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Late Quaternary environmental changes from a pollen and diatom record in the southern tropics (Lake Tritrivakely, Madagascar)

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Abstract

A pollen and diatom study of a 40 m-sedimentary sequence from Lake Tritrivakely in the central highlands of Madagascar provides evidence for climatic and environmental changes during the late Pleistocene and the Holocene. The major features of the modern regional climate and vegetation distribution and the hydrological characteristics of the lake basin are first summarized. Lithological units and specific methods used to establish the pollen and the diatom biozones are then presented. The chronology of the upper 13 m of the sequence (0–41 kyr) is supported by AMS radiocarbon dates. It has not been possible to acquire absolute ages for the lower 27 m of the core. However, a tentative age model based on comparisons between the terrestrial pollen and the Vostok δD isotopic temperature records suggests an age of about 150 kyr for the core base. The vegetation primarily responded to variations in temperature. Six major cold/warm cycles are identified. During the cold phases, Ericaceous bush surrounded the site. Assuming that the age model is correct, cold phases (prior to 143, 115–110, 94–88, 75–69, and 22–17 kyr) coincide with periods of high local summer insolation. The warm phases are of different amplitude. They show first the development of a wooded grassland under a dry climate, which may coincide with periods of low summer insolation (around 125, 100, 83, 60 and 10–5 kyr), and then the growth of mid-latitude trees under wetter conditions. The diatom record primarily documents changes in the precipitation minus evaporation balance ($P - E$) in the lake catchment, which appear consistent with orbitally-induced changes in P and seasonal contrasts as suggested by our pollen-based age model and the ^{14}C -dated section of the record. An overall trend from a relatively deep, nutrient-rich lake to a shallow, oligotrophic peat-marsh, is partly attributed to the basin infilling. However, wet–dry oscillations are superimposed over this trend. The two first lake high stands (before 143 and around 115 kyr if the age model is correct) and low stands (around 125 and 105 kyr) match pollen-inferred cold and warming phases, respectively. Later, periods of low $P - E$ also fit cold phases, and occur apparently every 12–10 kyr. Summer rain during phases of high summer insolation was not heavy enough to compensate for the large evaporation–evapotranspiration losses during warm summers and dry winters, especially during the cold Last Glacial Maximum, which was drier than today. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

The changes in the continental climate and environment in the southern tropics during the last glacial–interglacial cycle are still poorly known, partly due to a scarcity of long, continuous records.

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New observations from the southern tropics are needed to analyze the response of the vegetation- and hydro-systems to the changes in summer insolation, which are out of phase between the Northern and the Southern Hemispheres (Berger, 1978). The nearly synchronous northern and southern glaciations also raise the question of the amplitude and timing of glacial coolings in tropical regions (Lowell et al., 1995).

Here, we present a pollen and diatom record from a small crater lake in the central highlands of Madagascar, Tritrivakely ($19^{\circ}47'S$, $46^{\circ}55'E$, 1778 m). This site, first investigated by Burney (1987), has presented a 40 m sequence of sediments varying from pure diatomite, clay and silt, to peat, with a few fine sand layers. The upper 13 m have provided a 40,000-yr multi-proxy record (Gasse et al., 1994), for which detailed results on organic matter properties (Siffedine et al., 1995), rock magnetic properties (Williamson et al., 1998), pollen and diatoms (Gasse and Van Campo, 1998) have been already published. The results show: (i) cool conditions during the last glacial period, which contains short-term warmer–drier events; (ii) a positive mean annual water balance (precipitation minus evaporation; $P - E$) from about 39 to 32 kyr (kyr means 10^3 cal. yr B.P.), and from ca. 17 to 10 kyr; (iii) a Last Glacial Maximum (LGM; ca. 23–17 kyr) drier than today. The deglacial warming/wetting started around 17.5–17 kyr, earlier than the major wetting events that followed the LGM in the northern tropics.

This 40,000-yr record is complemented here by the pollen and diatom analysis of the 40 m-sedimentary profile. The pollen record primarily documents changes in regional temperature and shows six major cold/warm climatic phases. For lack of radiometric dates below 13 m, an age model based on comparisons between this pollen record and other paleoclimatic records from the southern hemisphere is proposed, which suggests an age of about 150 kyr for the bottom of the sequence. The diatom record documents changes in the lake water budget (precipitation minus evaporation in the lake catchment area; $P - E$). Tropical crater lakes are sensitive to changes in $P - E$ (e.g. Verschuren et al., 2000); lake level fluctuations can be used as paleoclimatic proxies (e.g. Harrison and Digerfeldt, 1993),

provided that groundwater losses are negligible. However, the respective roles of P and E on the lake status are difficult to identify. Comparison between the pollen-inferred climatic changes and hydrological changes at Lake Tritrivakely helps understanding of the response of the waterbody to local summer insolation forcing.

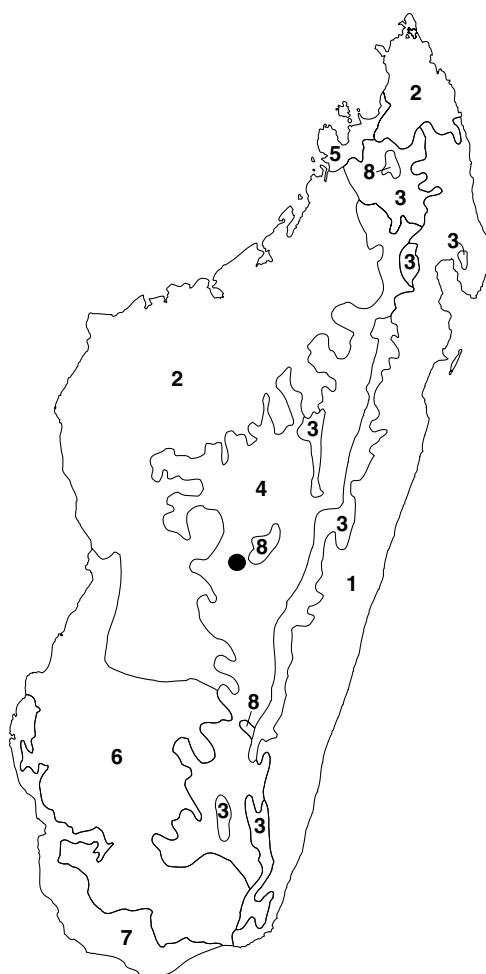


Fig. 1. Main climax vegetation types of Madagascar Island. 1 — dense rain forest; 2 — dense dry forest; 3 — submontane evergreen seasonal forest; 4 — low sclerophyllous forest at medium-altitude; 5 — rain forest of Sambirano; 6 — deciduous thicket; 7 — deciduous woodland with *Didereaceae* and *Euphorbia*; 8 — sclerophyllous montane forest and thicket. From Blasco et al. (2000). Black dot indicates the location of Lake Tritrivakely.

2. Modern environmental setting

2.1. Climate and vegetation

The climate of Madagascar is controlled by large-scale atmospheric circulation patterns and by topography. Two main climatic mechanisms affect the island: (i) the southeast trade wind originating from the southern subtropical Indian Ocean High (the Mascareignes Anticyclone) brings warm and humid air, and year-round precipitation over the eastern escarpment; and (ii) during the austral summer, the Asian northeast trade wind crosses the equator, following the southward displacement of the ITCZ, and deviates to its left. The resulting northwest currents, here called monsoon, bring heavy rains on the northern half of the island (Donque, 1972). Summer tropical cyclones are also frequent. In the south, intrusions of the cold southwesterly fronts occasionally bring cold air masses and light rains in winter.

The region of Tritrivakely in the central highlands is characterized by a tropical mountain climate with warm summers receiving 85–90% of the total annual precipitation, and cool and dry winters (Chaperon et al., 1993). The eastern circulation only brings drizzle and fog that may affect the hydrological cycle and the vegetation by increasing air humidity (Paulian et al., 1971). At Antsirabe, the mean annual values of P and temperature (T) are respectively 1354 mm/yr and 15°C, with large interannual variability. At Tritrivakely, P varied from 1557 to 1276 mm/yr between 1995 and 1997 (Ferry and Robison, pers. comm., 1999).

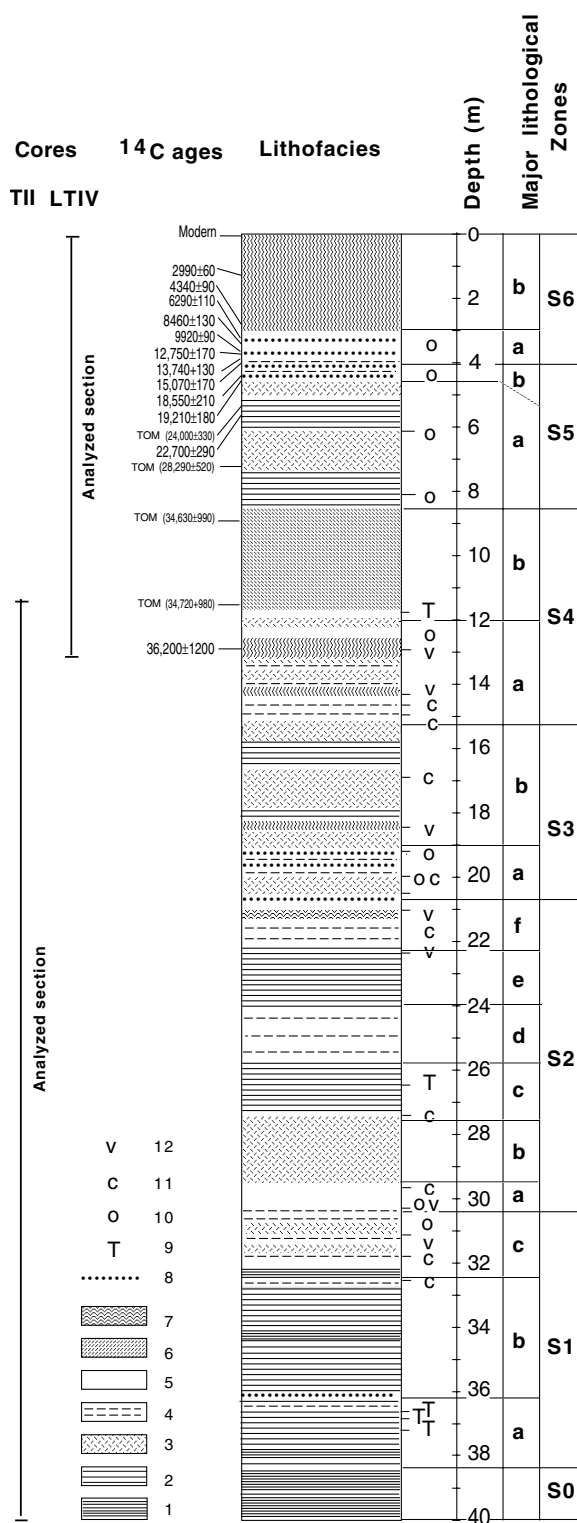
Lake Tritrivakely is presently surrounded by grassland and terrace agriculture. The original vegetation (Fig. 1) of the western slopes of the central highlands (800–1800 m; $T = 20^\circ\text{C}$; $P = 1000$ –1500 mm; 5–7 dry months) consists of a sclerophyllous forest with *Uapaca bojerii*, but as a result of strong human interference, it now occupies only isolated patches (Harisoa, 1988). Frequent fires occur, both human- and lightning-caused. At similar altitudes on the eastern escarpment, the medium-altitude dense rainforest ($T = 15$ – 20°C ; $P = 1000$ –1500 mm; two dry months) 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 *Podocarpus* and many bamboos. The main ecological difference from the lower-altitude forest is a lower minimum temperature. The ericaceous bush is characteristic of high mountains (>2000 m; $T \sim 10^\circ\text{C}$; $P > 2000$ mm); it survives severe variations in humidity, solar radiation, temperature, and winter frost (Humbert and Cours-Darne, 1965; Koechlin et al., 1974).

