



# An evaluation of the Lost World and Vertical Displacement hypotheses in the Chimantá Massif, Venezuelan Guayana

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## ABSTRACT

**Aim** To document the occurrence of vertical displacements of vegetation in the high plateaus of the Venezuelan Guayana (*tepuis*) over the last c. 6000 years, and to discuss their significance for the origin of their flora, especially the endemism patterns observed in their flat summits. Two hypotheses have been proposed for the origin of the summit flora. One (the Lost World hypothesis) proposes a long history of evolution in isolation from the surrounding plains, while the other (the Vertical Displacement hypothesis) suggests that vertical movements of vegetation during the Pleistocene glacial-interglacial cycles would have resulted in floristic mixing within the lowlands, and genetic interchange among plateau summits.

**Location** This work has been conducted on the flat summit of the Churí-tepui, in the Chimantá massif, at 5°15' Lat. N and 62°01' Long. W, around 2250 m altitude.

**Methods** Pollen analysis and radiocarbon dating of two peat outcrops, using modern analogue technique and numerical methods for palaeoecological interpretation were used.

**Results** The replacement of a high-altitude plant community (a paramoid *Chimantaea* shrubland) by a lower elevation (< 2300 m) *Stegolepis* meadow, occurred about 2500 years before present (yr BP). This vegetation change is inferred to have resulted from a regional climatic shift to higher temperature and moisture. A subsequent decrease in temperature and moisture led to the establishment of present conditions after about 1450 yr BP.

**Main conclusions** The highland vegetation of the *tepuis* responded to climate shifts with vertical displacements, supporting the hypothesis of vertical mixing. However, a physiographical analysis shows that around half of the *tepuis* would never have been connected by lowlands. Therefore, both hypotheses are needed to explain the origins of the summit flora in the *tepuis*.

## Keywords

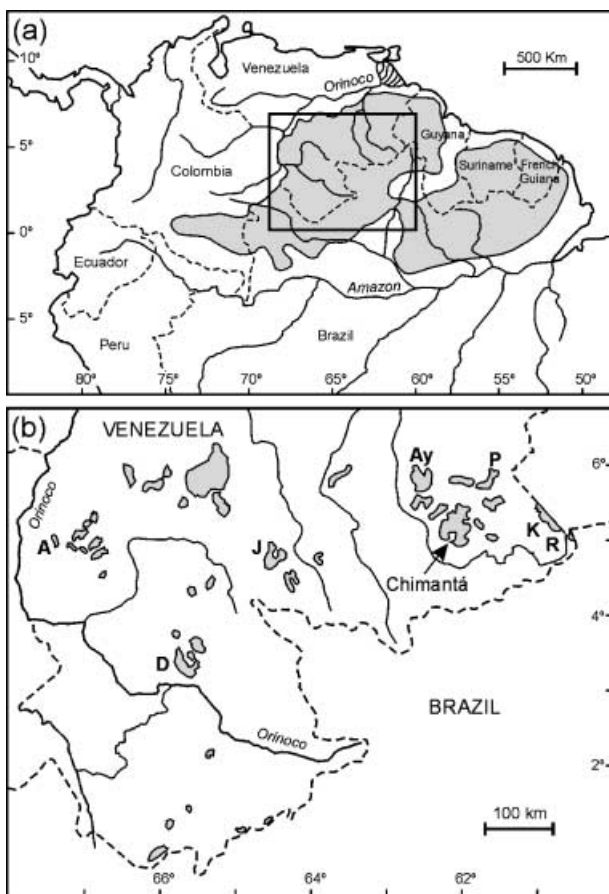
Endemism, historical biogeography, Holocene, palynology, *Pantepui*, *tepuis*, vegetation change, Venezuelan Guayana.

