

# Preliminary palynological analysis of a Holocene peat bog from Apakará-tepui (Chimantá Massif, Venezuelan Guayana)

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## Abstract

Preliminary palynological analysis of a Holocene peat bog from Apakará-tepui (Chimantá Massif, Venezuelan Guayana).- This paper reports the preliminary palynological results, at a millennial scale, of a Holocene peat bog sequence, since around 8.0 cal kyr BP to the present, obtained in the summit of the Apakará-tepui (2170 m elevation), in the Chimantá massif, located in the neotropical Venezuelan Guayana. The early Holocene was characterized by a vegetation different to the present, in which trees and shrubs dominated and *Myrica* (Myricaceae) was the main element of the gallery forests around a permanent water body, as indicated by the continuous presence of *Isoëtes* (Isoëtaceae) in high percentages. Around the middle Holocene (5.3 cal kyr BP), a shift towards more herbaceous and non-flooded communities occurred, and the present day vegetation established. This has been interpreted as a shift from warmer and wetter climates to cooler and drier conditions. The first phase, from 8.0 to 5.3 cal kyr BP, falls within a warming phase widely documented worldwide, known as the Holocene Thermal Maximum. The millennial trends shown here will be refined with further studies at centennial to decadal time scales. These results support the hypothesis that the best sites to detect paleoenvironmental changes in the summits of the tabular Guayana mountains are close to altitudinal ecotones.

Key words: Neotropics; Paleoclimatology; Paleoecology; Palynology; Quaternary.

## Resumen

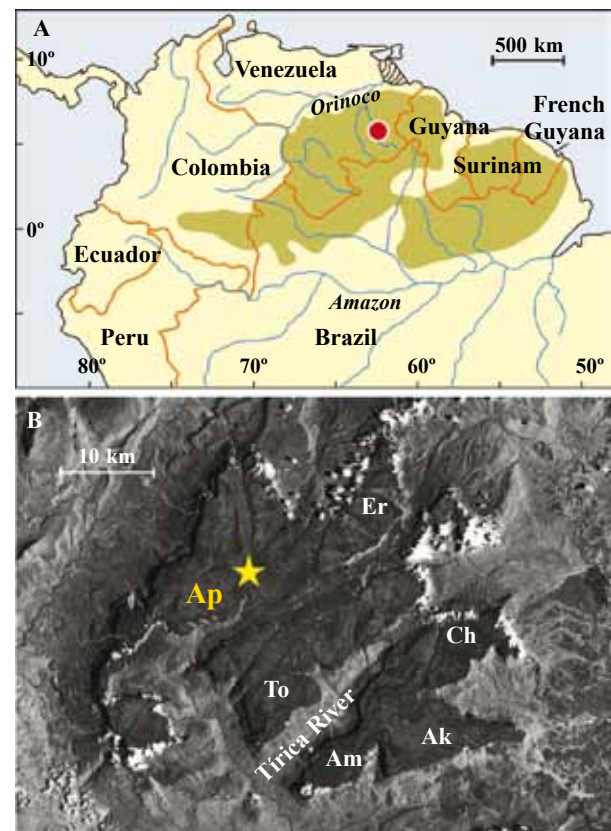
Análisis palinológico preliminar de una turbera holocena del Apakará-tepui (Macizo de Chimantá, Guayana venezolana).- Este artículo presenta los resultados palinológicos preliminares, a escala de milenios, de una secuencia holocena, desde 8.0 cal kyr BP hasta la actualidad, obtenida en la cima del Apakará-tepui (2170 m de altitud), en el Macizo del Chimantá, situado en la región neotropical de la Guayana venezolana. El Holoceno temprano se caracterizó por una vegetación diferente a la actual, dominada por árboles y arbustos, en la que *Myrica* L. (Myricaceae) era el elemento principal de los bosques de ribera que circundaban un cuerpo de agua permanente, como indica la presencia continua de *Isoëtes* L. (Isoëtaceae). Durante el Holoceno medio (5.3 cal kyr BP), se produjo un cambio a una vegetación más herbácea, estableciéndose las comunidades que actualmente ocupan el área. Ésto se interpreta como indicativo de un cambio desde climas más cálidos y húmedos a condiciones más frías y secas. La primera fase, de 8.0 a 5.3 cal kyr BP, coincide con una fase climática cálida ampliamente documentada a nivel global, conocida como el Máximo Térmico del Holoceno. Las tendencias milenarias obtenidas en este trabajo se refinarán con futuros estudios a escala de siglos y décadas. Estos resultados apoyan la hipótesis de que las mejores localidades para estudios paleoambientales en las montañas tabulares de Guayana se encuentran alrededor de los ecotonos altitudinales.