2.2. The modern waterbody

Tritrivakely is a small waterbody without surface outlet, which occupies the center of a crater, 90 m deep, and 550 m wide. Depending on the seasonal and interannual climatic fluctuations, it varies from a small lake with circumneutral water to an acidic bog with Cyperaceae hummocks and water holes. A detailed investigation conducted from 1992 to 1997 (Ferry and Robison, pers. comm., 1999) provided the following characteristics. The catchment and lake areas are 27.7 and ca. 6 ha, respectively. The lake has a mean depth of 1.32 m. Water level fluctuations ranged over 1.8 m during 1995–1997. The magnesium bicarbonate water has a very low electric conductivity ($\text{EC} = 18.4$ – $70.2 \mu\text{S cm}^{-1}$; mean = $41 \mu\text{S cm}^{-1}$), indicating a short water residence time; pH varies from 5.4 to 8.6 (mean = 7.2). The water budget is controlled by rainfall in, and evapotranspiration from the crater, and by groundwater inflow and outflow. A shallow aquifer maintains the waterbody during the dry season, but receives water from the lake in summer when the lake level is high.

The waterbody is colonized by emergent and aquatic plants. Cyperaceae dominate the biomass. Fourteen species were identified (Ranarijoana, 1999), among which Cyperaceae, Alismataceae, *Nymphaea*, *Nymphoides*, *Polygonum*, and *Potamogeton* are represented in the pollen spectrum. The diatom communities (12 samples collected in 1992–1997) reflect microhabitats and seasonal/interannual hydrological changes. Detailed results will be presented elsewhere. The epiphytic, aerophilous flora on the Cyperaceae hummocks is dominated by *Eunotia* spp. and small *Pinnularia*. During very low stands, finely punctated *Aulacoseira* close to *A. laevisima*, and *Fragilaria* gr. *tenera* are common in water hollows and on bottom



mud. During high stands, *A. muzzanensis* associated with rare *A. granulata*, *A. ambigua* and *Fragilaria* gr. *tenera* live in open water; the periphyton is rich in *Gomphonema* (*G.* cf. *gracile* mainly), *Achnanthes minutissima*, and small *Navicula* species (e.g. *N. minima*, *N. sp. af. utermohlii*).

3. Material and methods. Definition of the lithofacies, pollen and diatom zones

Our pollen and diatom studies derived from two cores collected at the crater center in 1992, using a Wright (core LT4; 13 m) and a Wieckowski piston corer (core TII; 0–40 m). These two cores were cross-correlated according to magnetic susceptibility data (Williamson et al., 1998). We present here a composite record (TII = 40–13 m, and LT IV = 13–0 m).

3.1. Core lithology

The profile reveals an accumulation of lacustrine and palustral sediments with a few fine sand layers and peat-marsh deposits (Fig. 2). There is no indication of important sedimentation gaps, although peat-marsh and oxidized sediment layers suggest episodes of very shallow water of increasing occurrence towards the top of the sequence, and even short-term (seasonal, interannual?) desiccation phases. The lithofacies reflect water level fluctuations that are superimposed over a trend of gradual shallowing. The major sedimentary features are the following (Fig. 2).

The section 4002–3830 cm (S0) consists of a finely laminated diatomite (couplets of dark–white laminae: 0.2–1 mm thick), with a few centimetric homogeneous bands, followed by a silt layer.

The section 3830–3044 cm (S1) begins with a dark

Fig. 2. Simplified stratigraphic log of the lake Tritrivakely lacustrine sequence. The composite profile is derived from core LT4 (13 m; after Gasse and Van Campo, 1998) and TII (40 m). Sections analyzed for pollen and diatoms are indicated by full vertical lines on the left. 1 — finely laminated diatomite; 2 — coarsely laminated diatomite; 3 — homogeneous to laminated silt; 4 — homogeneous to laminated clay; 5 — homogeneous to laminated organic mud; 6 — diatomaceous clay; 7 — peat composed of macrophyte debris; 8 — sand; 9 — in situ tephra; 10 — oxidized levels; 11 — charcoals; 12 — vegetal debris. On the right, major stratigraphical sections.

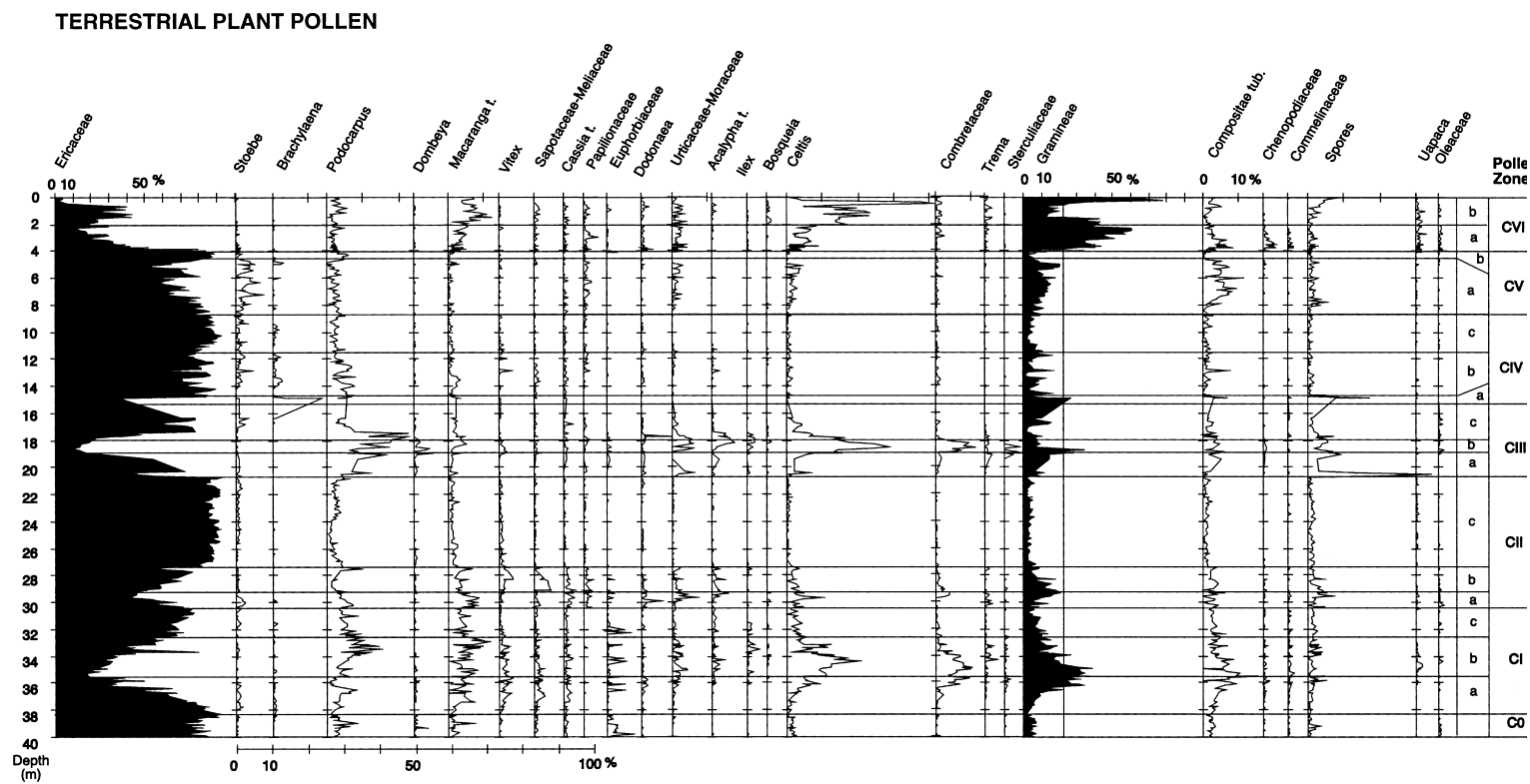


Fig. 3. Pollen diagram of major terrestrial pollen taxa. Spores of pteridophytes are also shown.