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## INTRODUCTION

One of the most striking features of the flora of the Guayana (= Guiana) region is the high degree of specialization and endemism, which is particularly apparent on the remote summits of the table mountains (*tepuis*), characteristic of the Guayana landscape (Figs 1 and 2). Earlier workers overestimated the degree of endemism of *Pantepui*, a discontinuous biogeographical province formed by the ensemble of the *tepuis* summits above 1500 m elevation (Huber, 1995a). For example, Maguire (1970) estimated

that the *Pantepui* flora might contain around 2000 species, of which 90–95% were endemic to this region. This fact, together with the implicit idea that the *tepuis* summits were geographically isolated from each other and from the surrounding lowlands, led to the Lost World (Doyle, 1912) hypothesis, according to which, the *Pantepui* flora would be relictual, after millions of years of isolated evolution (Maguire, 1970; Brewer-Carías, 1978). The amount of apparent endemism decreased as botanical exploration of the region intensified. At present, it is known that of 2322 species recorded so far in *Pantepui*, 'only' 33.0% are endemic



**Figure 1** Location map showing: (a) the extension of the Precambrian Guiana Shield (grey area), which defines the Guayana or Guiana region, and (b) the distribution of the *Pantepui* province (grey areas), indicating the Chimantá massif, the location of this study, and other important *tepui*s: A = Autana, Ay = Auyán, D = Duida, J = Jaua, K = Kukenán, P = Ptari, R = Roraima. Base map from Huber (1995a).



**Figure 2** Typical landscape of the Venezuelan Guayana, showing the flat *tepui* summits and the vertical cliffs separating them from the surrounding lowlands.

(Berry *et al.*, 1995). The more comprehensive collection also revealed that many taxa have a wider elevational range than previously known, and that taxa from both highlands and lowlands merge at intermediate altitudes (Steyermark & Dunsterville, 1980; Huber, 1988). Also, the myth of total geographical isolation has been questioned, because large valleys and ridges effectively connect many (although not all) *tepui* summits with the surrounding lowlands (Huber, 1988). In this way, the idea of evolution in isolation progressively lost credibility and the Vertical Displacement hypothesis emerged. According to Steyermark & Dunsterville (1980), connection between the ecosystems of the *tepui* summits is possible. They propose two mechanisms: (1) migrations using river valleys, and (2) vertical displacement during Pleistocene glacial-interglacial cycles. Consistent with this hypothesis is the occurrence of patches of *tepuian*-like vegetation in the plains surrounding the *tepui* summits. These communities have been considered relicts of glacial times, when the *tepuian* vegetation was vertically displaced (Huber, 1995b). The Vertical Displacement hypothesis has two main constraints. Firstly, it was developed for a low to intermediate *tepui* summit (the Guaiquinima, ranging from about 700–1650 m elevation), where connections with the surrounding lowlands are evident and extensive. The situation could be different for other, higher elevation *tepuis*. Secondly, although definite altitudinal vegetation patterns have been proposed for the Guayana region (Huber, 1988), past vertical floristic displacements have not been demonstrated so far.

Fortunately, these hypotheses are testable through palaeoecological studies. Pollen records presented in this paper document an altitudinal displacement of highland vegetation at sites above 2000 m altitude. Previous pollen analyses in several *Pantepui* localities were not conclusive in evaluating these hypotheses (Rull, 1991), due to severe constraints imposed by the lack of knowledge of this remote area, mainly in relation to pollen identification and interpretative capacity. However, in the last years, the situation has changed markedly. New pollen-morphological studies (Rull, 2003) have increased the reliability of pollen identification and the number of pollen types identified. Furthermore, our ability to interpret observed changes in the pollen record has been enhanced by the recent publication of detailed ecological and biogeographical information of parent taxa (Berry *et al.*, 1995; Marchant *et al.*, 2002). Therefore, at present, accurate vegetation reconstructions based on pollen analysis are possible.

## METHODS

### Study area: physiography, climate and vegetation

This study was carried out in the Churí-*tepui*, belonging to the Chimantá massif, a spectacular complex of *tepui* summits situated at about 05°07′–05°27′-N lat. and 61°65′–62°19′-W long. (Fig. 1). The total surface of the massif is about 1470 km<sup>2</sup>, its summit ranging from 1700 to 2700 m elevation (Huber, 1992). Like the other *tepuis* and *tepui* massifs, the Chimantá is developed on Precambrian sandstones and quartzites of the Roraima

Group overlying the Guiana Shield (Gibbs & Barron, 1983), and is part of the discontinuous Auyán-tepui erosion surface, the highest of the six such surfaces in the Venezuelan Guayana (Schubert, 1987; Briceño & Schubert, 1990, 1992a,b).

