epidermis (40x); **F**, ornamentation of epidermal cells; **G**, paracytic stomata; **H**, pelted trichome; **I**, pelted trichome under fluorescence microscopy (40x). **J–L**, Morphotype 5 (specimen CCU 013A). **J**, illustration; **K**, CCU 013A; **L**, detail of the craspedodromous venation (black arrow). A–C, J–K = 10 mm; D = 5000 μm; E = 500 μm; F–I = 50 μm; L = 2 mm.

trichome type, solitary occurrence. Nature of multicellular trichome, apex of multicellular flat trichome more than one cell thick and arranged radially (Figures 8 H–I), diameter 71 to 194 µm, ornamentation present.

Remarks. The material represents a single incomplete leaf specimen that, despite having some anatomical characters, did not show enough features to allow its taxonomic classification, with the main difference from the other morphotypes analyzed being the shape of its trichome.

Morphotype 5
(Figures 8J–L)

Material. CCU013A.

Morphological description. Leaf with marginal lamina attachment, laminar size microphyll, laminar shape elliptic, symmetrical, unlobed, margin entire, obtuse apex angle, and rounded apex. Primary venation pinnate with no naked basal veins and agrophic veins absent. Major secondaries reticulodromous with marginal secondary perimarginal veins (Figure 8L). Excurrent attachment of major secondary to midvein. Regular reticulate intercostal tertiary veins fabric with perpendicular angle. Irregular reticulate quaternary vein fabric (Figure 8L).

Remarks. The material refers to a single incomplete specimen of, probably, a leaflet, common to several taxa, and which has insufficient characters for a taxonomic classification until more complete specimens can be found.

Morphotype 6
(Figures 9A–E)