Palabras clave: Cuaternario; Neotrópico; Paleoclimatología; Paleoecología; Palinología.

## INTRODUCTION

Peat bogs in the summits of the table mountains (*tepuis*) from the neotropical Guayana Highlands (Fig. 1) have been considered *a priori* excellent locations to record late Pleistocene and Holocene paleoecological and paleoenvironmental changes, due to its pristine nature, which excludes human interference (Rull, 2007a; 2010). So far, however, palynological studies conducted on these summits have not been able to find consistent regional patterns of climate/vegetation in time and space. Indeed, whereas most records from the summits of the Chimantá massif (Akopán-tepui, Amurí-tepui and Toronó-tepui) have shown heterogeneous patterns of change likely due to the dominance of local micro- and meso-climatic processes over general paleoclimatic trends (Rull, 2005a), other sequences (Churí-tepui and Guaiquinima massif) suggested vegetation shifts linked to temperature and moisture variations of potential regional extent (Rull, 2004; 2005b). The main reason for this disagreement was assumed to be the different degree of sensitivity of the localities surveyed to past environmental changes, depending on their elevation. The better suited sites to document paleoecological shifts associated to climate changes were considered to be close to key altitudinal ecotones, and the highest mountaintops (Rull, 2005a). For example, in the Churí-tepui, the study site was close to the upper altitudinal boundary of grasslands dominated by *Stegolepis* Klossch ex Körn (Rapateaceae), in their contact with the *Chimantaea* Maguire, Steyerl. & Wurdack (Asteraceae) shrublands (Rull, 2004). On the contrary, localities situated within the grasslands and far from this ecotone, as for example the other Chimantá sites, would be less useful to record paleoenvironmental changes (Rull, 2005a). A study in one of the highest Chimantá mountaintops (Eruoda-tepui) also showed remarkable vegetation constancy during the Holocene; therefore, ecotonal localities seem to be the preferred tepuian sites for paleoecological reconstruction (Nogué *et al.*, 2009a).

This paper reports a preliminary palynological study in the Apakará-tepui (Chimantá massif), which is close to the mentioned grassland-shrubland altitudinal ecotone, at an elevation similar to the Churí-tepui, where a conspicuous vegetation shift was recorded during the late



**Figure 1.** Location map. A) Schematic map of northern South America indicating the position of the Chimantá massif (red dot). The approximate extension of the Guayana Shield is depicted as a brown area. B) radar image of the Chimantá massif (courtesy of ANAPRO Digital), indicating the Apakará coring site studied here (yellow star) and the other localities mentioned in the text. AP – Apakará, Er – Eruoda, To – Toronó, Am – Amurí, Ak – Akopán, Ch – Churí.

Holocene, and attributed to a temperature shift. The section embraces the last ~8.0 cal kyr BP (calendar kilo-years before present) and the resolution is millennial, thus recording the main Holocene trends. Further studies at higher resolution will refine the vegetational and climatic history of the site. This type of studies are useful not only to increase the ecological and paleoecological knowledge of these singular neotropical ecosystems but also to improve biodiversity conservation strategies in the face of the predicted global warming (Rull & Vegas-Vilarrúbia, 2006; Nogué *et al.*, 2009b; Rull *et al.*, 2009; Vegas-Vilarrúbia *et al.*, 2011).



**Figure 2.** Aerial view of the Chimant massif showing the valley of the Trica river in the center, and the characteristic tepuian summits at both sides (Photo: V. Rull).

## MATERIALS AND METHODS

### Coring site

The coring site is located on the summit of the Apakar-tepui, in the Chimant massif ( $5^{\circ} 19' 21.68''$  N –  $62^{\circ} 13' 34.14''$  W, 2170 m elevation). It lies within a relatively narrow valley modeled by an affluent of the Trica river running to the SE (Figs. 1 & 2). The site is part of the Guayana Highlands (those situated above 1500 m elevation), under mesothermic ombrophylous climate with annual average temperatures between 12 and 18 °C and very high rainfall (2500-3500 mm per year in average), without any true dry season. Additional moisture is provided by frequent and dense mists. Winds and thunderstorms are also frequent, especially when the Intertropical Convergence Zone (ITCZ) is around the region (March to November) (Huber, 1995a).

