

# A 40,000-yr Pollen and Diatom Record from Lake Tritrivakely, Madagascar, in the Southern Tropics

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**Links between southern and northern hemisphere climates during the Late Quaternary are poorly known, partly due to the scarcity of continuous climatic records in the southern tropics. Pollen and diatom evidence from Lake Tritrivakely (19°47'S) provides information on vegetational and hydrological changes in the central highlands of Madagascar over the past 40,000 yr. Most of the record reflects natural environmental variability since humans arrived on the island ca. 2000 yr B.P. During glacial times, the migration of mountain plants toward lower altitudes is consistent with a temperature decrease and with reduced atmospheric CO<sub>2</sub> levels. In the lake, a positive mean annual hydrologic balance, from 38,000 to 36,000 and from 17,500 to 9800 cal yr B.P., coincided with periods of decreasing summer insolation and preceded by several millennia lake rises in the northern tropics. A negative hydrologic budget during periods of maximum seasonal contrast in solar radiation is partly attributed to high summer evaporation rate. The last glacial maximum was cool and dry. The deglacial warming occurred in two steps. The first step, accompanied by an increase in wetness, occurred abruptly at ca. 17,000 cal yr B.P., about two millennia earlier than in the northern hemisphere. It is abundantly documented in southern terrestrial data. The second step, at 15,000 cal yr B.P., was in phase with the first major temperature change in the northern hemisphere.** © 1998 University of Washington.

## INTRODUCTION

Little is known about how the tropics respond to changes in major climate-forcing factors and how the tropics influenced climate globally during the last glacial–interglacial cycle. Proxy data thus far available from southern hemisphere land areas suggest that solar forcing can explain only part of the recorded pattern of paleoclimate changes (Partridge, 1997). In recent years, robust evidence of a substantial cooling in tropical lands during the last glacial maximum (LGM) has been provided from various continental archives

(e.g., Bonnefille *et al.*, 1992; Holmgren *et al.*, 1995; Stute, 1998). Corals (Beck *et al.*, 1997) and deep-sea records (Van Campo *et al.*, 1990; Bard *et al.*, 1997) also show that tropical LGM sea-surface temperature (SST) fell 2.5 to 6°C, contrary to CLIMAP (1981) estimates. However, the external force capable of provoking the glacial cooling in the tropics has not been identified. Climate-model simulations incorporating the modern pattern of heat transport in the oceans in a standard ice-age simulation produced substantial cooling of the tropics and subtropics (Webb *et al.*, 1997). A recent coupled ocean–atmosphere climate model simulated reduced oceanic meridional heat flux in the Atlantic and a tropical cooling of 3–5°C in most of the southern tropics (Ganopolski *et al.*, 1998).

The hydrologic response of tropical land systems to glacial–interglacial SST variations and related changes in atmospheric water vapor availability is poorly known. The timing of deglaciation in the southern tropics is also poorly constrained. The interhemispheric synchrony of abrupt postglacial warming has been thought to be in phase with that of the northern hemisphere at 15,000 cal yr B.P. (Bard *et al.*, 1997), lagging Antarctic warming by several millennia. However, there is widespread evidence for earlier rapid warming in the southern hemisphere (Partridge, 1997; Lowell *et al.*, 1995). Further observations are required to reconcile tropical land, ocean, and polar ice records from both hemispheres.

Here, we present a 40,000-yr pollen- and diatom-based paleoenvironmental record from a crater lake, Tritrivakely, in the Madagascar highlands (19°47'S, 46°55'E, 1778m). The site was first investigated by Burney (1987a,b,c), who published pollen and charcoal results from a 5-m sediment core covering the last 11,000 yr. It features: (i) natural environment variability since human arrival 2000 yr ago (Mac Phee and Burney, 1991); (ii) high sensitivity to changes in

the seasonal migration of the Intertropical Convergence Zone (ITCZ) and related heavy summer rains; (iii) high sensitivity to changes in temperature and atmospheric CO<sub>2</sub> concentration, as it lies close to the lower limit of mountain vegetation; and (iv) easy interpretation of the sedimentary and hydrologic record because of a restricted watershed.

Our study aims at understanding the response of a southern tropical land area to changes in (i) solar radiation, (ii) glacial/postglacial atmospheric temperature, and (iii) tropical SST. It provides new insights into the timing of the last deglacial warming and hydrological changes.

## MODERN ENVIRONMENTAL SETTING

### *Climate and Vegetation*

The climate of Madagascar is controlled by two major precipitation mechanisms modulated by the effects of topography (Donque, 1972): (i) the southeast trade wind is generated by the southern subtropical Indian Ocean High (the Mascareignes Anticyclone); it brings warm and humid air, and year-round precipitation over eastern regions; (ii) during austral summer, the ITCZ reaches about 18°S. The northeasterlies emanating from southern Asia are deviated south of the Equator. This airstream extends in the southern hemisphere as the northwest monsoon. These winds generate heavy thunderstorm rains on the northern half of Madagascar. Summer tropical cyclones are also frequent. They usually originate around 10°S and 60°E in the Indian Ocean, and off Cap Saint-André in the Mozambique Channel (Donque, 1972). To the south, intrusions of the polar front occasionally bring cold air masses and light rains in winter.

The tropical mountain climate in the central highlands is characterized by warm and wet summers, and cool and dry winters. The eastern circulation only brings drizzle and fog that may have a significant role on the hydrologic cycle and vegetation by increasing air humidity (Paulian *et al.*, 1971). Summer rains represent about 80–90% of the total annual precipitation (Chaperon *et al.*, 1993). At Antsirabe, the meteorological station closest to Tritrivakely, mean annual temperature (*T*) is 15.3°C (minimum: June–August), precipitation (*P*) 1412 mm (maximum: January–April), and air humidity 67%. Mean annual pan evaporation (*E*) slightly exceeds *P* (maximum: September–December).

Relief and prevailing winds determine the distribution of major plant formations, although most of the climax vegetation is presently perturbed under the effect of human action, mainly in the central highlands (Harisoa, 1988). The vegetation near lake Tritrivakely is dominated by grassland and terrace agriculture. Frequent fires occur, both human- and lightning-caused. The original vegetation of the western slopes of the central highlands (800–1800 m; *T* = 20°C; *P* = 1000–1500 mm; 5–7 dry months) consists of a sclerophyllous forest with *Uapaca bojerii*. The ericaceous bush is

characteristic of high mountains (>2000 m, *T* 10°C, *P* > 2000 mm), which experience severe variations in humidity, solar radiation, temperature, and winter frost (Koechlin *et al.*, 1974). The mountains form a wooded landscape, with numerous microphyllous species, among which *Stoebe* is well represented (Humbert and Cours-Darne, 1965; Koechlin *et al.*, 1974). On the eastern escarpment, the medium-altitude dense rainforest ranges between ca. 800 and 1800 m, with *T* oscillating between 15 and 20°C, and *P* between 1000 and >1500 mm. A short dry season lasts up to 2 months. The vegetation is characterized by a substantial extent of herbaceous undergrowth and the development of mossy plants. *Tambourissa*, *Weinmannia*, and *Symphonia* are among the best-represented tree genera. The sclerophyllous lichen forest replaces the mossy forest between 1800 and 2000 m, with the presence of the Gymnosperm tree *Podocarpus*, *Vitex*, *Dombeya*, and many bamboos. The main ecological difference with the lower-altitude forest is a lower minimum temperature. Numerous species are typical of this forest, among which is the only Chloranthaceae found in Madagascar, *Ascarinopsis coursii*.

### *The Modern Lake*

Tritrivakely is an 80-m-deep maar of the Ankaratra volcanic chain in central Madagascar. The slopes (30–40°) consist of basaltic tuff, occupied today by agriculture. The lake, about 1 km wide, is mainly supplied by rain falling in the crater, has no surface outlet, and is very sensitive to seasonal and interannual changes in *P*–*E*. During dry seasons or years (e.g., November, 1992), the water body is an ombrotrophic Cyperaceae marsh with permanent water hollows. Water characteristics are close to those of rain water (electric conductivity, *C*: 20.6–37  $\mu\text{S cm}^{-1}$ ; pH 5.2–6.3; SiO<sub>2</sub> content: 1 mg l<sup>-1</sup>), with maximum values in water hollows. After rains of exceptionally wet years (e.g., May 1994), Tritrivakely becomes a shallow lake, 2–3 m deep. Runoff into the lake tends to increase *C* (100  $\mu\text{S cm}^{-1}$ ), pH (6–6.7), and SiO<sub>2</sub> content (4.6 mg l<sup>-1</sup>). However, no significant change in water turbidity takes place because the particle load from the catchment is filtered by vegetation.