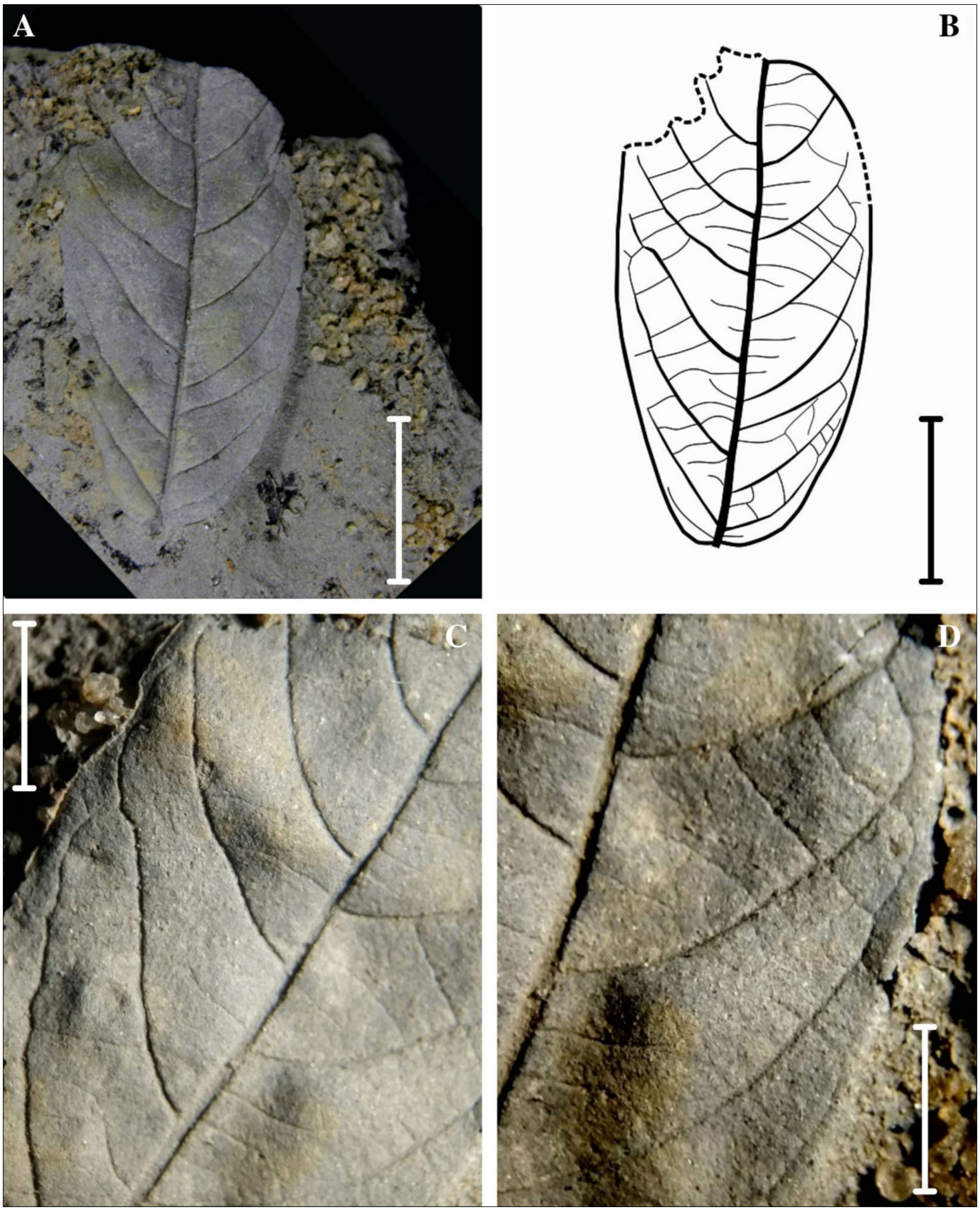

Figure 9. Morphotype 6 (specimen CCU 033). **A**, CCU 033; **B**, illustration detailing the venations; **C–D**, detail of secondary and tertiary venations. A–B = 10 mm; C–D = 3 mm.

Material. CCU 033.

Morphological description. Leaf probably with marginal lamina attachment, laminar size microphyll, laminar shape ovate, symmetrical, unlobed, margin entire, obtuse apex angle, and rounded apex. Primary venation pinnate with no naked basal veins and two pairs of basalvens, agrophic veins absent. Major secondaries brochidodromous. Minor secondary course simple brochidodromous, major secondaries spacing irregular, and variation of angle to midvein decreasing proximally. Excurrent attachment of major secondary to midvein. Intersecondary proximal course perpendicular to midvein, distal course parallel to major secondary, length less than 50% of subjacent secondaries and frequency more than 1 per intercostal area. Intercostal tertiary veins mixed percurrent with acute angle decreasing proximally. Epimedial tertiary fabric opposite percurrent. Quaternary vein fabric opposite percurrent.

Remarks. The material has morphological similarities with *Psidium* L. (Myrtaceae), presenting major secondary veins brochidodromous forming loops and intersecondary venation present. These characteristics, however, are common to several members of Myrtaceae (Oliveira *et al*., 2017) and the absence of more specimens and anatomical data makes it difficult to advance in comparisons.

DISCUSSION

Age

Although the material described has been found outside the original stratigraphic unit, its preservational characteristics indicate that it is a relatively recent deposit and little transported, given the poorly consolidated characteristic of the sedimentary matrix. In the Takutu Basin, the fossiliferous stratigraphic unit known for the Cenozoic is the Boa Vista Formation, which outcrops in the vicinity of the studied location (Figure 1) and has mineralogical and lithological similarities with the clayey matrices of the fossiliferous samples. Wankler & Marques-de-Souza (2018) had already suggested this correlation of fossiliferous intraclasts with the Boa Vista Formation. In that study, however, the authors compared the fossiliferous samples with samples from other portions of the Takutu Basin, far from the study area. In order to find more evidence of this correlation, the present study carried out the systematic collection of samples from two outcrops close to the fossil collection area and the results obtained suggest that the fossils correspond to the Boa Vista Formation. This unit almost completely covers the Takutu hemigraben region (Eiras & Kinoshida, 1990) and has its deposition attributed to the Late Pleistocene–Holocene interval (Stern, 2019; Zular, 2019; Oliveira, 2020).

The first record of the possible occurrence of fossils in the Boa Vista Formation was reported by Marques-de-Souza *et al.* (2018) and Wankler & Marques-de-Souza (2018). Recently, Oliveira (2020) recorded and described fragments of charcoal as indicators of environmental paleofires from this formation. In the same study, Oliveira (2020) indicated that the OSL and ^{14}C datings carried out with the material indicate a Late Pleistocene–Holocene age to this stratigraphic unit (from 4,400 ± 200 and 2,700 ± 1.0 Ka-profile 1; of 36,600 ± 3.1 and 6,700 ± 400 Ka - profile 2; and 105,200 ± 4.3 and 3,200 ± 300 Ka - profile 3; 98,100 ± 6.4 and 14,500 ± 700 Ka - profile 4) (Oliveira, 2020).