The coring was made at about 50 m from the river, within herbaceous vegetation but close to a *Chimantaea mirabilis* Maguire, Steyerm. & Wurdack (Asteraceae) paramoid shrubland (Fig. 3). These shrublands typically occur between 1900

and 2500 m altitude, which is the altitudinal range of the dominant species in the Chimant massif (Huber, 1995b; Pruski, 1997); and are usually composed by two layers, one shrubby and the other



**Figure 3.** View of a *Chimantaea mirabilis* shrubland from the Apakar-tepui summit, close to the sampling site (Photo: V. Rull).

herbaceous, dominated by *Chimantaea mirabilis* and the bambusoid grass *Myriocladus steyermarkii* Swallen (Poaceae), respectively (Huber, 1992b). Other important shrubs are *Notopora cardonae* A. C. Sm. (Ericaceae), *Mycerinus chimantensis* Maguire, Steyererm. & Wurdack (Ericaceae), *Weinmannia laxiramea* Killip & A. C. Sm. (Cunoniaceae), *Ilex retusa* Klotszch in Mat. (Aquifoliaceae), *Drymis roraimensis* (A. C. Sm.) Ehrend & Gootsb. (Winteraceae), and *Cyrilla racemiflora* L. (Cyrillaceae). In the herbaceous layer, *Lindmannia* Mez sp. (Bromeliaceae), *Everardia* sp. (Cyperaceae), *Heliamphora minor* Gleason (Sarraceniaceae), and several Xyridaceae and Eriocaulaceae species may co-dominate (Huber, 1992b; 1995b).

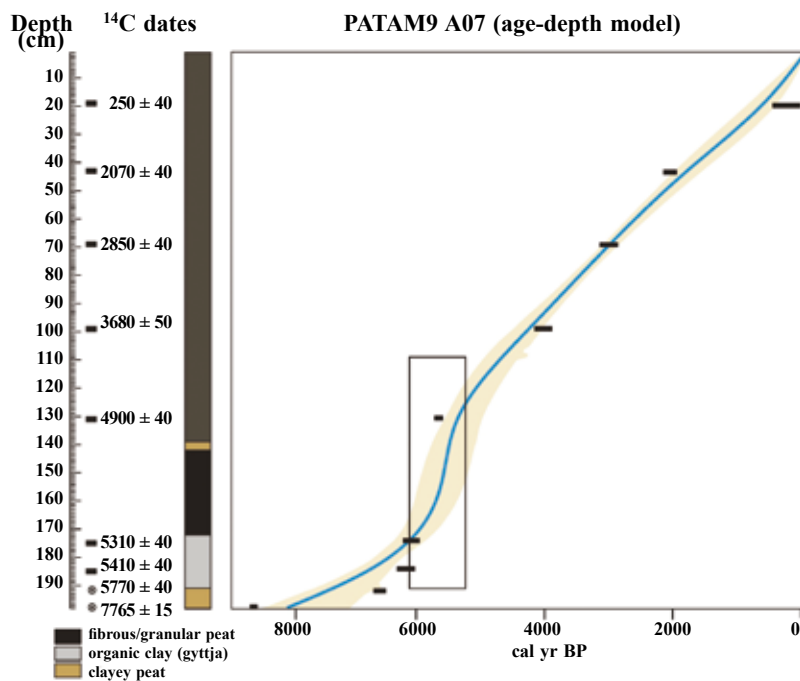
In the coring site, other shrubs as for example *Tepuia venusta* Camp (Ericaceae) and *Rhamnus chimantensis* Steyererm. & Maguire (Rhamnaceae) are also noteworthy; whereas among herbs, *Panicum eligulatum* N. E. Br. (Poaceae), *Stegolepis ligulata* Maguire (Rapateaceae), *Everardia angusta* N. E. Br. (Cyperaceae), *Rondonanthus acopanensis* (Moldenke) Hensold & Giul. (Eriocaulaceae), *Paepalanthus chimantensis* Hensold (Eriocaulaceae), and *Sphagnum* L. (Sphagnaceae) mosses, are worth mentioning. These mosses do not form real *Sphagnum* peat bogs, as in many other similar environments, but may be locally abundant, especially along water courses (Ahti, 1992). In addition, a gallery forest dominated by *Schefflera cf. clavigera* Frodin (Araliaceae), *Cyrilla racemiflora*, *Podocarpus buchholzii* de Laub. In Luces & Steyererm. (Podocarpaceae), *Gaiadendron punctatum* (Ruiz & Pav.) G. Don (Loranthaceae), *Drymis winteri* J. R. Forst. & G. Forst (Winteraceae), and *Weinmannia cf. laxiramea* grow along the nearby river. In other parts of the river margin, more open sandstone outcrops are covered by shrubs of *Mallophyton chimantense* Wurdack (Melastomataceae), *Adenanthe bicarpellata* Maguire, Steyererm. & Wurdack (Ochnaceae), *Bonnetia roraimae* Oliv. (Bonnetiaceae) and *Quelchia bracteata* Maguire, Steyererm. & Wurdack (Asteraceae).