The water body is colonized by emergent and aquatic plants, among which are *Polygonum glabrum*, Gramineae (sp. 1 and *Leersia hexandra*), Cyperaceae (*Heleocharis equisetina*, *Cyperus madagascariensis* dominant), *Nymphaea lotus*, *Nymphoides* sp., and *Naja australis* (H. L. Ranarijoana, pers. commun., 1997). Diatom communities reflect microhabitats and seasonal/interannual hydrological changes. The epiphytic, subaerial flora on Cyperaceae is mainly composed of *Eunotia* spp. (*E. flexuosa*, *E. naegelli*, *E. bilunaris* var. *mucicola*, and *E. incisa* dominant). On littoral surficial mud (<10 cm water), these *Eunotia* are accompanied by *Gomphonema* spp. (*G. gracile*, *G. parvulum*, *G. sp. aff. pseudotenellum*, *G. intricatum*), acidophilous *Cymbella* (e.g., *C.*

*cesatii*, *C. gracilis*), *Stauroneis producta*, *S. phoenicenteron*, *Frustulia rhomboides*, and diversified *Pinnularia* (e.g., *P. borealis*, *P. major*, *P. obscura*, *P. sp. aff. hemiptera*, *P. viridis*). In permanent water hollows, the flora is characterized by *Aulacoseira nygaardii* (up to 26% of the communities) and *Fragilaria nanana*. These species are associated with *A. granulata* and var. (up to 15%) and *A. ambigua* in open water during high water stands. The modern environment is not suitable for diatom preservation. Poorly silicified species, e.g., *Stenopterobia* or delicate *Eunotia* disappear in the uppermost centimeters of sediment. Biogenic silica dissolution during and after burial is attributed to subaerial conditions and frequent emersions, weathering by rainfall, and Si-poor lake and interstitial water.

## MATERIAL AND METHODS

In 1992, a 40-m sedimentary profile was collected by a French-Malagasy team at the center of Tritrivakely crater using a Wright (core LT; 13 m) and a Wieckowski piston corer (cores TI–TIV; 13 to 40 m). The profile reveals a continuous accumulation of lacustrine and palustral sediments with a few fine sand layers. Preliminary results about the  $^{14}\text{C}$  chronology, sedimentology, organic matter, and biological remains of core LT, dated 36,200  $^{14}\text{C}$  yr B.P. at its base, have been published (Gasse *et al.*). Centimeter-scale stratigraphic correlations between the upper 16 m of the five cores were established using high-resolution profiles of sediment magnetic properties (Williamson *et al.*, 1998). Total organic carbon (TOC), hydrogen index (HI: mg hydrocarbon/g TOC), and organic components in the upper 16 m of core TII were thoroughly analyzed (Sifeddine *et al.*, 1995). The C/N ratios and  $^{13}\text{C}$ -contents of total organic matter (TOM) and of isolated plant fragments for some levels were measured along core LT (E. Gibert, personal communication, 1997).

### Lithofacies and Chronology of Core LT

The chronology is based on fourteen  $^{14}\text{C}$  AMS dates of Cyperaceae debris and charcoal (Fig. 1). No macrorests were found within the 1300- to 572-cm interval. Radiocarbon ages measured on TOM were rejected because the palynofacies analysis (Sifeddine *et al.*, 1995) showed the contribution of detrital particles in sedimented OM. Measured ages are thus older than actual ages. The valid  $^{14}\text{C}$  ages were converted to calendar ages (cal yr B.P.; Williamson *et al.*, 1998) using the Stuiver and Reimer (1993) calibration back to 10,000  $^{14}\text{C}$  yr B.P., Eq. (1) between 10,000 and 18,000  $^{14}\text{C}$  yr B.P. (Bard *et al.*, 1993), and Eq. (2) for ages >18,000  $^{14}\text{C}$  yr B.P. (Bard *et al.*, 1997):

$$\text{cal age} = 1.24 \times (^{14}\text{C age}) - 840 \quad (1)$$

$$\begin{aligned} \text{cal age} = & -5.85 \times 10^{-6} \times (^{14}\text{C age})^2 \\ & + 1.39 \times (^{14}\text{C age}) - 1,807 \quad (2) \end{aligned}$$

The depth-scale was converted to cal yr B.P. assuming constant sedimentation rate between successive calibrated ages.

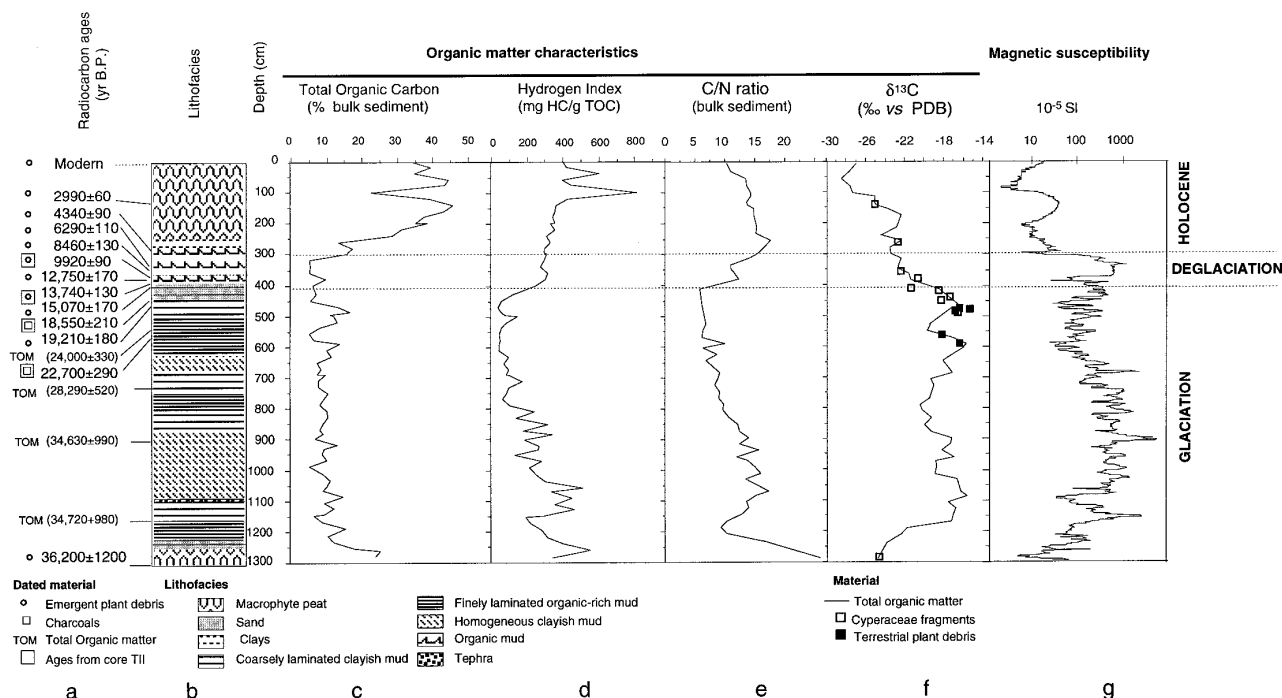
Our core represents the last glaciation (1300–452 cm) and postglacial time (452–0 cm). At the core base (1300–1250 cm; 40,800–40,000 cal yr B.P.) is a peat rich in macrophyte debris. High TOC (>20%), HI, and C/N values reflect a large contribution of autochthonous OM. Magnetic properties suggest low runoff and/or shallow/oxic environments. From 1250 to 1143 cm (40,000–38,000 cal yr B.P.), dark organic-rich clay layers alternate with oxidized clay and fine sand layers. An airfall tephra occurs at 1175–1170 cm. The interval 1143–452 cm (38,000–22,000 cal yr B.P.) is composed of brownish lacustrine clay coarsely laminated from 860 to 760 cm and from 610 to 460 cm. Organic compounds and magnetic properties indicate high terrigenous input to the lake between 1000 and 760 cm (35,500–30,500 cal yr B.P.), then a weakening of runoff and the development of subaquatic macrophytes from 760 to 452 cm (30,500–22,000 cal yr B.P.). Oxidized sediments are observed at 602 cm (27,200 cal yr B.P.) and 503 cm (24,200 cal yr B.P.).

The drastic drop in apparent mean sedimentation rate observed from 452 to 340 cm (22,000–7000 cal yr B.P.) suggests discontinuous deposition during the LGM and the early Holocene. However, no evidence of long hiatuses can be detected. In the LGM part of the section (452–402 cm; 22,000–16,900 cal yr B.P.), fine sand lenses are interbedded within oxidized clay. Several indicators show that the lake was commonly dry: (i) oxidized sediments and sand lenses, (ii) very low mean sedimentation rate, (iii) minimum TOC and HI values, (iv) an important contribution of terrigenous components documented by palynofacies and magnetic properties, and (v) no algal material in the TOM.

From 402 to 300 cm (16,900–4850 cal yr B.P.), dark organic mud predominates, but it is interrupted by thin oxidized clayish or sandy layers. Abundant algal-derived organic matter documents a lacustrine phase from 17,000 to 7000 cal yr B.P. Then sedge debris prevails in sedimented OM. The three upper meters (4800–0 cal yr B.P.) consist of Cyperaceae peat that accumulated under anoxic conditions, as indicated by high TOC and HI values. Magnetic susceptibility is very low, although a significant increase between 200 and 100 cm (4000–2300 cal yr B.P.) reflects enhanced detrital inputs to the core site.

### Pollen

Standard palynological techniques were used in the preparation of samples collected at 10-cm intervals or every centi-



**FIG. 1.** Characteristics of Tritrivakely core LT. (a) Radiocarbon ages. Cores LT and TII were correlated on the basis of magnetic properties (Williamson *et al.*, 1998; see text). Ages on TOM are biased by the contribution of a detrital fraction. (b–d) after Gasse *et al.* (1994). (e–f) after Gibert personal communication (1997). (g) after Williamson *et al.* (1998). High TOC-values correspond to peat sedimentation. High HI values reflect high local OM production and good OM preservation. High C/N values indicate a high contribution of higher plant debris reworked from the catchment or from local emergent plants. Low susceptibility values indicate low runoff and/or filtering of magnetic particles from the catchment subaquatic vegetation.