Physiographically, Venezuelan Guayana is subdivided into lowlands (0–500 m elevation), uplands (500–1500 m) and highlands (1500–3000 m). This topography provides a gradient of climatic conditions, mainly temperature, resulting in the altitudinal succession of life zones, each with characteristic vegetation. These are the piedmont (50–400 m), the slopes (400–2000 m), and the *tepui* summits or high-*tepui* zone (2000–3000 m). The piedmont corresponds climatically to the macrothermic belt. The slopes are subdivided in turn into three levels: lower montane or submontane (400–800 m), montane (800–1500 m) and upper montane (1500–2000 m). The *tepui* summits, the zone with which the present paper is concerned, are between the mesothermic and submicrothermic belts, and include several vegetation types, such as low *tepui* forests, scrubs, and high-mountain meadows and grasslands (Huber, 1995b). The ecosystems from the *tepui* summits correspond to the same uppermost montane life zone that is present worldwide above the treeline (Huber, 1988). Forests occur as gallery forests along some water courses (riverine forests), or in areas with specific geological and edaphic characteristics (low *tepuian* forests).

The climate of the Chimantá massif is mild and humid. The estimated mean annual temperature is 14.1 °C, with a maximum difference of 2 °C average between the warmest and the coldest month. The estimated average total annual precipitation is 3351 mm, with 8 months (April to November) over 200 mm (up to 500 mm in June). Potential evapotranspiration rates (Holdridge, 1959) are below 70 mm/month on average, reaching 819 mm per year. Strong winds and sudden changes in most climatic parameters are frequent (Galán, 1992). The vegetation is arranged in a heterogeneous mosaic pattern, related to the great diversity of environments and altitudes. Riverine forests (4–8 m tall) are dominated by *Bonnetia roraimae* (Theaceae), with *Schefflera* (Araliaceae) and *Spathelia* (Rutaceae) as other important components. The low *tepuian* forests grow on intrusive rocks (diabase), and are similar in composition to riverine forests, except that *B. roraimae* is not dominant and the other components are more abundant. The predominant vegetation types are several types of shrublands and herbaceous communities dominated either by Poaceae and Cyperaceae (grasslands) or by Rapateaceae and Xyridaceae (meadows). Of them, the *paramoid* shrublands and the meadows will be described in more detail, because of their significance for the present study.

The highland *tepui* meadows (*herbazales*) are herbaceous communities growing on thick peat accumulations, and dominated by the families Rapateaceae and Xyridaceae, with Cyperaceae and the Poaceae as subordinate components. In the Chimantá massif, these communities are typically 0.3–1 m high, and the absolute dominant taxon is the endemic *Stegolepis ligulata* (Rapateaceae). Co-dominant taxa are several species of *Xyris* (Xyridaceae), *Everardia* and *Lagenocarpus* (Cyperaceae), *Lindmania* and *Brocchinia* (Bromeliaceae), *Heliamphora* (Sarraceniaceae), and *Syngonanthus* (Eriocaulaceae). Other components

include several members of the families Orchidaceae, Iridaceae, Liliaceae and Lentibulariaceae. Among the occasional shrubs (up to 2 m tall), the families Theaceae, Ericaceae, Melastomataceae, Asteraceae, Ochnaceae, Rubiaceae and Santalaceae are present at low densities (Huber, 1995b). The upper altitudinal limit of *Stegolepis ligulata* occurs at about 2300 m (Huber, 1992).