The Apakará coring site studied here lies close to the upper altitudinal boundary of the tepuian meadows dominated by *Stegolepis ligulata*, which is around 2200-2300 m (Huber, 1992b). These meadows are widespread throughout the Chimantá massif and, in them, *Stegolepis ligulata* is accompanied by several species of *Xyris* L. (Xyri-

daceae), *Everardia* Ridl. Ex Thurn (Cyperaceae), *Lagenocarpus* Nees (Cyperaceae), *Lindmania* Mez (Bromeliaceae), *Brocchinia* Schlut. F. (Bromeliaceae), *Heliamphora* Benth. (Sarraceniaceae), and *Syngonanthus* Ruhland. (Eriocaulaceae). Poaceae are represented by a single species, *Panicum eligulatum*, which occurs very scarcely. Shrubs are also scarce and scattered, with *Maguireothamnus speciosus* (N. E. Br.) Steyererm. (Rubiaceae), *Digomphia laurifolia* Benth. (Bignoniaceae), *Macairea cardonae* Wurdack (Melastomataceae), *Stomatochaeta condensata* (Baker) Maguire & Wurdack (Asteraceae) and *Cyrilla racemiflora* L. (Cyrillaceae), as the main representatives. *Stegolepis ligulata* may occur slightly above the upper boundary of the meadows it dominates, but in small and scattered stands (Huber, 1987).

### Sampling and pollen-analytical procedures

A 200 cm peat core called PATAM9-A07 was obtained with a Russian borer. Samples for pollen analysis were taken in the field at every 2 cm. In this preliminary analysis, samples are analyzed every 10 cm. A surface sample was taken in the coring point for comparison. Around 3 g of each of these samples were processed after addition of *Lycopodium* L. (Lycopodiaceae) tablets (batch n° 177745; 18,584 spores/tablet). The laboratory processing included KOH, HCl and HF digestions, and acetolysis; slides were mounted with silicone oil without sealing (Nogué *et al.*, 2009a; Rull *et al.*, 2010b). The palynomorphs considered were pollen, pteridophyte spores, algae and animal remains, and fungal spores. Counting was conducted until a minimum of 300 pollen and pterophyte spores (including a minimum pollen sum of 200), and the saturation of diversity (Rull, 1987). The pollen sum included all pollen types, except those from aquatic and semi-aquatic plants. Identification was based on local and regional pollen and spore floras (Absy, 1979; Roubik & Moreno, 1991; Salgado-Labouriau & Villar, 1992; Jiménez, 1996; Herrera & Urrego, 1996; Colinvaux *et al.*, 1999; Rull, 2003; Burn & Mayle, 2008; Leal, 2010; López-Martínez *et al.*, 2010), some general palynological catalogs (Erdtman, 1952; Tryon & Lugardon, 1991), and the Neotropical Pollen Database (Bush & Weng, 2006). Pollen diagrams were plotted and zoned using *psimpoll 4.27*, the Optimal Splitting by Information



**Figure 4.** Stratigraphy and age-depth model of core PATAM9 A07. Dates are represented as horizontal bars indicating their respective confidence intervals. The smooth spline model (Blaauw, 2010) is represented as a solid blue line and its confidence interval as a light brown band. The box indicates a significant acceleration in peat accumulation rates.