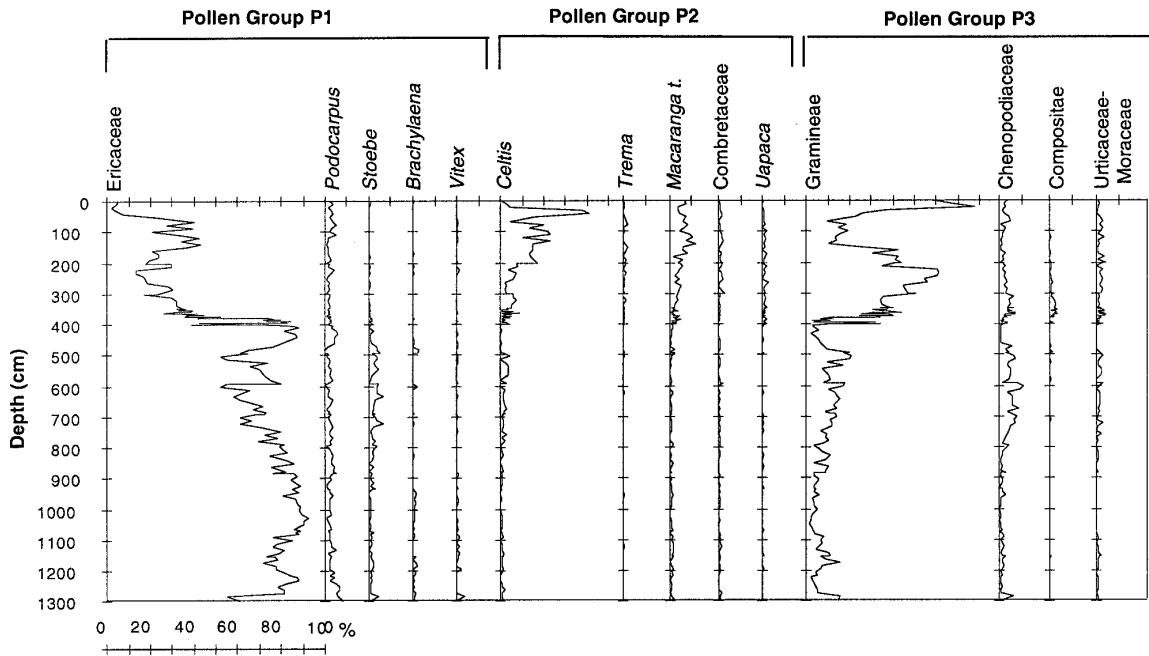
meter within zones of very low sedimentation rate. Pollen was well preserved and concentrations ranged from  $2 \times 10^4$  to  $144 \times 10^4$  grains  $g^{-1}$ . On the average, 585 pollen grains (169 to 1338) were counted in each sample. A total of 266 pollen and spore types were identified, mainly using the “Palynologia Madagassica et Mascarenica” series (Straka, 1991). Identifications to genus were suffixed with “type,” when pollen from other genera were comparable. Total unknowns ranged from 1 to 10% for all levels.

Terrestrial pollen results are given as percentage diagrams of selected taxa (Fig. 2a). The basic sum excludes pollen from aquatic and marsh vegetation. Gramineae may have formed part of either the regional or the local vegetation. In view of low grass pollen concentrations as compared with Cyperaceae, the latter undoubtedly being due to local conditions, we here consider that Gramineae should mainly have originated in the regional vegetation and thus include it in the basic sum. Moreover, the general pattern of the terrestrial curves is not affected when excluding Gramineae from the basic sum. Aquatic and paludal pollen types can reach high percentages of the raw (terrestrial + paludal + aquatic) pollen sum, such as Cyperaceae, *Aponogeton*, *Polygonum*, *Alismataceae*, *Potamogeton*, and *Myriophyllum* (Fig. 2b). *Aponogeton* is represented by seven species in Madagascar (Jumelle, 1936), but has not been found in the modern lake.

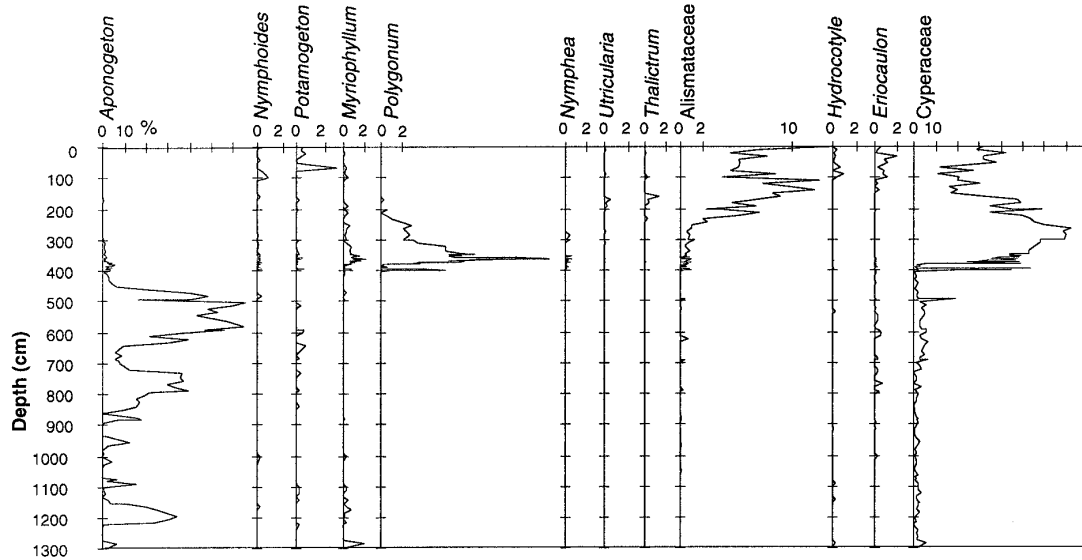
Major pollen groups, P1 to P3, were identified by correspondence factor analysis (CFA) of the most abundant relative terrestrial pollen taxa frequencies (Fig. 3). Group P1 is mainly defined by Ericaceae pollen, ranging from 2 to 93%. *Philippia* is the most common genus of this family in Madagascar, although others like *Agauria* and *Vaccinium* are found (Humbert and Cours-Darne, 1965; Koechlin *et al.*, 1974). Pollen representation of Ericaceae above 70% is seen only in surface samples within the ericaceous bush at altitudes ranging from 2200 to 2500 m (Burney, 1988; Straka, 1991). They are associated with *Stoebe* and woody elements of montane forests (*Podocarpus*, *Brachylaena*, and *Buxus*). *Buxus* is the only genus of the Buxaceae family in Madagascar, now endemic in the northwestern mountains, between 600 and 1600 m. The conifer tree *Podocarpus*, characteristic of the sclerophyllous lichen forest, is developed in the central highlands at the most cloudy level. The aborescent Compositae *Brachylaena* is well represented in mountain forests.

Group P2 is defined by the arboreal taxa *Celtis*, *Trema*, *Combretaceae*, *Macaranga*-type, and *Uapaca*. These arboreal taxa are found in middle-altitude forests (800–1800 m) and are also represented in various proportions in modern pollen spectra of woodland/grassland mosaic, open formations, and mountain forests (Burney, 1988; Straka, 1991). *Celtis* comprises up to 40% of terrestrial plants in the upper

**a. Terrestrial plant pollen**



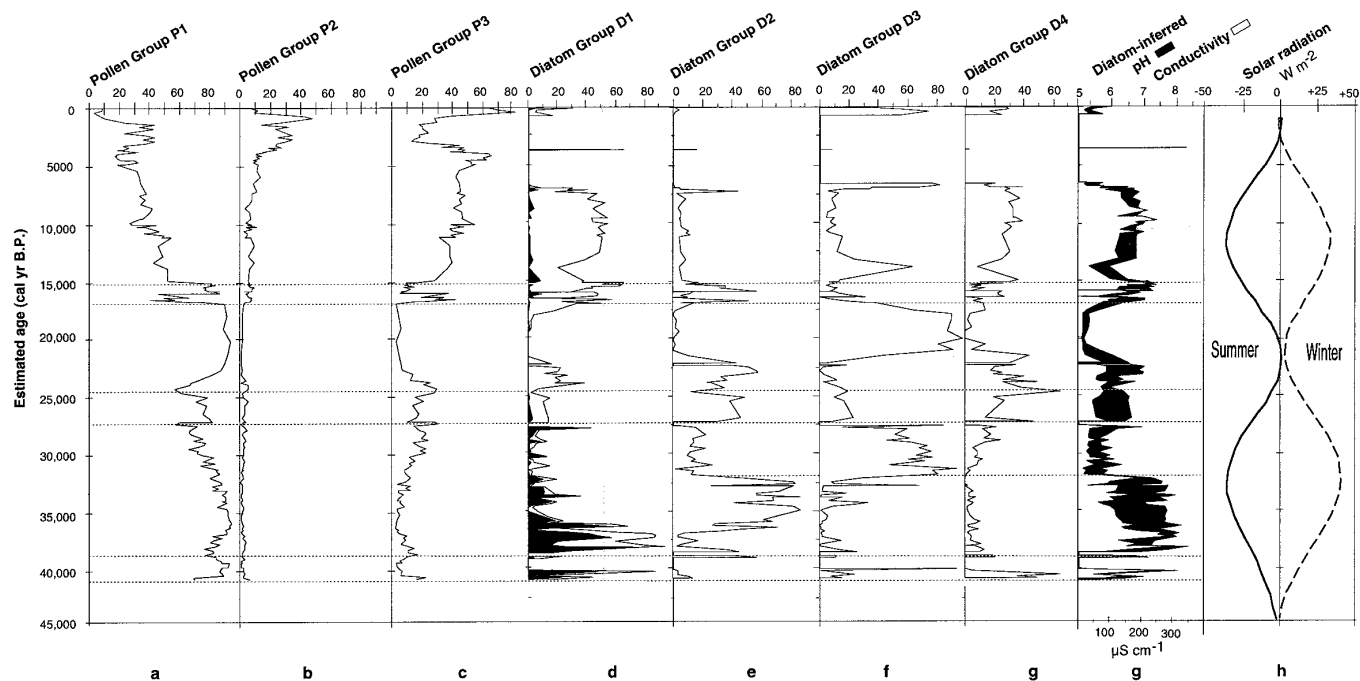
### b. Emergent and aquatic plant pollen