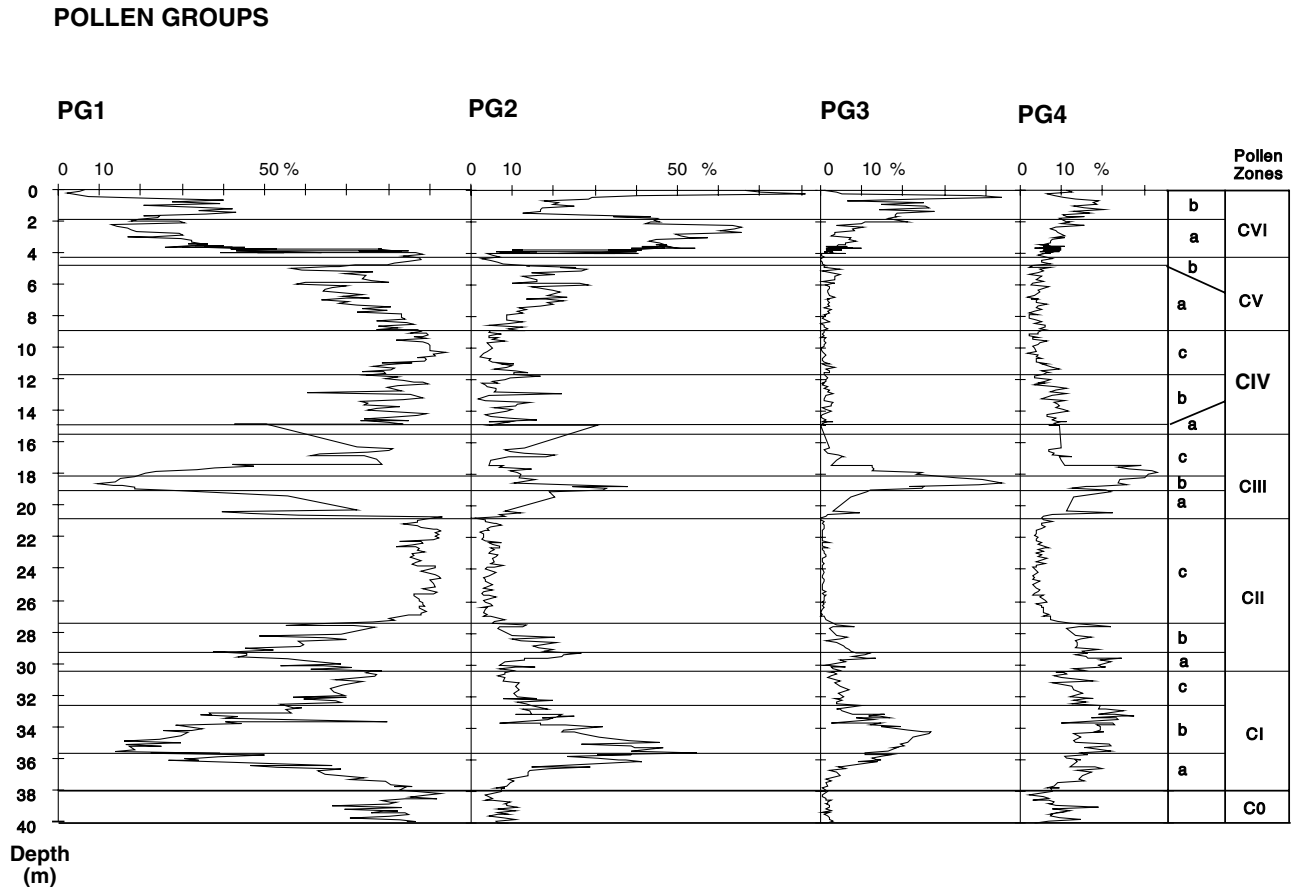


Fig. 4. Pollen diagram of major pollen groups (PG1–PG4); PG1 — defined by Ericaceae, *Stoebe* and the arborescent Compositae *Brachylaena*; PG2 — composed of the herbaceous plant families Gramineae, Chenopodiaceae, Compositae (Tubiflorae type), Caryophyllaceae and other taxa of open formations; PG3 — arboreal taxa at medium-altitude forests and woodlands; PG4 — *Podocarpus* and other components of montane forest.

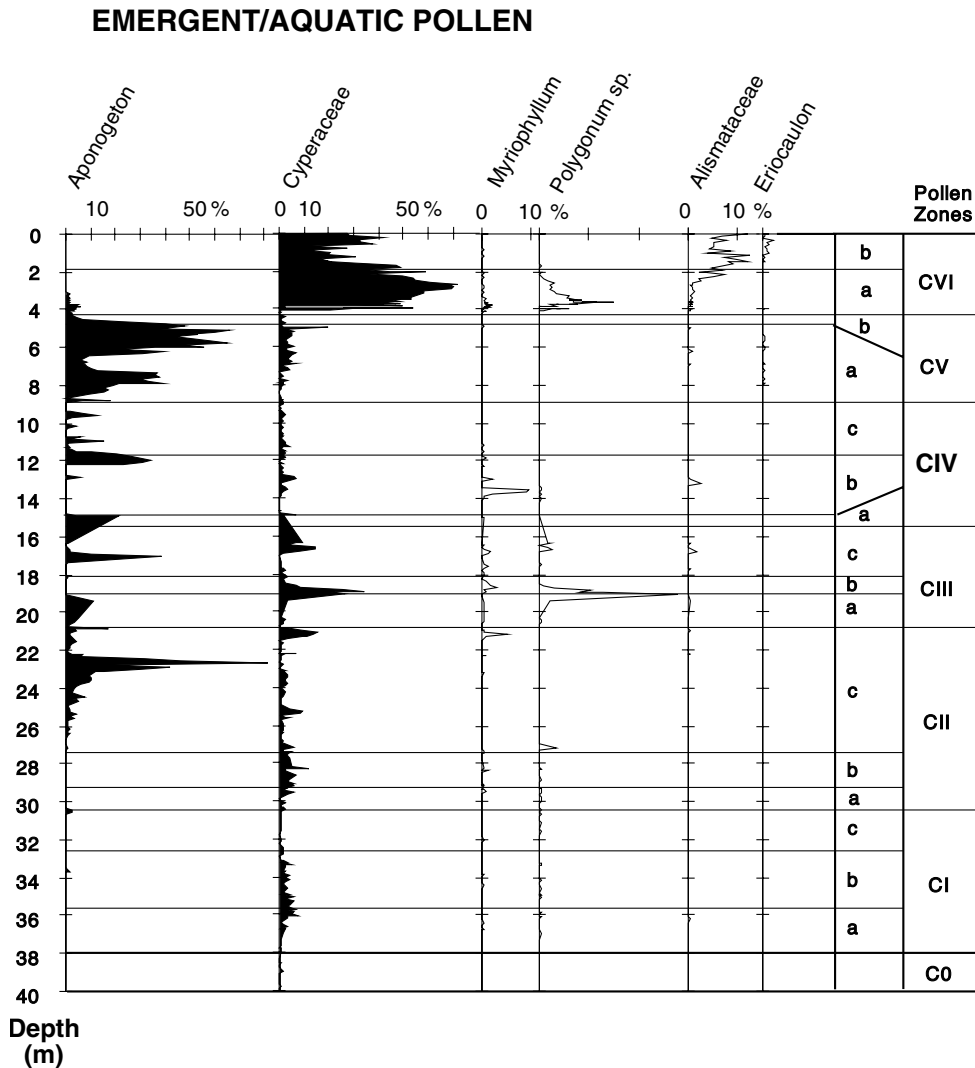


Fig. 5. Pollen diagram of aquatic and paludal plants: percentages are calculated on the raw (terrestrial + aquatic/paludal) pollen sum. Pollen zones (on the right) are those defined from the terrestrial pollen spectra (Figs. 3 and 4).

to pale gray diatomite with several finely laminated intervals, interrupted by tephra layers at 3720, 3675 and 3685 cm, and by a thin bed of fine sand at 3627 cm, which suggests a low stand ending stage SIa. A banded to finely laminated diatomite enriched in silt and clay above 3300 cm dominates SIb, and switches to an organic mud with vegetal debris above 3240 cm (SIc).

From 3044 to 2071 cm (S2), the sediments are more silty, and do not show the well defined, fine laminations observed below, although several intervals are

banded to laminated. This section starts with a coarsely laminated organic mud (S2a) containing abundant vegetal fragments lying in horizontal layers and oxidized silt levels, which indicate shallow, swampy conditions at the core site. Silt and silty diatomite (S2b,c,e) then alternate with organic-rich clay (S2d). A tephra layer occurs at 2654 cm. This section ends with a peat bed (2132–2105 cm) and organic-rich clay (S2f).

The section 2071–1525 cm (S3) begins (S3a) with a dark coarse sand composed of reworked volcanic

material (2071–2060 cm) and gray silt. At 1970–1942 cm, oxidized sandy silt and dark sandy clay suggest conditions close to dry. Above 1900 cm (S3b), gray homogeneous silt, and dark, banded to laminated diatomaceous clay rich in vivianite and siderite are observed. Vegetal debris and charcoals are abundant, and form a peat layer around 1838 cm.

From 1525 to 860 cm (S4), organic mud and peat beds alternate with oxidized sandy silt and clay from 1540 to 1175 cm (S4a). An airfall tephra occurs at 1175–1170 cm. Then, a brownish, siderite-rich, diatomaceous clay is observed (S4b).

Diatomaceous silt, coarsely laminated from 860 to 760 cm and 610 to 460 cm, then prevails up to 452 cm (S5a). Oxidized surfaces are observed at 802, 612, and 503 cm. From 452 to 402 cm (S5b), fine sand lenses are interbedded within oxidized silt and clay, reflecting very shallow to dry conditions.

Then, dark organic mud predominates (402–300 cm; S6a), but contains several thin oxidized clayish or sandy layers. The upper 3 m consist of Cyperaceae peat (S6b).

Seventeen ^{14}C AMS dates of Cyperaceae debris and charcoals provided the chronology of the upper 13 m of the sequence (Gasse et al., 1994). Radiocarbon ages measured on total organic matter (TOM) were rejected because of the occurrence in the sediment of organic detrital particles reworked from soils in the catchment (Siffedine et al., 1995); ages on TOM are somewhat older than real ages. The 14 valid ^{14}C ages were converted to calendar ages (cal. yr B.P.; Williamson et al., 1998; Gasse and Van Campo, 1998), using the CALIB.3 program (Stuiver and Reimer, 1993). The tephra layers around 3720, 3685, 3675, 2654, and 1175 cm document nearby volcanic explosions. Their Ar/Ar radiometric dating failed due to the scarcity and bad preservation of sanidine crystals. The Th/U-disequilibrium dating method was also attempted on siderite, without success because the geochemical system was not closed.

Samples for pollen and diatom analyses were taken at 10 cm intervals along the profile, or at every centimeter within zones of very low sedimentation rate of core LT4. Pollen and diatom slides were performed according to standard techniques (Gasse and Van Campo, 1998).

3.2. Pollen

The Atlases of the “Palynologia Madagassica et Mascarenica” series (Straka, 1991) were the basic reference for the identification of pollen types, given to the family or genus level, rarely to the species level. In many cases, a pollen type does not represent a single genus. The suffix “type” is then added, indicating that it may include several genera within the family. Pollen was abundant and well preserved, and an average of 778 pollen and spores (182–4773) were counted in each sample. When a pollen type was dominant in a sample (for example Ericaceae), a minimum of 100 additional pollen grains were counted. The pollen results are given as percentage diagrams of selected taxa (Figs. 3–5).