Content (OSIC) method, and the broken-stick model for significance testing (Bennett, 1996). Only pollen types over 0.5% were considered for zonation. Pollen grouping according to habits and vegetation types follows Huber (1992a, b; 1995b) and the Flora of the Venezuelan Guayana (Steyermark *et al.*, 1995-2005), which is also the taxonomic reference. AMS radiocarbon dating was performed in the Kek Crabon Cycle AMS Laboratory (University of California, Irvine) and Beta Analytic Inc., on nine samples consisting of plant macroremains. Age calibration and the age-depth model were performed with *clam.R* (Blaauw, 2010), using the *IntCal09.14c* database (Reimer *et al.*, 2009).

## RESULTS AND DISCUSSION

### Lithostratigraphy and chronology

The core is mainly composed of dark-brown peat, with some clayey intervals at the base (Fig. 4). The very basal layer (199-190 cm) is of clayey peat, followed by a ~20 cm interval of dark organic

peat (gyttja). The rest of the core, from ~170 cm onwards, is dark-brown fibrous/granular peat, except for a ~5 cm clayey layer around 140 cm. The age-depth model is based on the nine radiocarbon ages measured (Table 1). The best fit was obtained with a spline smooth model (Fig. 4). Peat accumulation rates changed two times along the sequence. At the base, they were of 0.24 mm/y but they abruptly increased to 0.55 mm/y around 6100 cal yr BP, coinciding with the lithostratigraphic change from gyttja to fibrous/granular peat. A subsequent lowering to 0.13 mm/y occurred around 5200 cal yr BP, which remained until the present.

### Palynology

A total of 67 pollen and 15 pteridophyte spore types were found in this study. The average count was 359 (minimum 319, maximum 422), and the average pollen sum was 265 (minimum 231, maximum 305). The surface sample (Fig. 5) is dominated by herbs, mainly Poaceae, Cyperaceae and *Xyris*, followed by some ligneous elements, mainly *Cyrilla* Garden ex L. (Cyrillaceae) and *Weinmannia* L. (Cunoniaceae).

**Table 1.** AMS radiocarbon dates from pnat macrofossils. Beta – Beta Analytic Inc., UCI – Kek Crabon Cycle AMS Laboratory (University of California, Irvine).

Sample	Depth (cm)	Lab code	<sup>14</sup> C BP	cal BP (2σ)
PATAM9_A07/10	18-20	Beta-242284	250 ± 40	268-333
PATAM9_A07/22	42-44	Beta-269200	2070 ± 40	1946-2144
PATAM9_A07/35	68-70	Beta-242285	2850 ± 40	2855-3078
PATAM9_A07/50	98-100	Beta-269201	3680 ± 40	3879-4150
PATAM9_A07/66	130-132	Beta-242286	4900 ± 40	5587-5669
PATAM9_A07/88	174-176	Beta-242287	5310 ± 40	5989-6207
PATAM9_A07/93	184-186	Beta-262202	5410 ± 40	6176-6295
PATAM9_A07/97	192	Beta-277187	5770 ± 40	6473-6666
PATAM9_A07/100	198	UCI-37505	7765 ± 15	8536-8592

Among pteridophyte spores, Cyatheaceae are the more abundant. Some significant elements of the tepuian vegetation such as *Bonnetia* Mart. Ex Nees & Marth. (Bonnetiaceae) and *Stegolepis* are scarce or absent. Concerning *Chimantaea*, despite the proximity of a shrubland dominated by *Chimantaea mirabilis*, its pollen is under 5%. Less abundant but worth mentioning elements are Clusiaceae (*Tovomita*-type Aubl.), *Adenanthe* Maguire, Steyerl. & Wurdack (Ochnaceae) and *Ilex* (ligneous), *Brocchinia* (herbaceous), and *Hymenophyllum* Sm./*Trichomanes* L. (Hymenophyllaceae), *Lycopodiella contexta* (Mart.) Holub. (Lycopodiaceae) and *Pterozonium* Fée (Pteridaceae) (pteridophytes).