**FIG. 2.** Pollen diagrams for Lake Tritrivakely. (a) Pollen diagram of major terrestrial pollen taxa of groups P1 (mountain elements), P2 (arboreal elements of middle altitude forests), and P3 (elements of open formations). (b) Pollen diagram of pollen of aquatic and paludal plants. Percentages are calculated on the raw pollen sum (terrestrial + aquatic/paludal).

part of the diagram. The 2-porate *Trema* pollen type, which has been distinguished from the 3-porate *Celtis* type, shows the same trend. Among the three *Celtis* species present in Madagascar, the deciduous *C. gomphophylla* is the only one reported in the central highlands, between 700 and 1300 m (Leroy, 1952). It is also present in upland forests from tropical western and eastern Africa and in cloud forests of south-

ern Africa (White and Moll, 1978). *Trema* is characteristic of the upper limit (1000–1400 m) of the dense rainforest (Rajeriarison, 1984). *Macaranga*-type includes other Euphorbiaceae pollen of comparable pollen type. This genus is well represented in African swamp forests. *Uapaca* is typical of the sclerophyllous western slope forests, subject to the foehn effect of desiccated trade winds.



**FIG. 3.** Summary results of pollen and diatom records as a function of calendar age. (a–c) Terrestrial Pollen groups (see text and Fig. 2). (d–g) Diatom ecological groups (see text and Fig. 4). (h) Diatom-inferred pH and conductivity (C). Optimum values for individual taxa are taken from Gasse *et al.* (1995) and from their occurrence in modern, acidic-water samples from Madagascar for 12 taxa (*Aulocoseira nygaardii*, *A. lirata* var. *lacustris*, *Eunotia incisa*, *E. bilunaris* and var., *Frustulia rhomboides*, *Gomphonema* sp. aff. *pseudotenellum*, *Stauroneis producta*, *Pinnularia* sp. aff. *hemiptera*, *P.* sp. aff. *legumen*, *Neidium iridis*, *N. bisulcatum*). The robustness of the transfert functions is low for samples with low-inferred values, especially during the LGM. (i) Variations in solar radiation at 20°S.

High frequencies of Gramineae, Compositae, and Chenopodiaceae are the main elements of group P3. They suggest open formations. Gramineae is the prevalent herbaceous pollen type. Although some Gramineae pollen may derive from the local swampy environment, the highest percentages are found in grassland or woodland/grassland mosaics (Burney, 1988). Some miscellaneous types are represented in significant amounts, such as *Anthospermum*, Urticaceae–Moraceae, *Dodonea*, or Sapotaceae–Meliaceae. Pteridophyte trilete and monolete spores have low representation, they roughly conform to the pattern shown by the P3 elements. Although varying strongly in relative abundance, almost all identified terrestrial plant taxa do occur along the whole sequence. This suggests that if changing climatic conditions were strong enough to disorganize the vegetation structure and spatial distribution, they cause no drastic changes in the main regional flora components.

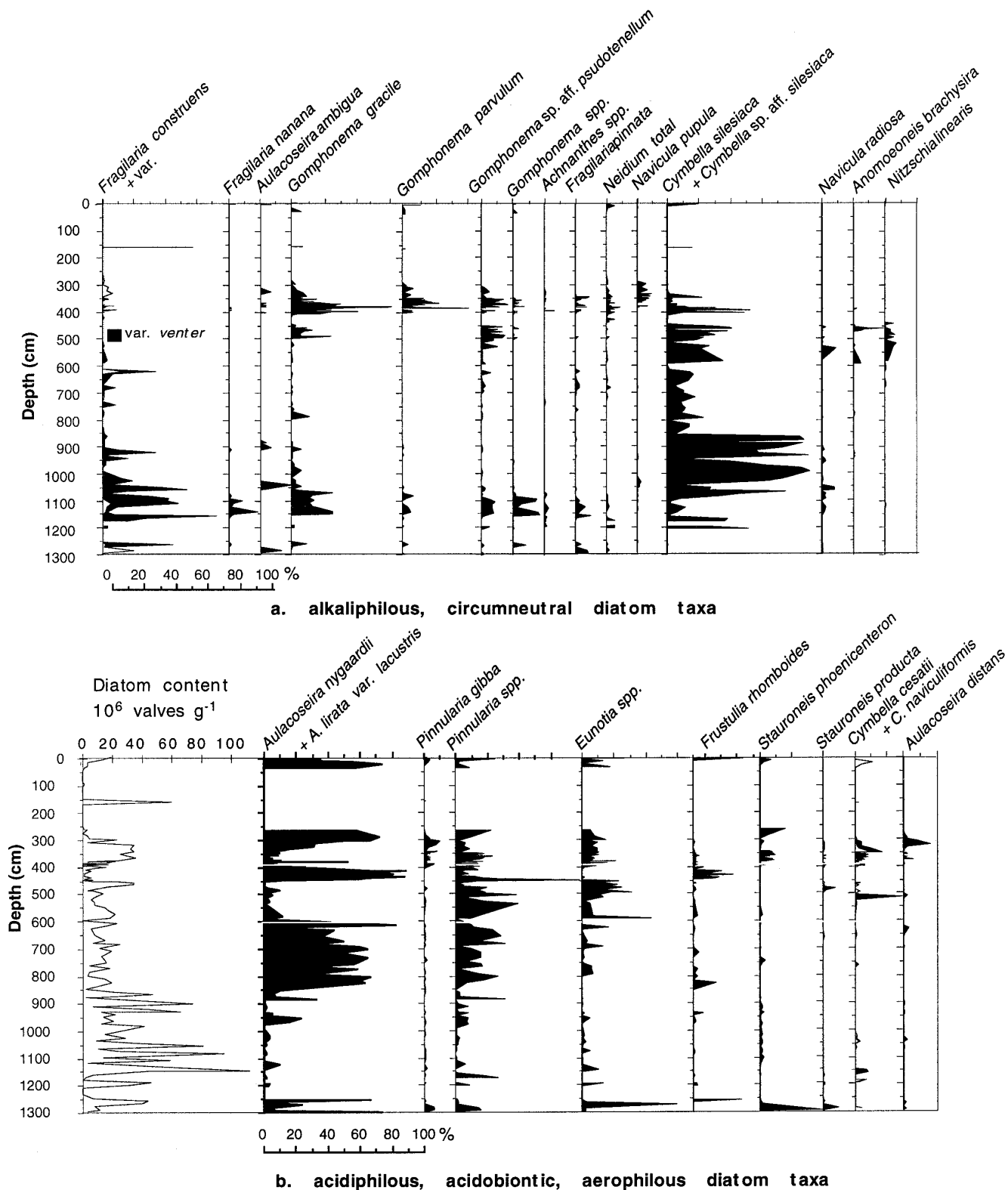
### Diatoms

Diatom slides were prepared following standard techniques using samples collected at 10-cm intervals along the profile, but at 1 to 5 cm in zones of low sedimentation rate. Diatom content (0 to  $10^8$  valves  $g^{-1}$ ) and preservation vary drastically along the profile. The absence of diatoms in sev-

eral levels is most likely due to dissolution. Countings were performed for 154 samples (400 to 600 valves when diatom content is  $>5 \times 10^5$  valves/mg; 60 to 300 valves for others).

The 141 taxa present were identified using mainly the works by Manguin (1941, 1952), Gasse (1986), Krammer and Lange-Bertalot (1985, 1991), Lange-Bertalot and Krammer (1987), and literature on dilute/acidic lakes of high latitudes (e.g., Florin, 1981; Camburn and Kingston, 1986). Most taxa not appearing in the literature were encountered in our modern reference samples from Tritrivakely and/or in neighboring lakes. An open nomenclature is adopted for these taxa. Results are given as percentage of selected taxa (Fig. 4).