The *paramoid* shrublands or scrubs are situated at higher elevations up to 2600 m. These shrublands are a unique vegetation type of the Chimantá massif, dominated by one of the three species of *Chimantaea* (Asteraceae), a genus endemic to the Chimantá and some adjacent *tepuis*. This vegetation type has physiognomic and taxonomic affinities with some upper Andean shrublands called  *páramos*, because of the dominance of the caulirosette (columnar rosette) growth forms belonging to the Asteraceae. In the Churí-tepui, the *paramoid* shrublands are dominated by *Chimantaea humilis* (0.5–1.5 m high), growing on water-saturated, peaty soils up to 1 m in depth. The terrestrial tubular bromeliad *Brocchinia hechtioides* is a conspicuous element of this vegetation type: accompanying elements are *Stegolepis ligulata* (up to 2300 m elevation), *Stomatochaeta cymbifolia* (Asteraceae), *Ledothamnus luteus* (Ericaceae), *Maguireothamnus speciosus* and *Aphanocarpus steyermarkii* (Rubiaceae), *Macairea cardonae* and *Comolia coriacea* (Melastomataceae), *Heliamphora minor* (Sarraceniaceae), and several Xyridaceae, Eriocaulaceae and Cyperaceae (Huber, 1992). The other types of *paramoid* shrublands are dominated either by *Chimantaea mirabilis* (centre-north of the massif) or *Chimantaea lanocaulis* (restricted to the highest areas of the NE, Apakará-tepui and Eruoda-tepui); while *Stegolepis ligulata* is absent, due to altitudinal constraints.

## Materials and methods

Two peat outcrops situated near the upper limit of the altitudinal distribution of *Stegolepis ligulata* were sampled for pollen analysis and radiocarbon dating. The sites are in the locality VIII of Huber (1992), situated in the SE sector of the massif, at about 2250 m altitude, on an extensive plain with a gentle slope towards the NW. The dominant vegetation is *paramoid* shrubland, with patches of riverine forests. The two sections sampled were labelled CHIM-1 (55 cm depth) and CHIM-2 (83 cm depth). Each 5 cm, a sample was taken for pollen analysis. Samples for radiocarbon dating were taken only in CHIM-2, at three intervals (20–31 cm, 42–55 cm and 69–83 cm). Laboratory methods include HCl and HF digestion and acetolysis. Slides were mounted in silicone oil without sealing. Identification followed mainly Salgado-Labouriau & Villar (1992) and Rull (2003), with the help of other pollen and spores atlases and books (Roubik & Moreno, 1991; Tryon & Lugardon, 1991; Herrera & Urrego, 1996; Colinvaux *et al.*, 1999). Taxonomy follows Berry *et al.* (1995). A minimum of 200 pollen grains were counted, but counts were not stopped until the diversity saturation criterion was fulfilled (Rull, 1987). Pollen diagrams were plotted with Pspimoll 4.10 (Bennett, 1994, 2002) and weighting average ordering of taxa was performed using Tran 1.8 (written by S. Juggins, University Newcastle). Statistical analyses were carried out using

MVSP 3.1 for Windows (Kovach, 1989, 1999). The program CALIB 4.3 was used to calibrate  $^{14}\text{C}$  dates (Stuiver *et al.*, 1998a,b).

## RESULTS

### Vegetational interpretation

The results of radiocarbon dating for section CHIM-2 are shown in Table 1, and the palynological diagrams for both sections are depicted in Fig. 3. Visually, both diagrams show a sharp and conspicuous subdivision into two sections: the lowermost section dominated by *Chimantaea* and *Xyris*, with *Stegolepis* almost absent; and the upper section, in which *Chimantaea* and *Xyris* are notably lower (especially the former), whereas *Stegolepis* and Poaceae are dominant. These patterns of change were examined using an assemblage approach. In this way, it is possible to verify that the observed changes are not due to minor internal reorganizations in the taxonomic composition of the communities (i.e. modulated successions) but to actual community substitutions (*sensu* Rull, 1990). Two pollen assemblages were obtained in each locality by cluster analysis, using the Pearson correlation coefficient, and the centroid agglomerative method (Kovach, 1989, 1999). Both groups show a strong homogeneity in both localities. Indeed, group A is characterized by *Stegolepis*, Poaceae, *Ilex* and *Cyrilla*, and group B is defined by *Chimantaea*, *Xyris* and Ericaceae (Fig. 4). These are the dominant elements of the pollen diagrams, and include the most characteristic taxa that define the two communities under consideration: the *Chimantaea* shrublands, and the *Stegolepis* meadows (Huber, 1992, 1995b). Therefore, numerical analysis confirms that a community replacement has taken place. Cyperaceae is the only element that shows no fidelity to any of the two assemblages. This is a broad category because of the difficulty of pollen differentiation below the family level (Rull, 2003). Therefore, several Cyperaceae genera and species with different ecological requirements are likely to be represented. The same could be true for Ericaceae and Poaceae, but they belong to definite groups (B and A, respectively). This is not surprising, because it is known that some Ericaceae genera and species are common and typical elements of the *Chimantaea* shrublands, whilst grasses are not (Huber, 1992). In the *tepuian* summits, Poaceae are important only in grasslands restricted to some flooded valley bottoms (Huber, 1995b).