3.2.1. Terrestrial pollen

A correspondence analysis (CA; Benzécri, 1980) was carried out on the most abundant terrestrial pollen types (Fig. 3), gathering pollen types that we considered according to the physiognomy and habitat of the plant species they include, taken from the *Flore de Madagascar et des Comores* (Humbert et al., 1936). The first two axes account for 39 and 13% of the total variance, respectively. Axes 3 and 4 still represent 10% of the total variance but their significance is less clear. The CA yields four major pollen groups depending on their contribution to Axes 1–4 (PG; Fig. 4), whose ecological meaning obviously contains ambiguities, because they include taxa that are represented in different formations, such as montane and middle-altitude forests, woodland/grassland mosaics, and open formations (Burney, 1988; Straka, 1991).

PG1 is mainly defined by Ericaceae, *Stoebe* and the arborescent Compositae *Brachylaena*, which are modern components of the South African temperate fynbos communities (Taylor, 1978). High pollen representation of Ericaceae (>70%) only appears in modern pollen spectra within the ericaceous bush above 2000 m (Burney, 1988; Straka, 1991). The microphyllous species of *Stoebe* are associated with this vegetation type. The high values of PG1 reveal the occurrence of an ericaceous bush in the catchment, under colder conditions than present, although vegetation model simulations show that lower atmospheric CO_2 concentrations may have contributed to the

ericaceous bush descent, at the expense of montane forest taxa (Jolly and Haxeltine, 1997).

PG2 is mostly composed of the herbaceous plant families Gramineae, Chenopodiaceae, Compositae (Tubiflorae type), Caryophyllaceae and other taxa that are primarily found in open formations. Although some Gramineae pollen may derive from the local swamp, the high PG2 values clearly indicate grassland or wooded grassland (Burney, 1988; Straka, 1991). Two arboreal pollen *Uapaca* and *Antidesma*, associated with the driest types of forest, also belong to PG2. The fire-resistant tree *U. bojeri* is typical of the sclerophyllous forest of the western slopes in the central highlands (Koechlin, 1972). *Antidesma* trees or shrubs are found in the dry forest of the West Domain (Rajeriarison, 1984), commonly along rivers (Léandri, 1958).

PG3 includes arboreal taxa of medium-altitude forests and woodlands. Some of them, like Combretaceae, have low indicative values, since the plant species occur in forests, woodlands, and woodland/grassland mosaics, and are represented by various proportions in the modern pollen spectra of these vegetation types (Burney, 1988; Straka, 1991). *Celtis* may reach more than 30% of the terrestrial pollen. The tall tree *C. gomphophylla* is the only of the three species present in Madagascar reported in the forests of the central highlands, between 700 and 1300 m (Leroy, 1952). *Trema* pollen is much less abundant in the pollen diagram. *T. humbertii* is characteristic of the upper limit of the middle-altitude dense rainforest (Rajeriarison, 1984), whereas *T. orientalis* is ubiquitous in the Island (Leroy, 1952). *Acalypha* species usually grow at the forest edges. *Ilex mitis* is a common tree in the forests above 800 m (Perrier de la Bathie, 1946). *Bosqueia* are present in all forest types, and *Acalypha* species usually grow as pioneer species at forest edges.

A primary component of PG4 is *Podocarpus*, characteristic of the montane lichen forest in the central highlands, between 1300 and 2000 m, at the most cloudy level (Koechlin, 1972). Owing to the high dispersal ability of *Podocarpus* pollen, only percentages of $\pm 20\%$ indicate the close proximity of the *Podocarpus* forest (Coetzee, 1967). PG4 also includes *Dombeya* and *Vitex* trees, represented by many species, especially in the montane forests (Arènes, 1959; Moldenke, 1956). The *Macaranga* pollen type is abundant in the pollen diagram; more than 15 forest

tree or shrub species occur in Madagascar. Several miscellaneous pollen types, such as Urticaceae–Moraceae, *Dodonaea*, or Sapotaceae–Meliaceae are present in significant amounts.

To sum up, and assuming that the highest representations of the PG1 pollen group are related to the coldest temperatures, the terrestrial pollen record shows six cold/warm cycles (C0–CVI; Figs. 3 and 4). Each cycle includes a warming phase (labelled CIa to CIVa) and a return to cold conditions, which induces the development of an ericaceous bush around the site. The six warming phases are of various amplitudes. They start at 3800 (CIa), 3044 (CIIa), 2071 (CIIIa), around 1525 (CIVa), 860 (CVa), and 402 cm (CIVa). The major warm phases (CI, CIII and CVI) are defined by the successive stages observed in the vegetation history: (i) at the onset of a warm phase, the ericaceous bush (PG1) disappears, migrating to higher altitudes; the temperature increase, without a sufficient parallel moisture rise, first produces a wooded grassland (PG2); (ii) following a further moisture increase, trees grow denser, especially along the lake shore; and (iii) with the cooling re-initiation, the montane forest migrates around the site, before the onset of a new cold phase.

3.3. Emergent and aquatic plant pollen

The emergent plant pollen (Fig. 5) mainly consist of *Aponogeton* and Cyperaceae (nearly 90% of the total aquatic/paludal pollen). *Aponogeton*, which live through the dry season as a dormant tuber, are not found today at Tiritivakely, but rather in fresh, cool waters (Raynal-Roques, 1980). It is the only genus of the family Aponogetonaceae and is represented by seven species in Madagascar (Jumelle, 1936). In the core, *Aponogeton* reaches high frequencies in several intervals between 2600 and 300 cm, and then disappears. Cyperaceae occur with significant percentages at different levels and become dominant above 400 cm. Other emergent and aquatic plant pollen occur in relatively low numbers. The high frequencies of sedge pollen indicate shallow conditions. Increasing frequencies from the core base to the top reflect an overall decrease in water depth, but this trend is not linear. The peaks of *Aponogeton* and Cyperaceae suggest episodes of low water level

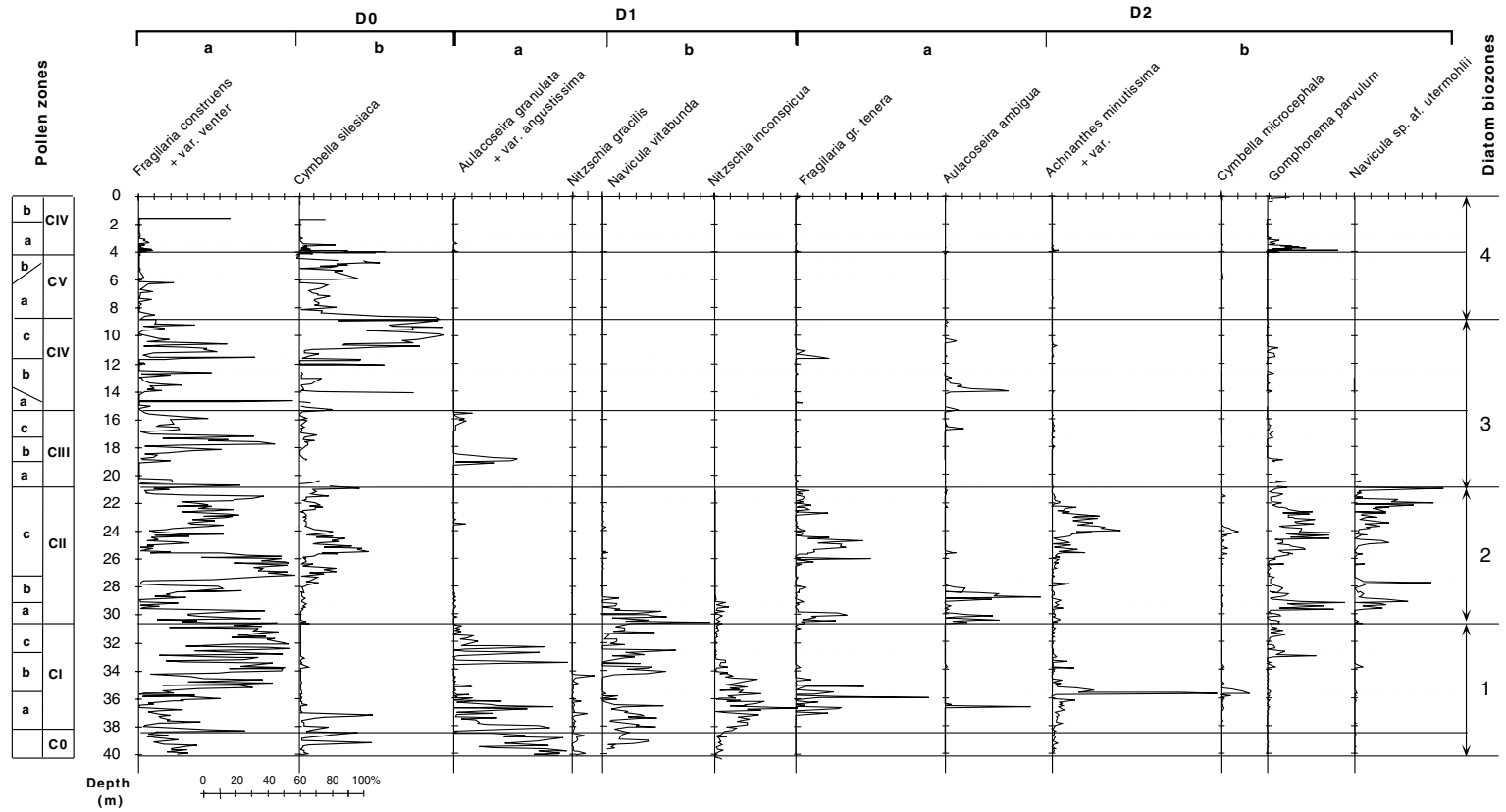


Fig. 6. Diatom diagrams for Lake Tritrivalley, illustrating the succession of major diatom taxa and diatom groups from the core base to the top. Diatom taxa of group D0, which reaches high percentages in many intervals along the core, and of groups D1 and D2 dominant in the lower 20 m of the profile. Diatom taxa of groups D3 and D4 dominant in the upper 20 m of the profile. Diatom groups D1–D4 tend to replace one another from the core base to the top, and define Diatom Zones (1–4). For comparison, the Pollen Zones are plotted on the left of the diagrams 6(a) and (b). Full horizontal lines coincide with the limits of major pollen zones. Full and dotted horizontal lines separate the diatom sub-zones.

