

## Late Holocene Vegetational Change in Central Madagascar

DAVID A. BURNEY

*Department of Zoology, Duke University, Durham, North Carolina 27706*

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A sediment core from Lake Kavitaha, central Madagascar, provides a stratigraphic record of changes in pollen spectra and charcoal influx in the late Holocene. The earliest pollen spectra distantly resemble the modern pollen rain of a vegetational mosaic in northern Madagascar, although results of principal component analysis suggest no close modern analog. At about 1300 yr B.P., a marked rise in charcoal is followed by a decline in pollen of woody taxa, culminating in a change to grass-dominated pollen spectra within about 4 centuries. Pollen of woody taxa decline below 15% of total terrestrial pollen and spores beginning about 600 yr B.P. The influx of charcoal from graminoid sources remains high until recent centuries. The late Holocene changes in vegetation and fire ecology at the site were approximately contemporaneous with the latest  $^{14}\text{C}$  dates for the extinct megafauna and the earliest dates for human occupation. © 1987 University of Washington.

### INTRODUCTION

At least 17 species of mammals, birds, and reptiles became extinct in Madagascar during the late Holocene, leaving the island devoid of indigenous terrestrial vertebrates with a body weight  $>12$  kg (Burney *et al.*, 1986). Plants of the Ericaceae family, however, "subfossil fauna," as it is often called, disappeared within the last millennium, the cause of this major extinction event is unknown (Dewar, 1984; MacPhee *et al.*, 1985). The century-long debate concerning these extinctions has generated few testable hypotheses. Jull (1899) blamed catastrophic geological events, but no evidence for an island-wide event has ever been found. Decary (1930) and Mahé and Sourdat (1972) have suggested that climatic changes could have caused some extinctions, particularly in the arid southwest, where geomorphological and pedological evidence for climatic changes has been described.

The human-agency hypothesis is the only widely held explanation for the extinction of the island's megafauna. Evidence from archaeology (Battistini *et al.*, 1963; Vérin, 1975; Dewar, 1984) and linguistics (Vérin *et al.*, 1970; Dahl, 1951) sug-

gests that human settlement began in Madagascar about 1500 yr B.P. Since remains of extinct megafauna have been recovered from sites dated as recently as  $980 \pm 200$  yr B.P. (Mahé and Sourdat, 1972) and  $830 \pm 100$  yr B.P. (R. E. Dewar, unpublished data), human settlement may have antedated at least some of the extinctions. Perrier de la Bathie (1921, 1936) and Humbert (1927, 1949, 1955) argued from floristic distributions and limited plant macrofossil evidence (two undated sites) that Cenozoic Madagascar was entirely covered by essentially "climax" forest prior to the arrival of humans. According to their hypothesis, the extinctions were one consequence of the loss of this continuous forest cover, which they believed occurred as a result of the felling and burning activities of the first human inhabitants.

Koechlin *et al.*, (1974) and Dewar (1984) question the "continuous forest" idea in relation to prehistoric Madagascar and the corollary that human disruption of this ecosystem caused the megafaunal extinctions. Koechlin points out many examples of floristic distributions that seem to support the opposite conclusion, namely, that many forest remnants appear to have existed in isolation from other forests for a much

longer period than the 2 millennia or less that man is thought to have been in Madagascar. Dewar suggests that a forest-woodland-grassland mosaic was more likely in the central highlands during the Holocene than any sort of continuous formation.

In partial corroboration of this idea, recently published early Holocene pollen spectra from  $^{14}\text{C}$ -dated horizons in the fossil beds of Ampasambazimba suggest that a mosaic of swamp forest, woodland, bushland, and grassland existed close to this important vertebrate fossil site about 7000–8000 yr B.P. (MacPhee *et al.*, 1985). Likewise, a Holocene pollen and charcoal record from Lake Tritrivakely in central Madagascar (Burney, 1987) indicates that grassland and ericoid bushland alternated dominance at this site during the early and middle Holocene, with an increase in diversity of wooded savanna and riparian taxa after 4000 yr B.P.

The fact remains that 72% of the modern land surface of Madagascar is covered by depauperate grassland (Guichon, 1960). On all sides of this vast monotonous grassland which sprawls across the center of the island, there exist highly diverse forests, woodlands, and bushlands with high endemism, but no large animals. Yet most of the sites containing abundant remains of the subfossil megafauna, many but not all of which were almost certainly arboreal in habit, are located in the grasslands of the center and the bushland thickets of the south. The notion that vegetation change and the late Holocene extinctions are somehow connected is thus very attractive.

The purpose of this study is to test the hypothesis that the late Holocene extinction of the megafauna in Madagascar was temporally associated with vegetation changes. Evidence from fossil pollen and charcoal in the sediments of a core collected from a small lake in central Madagascar is examined. The stratigraphic record covers the period of time from just prior to the earliest-dated archaeological

sites on the island up to the present day, including the 5 centuries or more in which the radiocarbon record suggests that man and megafauna may have coexisted in Madagascar.

## METHODS

Lake Kavitaha (12.5 ha) is a small lava-barrier lake immediately below the outlet of Lake Itasy (Fig. 1). Kavitaha empties directly into the Lily River, and lies 13 km southeast of Ampasambazimba, a Holocene fossil site containing abundant remains of the extinct megafauna. Lake Kavitaha is 650 m  $\times$  200 m, with a maximum depth of 16 m near the south end.