Taken as a whole, the pollen assemblages defined show a consistent stratigraphic pattern in both CHIM-1 and CHIM-2

(Fig. 5). The *Chimantaea* shrubland zone has practically no *Stegolepis*, like the present-day paramoid shrublands of the uppermost altitudinal levels in the Chimantá massif. Therefore, these vegetation types were at lower elevations compared with the present situation (the coring site is close to the uppermost limit of distribution of *Stegolepis*, see above). The sudden increase in *Stegolepis* occurs at about 30 cm in CHIM-1 and 55 cm in CHIM-2, at an interpolated age of 2552 cal.  $^{14}\text{C}$  yr BP. Therefore, after this date, vegetation moved upward, leading to a situation similar to the present; or moved possibly even higher, because the percentages of *Stegolepis* are higher than in the present-day paramoid shrubland with *Stegolepis*, and rather more similar to those of well-developed *Stegolepis* meadows, at lower elevations (Rull, 1991). In CHIM-2, a third zone can be distinguished above 37 cm (< 1330 cal.  $^{14}\text{C}$  yr BP), characterized by intermediate percentages of shrubland and meadow assemblages, and of *Chimantaea* and *Stegolepis*, respectively. This can be interpreted as a *Chimantaea* shrubland with *Stegolepis*, comparable to the present-day vegetation of the study area. This zone is not so evident in CHIM-1, either because it could be absent (eroded?) or because it is subsumed within the *Stegolepis* meadow zone (Fig. 5).

### Palaeoclimatic interpretation and correlations

The altitude of vegetation types depends principally on average annual temperatures (Galán, 1992), hence these elevational shifts reflect temperature changes. The present-day lapse rate of the region is  $-0.6\text{ }^{\circ}\text{C}/100\text{ m}$  altitude (Galán, 1992). Unfortunately, the scarcity of modern analogues for the *tepuí* summits (Rull, 1991) does not allow us to estimate quantitatively the vertical displacement recorded in these diagrams and therefore to estimate the temperature change. However, a maximum altitudinal displacement of one to a few hundreds of metres is likely to have occurred. In summary, the diagrams reflect an initial phase colder than today before 2552 cal.  $^{14}\text{C}$  yr BP and a shift towards a phase like today or slightly warmer after this date. The present-day climatic and vegetational conditions appear to have been developed shortly after 1330 cal.  $^{14}\text{C}$  yr BP (AD 620).

The upward shift around 2500 BP coincided with a general expansion of gallery forests on other *tepuí* summits, and with high lake levels in the surrounding lowlands of the *Gran Sabana*, indicating a general increase in moisture (Rull, 1991, 1992, 1996). It also started at the same time as the Miranda warm phase of the northern Andes, interpreted as a temperature and moisture increase, on the basis of pollen records (Salgado-Labouriau *et al.*, 1988; Salgado-Labouriau, 1989). Titanium and Fe records from ODP site 1002 located at the Cariaco basin, about  $5^{\circ}$  latitude north of the Chimanta massif, favour a shift to higher precipitation after 2800 y BP (Haug *et al.*, 2001). Therefore, the upward displacement recorded here is most probably the result of a widespread climate shift towards higher temperatures and moisture. The subsequent shift initiated around AD 620 coincides with the onset of abrupt but persistent drought episodes recorded isotopically in the Yucatán Peninsula (Mexico) since AD 600–1400, and implicated in the collapse of the Maya