Vegetation Formation

The current region is covered by savannas vegetation known locally as "*lavrado*" (Carneiro-Filho, 1992; Barbosa & Miranda, 2004; Barbosa *et al*., 2007; Nascimento & Lins, 2018), which consists of grasses and sedges, in open areas, and added with shrub and tree species in areas of more closed vegetation (Miranda & Absy, 2000; Barbosa & Miranda, 2004; Hollowell *et al*., 2007; Morais & Carvalho, 2015; Araújo *et al*., 2017). The "*lavrado*" is also formed by an undefined network of islands of forests dominated by *Mauritia flexuosa* L.f., being part of the drainage system sometimes associated with paleochannels, called "veredas" (Palm swamps) (Barbosa & Miranda, 2004; Morais & Carvalho, 2015). All taxa (CCU 003, CCU 005aA-005aB, CCU 006a,b, CCU 007, CCU 008, CCU 011, CCU 016abA, CCU 024aA-024aB-024bA-024bB-024bE, CCU 033, CCU 034aA and CCU 035) shown in this study are fossils of species that compose the current vegetation of the "*lavrado*".

Paleoecological aspects

The anatomical-cuticular characteristics have played an important role in the interpretation of the environmental conditions of the flora. According to Stace (1965), xeromorphic plants predominantly present cells with straight walls, as observed in the fossil specimens of this study. In addition, most records with anatomical preservation indicated the presence of hypostomatic leaves, that is, with stomata present predominantly on the abaxial surface of the leaf epidermis, corroborating the analysis carried out by Ferreira *et al.* (2015) with predominant woody species in the "*lavrado*" in Roraima. The occurrence of stomata on the lower epidermis is also considered a xerophytic trait (Ullah *et al*., 2014).

Another relevant aspect that must be considered is that the stomatal guard cells of xeromorphic plants tend to be "sunken" in the epidermis (Stace, 1965), since they are superimposed by the subsidiary cells, making it difficult to observe them in frontal microscopy. This feature was quite recurrent in the observations of the slides produced with the studied fossils. Finally, the presence of high numbers of trichomes characterizes an adaptation to environments with arid conditions, and the trichomes, in this case, would have the function of decreasing the transpiration rate and assisting in the absorption of water (Metcalfe & Chalk, 1979).

As seen, there is a great similarity between the fossil leaves and typical species of the "*lavrado*", leading to the conclusion that they represent a relatively recent record of the flora of that region. However, the absence of botanical studies with anatomical-cuticular data of the current flora makes comparative paleobotanical studies difficult since most species and other higher taxa of angiosperms are defined based on their reproductive structures. For this reason, the material studied was determined only at the genus and/or family levels, corroborating hypothesis held for a long time in this field of knowledge (Wilf, 2008; Wilf *et al*., 2021).

CONCLUDING REMARKS

The present study presents the first records of fossil leaves from the Late Pleistocene–Holocene of the Takutu Basin. Comparative analyses carried out using XRD and LIBS indicated chemical and mineralogical similarities of the fossiliferous samples with samples from the Boa Vista Formation, supporting the indication of this unit as the source of the material studied.

In the taxonomic study, 15 specimens were analyzed and identified as representatives of *Byrsonima* Rich ex Kunth, and *Zanthoxylum* L., as well as representatives of the Dilleniaceae. Another eight samples were described and grouped into five morphotypes due to the incompleteness of the respective specimens, which prevented their taxonomic classification.

The studied taxa still occur today in the region and are typical elements of the savanna formation "*lavrado*" of Roraima, indicating that they are fossils of Late Pleistocene–Holocene age, corroborating their origin from deposits of the Boa vista Formation, as suggested by the similarity chemistry and mineralogical rock matrix.

Finally, the anatomical-cuticular characters indicated the dominance of hypostomatic cuticles and high numbers of trichomes in the epidermis, conditions observed in xeromorphic plants and in the current woody species predominant in the "*lavrado*" in Roraima; thus corroborating that it is the fossil record of this plant formation that lived under the same conditions during the Late Pleistocene–Holocene.

ACKNOWLEDGMENTS

The authors would like to thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the financial support through scholarships (Process 141042/2009-5), which were vitally important for conducting this study. The authors are also grateful to Casa de Cultura Britânica, UFC, for revising the English of the final manuscript.

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Received in 20 April, 2022; accepted in 11 November, 2022.