Past pH and conductivity ( $C$ ;  $\mu S\ cm^{-1}$ ) of the lake water were tentatively inferred from hydrochemical transfer functions established for Africa (Gasse *et al.*, 1995), from which optimum conditions and tolerances can be assigned to 89 taxa. Their cumulative percentage is 70% in 79 samples. For other abundant taxa, we assumed that optimum growth conditions are met in modern habitats in Tritrivakely and/or in neighboring lakes where they are well represented. Empirical pH and  $C$  “optimum values” were thus assigned to 12 taxa. This makes percentages of “unknown” taxa 10% in 130 samples and 31% in all samples. Empirically enlarged



**FIG. 4.** Diatom data from Lake Tritrivakely. (a) Diatom diagram of major lacustrine, alkaliphilous diatom taxa of groups D1 and D2. (b) Diatom diagram of major lacustrine, acidophilous, acidobiontic, aerophilous diatom taxa of groups D3 and D4.

transfer functions applied to some modern samples yielded satisfactory results. They were therefore applied to the fossil sequence (Fig. 3). Large uncertainties for inferred-values are due to (i) the prediction error for established transfer functions (Gasse *et al.*, 1995; log C:  $\pm 0.32$ ; pH:  $\pm 0.48$ ), (ii) the use of species parameters from another biogeographical area, (iii) the introduction of empirical parameters, and (iv) distortion by selective dissolution in poorly preserved samples.

Diatom taxa were classified through CFA in four major groups, D1 to D4 (Fig. 3), which form a continuum between two extremes: (i) a permanent, slightly alkaline lake favorable for diatom preservation and (ii) acidic, subaerial conditions where diatoms are strongly altered by dissolution.

Group D1 reflects a permanent, circumneutral to slightly alkaline, shallow lake. Subgroup D1a is dominated by planktonic or facultative planktonic *Fragilaria* (*F. nanana*, *F. construens*, and var. *venter*) accompanied by *Aulacoseira ambigua* and *A. granulata*. It indicates open water in a mesotrophic waterbody. Subgroup D1b consists mainly of the *Gomphonema* spp. found in the modern lake, associated with *Achnanthes exigua*, *A. lanceolata*, *A. minutissima*, *Amphora libyca*, *Fragilaria pinnata*, *Navicula pupula*, *N. americana*, and *Neidium* spp. This group registers colonization by macrophytes. When D1 predominates, diatom valves do not show marked dissolution effects. Diatom content, inferred pH, and C reach their maximum. This suggests high nutrient availability and silica input from the catchment, and high primary productivity in the lake.

Group D2 is defined by the predominance of epiphytic *Cymbella* (*C. silesiaca*, *C. minuta*), accompanied by *Anomoeoneis brachysira*, *Navicula* sp. aff. *leptostriata*, *Nitzschia linearis*, and *Stauroneis* (*S. anceps*, *S. smithii*). These taxa are usually found as epipellic and circumneutral, freshwater swamps. This is in good agreement with inferred pH and C. *Cymbella* spp. may represent up to 70% of the taphocenose. In these cases, valves are commonly reduced to their axial area. Partial dissolution is attributed to low silica content in the water and/or frequent emersions.

Group D3 mainly consists of *Aulacoseira nygaardii* and rare *A. lirata* var. *lacustris*. These species live today at Tritrivakely and/or at Ifahrimene, a neighboring crater lake (2200 m altitude; C = 17–46  $\mu\text{S cm}^{-1}$ , pH 5.8–6.6) which also partly desiccates during dry seasons or years. They reflect acidic, relatively deep water with very low ionic content as occurs during wet seasons or years in these temporary mountain lakes. They are associated with coarse aerophilous, acidobiontic forms, e.g., *P. legumen*, *P. major*, *Frustulia rhomboides*, and *Eunotia formica*. Valves are commonly reduced to their highly silicified parts.

Groups D4 represents aerophilous communities in an acidic marsh. Almost all species occur in modern subaerial microhabitats. Subgroup D5a is dominated by *Eunotia* spp. found as epiphytic on Cyperaceae, small *Pinnularia* (*P. ap-*

*pendiculata*, *P. subrostrata*, *P. obscura*, *P. borealis*), *Aulacoseira distans*, acidophilous *Cymbella* and *Navicula* (e.g., *N. subtilissima*), and *Stenopterobia* sp. Group D5b consists of poorly preserved valves of large *Pinnularia*, e.g., *P. viridis*, *P. sp. aff. hemiptera*, and *Stauroneis phoenicenteron*.

High frequencies of Groups D3 and D4 correspond to very low diatom content, attributed to low productivity in an oligotrophic waterbody and poor preservation. Although inferred pH and C are obviously biased by selective dissolution, very low values are consistent with the ombrotrophic/ephemeral conditions in which abundant D3 and D4 species live today in Madagascar.

## MAJOR ENVIRONMENTAL CHANGES

### Glacial Period (1300–402 cm Depth; 40,800–17,000 cal yr B.P.)

Terrestrial vegetation is characterized by predominance of P1. Ericaceae dominate the diagram and do not fall below 50%. P2 and P3 have low representation. The site was surrounded by an ericaceous bush, indicating a substantially lower average temperature than at present. During the LGM, the Ericaceous bush was also developed around Torotorofotsy at 986 m altitude (Straka, 1993). This is consistent with a temperature at least 4°C colder than today. A lower atmospheric CO<sub>2</sub> concentration may also have contributed to the altitudinal shift of Ericaceous bush (Street-Perrott *et al.*, 1997). Intervals that contain the highest P1 values are considered as being the coldest periods, at 40,000–39,000 and 37,000–32,400 cal yr B.P., and during the LGM from 22,700 to 16,900 cal yr B.P.. There is a general tendency toward drier/warmer conditions from 35,800 to 24,200 cal yr B.P., an interval characterized by a decrease in P1 and slight increase in middle-altitude trees such as *Celtis*, but above all by an increase in open vegetation elements (P3).

In the lake, the diatom flora documents a peat-marsh at ca. 40,800 cal yr B.P. (D4 dominant). Then, hydrologic conditions fluctuated (shifts between D1, D3, D4); drought periods alternated with sudden floods. From ca. 38,000 to 36,000 cal yr B.P., a permanent, slightly alkaline, mesotrophic lake received dissolved salts and nutrients from the crater slopes (D1 dominant). A swamp recorded by the predominance of D2 developed from ca. 36,000 to 32,000 cal yr B.P. and received abundant detrital organic debris from the catchment (Sifeddine *et al.*, 1995). Between ca 32,000 and 22,300 cal yr B.P., the most characteristic feature is an overall increase in subaerial diatom species (D5) and in the subaquatic pollen elements, *Aponogeton* and Cyperaceae. *Aponogetonaceae*, which tolerate temporary floods (Raynal-Roques, 1980), do not live today at Tritrivakely, but rather in fresh, cool water in Madagascar (Jumelle, 1936). Tritrivakely evolved from an acidic lake, possibly ephemeral (32,500–27,200 cal yr B.P.), to a slightly acidic swamp (27,000–22,300 cal yr



B.P.). This trend agrees with an increasing contribution of autochthonous macrophyte material in TOM (Sifeddine *et al.*, 1995).

During the LGM, aquatic pollen are absent. Diatom content and preservation are extremely poor. Several levels are devoid of diatoms. Group D3 predominates, consisting of up to 95% of the taphocenoses, with *Aulacoseira* up to 80%. Valves are commonly reduced to their sulcus. The other 20% are fragments of subaerial species. In agreement with other indicators that suggest a deficit in the mean annual water balance, the diatom flora is interpreted as the result of occasional floods followed by seasonal or interannual droughts; *Aulacoseira* grew during the wet seasons or years and was replaced by subaerial communities when the water table dropped before total desiccation. Ericaceae, which are adapted to survive strong seasonal drought, could have persisted through the dry period of the LGM (D. A. Burney, pers. commun., 1996).

Superimposed on the long-term trends, the pollen record documents short-term warmer–drier events centered around 40,000, 27,100, and 24,200 cal yr B.P. These spells coincide with narrow peaks of the diatom groups D3–D4 and abrupt pH and C decreases. The peaks are immediately followed by total disappearance of diatoms in oxidized layers. As during the LGM, this is attributed to the establishment of ephemeral/ombrotrophic conditions preceding short-term desiccation events.

#### *Glacial–Interglacial Transition (402–381 cm Depth; 17,000–9800 cal yr B.P.)*

This interval shows the major terrestrial vegetation change registered in the diagram, characterized by a very important fall of Ericaceae values, from 86% at 16,900 cal yr B.P. to 39% at 16,500 cal yr B.P. This change suggests an extremely rapid disintegration of the ericaceous bush, which probably migrated to higher altitudes. This is attributed to an abrupt warming that occurred within less than a few centuries. This interval is contemporaneous with significant increases in most of the woody taxa from middle-altitude forests and wooded grassland.

An abrupt return to glacial conditions is registered from ca. 16,000 to 15,100 cal yr B.P., with pollen spectra very close to those of the LGM. After 15,100 cal yr B.P., interglacial conditions were suddenly reestablished, with the permanent fall of the Ericaceae pollen below 45%. The abruptness of the transition cannot be attributed to a sedimentary artifact because other proxies (e.g., magnetic properties and diatoms) do not show such a clear-cut change. From 15,100 to 9800 cal yr B.P., a decreasing trend in the Ericaceae values is synchronous with the regular, although weak, occurrence of various woody pollen types of middle and even low altitudes and with the increase in Gramineae, Compositae, and Amaranthaceae–Chenopodiaceae. This is interpreted as reflecting

the establishment of a wooded grassland or woodland/grassland mosaic.