**Table 1** Results of radiocarbon dating (Schubert & Fritz, 1985; Schubert *et al.*, 1986) and calibration (Stuiver *et al.*, 1998a,b). One sigma confidence interval for calibrated ages is given in brackets

Sample	Laboratory number	Depth (cm)	$^{14}\text{C}$ years BP	Cal. $^{14}\text{C}$ years BP
CHIM-11	WAT-1163	20–31	Modern (105%)	—
CHIM-12	WAT-1173	42–55	1450 ± 60	1330 (1294–1406)
CHIM-13	WAT-1164	69–83	5740 ± 100	6499 (6409–6663)



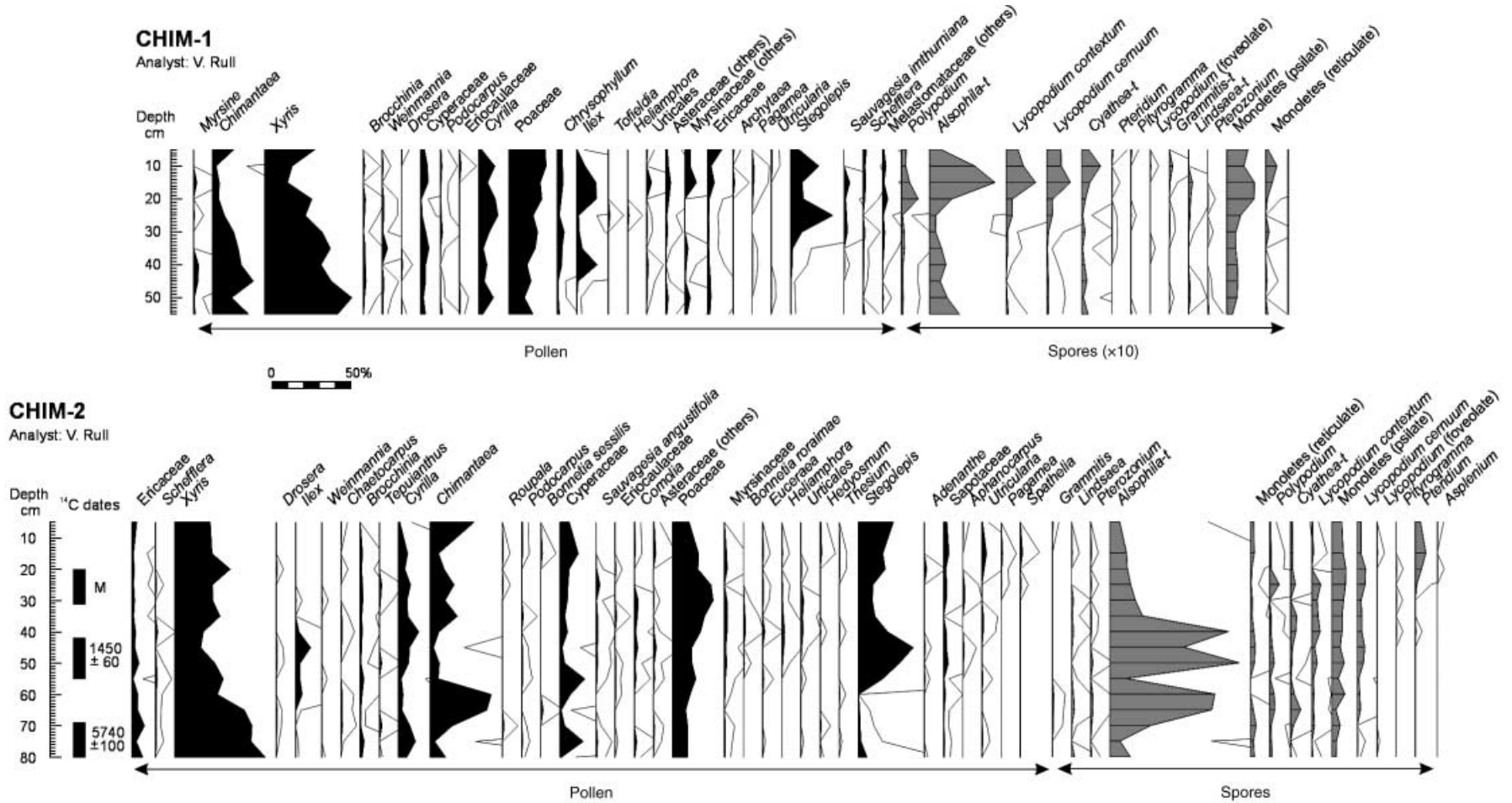