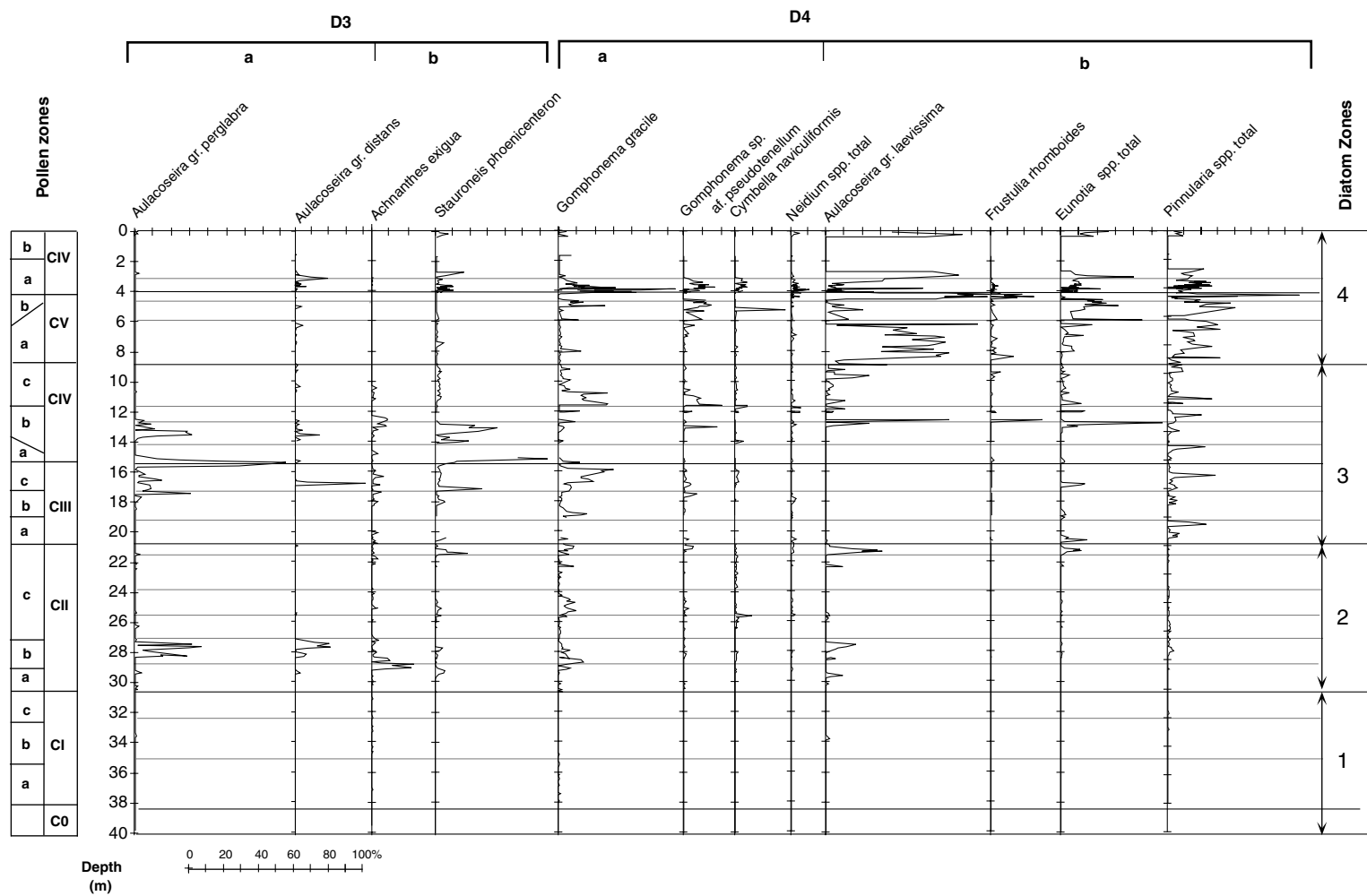


Fig. 6. (continued)

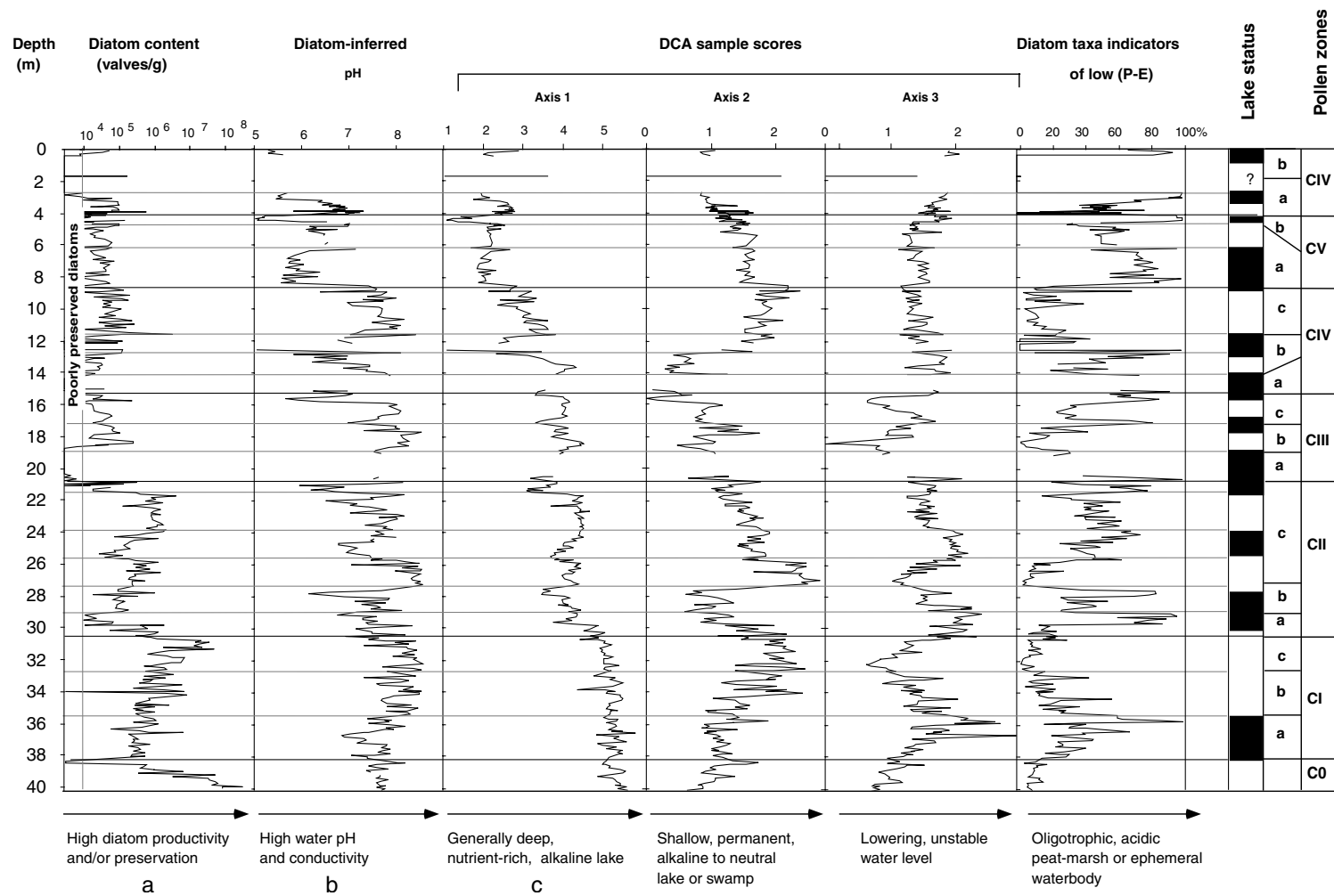


Fig. 7. Summary diatom diagram illustrating the waterbody evolution. (a) Diatom content (valves/g dry sediment). (b) Diatom-inferred-pH, which evolved in parallel with diatom-inferred electric conductivity (CE; not represented here), based on the transfer function established for East African diatoms (Gasse and Tekaia, 1983, and Gasse, unpubl. data). (c)–(e) Detrended Canonical Analysis (DCA). Samples scores, Axes 1–3 (see text for explanation). (f) Total percentages of diatom species indicating periods of water deficit (low $P - E$) and low nutrient content. These species are those assigned to sub-group b in each major diatom group/biozone (D1–D4; see text and Fig. 6a,b). (g) “Lake status”. White rectangles represent relatively high $P - E$ and nutrient content (status a). Black rectangles indicate periods of water deficit (low $P - E$) and low nutrient content. Discontinuities in the diatom curves correspond to intervals with no or very poorly preserved diatom valves, interpreted as periods of water deficit. For comparison, the Pollen Zones are plotted on the left. Full horizontal lines coincide with the limits of major pollen zones. Full and dotted horizontal lines separate the diatom sub-zones.

centered around 3600, 2900, 2200–1900, 1700–1500, 1200, between 800 and 450, and above 400 cm.

3.4. Diatoms

Taxon identification (266) was conducted using works on African diatoms (Manguin, 1941, 1952; Hustedt, 1949; Gasse, 1986), and literature on acidic, oligotrophic lakes of temperate or high northern latitudes (mainly, Lange-Bertalot and Krammer, 1987; Krammer and Lange-Bertalot, 1985, 1986, 1991, 1997; Krammer, 1991; Lange-Bertalot, 1995, 1996a–c, 1998, 1999; Florin, 1981; Camburn and Kingston, 1986). Several taxa not appearing in the literature were found in our modern reference samples from Tritrivakely and/or in neighboring lakes. An open nomenclature is adopted for these taxa. Counts (300–750 valves per sample) are given as percentage of selected taxa (Fig. 6a,b). The diatom concentration (valves per mg/dry sediment) varies drastically (Fig. 7) and is clearly linked to diatom preservation, i.e. badly preserved valves in diatom-poor samples, and vice versa. Countings are regarded as significant in the 386 samples that contain more than ca. 10,000 valves g^{-1} . In others, selective dissolution may have significantly distorted the original assemblage.

The diatom assemblages resemble those found in mid-altitude, volcanic regions of East Africa. The ecological interpretation is based on our modern diatom/hydrochemistry dataset from these regions (Gasse et al., 1983, 1995; Gasse and Tekaia, 1983; Gasse, 1986), complemented by 12 reference samples from Tritrivakely and 15 from other lakes in Madagascar for which environmental conditions are known (Gasse and Robison, unpubl. data). Past pH and EC of the lake water were tentatively inferred from transfer functions established for northern Africa (Gasse and Tekaia, 1983; Gasse et al., 1995). Optimum conditions can be assigned for 102 taxa. The inferred values suffer large uncertainties because: (i) several taxa, or morphotypes, abundant here are not represented in the training set; and (ii) selective dissolution may bias inferences in diatom-poor samples. However, the results reflect major fluctuations and appear significant when compared with our modern references. The inferred EC and pH values at the core top are in agreement with the modern measured values. The diatom record reflects freshwater conditions through-

out the profile. The diatom-inferred conductivity reaches a maximum at $650 \mu\text{S cm}^{-1}$ around 3600–3400 cm; it decreases irregularly upward and frequently falls below $50 \mu\text{S cm}^{-1}$. It fluctuates in phase with pH-values that range between 8.2 and 5.5 (Fig. 7). In the absence of a surface outlet, these freshwater conditions imply that salt regulation was ensured by infiltration. The lake was hydrologically open, as it is today.