The reestablishment of a water body favorable to aquatic life occurred in two steps, separated by a return toward drier conditions, in phase with terrestrial vegetation changes. Diatoms representing a permanent, shallow, slightly alkaline to circumneutral lake (D1, D2) reappear at 17,500 cal yr B.P. They predominate at ca 16,500 cal yr B.P., during the cooling event from ca 16,000 to 15,000 cal yr B.P., and after 12,500 cal yr B.P. However, diatoms are absent from several levels, and abrupt decreases in C and pH observed between ca. 16,700 and 16,300 cal yr B.P. and at 13,900 cal yr B.P. reflect short-term episodes of desiccation. The relative abundance of the diatom group D4 is consistent with the development of plants with aerial or floating leaves. Emergent (e.g., Cyperaceae, *Polygonum*) and aquatic (*Nymphaea*, *Nymphaoides*, *Myriophyllum*, *Potamogeton*) pollen increase suddenly at 16,900 and 15,100 cal yr B.P. Maximum aquatic plants occur at 9800 cal yr B.P. in phase with a maximum in C and pH values.

#### *Holocene Period (360–0 cm Depth; 9800–0 cal yr B.P.)*

After 9800 cal yr B.P., the P1 fluctuations show that the preceding warming trend stops, and even slightly reverses from 9600 to 8600 cal yr B.P. The maximum representation of Gramineae, centered on 4000 cal yr B.P., marks the driest/warmest period (P1 minimum). In the water body, diatom-inferred pH and C decrease from 9800 to 7000 cal yr B.P. The subsequent disappearance of diatoms is attributed to dissolution under ombrotrophic conditions. The maximum of Cyperaceae centers on 4500–4400 cal yr B.P. Aquatic plant pollen percentages shift down to minimum at 4000 cal yr B.P.

From 3500 to 2800 cal yr B.P., the P1 and P2 elements increase, reflecting a return toward higher effective moisture and lower temperature. This is consistent with the development of a riparian forest around the lake, and of *Anthospermum*, indicative of high-altitude cool, dry conditions or moist disturbed areas (Burney, 1988). Cyperaceae decrease while aquatic Alismataceae develop, and diatoms record a brief episode with deeper and alkaline water about 3200 cal yr B.P. Cool conditions persist until 1000 cal yr B.P. From 1000 to 700 cal yr B.P., the Ericaceae decrease, in favor of deciduous *Celtis*, which probably expands around the lake under warming conditions. After 700 cal yr B.P., high values of Gramineae reflect strong human impact. The diatom flora indicates hydrologic conditions close to modern. *Cannabis*/*Humulus* pollen occur as traces since 2200 cal yr. *Pinus*, introduced at the beginning of the 20th century (Rajeriarison, 1984), is well represented in the top level, although a few grains occur in the uppermost 20 cm of the core.

## DISCUSSION AND CONCLUSION

Our record shows (i) cooler conditions during glacial times, (ii) a deglacial warming in two steps, commencing at 17,000 and 15,000 cal yr B.P., (iii) episodes of positive mean annual  $P-E$  balance from 38,000 to 32,000 and 17,000 to 9800 cal yr B.P., and (iv) a LGM climate drier than today.

During glacial times, the migration of mountain plants to lower altitudes is consistent with a temperature decrease and with reduced atmospheric  $\text{CO}_2$  levels (Jolly and Haxeltine, 1997; Street-Perrott *et al.*, 1997). The hypothesis of  $\text{CO}_2$ -related climatic impact was recently reinforced by a  $\delta^{13}\text{C}$  record at Tritrivakely (E. Gibert, pers. commun., 1997), which suggests that lower atmospheric  $\text{CO}_2$  concentration has decreased carbon-isotope discrimination in  $\text{C}_3$  land plants (Gasse and Lin, in press). Dry/warm spells recorded by both terrestrial pollen and diatom data occurred about 40,000, at 27,100, and at 24,200 cal yr B.P. Uncertainties in our chronology for this period do not justify any correlations with Dansgaard-Oeschger events or changes in greenhouse gas concentration.

Lake Tritrivakely experienced stages of positive mean annual hydrologic balance (compared to modern) leading to a permanent water body in the intervals 38,000–32,000 and 17,500–7000 cal yr B.P., although the latter is interrupted by several dry spells. These intervals precede by several millennia the lake rises in the northern African tropics, where a Late Pleistocene highstand is centered on 32,000–27,000 cal yr B.P. and a postglacial one on 15,000–5000 cal yr B.P. (e.g., Williams and Faure, 1980; Street-Perrott *et al.*, 1989), with abrupt returns to dry conditions during the Younger Dryas event and about 9000–8000 cal yr B.P. (Gasse and Van Campo, 1994). These interhemispheric dissimilarities can be partly accounted for by orbital forcing. Rise of the water table coincides with periods of decreasing seasonal contrast in solar radiation, i.e., decreasing summer insolation (Fig. 3). Therefore, high  $P-E$  values cannot be explained by reinforced monsoon rain induced by enhanced summer land heating, but rather by a decrease in evaporation rate during summers that were cooler than today. Drizzle and fog of eastern origin, and some winter polar rains, may also have contributed to maintain the year-round lake level. Conversely, periods of marked negative  $P-E$  (about 40,000, 22,500–17,500, and 4000 cal yr B.P.) correspond to times of maximum summer solar radiation. About 40,000 yr B.P. and during the Late Holocene period, heavy monsoon rainfall did not compensate for the large evaporation–evapotranspiration losses from the peat-rich swamp during warm summers and dry winters, as today. During the LGM, Tritrivakely was most commonly dry, with occasional floods. Associated with cooler LGM conditions, this implies a significant decrease in precipitation.

Dry, cool climate conditions during the LGM in the southern tropics are documented from many sites. In the summer

rainfall area of southern Africa, a precipitation decline of >15–20% is evident from pollen and from sediment texture in Pretoria Salt Pan (Partridge, 1997; Partridge *et al.*, 1997). A precipitation decrease of 11 to 17% was estimated for the Tanganyika basin from pollen (Chalié, 1995) and a water–energy balance model for 21,000 cal yr B.P. when the lake was low (Bergonzini *et al.*, 1997). A LGM highstand of Lake Malawi (Finney *et al.*, 1996) appears as an exception, and may be explained by the regional precipitation pattern in southeastern Africa (Richard, 1994). The simultaneous development of drier and cooler glacial conditions in northern and southern Africa has been attributed to the coeval expansion of northern and southern hemisphere polar ice sheets and their influence on subtropical African climate (deMenocal, 1995). A variety of lake, pollen, and glacial evidence from tropical South America also shows cold/dry conditions about 21,000 cal yr B.P. when Lake Titicaca was very low (Servant *et al.*, 1995).

At Tritrivakely, the last deglacial warming occurred in two steps, shortly after 16,900 (WS1) and after 15,000 cal yr B.P. (WS2). The reestablishment of a positive water balance in the lake appears at 17,500 cal yr B.P.

The WS1 event, accompanied by increased wetness, is abundantly evidenced in the southern hemisphere land areas. Pollen-inferred temperature in the southern part of the Tanganyika basin increased by  $4^\circ\text{C}$  from about 17,000 to 15,000 cal yr B.P. (Chalié, 1995) when lake level rose (Gasse *et al.*, 1989). Similar and contemporaneous trends are observed in eastern South Africa (Partridge, 1997) and in the American tropics south of  $15^\circ\text{S}$  (Argollo and Mourguiart, 1995). In the Chilean Andes, the culmination of the last glacial advance ca. 17,000 cal yr B.P. was followed by a widespread retreat by 16,500 cal yr B.P. associated with an abrupt warming documented by pollen and beetle assemblages from the Chilean lake region (Ashworth and Hoganson, 1993; Lowell *et al.*, 1995). In Antarctica, the  $\delta^{18}\text{O}$  record from the Byrd ice core (Johnsen *et al.*, 1992) shows deglacial isotopic temperature increase at 18,000 cal yr B.P. The start of the SST increase in the southern ocean is dated at 17,000 cal yr B.P. (Pichon *et al.*, 1992), in phase with a first increase in tropical SST registered in the Barbados coral record (Guilderson *et al.*, 1994). Comparison of deglacial climate records by Sowers and Bender (1995) show that the  $\text{CH}_4$  and  $\text{CO}_2$  atmospheric concentrations began to rise 2000 to 3000 yr before the warming began in Greenland.

The WS2 event was synchronous with the major warming seen in Greenland ice cores (Johnsen *et al.*, 1992), with an increase in North Atlantic SST (Lehman and Keigwin, 1992), with European terrestrial data (Lowe *et al.*, 1980) at the onset of the Bölling interval and with the first lake rise in the African northern tropics (Gasse *et al.*, 1990). It appears coincident with a rapid southward retreat of the northern limit of Antarctic sea ice associated with reactivation of

North Atlantic deep-water formation, which is reflected in benthic  $\delta^{13}\text{C}$  values in the North Atlantic and Southern Ocean (Charles and Fairbanks, 1992). It is also coincident with the drastic decrease of Antarctic dust influx attributed to the submergence of a large portion of the Argentina continental shelf (14,600 cal yr B.P.; Jouzel *et al.*, 1995). In core MD79257 from the Mozambique Channel, the deglacial SST warming is centered at 15,100 cal yr B.P., but took place from ca. 17,000 to 14,500 cal yr B.P. This is inferred from alkenone paleothermometry which shows a  $1.5^\circ\text{C}$  increase in SST during this interval (Bard *et al.*, 1997). In the same core, foraminifera-inferred winter SST increases by  $4^\circ\text{C}$  (J. C. Duplessy and J. Duprat, pers. commun., 1995) during the same interval. These SST estimates do not show the two deglacial steps separated by a cold reversal between 16,000 and 15,000 cal yr B.P.