Figure 3 Percentage pollen diagrams of CHIM-1 and CHIM-2 from Churi-tepui. Pollen types are in black and fern (and allied) spores in grey.

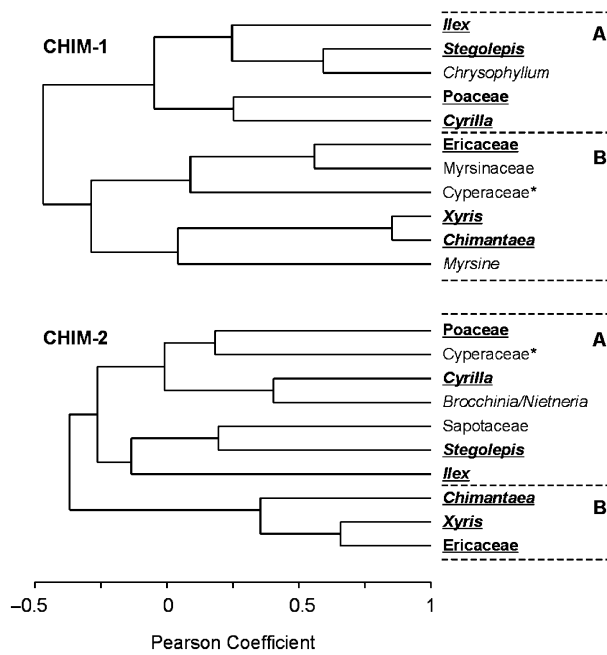


Figure 4 Dendrogram showing the results of cluster analysis on CHIM-1 and CHIM-2 pollen data, using the Pearson correlation coefficient and the centroid agglomerative method (see text for details).

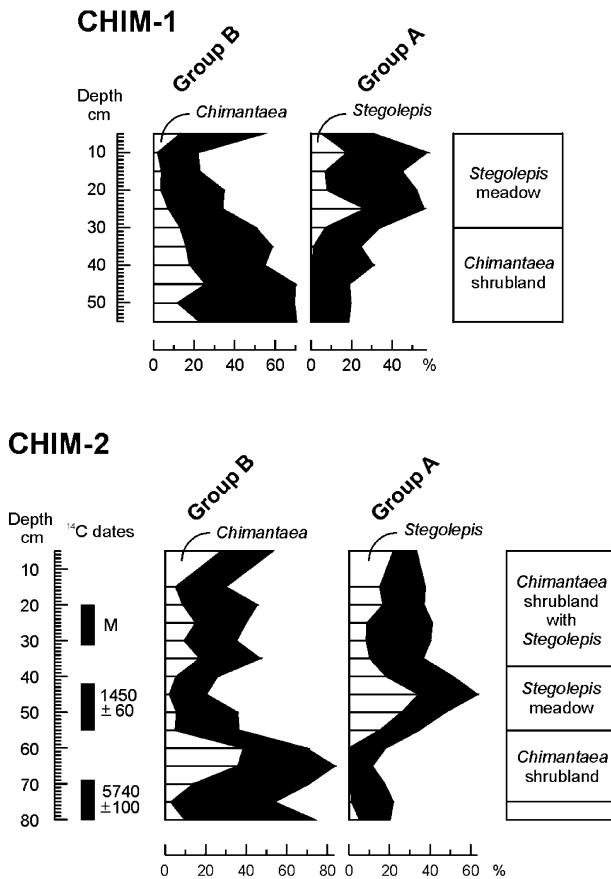


Figure 5 Stratigraphic distribution of groups A and B resulting from cluster analysis, and interpreted vegetation zones.