Nutrient content is a crucial factor for diatom species distribution (e.g. Kilham et al., 1986; Bennion, 1995; Lange-Bertalot et al., 1996a), but no quantitative reconstruction can be performed here due to the scarcity of information on modern African lakes with regard to this variable. Volcanic tephra deposition may induce sudden changes in the water-Si content, Si:P ratio and light penetration (Birks and Lotte, 1994). Although some blooms of *Fragilaria tenera* may have been favored by volcanic silica inputs, no clear impact on diatom assemblages can be detected in our record.

A Detrended Canonical Analysis (DCA; ter Braak and Smilauer, 1998) was based on 386 samples and the best represented taxa or groups of taxa (122). Sample scores are presented for Axes 1–3 (Fig. 7), which have eigenvalues of 0.59, 0.19, and 0.13, respectively. Five major taxa groups (D0–D4) were defined using their contribution to the DCA axes. Each group was subdivided into two sub-groups, a and b, representing the hydrological status: (a) high ($P - E$) values, relatively deep, nutrient rich water, and a high concentration of well preserved diatoms in the sediments; and (b) low ($P - E$) values, relatively shallow water or ephemeral conditions, a lower nutrient concentration, and a lower diatom content and preservation.

The only group reaching high percentages throughout the profile is D0 (Fig. 6a). The characteristic taxa of D0 are strongly and positively correlated with DCA Axis 2. D0a consists of the small chain-forming *Fragilaria*, mainly delicate forms assigned to *F. construens* var. *venter*, and associated with *F. brevis-triata* and *F. construens* var. *construens* below 1500 cm. *F. construens* var. *venter* has the highest loading on Axis 2. *F. construens* and its variety *venter* are facultative planktonic forms common in many East African lakes and in the plankton and bottom mud of the crater Lake Andrianakibo in the

Madagascar highlands. These live either as suspended forms or in nutrient-enriched environments of the lake bottom (Bennion, 1995). D0a predominates in the intervals 3420–3040, 2750–2580 and 1175–860 cm and around 160 cm, rich in well preserved diatom valves. D0b is primarily composed of the epiphytic form *Cymbella silesiaca*. This taxon predominates from 1100 to 860 cm, but its valves are poorly preserved in this interval. Both *Fragilaria* and *C. silesiaca* inhabit the photic zone in shallow, circumneutral waterbodies.

The components of groups D1–D4 have decreasing coordinates along DCA Axis 1, from the heaviest positive (D1) to the heaviest negative loadings (D4). Groups D1–D4 tend to replace one another from the core base to the top, and thus define biozones 1–4 (Fig. 6).

D1 characterizes the interval 4000–3044 cm (Fig. 6a), and reflects relatively high pH, EC and nutrient content. D1a includes primarily the euplanktonic forms *A. granulata* and its variety *angustissima*, which thrive in numerous well-mixed, mesotrophic lakes; other planktonic forms, e.g. *Nitzschia gracilis*, *N. lancettula*, and *N. subacicularis*, are widespread in alkaline East African lakes but occur in low numbers here. The associated periphytic forms, *Navicula vitabunda*, the rare *Amphora perpusilla*, *Epithemia adnata*, *E. sorex*, *Nitzschia amphibia*, *N. palea*..., are alkaliphilous. D1b is primarily defined by *Nitzschia inconspicua*, which survives aerophilous conditions as shown by its predominance on emergent macrophytes at Lake Alaotra (northeastern Madagascar; unpubl. data).

D2 elements reach high frequencies below 2071 cm, but are the best characteristics of the interval 3044–2071 cm (Fig. 6a). They have high positive loadings on Axis 3. D2a consists of *Fragilaria* gr. *tenera*, and the obligate planktonic *Aulacoseira ambigua*, which has low nutrient requirements compared to *A. granulata* (Kilham et al., 1986). These two species compete in the plankton of several, slightly alkaline African crater lakes, e.g. Lake Naivasha (Kenya) and Lake Ambatamahita (North Madagascar). *F. gr. tenera* was found, however, in the modern shallow lake Tritrivakely. It is thus regarded here as a facultative planktonic form. D2b associates typical periphytic species common in the modern lake during wet years/seasons, mainly *Achnanthes minutissima*,

Cymbella microcephala, *Gomphonema parvulum*, *Navicula* sp. af. *utermohlii*. D2 reflects an unstable waterbody: marshy intervals are bracketed by short phases deep enough to allow plankton growth.

D3 taxa, negatively correlated to Axis 2, are represented from 2800 cm, but show maximum percentages from 1904 to 1500 cm (Fig. 6b). D3a is primarily defined by the facultative planktonic forms *Aulacoseira* gr. *perglabra* and *A. gr. distans*, similar to those found in the bottom mud of the shallow Lake Kioga (Uganda; EC = 212 $\mu\text{S cm}^{-1}$; pH 6.6), and in the oligo-/dystrophic lake Julma Ölkky (Finland; EC = 17 $\mu\text{S cm}^{-1}$; Lange-Bertalot, 1996a). These taxa are closely associated with the acidophilous species *Stauroneis phoenicenteron*. D3b is mainly composed of *Achnanthes exigua*, *A. lanceolata* and *Fragilaria pinnata*, periphytic in neutral swamps.

D4 elements appear around 3000 cm but are best represented above 860 cm (Fig. 6b). D4a includes *Gomphonema* gr. *gracile*, *G. sp. af. pseudotenellum*, *Cymbella naviculiformis*, *Neidium* spp., common in oligotrophic, circumneutral to acidic swamps. D4b is opposite to D1 along Axis 1, and is positively correlated with Axis 3. D4b reflects ephemeral or subaerial, acidic, oligotrophic conditions. The group of *Aulacoseira* gr. *laevissima*, which dominates in the intervals 850–612 and 450–412, and above 300 cm, lives today at Tritrivakely and at Ifahrimene, a neighboring crater lake, which also desiccates during dry seasons or years, in shallow waters with extremely low ionic concentration (EC = 17–46 $\mu\text{S cm}^{-1}$, pH 5.8–6.6). Other significant taxa are *Eunotia* (*E. incisa*, *E. minor*, *E. flexuosa*...) and *Pinnularia* (*P. major*, *P. viridis*, *P. sp. af. legumen*, *P. appendiculata*, *P. borealis*...), found today as epiphytic or epipelic at Tritrivakely. D4b corresponds to very low diatom content and bad preservation. Large peaks of *A. gr. laevissima* are commonly followed by a total disappearance of diatoms, attributed to short-term desiccation phases.

To sum up, the successive biozones D1–D4 reflect an overall trend from a relatively deep, alkaline, nutrient-rich lake, where the diatom silica largely contributes to sedimentation, to acidic, oligo-dystrophic, ephemeral or subaerial conditions unfavorable to diatom production and/or preservation. This overall shallowing/acidification/oligotrophication trend is well recorded by DCA sample scores along Axis 1 and the pH curve (Fig. 7). This evolution is in good

agreement with changes in lithofacies and with the increasing frequencies of emergent plant pollen. This evolution can be partly caused by gradual basin infilling. However, an alternation of relatively wet, nutrient-rich, and dry, oligotrophic episodes (hydrological status a and b) is superimposed over this general trend (Fig. 7). The intervals with high sample scores along DCA Axis 2, due to D0, correspond to a permanent, circumneutral swamp or shallow lake. The high DCA Axis 3 values appear to reflect periods of hydrological deficit (low $P - E$) and/or low nutrient concentration within the successive biozones. Due to the general shallowing, diatom indicators of relatively high and low stands (represented by sub-groups D1a–D4a and D1b–D4b, respectively) are specific of individual biozones. In order to confirm the significance of DCA3 and to amplify the diatom signal of the hydrological fluctuations, we estimated the total percentages of the taxa indicators of negative water budget and low nutrient content (sub-groups b) in the successive biozones D1–D4 (Fig. 7).

The abruptness of the shifts between status a and b suggests some threshold hydrological mechanisms, linked with connections/disconnections between the lake and the aquifer, as occurring today at the seasonal and interannual scales. During periods of high $P - E$ balance in the catchment, the aquifer rose and sustained a permanent lake with a relatively high residence time; substantial weathering of the crater slopes also brought nutrients. When $P - E$ decreased in the watershed, the groundwater table fell below the altitude of the lake bottom, and the waterbody turned to an ombrotrophic, oligotrophic peat-marsh.

4. Reconstruction of major environmental changes

4.1. Tentative age model

From the ^{14}C -dated part of the sequence (13 m; 0–40.8 kyr), we have shown (Gasse and Van Campo, 1998) that the deglacial warming phase, from ca. 17 to 10 kyr, coincides with a steep increase in temperature in southern low latitudes as recorded at Vostok. In the absence of direct chronological control prior to 40.8 kyr, a tentative age model is proposed, primarily based on comparisons between the Tritrivakely terrestrial pollen record and the

Vostok temperature curve (Jouzel et al., 1993, 1996). We assume that highest representations of the PG1 pollen group (Ericaceous bush close to the core site) reflect the coldest temperatures, and that the temperature in the central highlands of Madagascar roughly covaries with the air temperature over Antarctica. Different timescales have been used for the interpretation of the Vostok ice core records. We use the chronology of Waelbroeck et al. (1995) who applied the orbital tuning approach to the deuterium record to derive a timescale that is consistent with the SPECMAP marine timescale (Martinson et al., 1987). The Vostok δD isotopic temperature signal is correlated with the insolation at 65°N assuming that insolation is the dominant force in northern high latitudes (Imbrie et al., 1992). An age model was then obtained by peak to peak correlation between the Vostok temperatures and the PG1 percentages from 4002 to 1300 cm. (Fig. 7). We suggest that the major warming at 3600–3500 m at Tritrivakely coincides with the marine isotope stage 5e. Support for this is the comparison of the Tritrivakely record with the reconstruction of the lowland terrestrial temperatures in southeast tropical Africa for the last 135 kyr, based on pollen data of core MD79254, lying in the Mozambique channel off the Zambezi river (Van Campo et al., 1990). Temperature fluctuations derived from the marine pollen are in good phasing with Tritrivakely, although the low resolution of the marine data does not allow detailed comparisons between both series.