Jouzel *et al.* (1995) recently showed that deglaciation in Antarctica was also a two-step process. However, the Antarctic cold reversal, centered around 13,000 cal yr B.P., lags our cold reversal (16,000–15,000 cal yr B.P.) and leads the Younger Dryas (12,600–11,100 cal yr B.P.). The Uyuni–Coipasca basin in the southern part of the Titicaca catchment area (Bolivia) experienced a lake highstand synchronous with the cold reversal observed in our record. This highstand reflects a wet episode called the “Tauca phase” documented in northern Chile ( $23^\circ\text{S}$ ) (Messerli *et al.*, 1993). This interval has also been recognized by Benson *et al.* (1992) as the last highstand of Lake Lahontan. Broecker’s (1994) hypothesis about this interval occurring between Heinrich event 1 and the Bölling interval would involve a cessation of oceanic deep water formation. The nature of such connections is not identified.

The lake Tritrivakely 40,000-yr multiproxy paleoclimatic record clearly indicates that episodes of maximum  $P-E$  balance in the northern and southern tropics are out of phase, as expected from orbital forcing. However, drier conditions during the LGM are evident in both hemispheres. The deglaciation was a two-step process. The first step occurred abruptly 17,000 cal yr ago, about two millennia earlier than in the northern hemisphere, and in good agreement with terrestrial data from southern land areas. The second step was in phase with the first major temperature change in the northern hemisphere.

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## REFERENCES

- Argollo, J., and Mourguiart, P. (1995). Paleohidrologia de los ultimos 25 000 anos en los Andes bolivianos. *Bulletin de l'Institut Français des Etudes Andines* **24**(3), 551–562.
- Ashworth, A. C., and Hoganson, J. W. (1993). The magnitude and rapidity of the climate change marking the end of the Pleistocene in the mid-latitudes of South America. *Palaeogeography Palaeoclimatology Palaeoecology* **101**, 263–270.
- Bard, E., Arnold, M., Fairbanks, R. G., and Hamelin, B. (1993).  $^{230}\text{Th}$ ,  $^{234}\text{U}$  and  $^{14}\text{C}$  ages obtained by mass spectrometry on corals. *Radiocarbon* **35**(1), 191–199.
- Bard, E., Rostek, F., and Sonzogni, C. (1997). Interhemispheric synchrony of the last deglaciation inferred from alkenone palaeothermometry. *Nature* **385**, 707–710.
- Beck, J. W., Récy, J., Taylor, F., Edwards, R. L., and Cabioch, G. (1997). Abrupt changes in early Holocene tropical sea surface temperature derived from coral records. *Nature* **385**, 705–707.
- Benson, L., Currey, D., Lao, Y., and Hostetler, S. (1992). Lake-size variations in the Lahontan and Bonneville basins between 13,000 and 9000  $^{14}\text{C}$  yr BP. *Palaeogeography Palaeoclimatology Palaeoecology* **95**, 19–32.
- Bergonzini, L., Chalié, F., and Gasse, F. (1997). Paleoevaporation and paleoprecipitation in the Tanganyika Basin at 18,000 years B.P. inferred from hydrologic and vegetation proxies. *Quaternary Research* **47**, 295–305.
- Bonnefille, R., Chalié, F., Guiot, J., and Vincens, A. (1992). Quantitative estimates of full glacial temperatures in equatorial Africa from palynological data. *Climate Dynamics* **6**, 251–257.
- Broecker, W. S. (1994). Massive iceberg discharges as triggers for global climate change. *Nature* **372**, 421–424.
- Burney, D. A. (1987a). Presettlement changes at Lake Tritrivakely, Madagascar. *Palaeoecology of Africa* **18**, 350–381.
- Burney, D. A. (1987b). Late Holocene vegetational change in central Madagascar. *Quaternary Research* **28**, 130–143.
- Burney, D. A. (1987c). Late Quaternary stratigraphic charcoal records from Madagascar. *Quaternary Research* **28**, 274–280.
- Burney, D. A. (1988). Modern pollen spectra from Madagascar. *Palaeogeography Palaeoclimatology Palaeoecology* **66**, 63–75.
- Camburn, K. E., and Kingston, J. C. (1986). The genus *Melosira* from soft-water lakes with special reference to northern Michigan, Wisconsin and Minnesota. In “Diatoms and Lake Acidity” (J. P. Smol, R. W. Battarbee, R. B. Davis, and J. Meriläinen, Eds.), pp. 17–34. Junk, Dordrecht.
- Chalié, F. (1995). Paléoclimats du bassin Tanganyika Sud au cours des 25 derniers mille ans. Reconstruction quantitative par le traitement statistique des données polliniques. *Comptes Rendus de l'Académie des Sciences (Paris) Series 2* **320**(2), 205–208.
- Chaperon, P., Danioux, J., and Ferry, L. (1993). Fleuves et Rivières de Madagascar. ORSTOM, Paris, *Monographies Hydrologiques* **10**, 874.
- Charles, C., and Fairbanks, R. (1992). Evidence from Southern Ocean sediments for the effect of North Atlantic deep-water flux on climate. *Nature* **355**, 416–419.
- CLIMAP Members (1981). “Seasonal Reconstruction of the Earth’s Surface at the Last Glacial Maximum.” Geological Society of America Map Chart Series MC-36.
- deMenocal, P. B. (1995). Plio-Pleistocene African climate. *Science* **270**, 53–59.
- Donque, G. (1972). The climatology of Madagascar. In “Biogeography and Ecology of Madagascar” (G. Richard-Vindard and R. Battistini, Eds.), pp. 87–144. Junk, The Hague.