civilization (Hodell *et al.*, 1995; Curtis *et al.*, 1996). It also coincides with an increase in silt and charcoal influx to a lake from central Peru (AD 600–700), and a major dust event recorded at AD 620 in ice cores from the Peruvian Andes, both of which have been related to dry climatic conditions that appear to have affected pre-Incaic civilizations (Thompson *et al.*, 1995, 1988; Chepstow-Lusty *et al.*, 1996). Similar episodic drought events were recorded recently in the Cariaco basin, at about AD 760, 810, 860 and 910 (Haug *et al.*, 2003). Therefore, the event recorded herein from AD 620 onwards would represent part of a climatic shift of regional significance, with notable impact on human populations (Brenner *et al.*, 2001).

**CONCLUSIONS AND BIOGEOGRAPHICAL SIGNIFICANCE**

According to the results presented, the vertical displacements postulated by Steyermark & Dunsterville (1980) as a consequence of climatic changes seem to be a real phenomenon, even for the highest *tepu* summits. It is important to note that the vertical movements recorded here occurred during the Holocene, when climatic changes have been comparatively small. The magnitude of these movements is expected to have been notably higher during the Pleistocene glacial-interglacial cycles, by analogy with Neotropical high mountains situated at the same latitude. Therefore, the Vertical Displacement hypothesis seems to be supported by these results. The next question is if these vertical displacements have been frequent and intense enough to account for the evolution of the *Pantepui* flora.

The first evidence of widespread glaciation in the Northern Hemisphere, or the onset of glacial-interglacial cycles, is at 2.4–2.5 million years (My) BP. Between that time and 800,000 years (800 ky) BP, about 30 glacial/interglacial cycles occurred, with a periodicity of 41 ky. During the last 800 ky, the eight glacial cycles documented have been not only longer (100 ky periodicity) but also more intense (Raymo, 1994; Chapman, 2000). Another interesting fact is that glacial phases have been notably longer than interglacials, so glacial conditions have been the rule. Therefore, in theory, there have been roughly 40 opportunities for biotic interchange between the *tepu* summits during the last 2.5 Ma. In order to assess the intensity of both climatic and altitudinal oscillations, the Last Glacial Maximum, which occurred at about 18 <sup>14</sup>C ky BP, will be used as a reference for further comparisons. This has been the coldest phase of the Last Glaciation. In the Neotropics, average temperatures were about 8 °C lower than today in the Andes (Van der Hammen & Hooghiemstra, 2000), and around 5 °C below the present ones in the lowlands (Bush *et al.*, 2001). According to Van der Hammen & Cleef (1986), the treeline was 1300–1500 m lower than today in the Colombian Andes, situated at the same latitude as the *Pantepui* region. In the Venezuelan Andes, between about 8–9° N lat., a similar shift of 1200 m was recorded (Rull, 1998). Therefore, a lowering of the same magnitude might be expected for the *tepu*-ian vegetation. Is this repeated lowering of *tepu*-ian ecosystems towards and into the lowlands sufficient to allow biotic interchange among them? Huber (1987) gives detailed information

on the base-summit altitudinal differences for the most important *tepuis*. This difference is above 1300 m for more than half of them, hence they would have remained isolated during the Last Glacial Maximum. Since temperature shifts of former glaciations have been only as large or have been less pronounced than the LGM, especially before 800 ky BP, a higher degree of biogeographical connection is not likely to have occurred in previous glaciations. This means that a significant proportion of the *tepuí* summit vegetation would have never been connected, except for hypothetical mechanisms such as long-distance seed dispersal or migration through river valleys connecting lowlands and highlands. Therefore, both isolation as well as vertical displacement are needed to explain the composition of the *tepuian* vegetation.

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#### BIOSKETCH

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