The depth scale of the Tritrivakely profile was converted to an age scale assuming a constant sedimentation rate between successive estimated ages (Fig. 8). This assumption, as well as possible leads and lags between the Tritrivakely and the Vostok temperature records, makes our age model only tentative. In the sections below, the ages should be regarded as hypotheses, and may change if new dating methods are developed.

4.2. The cold/warm cycles and related changes in the lake status

The major environmental phases described below are based on cold–warm cycles inferred from the terrestrial pollen and pollen groups (Figs. 3, 4 and 8). Environmental conditions in the waterbody are

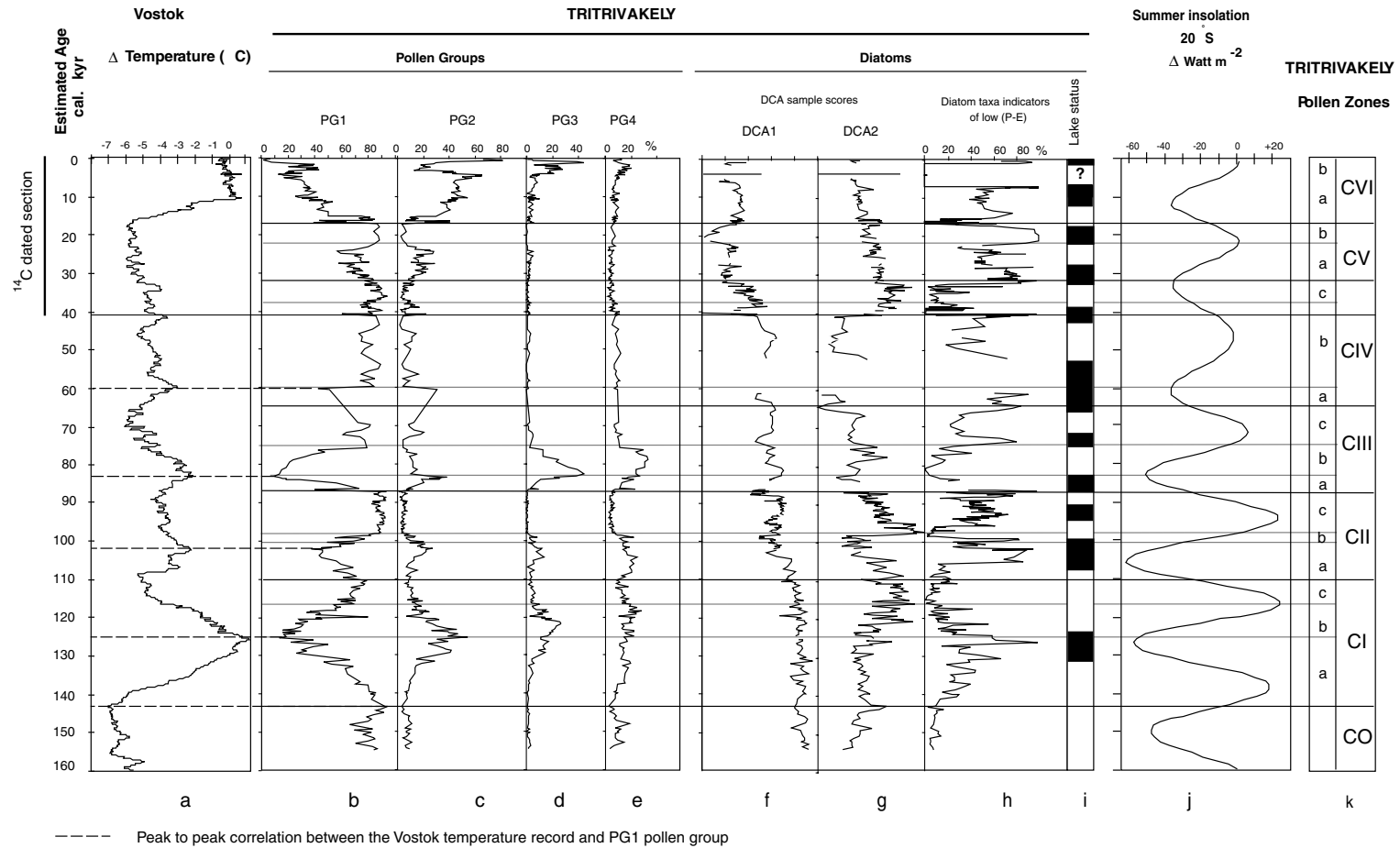


Fig. 8. Tentative interpretation of the Tritrivakely pollen and diatom records in terms of age. (a) the Vostok temperature curve (Jouzel et al., 1993) using the chronology of Waelbroeck et al. (1995). (b)–(i) The Tritrivakely record. From 0 to 40.8 cal. kyr (full line), the chronology is based on calibrated radiocarbon ages. Prior to 40.8 cal. kyr, the proposed age model is based on peak to peak correlations between the Vostok temperature and the percentages of the pollen group PG1 (dashed lines). All other curves for the Tritrivakely record are then scaled according to PG1 timescale and depth. (b)–(e) Major pollen groups, PG1–PG4 (b)–(e), illustrate warm/cold cycles. See text and Fig. 4 for the definition of the Pollen Groups. (f)–(i) Some major diatom indicators: samples scores for Axes 1 and 2 from the Detrended Canonical Analysis (DCA; (f), (g)); diatom taxa indicators of low ($P - E$) balance (h), and “lake status” (i) See text and Fig. 7 for explanation. (j) Summer insolation at 20°S (after Berger, 1978). (k) The Tritrivakely Pollen Zones.

derived from the lithology (Fig. 2), the aquatic and emergent plant pollen record (Fig. 5), and the diatom record (Figs. 6 and 7). The pollen stratigraphy is plotted together with some diatom indicators according to the age model proposed above in Fig. 8.

4.2.1. C0: 4002–3830 cm (estimated age 154–143 kyr)

The sequence begins with a cold phase, with temperatures significantly lower than today, as inferred from the high values of Ericaceae. However, the lowermost levels (4002–3900 cm) may represent the end of a previous warmer phase, on account of a small peak of PG4 pollen and still increasing Ericaceae percentage. Ericaceae reach peak values, corresponding to coldest conditions, around 3830 cm (143 kyr).

The C0 interval is characterized by the highest diatom content and preservation, and by the highest contribution of D1a. It represents a high stand. Although *A. granulata* and its varieties are favored by good mixing, the fine laminations observed in the sediments suggest lake stratification, at least seasonally. A shift in diatom content (3900–3830 cm) and a change in lithofacies mark the transition to the period CI.

4.2.2. CI: 3830–3044 cm (estimated age 143–110 kyr)

In sub-phase CIa (3830–3555 cm; 143–125 kyr), a strong decline of PG1, mirrored by increases of PG2 and PG4 values, marks the beginning of a warm phase. PG2 values, mainly Gramineae and Compositae (Tubiflorae type), increase sharply and reach a maximum (around 50%) at 3555 cm, paralleled by an increase in PG3 values. The dominance of the herbaceous component (PG2) indicates that the ericaceous bush is replaced by a grassland/woodland mosaic under warmer–drier conditions. From 3555 to 3250 cm (CIb; 125–116 kyr), the PG3 medium/low-altitude tree taxa (mainly *Celtis*/Combretaceae) reach a maximum, part of which may be riparian, while PG2 decreases. This PG3 maximum reflects the wettest conditions. Then a maximum of the montane lichen forest components (PG4), mainly *Podocarpus*, is observed, while Ericaceae increase. This indicates the beginning of a cooling trend (CIc, 3250–3044 cm; 116–110 kyr). The ericoid vegetation

(PG1) dominates again from 3250 cm and expands to a new peak at 3044 cm (110 kyr), not as high as the preceding one.

In the lake, CIa coincides with unstable hydrological conditions and a desiccation trend. This is reflected by increasing DCA3 values mainly due to the development of *Nitzschia inconspicua* (D1b) and *Achnanthes minutissima* (D2b), which reach a maximum at 3636 (129 kyr) and 3570 cm (126 kyr), respectively. The low stand is confirmed by fine sand layers around 3627 cm (Fig. 2) and a first increase in Cyperaceae pollen. However, a peak of *Aulacoseira ambigua* (3660 cm) and sediment packs with thin white laminae almost exclusively composed of *F. gr. tenera* (3700–3460 cm) suggest sudden water influxes (seasonal?) allowing these open water forms (D2a) to develop. A return to deeper conditions is then marked by increases of D0 and D1a during the warm–wet phase CIb. A shallow waterbody with circumneutral water (D0 dominant) maintained during the cold period CIc (high DAC2 values).

4.2.3. CII: 3044–2071 cm (estimated age 110–86.7 kyr)

A second sharp decrease of Ericaceae at the beginning of CII shows a return to warmer conditions (CIIa, 3044–2928 cm; 110–102 kyr). This warm pulse is weaker than CIa, as suggested by the lower Ericaceae fall, and the lower increases of PG2, PG3 and PG4 during sub-phases CIIb (2928–2735 cm; 102–98.5 kyr). Cold conditions favorable for Ericaceae growth were fully re-established at 2735 and maintained up to 2071 cm (CIIc; ca. 98.5–87 kyr).

In the lake, a low stand took place during the warm period CIIa–CIIb. Diatom content falls markedly. As for CIa, the dominance of typically periphytic forms (D2b and D3b) is bracketed by peaks of obligate or facultative planktonic taxa of D2a and D3a between 3044 and 2740 cm. The first occurrence of D4, a second increase of Cyperaceae pollen, and in situ vegetal fragments in the sediments confirm the development of a peat-marsh at the core site.

The following cooling phase CIIc begins with a return to lacustrine, shallow, circumneutral conditions, recorded by high DCA2 values from 2740 to 2600 cm (ca. 98.7–96 kyr) mainly due to D0a. Then, while the pollen spectra remain stable, the diatoms indicate several hydrological fluctuations. A low

stand is recorded by the development of D0b and D2b at 2600–2400 cm (ca. 96–93 kyr). It is followed by a minor moisture increase allowing D0a to develop again until 2200 cm. Finally, a dramatic negative shift in diatom content and an increase of D4 taxa indicate a new desiccation/acidification trend (2180–2075 cm; ca. 89–87 kyr), which started under still cold conditions. This is consistent with the development of emergent plants as indicated by the pollen record, and with the occurrence of a peat layer in the sediment core.