- Finney, B. P., Sholtz, C. A., Johnson, T. C., and Trumbore, S. (1996). Late Quaternary lake-level changes of Lake Malawi. In "The Limnology, Climatology and Paleoclimatology of the East African Lakes" (T. J. Johnson and E. O. Odada, Eds.), pp. 495–508, Gordon and Breach.
- Florin, B. B. (1981). "The Taxonomy of Some *Melosira* Species, a Comparative Morphological Study. II." Proceedings, Budapest Symposium on Diatoms 1980. Koeltz, Koenigstein, pp. 43–73.
- Ganopolski, A., Rahmstorf, S., Petoukhov, V., and Claussen, M. (1998). Simulation of modern and glacial climates with a coupled global model of intermediate complexity. *Nature* **391**, 351–356.
- Gasse, F. (1986). East African diatoms. Taxonomy, ecological distribution. *Bibliotheca Diatomologica* **11**, Cramer, Stuttgart.
- Gasse, F., Lédée, V., Massault, M., and Fontes, J. Ch. (1989). Water-level fluctuations of Lake Tanganyika in phase with oceanic changes during the last glaciation and deglaciation. *Nature* **342**, 57–69.
- Gasse, F., Téthet, R., Durand, A., Gibert, E., and Fontes, J. Ch. (1990). The arid–humid transition in the Sahara and the Sahel during the last deglaciation. *Nature* **346**, 141–156.
- Gasse, F., Cortijo, E., Disnar, J. R., Ferry, L., Gibert, E., Kissel, C., Lagouan-Défarage, F., Lallier-Vergès, E., Miskovsky, J. C., Ratsimbazafy, B., Ranaivo, F., Tucholka, P., Saos, J. L., Siffedine, A., Taieb, M., Van Campo, E., and Williamson, D. (1994). A 36 kyr environmental record in the southern tropics: Lake Tritrivakely. *Comptes Rendus de l'Académie des Sciences (Paris) Série 2* **318**, 1513–1519.
- Gasse, F., Juggins, S., and Ben Khelifa, L. (1995). Diatom-based transfer-functions for inferring past hydrochemical characteristics of African lakes. *Palaeogeography Palaeoclimatology Palaeoecology* **117**, 31–54.
- Gasse, F., and Van Campo, E. (1994). Abrupt post-glacial climate events in West Asia and North Africa monsoon domains. *Earth and Planetary Science Letters* **126**, 435–456.
- Gasse, F., and Lin, R. (1997). Lacustrine isotope archives of past climate and environmental changes in the tropics and subtropics. Some examples from Africa. In "Isotope Techniques in Studying Past and Current Environmental Changes in the Hydrosphere and the Atmosphere," IAEA-SM-349. In press.
- Guilderson, T. P., Fairbanks, R. G., and Rubenstone, J. L. (1994). Tropical temperature variations since 20,000 years ago: Modulating inter-hemispheric climate change. *Science* **263**, 663–665.
- Harisoa, F. M. (1988). "Etude de la végétation de Madagascar à l'aide des données spatiales." Thèse, Université de l'Université Paul Sabatier, Toulouse.
- Holmgren, K., Karlén, W., and Shaw, P. (1995). Paleoclimatic significance of the stable isotopic composition and petrology of a late Pleistocene stalagmite from Botswana. *Quaternary Research* **43**(3), 320–328.
- Humbert, H. (1955). Les territoires phytogéographiques de Madagascar. Leur cartographie. Colloque sur les régions écologiques du globe. Paris, 1954. *Annals of Biology* **31**(5–6), 439–448.
- Humbert, H., and Cours-Darne, G. (1965). Carte Internationale du Tapis Végétal et des conditions écologiques à 1/1 000 000 de Madagascar. Notice de la carte. *Travaux de la Section Scientifique et Technique Institut Français de Pondichery* **6**, 162.
- Johnsen, S. J., Clausen, H. B., Dansgaard, W., Fuhrer, K., Gundestrup, N., Hammer, C. U., Iversen, P., Jouzel, J., Stauffer, B., and Steffensen, J. P. (1992). Irregular glacial interstadials recorded in a new Greenland ice core. *Nature* **359**, 311–313.
- Jolly, D., and Haxeltine (1997). Effect of low atmospheric CO<sub>2</sub> on tropical african montane vegetation. *Science* **276**, 786–788.
- Johnsen, S. J., Dansgaard, W., Clausen, H. B., and Langway, C. C., Jr. (1972). Oxygen isotope profiles through Antarctic and Greenland ice sheets. *Nature* **235**, 429–434.
- Jouzel, J., Vaikmae, R., Petit, J. R., Martin, M., Duclos, Y., Stievenard, M., Lorius, C., Toots, M., Mélières, M. A., Burckle, I. H., Barkov, N. I., and Kotlyakov, V. M. (1995). The two-step shape and timing of the last deglaciation in Antarctica. *Climate Dynamics* **11**, 151–161.
- Jumelle, H. (1936). "Flore de Madagascar et des Comores," Fam. 23, Aponogetonaceae.
- Koechlin, J., Guillaumet, J. L., and Morat, P. (1974). "Flore et végétation de Madagascar." Cramer, Vaduz.
- Krammer, K., and Lange-Bertalot, H. (1991). *Bacillariophyceae* **3, 4**.
- Krammer, K., and Lange-Bertalot, H. (1985). *Bibliotheca Diatomologica* **9**.
- Lange-Bertalot, H., and Krammer, K. (1987). *Bibliotheca Diatomologica* **15**.
- Lehman, S. J., and Keigwin, L. D. (1992). Sudden changes in North Atlantic circulation during the last deglaciation. *Nature* **356**, 757–762.
- Leroy, J. F. (1952). "Flore de Madagascar et des Comores," Fam. 52–54. Salicaceae, Myricaceae, Ulmaceae.
- Lowe, J. J., Gray, J. M., and Robinson, J. E. (1980). "Studies in the Late Glacial of Northwest Europe." Pergamon, Oxford.
- Lowell, T. V., Heusser, C. J., Andersen, B. G., Moreno, P. I., Hauser, A., Heusser, L. E., Schlüchter, C., Marchant, D. R., and Denton, G. H. (1995). Interhemispheric Correlation of Late Pleistocene Glacial events. *Science* **269**, 1541–1549.
- Mac Phee, R. D. E., and Burney, D. A. (1991). Dating of modified femora of extinct dwarf Hippopotamus from southern Madagascar: Implications for constraining human colonization and vertebrate extinction events. *Journal of Archaeological Science* **18**, 695–706.
- Manguin, E. (1941). Contribution à la flore de diatomées d'eau douce de Madagascar. *Revue Algologique* **12**(1,2), 153–157.
- Manguin, E. (1952). Les diatomées fossiles du bassin d'Antsirabé, Ranomafana II. *Mem. Inst. Scient. Madagascar, Série B* **4**(1), 1–57.
- Messerli, B., Grosjean, M., Bonani, G., Burgi, A., Geyh, M. A., Graf, K., Ramseyer, K., Romero, H., Schotterer, U., Schreier, H., and Vuille, M. (1993). Climate change and natural resource dynamics of the Atacama Altiplano during the last 18,000 years: a preliminary synthesis. *Mountain Research and Development* **13**(2), 117–127.
- Partridge, T. C. (1997). Cainozoic environmental change in southern Africa, with special emphasis on the last 200 000 years. *Progress in Physical Geography* **21**(1), 3–22.
- Partridge, T. C., deMenocal, P. B., Lorentz, S. A., Paiker, M. J., and Vogel, J. C. (1997). Orbital forcing of climate over South Africa: A 200 000-year rainfall record from the Pretoria Saltpan. *Quaternary Science Reviews* **16**, 1–9.
- Paulian, R., Betsch, J. M., Guillaumet, J. L., Blanc, C., and Griveaud, P. (1971). Etude des écosystèmes montagnards dans la région malgache. Le massif de l'Andringitra. Géomorphologie, climatologie et groupements végétaux. *Bulletin de la Société Ecologique* **2**(2–3), 189–266.
- Perrier de la Bathie, H. (1921). La végétation malgache. *Annales du musée colonial de Marseille, 3ème série*, **9**.
- Pichon, J. J., Labeyrie, L. D., Bareille, G., Labracherie, M., Duprat, J., and Jouzel, J. (1992). Surface water temperature changes in the high latitudes of the Southern Hemisphere over the last glacial-interglacial cycle. *Palaeoceanography* **7**, 289–318.
- Rajeriarison, C. (1984). "Influences des formations végétales malgaches et des principaux facteurs climatiques dans la composition des flux polliniques atmosphériques de la région de Tananarive (Madagascar), au cours de 3 cycles annuels (1979, 1980 et 1981)." Thèse, Université de Montpellier.
- Raynal-Roques, A. (1980). Les Plantes Aquatiques. In "Flore et Faune

- aquatiques de l'Afrique sahélo-soudanienne'' (J. R. Durand and C. Lévêque, Eds.), pp. 63–152. ORSTOM, Paris.
- Richard, Y. (1994). Variabilité pluviométrique en Afrique du Sud-Est. *La Météorologie série* **8**, 11–21.
- Servant, M., Fournier, M., Argollo, J., Servant-Vildary, S., Sylvestre, F., Wirrmann, D., and Ybert, J. P. (1995). La dernière transition glaciaire/interglaciaire des Andes tropicales sud (Bolivie) d'après l'étude des variations des niveaux lacustres et des fluctuations glaciaires. *Comptes Rendus de l'Académie des Sciences (Paris) Série 2* **320**, 729–736.
- Sifeddine, A., Laggoun-Défarge, F., Lallier-Vergès, E., Disnar, J. R., Williamson, D., Gasse, F., and Gibert, E. (1995). La sédimentation organique lacustre en zone tropicale sud au cours des 36 000 dernières années (Lac Tritrivakely, Madagascar). *Comptes Rendus de l'Académie des Sciences (Paris) Série 2* **321**, 385–391.
- Sowers, T., and Bender, M. (1995). Climate Records Covering the Last Deglaciation. *Science* **269**, 210–214.
- Straka, H. (1991). Palynologia Madagassica et Mascarenica. 2. Echantillons de surface. *Tropische und subtropische Pflanzenwelt* **78**, 5–43.
- Straka, H. (1993). Beiträge zur Kenntnis der Vegetationsgeschichte von Madagaskar (Vorläufige Mitteilung). *Dissertationes Botanicae* **196**, 439–449.
- Street-Perrott, F. A., Marchand, D. S., Roberts, N., and Harrison, S. P. (1989). Global Lake-Level Variations from 18,000 to 0 Years Ago: A Palaeoclimatic Analysis'' (United States Department of Energy, Eds.), DOE/ER/60304-HI, pp. 1–213. U. S. Dept. Energy, Washington, DC.
- Street-Perrott, F. A., Huang, Y., Perrott, R. A., Eglington, G., Barker, P., Ben Khelifa, L., Harkness, D. D., and Olago, D. O. (1997). Impact of lower atmospheric CO<sub>2</sub> on tropical mountain ecosystems. *Science* **278**, 1422–1426.
- Stuiver, M., and Reimer, P. J. (1993). Extended <sup>14</sup>C data base and revised CALIB 3.0 <sup>14</sup>C age calibration program. *Radiocarbon* **35**, 215–230.
- Stute, M., and Talma, S. (1998). Glacial temperatures and moisture transport regimes reconstructed from noble gas and δ<sup>18</sup>O, Stampriet aquifer, Namibia. In "Isotope Techniques in Studying Past and Current Environmental Changes in the Hydrosphere and the Atmosphere," in press.
- Van Campo, E., Duplessy, J. C., Prell, W. L., Barratt, N., and Sabatier, R. (1990). Comparison of terrestrial and marine temperature estimates for the past 135 Kyr off southeast Africa: A test for GCM simulations of paleoclimates. *Nature* **348**, 208–212.
- Webb, R. S., Rind, D. H., Lehman, S. J., Healy, R. J., and Sigman, D. (1997). Influence of heat transport on the climate of the Last Glacial Maximum. *Nature* **385**, 695–699.
- Williams, M. A. J., and Faure, H. (1980). *The Sahara and the Nile*. Balkema, Rotterdam.
- Williamson, D., Jelinowska, A., Kissel, C., Tucholka, P., Gibert, E., Gasse, F., Massault, M., Taieb, M., Van Campo, E., and Wieckowski, K. (1998). Rock magnetic proxies of erosion/oxidation cycles in Late Quaternary maar lake sediments (Lake Tritrivakely Madagascar): paleoenvironmental implications. *Earth and Planetary Science Letters* **155**, 205–219.
- White, F., and Moll, E. (1978). The Indian Ocean coastal belt. In "Biogeography and ecology of Southern Africa'' (M. J. A. Werger, Ed.), pp. 563–598. Junk, The Hague.