The general pollen diagram (Fig. 5) represents the pollen and spore types over 0.5% of the pollen sum. This diagram was subdivided into 2 pollen zones:

#### *APK-I (199-129 cm, 8010-5310 cal yr BP)*

This zone is dominated by ligneous plants (trees and shrubs), reaching around 60% of the pollen sum. Among them, the more abundant are *Myrica* L. (Myricaceae), *Cyrilla*, *Ilex* and *Weinmannia*. It is noteworthy that *Myrica* rarely is below 10%, while it is almost absent at present. Clusiaceae (*Tovomita*-type) and *Chimantaea* are absent or less abundant than today. Among herbs, only Poaceae are worth mentioning, with percentages up to 40%, *Brocchinia* and *Xyris*, usually present today, are very scarce or absent in this zone. Cyperaceae are also scarcer than at present. Pteridophyte spores are also scanty, except for *Isoetes* that reached values over 60% of the pollen sum but experienced a dramatic

decrease from about 160 cm (5680 cal yr BP) until the top of the zone. *Hymenophyllum/Trichomanes* is almost absent, *Huperzia* Bernh. (Lycopodiaceae) shows a decreasing trend but of less magnitude than *Isoetes*, and *Pterozonium* has similar percentages than today. This zone differs from the surface sample, which represents the present-day vegetation, in the higher abundance of *Myrica*, *Isoetes* and *Pterozonium*, and the lower percentages of Clusiaceae (*Tovomita*-type), *Weinmannia*, *Brocchinia*, Poaceae and pteridophyte spores in general.

#### *APK-II (129-0 cm, 5310-0 cal yr BP)*

The more significant change with respect to the former zone is the remarkable decrease of *Myrica*, which reaches values similar to today (< 1%) and almost disappears at the top of the diagram. The other ligneous elements remain with percentages similar to the former zone, except for Clusiaceae (*Tovomita*-type) and Melastomataceae, which experienced a slight increase. There is a general increase of herbs (60-70%), which replace the ligneous plants in the dominance of the diagram. The more evident increase correspond to Poaceae (up to 50%), *Brocchinia* and *Xyris* also showed a consistent increase. *Stegolepis* appears occasionally without any definite trend. Cyperaceae also increase but it does not attain present-day values (14%). Among pteridophyte spores, the more outstanding shift is the dramatic decline of *Isoetes* (~1%). *Cyathea* Sm. (Cyatheaceae) spores slightly increase and *Pterozonium* declines in a similar way that *Myrica* and *Isoetes*, but at lower magnitudes.



*Hymenophyllum/Trichomanes* increases and attains values similar to present day conditions. This zone was subdivided into two subzones, namely a and b, with the boundary at 69 cm (2990 cal yr BP). As compared to APK-IIa, subzone APK-IIb shows a slight increase in some minor ligneous and herbaceous elements such as Clusiaceae (*Tovomita*-type), *Chimantaea*, *Weinmannia* and *Brocchinia*, as well as the appearance of *Bonnetia roraimae* and *Psychotria* L. (Rubiaceae) (absent in the rest of the diagram), and the decrease of Poaceae. In general, the zone APK-II is more similar to the surface sample.

### Paleoenvironmental interpretation

According to the former results, both the environment and the vegetation were different from the present ones between 8010 and 5310 cal yr BP. The high abundance of *Isoëtes* suggests a very wet environment, possibly permanent flooding, in the coring site. This moisture-loving genus of pteridophytes has three species in the Guayana region, one from the lowlands (*Isoëtes triangula* U. Weber, 50-200 m elevation) and two from the high-tepui summits (*Isoëtes killipii* C. V. Morton, 1900-2800 m elevation; and *Isoëtes vermiculata* Hickey, 2500-2700 m elevation) (Hickey & Smith, 1995). In the Chimantá massif, *Isoëtes killipii* grows in moist meadows, edges of pools, streams, wet crevices near waterfalls, between 1900 and 2800 m elevation (Huber, 1992a). In the Apakará diagram the presence of clayey sediments are indicative of standing water and support the interpretation of flooded vegetation or a small shallow pond (light availability is needed for *Isoëtes* to develop). Therefore, climates wetter than today could be inferred. This is supported by the increase of *Pterozonium*, a fern typical of humid tepuian environments (Lellinger, 1995), and the absence/scarcity of *Hymenophyllum/Trichomanes*, two genera of lithophilous ferns, in the Chimantá massif (Huber, 1992b). On the other hand, the dominance of *Myrica* (very scarce today) and the other forest elements indicates that these forests were different in composition than today. *Myrica rotundata* Steyerl. & Maguire (Myricaceae) is the only species of the family Myricaceae known from the Venezuelan Guayana (Miller, 2001). This species is typical from tropical mountains and, in the Cimantá massif, it is found in mixed *Bonnetia* forests and forested slopes between 1900 and 2200

m. The high abundance of *Myrica* pollen in contrast to today may be interpreted as more favorable environmental conditions for its development. Since the Apakará locality studied here (2170 m elevation) is close to the upper boundary limit of *Myrica rotundata*, a climate warmer than today could be assumed for the early to mid-Holocene interval studied here. In summary, the more likely climate for the 8010-5310 cal yr BP interval is warmer and wetter than today.