4.2.4. CIII: 2071–1525 cm (estimated age 87–65 kyr)

A new warm phase develops, with a significant fall of the Ericaceae percentage (CIIIa, 2071–1900 cm; ca. 87–84 kyr). The dynamics of vegetation changes is comparable with what is seen in CI. Under increasing temperatures, a grassland/woodland mosaic (PG2) replaces the high-altitude bush, before a short period when the density of medium-altitude trees (PG3) is a maximum in the landscape (CIIIb, 1900–1735 cm; 84–75 kyr). Then, in the following reversal phase, the presence of a montane forest (PG4) not far from the site is attested by the highest percentages of *Podocarpus*, reaching 23% at 1775 and 1745 cm. The ericaceous bush altitude shifts down to the lake site. PG1 reaches high values again above 1735 cm (CIIIc, 1735–1525 cm; 75–65 kyr).

During CIIIa, the absence of diatoms in the coarse detrital and oxidized material suggests an extremely low water table. However, the high frequencies of Cyperaceae and *Polygonum* pollen indicate the persistence of a wetland at the core site. The re-establishment of a shallow circumneutral lake is indicated by the high frequencies of D1a and D0, successively, during CIIIb. Despite its low resolution, the diatom record suggests that CIIIc is complex, with a very low stand, acidic and oligotrophic water from 1735 to 1640 cm (ca. 75–70 kyr), followed by somewhat wetter conditions after 70 kyr.

4.3. CIV: 1525–860 cm (estimated age 62–33 kyr)

This interval is difficult to interpret due to the apparently low sedimentation rate, possible sedimentation gaps, and the absence of diatoms in many layers.

This phase starts by a significant warm/dry interval (CIVa, 1525–1486 cm; 65–60 kyr) recorded

around 1489–1484 cm (ca. 60 kyr) by high PG2 frequencies. From 1486 to 1170 cm (CIVb; ca. 60–38 kyr), PG1 and PG 2 fluctuates markedly. PG2 commonly reaches frequencies >10%, and peaks at 22 and 17% at 1285 (40.6 kyr) and 1175 cm (38.6 kyr), respectively. Then (CIVc, 1170–860 cm; 38–33 kyr), PG1 increases to reach high frequencies that maintain up to ca. 860 cm (ca. 33 kyr), with a maximum at 1030 cm (ca. 36 kyr).

During phases CIVa and CIVb, several peat layers are devoid of diatoms (1500–1470; 1467–1410; 1285 and 1175 cm). The disappearance of diatoms is synchronous or immediately following peaks of PG2. A wet pulse is recorded during phase CIVb by a sharp peak of *A. ambigua* (D2a) around 1400 cm, followed by a return to peat-marsh or ephemeral lacustrine conditions indicated by D3 and D4b. A marked environmental change is observed at 1170 cm, when a shallow, neutral to slightly alkaline lake established during CIVc. This is indicated by the development of D0a and D0b in succession, and an increase in diatom content.

4.4. CV: 860–402 cm (33–17 kyr)

A warming phase of low, although significant, amplitude is characterized by declines of Ericaceae and significant increases in PG2 elements (CVa; 860–452 cm; 33–22 kyr). PG2 shows values >9% and peaks at 26–29% at 603–592 cm (27–27.5 kyr), and at 28% at 503 cm (ca. 24.2 kyr). These shifts are interpreted as a succession of short-term warmer–drier pulses. CV ends with very high values of Ericaceae, culminating between 452 and 402 cm and characterizing the cold LGM period (CVc; ca. 22–17 kyr).

The lake evolved from an ephemeral, acidic waterbody with D4b dominant (860–592 cm; ca. 33–27.5 kyr) to a slightly acidic swamp marked by a return of D4a (592–452 cm), but the overall increase in *Eunotia* and *Pinnularia* (D4b) and in emergent plant pollen elements, mainly *Aponogeton*, reflects a general tendency toward aridity. The pollen-inferred warmer–drier pulses, e.g. at 603–592 and 503 cm, coincide with the peaks of D4b taxa, or with a total disappearance of diatoms. During the LGM (CVb), the diatom concentration is extremely low to nil. D4 elements, mainly *Aulocoseira* gr. *laevissima* and

coarse *Pinnularia*, and often reduced to the most silicified parts of the valves, are found in oxidized, sandy sediments, suggesting occasional floods followed by seasonal or interannual droughts.

4.5. CVI: 402–0 cm (17–0 kyr)

During CVIa (402–200 cm, 17–4 kyr), the last deglacial warming, defined by the abrupt fall of the Ericaceae and increase in PG2 and PG3, occurred within less than a few centuries, and underwent a brief and sharp reversal, which is recorded by a return to pollen spectra close to those of the LGM, and corresponding glacial conditions. The abruptness of the transition cannot be caused by a sedimentary artifact since other proxies (e.g. magnetic properties and diatoms) do not show such a clear-cut change. After this event (17–15 kyr), the Ericaceae decrease steadily. The deglacial warming resumes with the establishment of a wooded grassland or woodland/grassland mosaic. Common features appear between CVI and previous cycles, in that the maximum representation of open vegetation elements (PG2) leads that of the middle-low elevation trees (PG3) above 200 cm (CVIb), consistent with the development of a riparian forest. A further peak in montane forest (PG4) is missing to obtain the full cycle model. That may be due to the present climatic conditions and/or the strong human impact reflected by very high Gramineae values in the uppermost part of the sequence.

A circumneutral swamp is re-established during stage CIVa. But the relative abundance of D4b, the absence of diatoms in several levels, the abundance of emergent plants, and the occurrence of oxidized fine sand layers reflect very shallow water, and even short-term episodes of desiccation. The increased proportions of D4b elements, and the subsequent disappearance of diatoms, then coincide with the establishment of a Cyperaceae peat-marsh. Besides a peak of D0a taxa at 166 cm and the reappearance of D4 species above 33 cm, the uppermost part of the sequence is devoid of diatoms.

5. Discussion and conclusions

The Tritrivakely sequence provides a new, long, nearly continuous paleoenvironmental record from

the southern tropics, based on pollen and diatom analyses. The terrestrial vegetation reflects changes in the regional climate. In the high-altitude Tritrivakely area, it primarily responded to variations in temperature. The terrestrial pollen record includes six cold/warm cycles of various amplitude, which were tentatively correlated with the Vostok temperature record, suggesting that the sequence represents about 150 kyr. The good consistency observed between major terrestrial pollen zones, changes in lithofacies, aquatic and emergent plant pollen, and diatom assemblages indicate that the hydrology of the small Lake Tritrivakely has also been controlled by the regional climate. The diatom record can be partly explained by the orbitally-induced changes in precipitation and seasonal contrasts as suggested by our age model.

To the extent that our age model for periods older than 41 kyr is correct, the following remarks arise from the Tritrivakely record.

1. The pollen-inferred cold phases at ca. 143, 115–110, 94–88, 75–69, 55–45, and 22–17 kyr (C0, CIIc–CIIIc and CVb; Fig. 8) are periods of high summer insolation at 20°S due to the geometry of orbital precession, which should result in high summer precipitation. Conversely, the initial stage of the warm phases (CIa–CVIa), which is reflected by the development of wooded grassland (PG2) ending around 125, 103, 83, 60, and 5 kyr, correlates with periods of low local summer insolation (Fig. 8) and thus, presumably, low monsoon precipitation. The subsequent development of woodland and montane forest (PG3 and PG4) requires wetter conditions than fits with the phases of increasing summer insolation, when *P* increases and *E* is still low. The cold period around 35 kyr, which is preceded and followed by warm pulses, is an exception, as it occurs during a period of low summer insolation. It may be considered to be the last of the short-duration cold events that punctuate zone CIV.
2. Pollen-inferred warming phases CIa to CIVa and CVIa coincide with periods of hydrological/nutrient deficit in the lake (lake status b; Fig. 8). This is consistent with low summer insolation and low *P* suggested by the age model, and with increasing evaporation rate (*E*) induced by warming.
3. The overall trend from a relatively deep lake to a

shallow waterbody from the sequence base to the top observed along the core can be partly accounted for by the basin infilling. This desiccation trend can also be enhanced by an overall, long-term decrease in monsoonal precipitation related to the decreasing amplitude of the precessional cycle in summer insolation after 100 kyr. Such a trend towards aridity appears in the south monsoon precipitation time series inferred from sedimentary variables in the Pretoria Salt Pan (South Africa; 30°S), which spans the last 200 kyr (Partridge et al., 1997).

4. Prior to 100 kyr, the amplitude of the precessional cycles in seasonal solar radiation is very large (Fig. 8). Changes in the lake hydrological balance and in terrestrial vegetation evolved in parallel. The highest water/nutrient levels observed in the whole record (prior to 143 and around 115 kyr), and subsequent low stands (around 130–125 and 105 kyr.) fit pollen-inferred cold and warm phases, respectively. The lake behavior can be explained by orbitally-induced changes in summer precipitation suggested by the age model, the lake response being enhanced by changes in evaporation rate related to temperature fluctuations.
5. After 100 kyr, periods of low ($P - E$) led to an ephemeral waterbody, a peat-marsh or even a wet soil at the core site. The waterbody became more and more sensitive to any hydrological deficit because of the basin infilling. The diatom record provides evidence for changes in ($P - E$) that are not recorded by pollen data. Such dry periods occurred around 96–93, 87–84, 75–72, 62–50, 42–39, 33–28, 22–17, and after 7 kyr. Besides the interval 60–50 kyr where the signal is unclear due to generally dry conditions and a low sedimentation rate, low stands occur apparently every 12–10 kyr, and also fit cold stages, such as the LGM. As proposed for the LGM (Gasse and Van Campo, 1998), summer monsoon rainfall during phases of high summer insolation may be not heavy enough to compensate for the large evaporation–evapotranspiration losses during warm summers and dry winters, while the ericoid vegetation tolerates these harsh conditions. Positive ($P - E$) re-established when summer insolation was in an increasing or decreasing phase.
6. The Triterivakely record also suggests that the cold stage around 140 kyr (glacial stage 6) was much

wetter than the LGM. The Pretoria Salt Pan rainfall reconstruction shows a rainfall amount of about 750 mm yr⁻¹ around 140 kyr, but very low precipitation (about 600 mm yr⁻¹) at 45–38 kyr and the minimum for the whole sequence (about 560 mm yr⁻¹) around 20 kyr (Partridge et al., 1997). In agreement with coupled ocean–atmosphere climate models (Bush and Philander, 1998), the Triterivakely and the Pretoria Salt Pan records show that the global hydrological cycle was considerably reduced during the LGM in the southern African tropics, compared with the previous glacial stage.

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