The upper pollen zone, ranging from 5310 cal yr BP to the present shows no remarkable differences with respect to present-day vegetation and a similar climate can be deduced. In the absence of more detailed studies, the minor oscillations in several pollen and spore types inside this zone that justified the subdivision into two subzones, before and after 2990 cal yr BP, could be tentatively attributed to minor community reorganizations, which cause is not yet known. It is noteworthy that the typical *Bonnetia* gallery forests did not appear until this date (2990 cal yr BP), as indicated by the first appearance of the dominant species (*Bonnetia roraimae*) and *Psychotria*, growing in the shrubby stratum of these forests (Huber, 1992a).

Comparison with other tepuian localities is problematic as most of them go back to 5-6 cal kyr BP at most, and do not record the early Holocene. Furthermore, as stated before, local reorganizations dominate over potential regional trends thus preventing generalizations (Rull, 2005a). Other areas available for comparison are the Andes, the Cariaco Basin and Lake Valencia (Rull *et al.*, 2010a). In the Andes, oxygen isotope records from the “Lagunas Verdes” lake cores showed a shift from wet climates during the early Holocene to drier ones in the middle Holocene (Polissar *et al.*, 2006), coinciding with the Apakará record. The Lake Valencia sediments also recorded wetter conditions during the early-mid Holocene, where maximum lake levels were recorded, with a further shift to drier conditions during the mid-late Holocene (Curtis *et al.*, 1999). The same trends were found in the Cariaco Basin using Titanium and Iron records, showing the occurrence of wetter climates during the early Holocene and a shift towards drier conditions since around 5.4 cal kyr BP (Haug *et al.*, 2001), which matches almost exactly with the Apakará sequence. These moisture fluctuations have been attributed to the latitudinal migration of the Intertropical Convergence Zone



(ITCZ), which is one of the main controls of the precipitation amount and regime in the Neotropics (Haug *et al.*, 2001).

Concerning temperature, the assumedly warmer Apakará phase (8.0 to 5.3 cal kyr BP) falls within the so called Holocene Thermal Maximum (HTM), recorded in the Northern Hemisphere between about 11.0 and 5.0 cal kyr BP, and attributed to changes in orbital forcing and oceanic circulation (Renssen *et al.*, 2009). The warming trend leading to the HTM (called Early Holocene Warming or EHW) was previously documented in two localities from the adjacent Gran Sabana midlands, around 800-900 elevation, coinciding with the first record of extensive savannas in the region (Rull, 2007b; Montoya *et al.*, 2011). Contrastingly with the apparent paleoclimatic heterogeneity recorded in many Guayana records as compared with others from the Neotropics (Rull *et al.*, 2010a), the Apakará sequence shows a convincing agreement in both temperature and hydrological balance, at a millennial scale. Further studies will show if this situation is maintained at decadal to centennial scales. The results obtained here are encouraging for the tepui summits as suitable locations to record regional and global paleoclimatic and paleoecological trends, and support the hypothesis of the altitudinal ecotones as the more sensitive sites (Rull, 2005a).

## CONCLUSIONS

Millennial-scale pollen analysis of a Holocene sequence from the summit of the Apakará summit, in the Chimantá massif, has documented the occurrence of a significant vegetation change around 5.3 cal kyr BP, which is considered to have been a consequence of an environmental change from early-mid Holocene warmer and wetter climates to mid-late Holocene cooler and drier conditions, similar to present. The warmer and wetter phase (8.0 to 5.3 cal kyr BP) agrees with most neotropical records, and also with the Northern Hemisphere Holocene Thermal Maximum. During the second phase (5.3 cal kyr BP to present), the present climates and vegetation established, with minor fluctuations. Studies at centennial to millennial scales are needed for a detailed reconstruction of the Holocene trends. This study supports the potential interest of tepui summits as paleoenvironmentally sensitive sites.

## ACKNOWLEDGEMENTS

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