A sediment core 3.5 m in length was collected with a 6.25-cm-diameter piston corer in a water depth of 6.2 m over a large flat-bottomed terrace near the north end of the lake. Essentially 100% recovery was achieved on all three pipe sections.

Pollen residues were prepared according to Faegri and Iversen (1975). Samples were handled quantitatively according to the method described by Kendall (1969), and the pollen residues were mounted in liquid glycerine and counted at 400 $\times$  and 1000 $\times$  oil immersion on a Leitz Orthoplan microscope with Nomarsky interference and po-

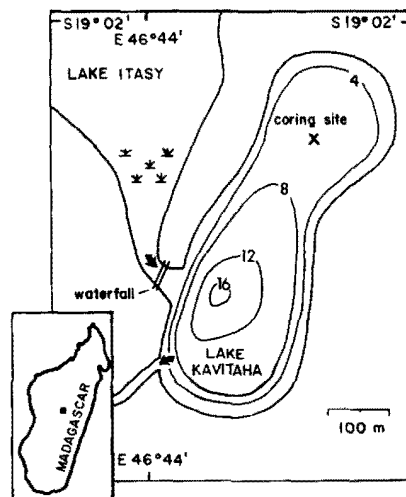


FIG. 1. Map showing the location and bathymetry of Lake Kavitaha, Madagascar. Depths in meters.

larization. Identifications were made by comparing fossil material with reference slides from the collection housed in the Duke University Zoology Department and by referring to the published illustrations and descriptions of the pollen morphology of certain families of plants indigenous to Madagascar (Senesse, 1980; Straka, 1966, 1980; Straka and Friedrich, 1983; Straka and Simon, 1967; Straka *et al.*, 1967). Charcoal was measured optically in pollen slides by the method described by Swain (1973, 1980). Loss-on-ignition data were obtained by using the two-step ignition method of Dean (1974).

Pollen zonation was discerned by Ward's Minimum Variance Hierarchical Cluster Analysis on a mainframe computer (SAS (Institute, Inc., 1982), a procedure in which the distance between two clusters is the sum of squares between the two clusters summed over all the variables. At each generation, the within-cluster sum of squares is minimized over all partitions obtainable by merging two clusters from the previous generation. This method tends to join clusters with approximately the same number of observations. All identified terrestrial taxa and distinctive unknown types were included in this analysis.

Principal component analysis of the pollen data was used to compare fossil and modern pollen spectra. All major terrestrial taxa were used in this analysis, and minor taxa were grouped by physiognomic category for inclusion.

## RESULTS

The top 1.5 m of sediment consists of olivaceous black gyttja (5Y 2.5/1) with abundant plant cuticles and diatoms. Silts and clays are present in variable amounts. Loss-on-ignition data show highly variable organic matter content (mean 25%, SD = 8.2%). At 149.5 cm below the sediment surface there is a 0.5-cm light-grayish-brown gritty band (2.5Y 6/2) with abundant subrounded silt grains. Between 1.5 and 2.9 m, sediments are black (N 2/0) with fewer

clastics and higher organic matter content (mean 41%, SD = 5.0%). From 2.9 m to the bottom of the core at 3.5 m, the amount of organic matter increases (mean 61%, SD = 4.6%), and clastic materials are very scarce. Carbonates are rare throughout the core, never exceeding 4% of dry weight and <1% at most levels.

Four  $^{14}\text{C}$  dates (Beta-14856, 15528, 14855, and 11730:  $670 \pm 80$ ,  $960 \pm 90$ ,  $1400 \pm 80$ , and  $1490 \pm 60$  yr B.P., respectively) have been used to construct a chronology (Fig. 2). The core provides a record of stratigraphic changes over about the last 1500 radiocarbon years. All dates have been corrected for isotopic fractionation. Plotting these dates against sediment depth shows that a straight line can be drawn through three of the four points, with the fourth within  $1.6 \times$  standard error from this line. This line intersects the point of origin for sediment depth and radiocarbon years.

Interpolation from this line might suggest that the slightly discordant date (if the sedimentation rate were indeed constant) perhaps should be revised from 1400 to about 1300 yr B.P. Correction of this date

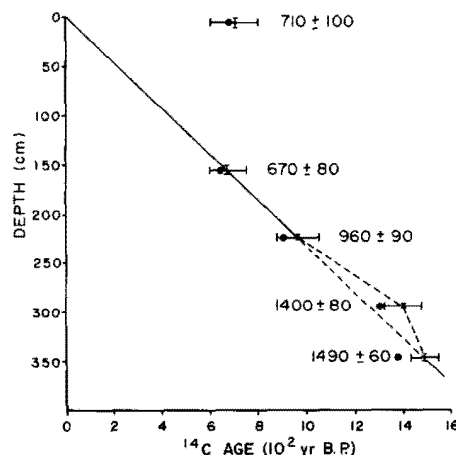


FIG. 2. Radiocarbon chronology of the Lake Kavutaha core. Several lines of evidence (see text) suggest that sedimentation increased briefly at about 1400–1300 yr B.P. Modern sediments apparently contain some old carbon, probably reworked from wetland agriculture along the shore. Solid circles indicate ages calibrated from Stuiver and Pearson (1986).

with the most recent calibration curve from the tree-ring chronology (Stuiver and Pearson, 1986), after subtracting 30 yr from each date for Southern Hemisphere  $^{14}\text{C}$  discrepancies noted by Lerman *et al.* (1970) and Vogel *et al.* (1986), also yields a revised date of 1300 yr B.P. However, if all the dates are thus calibrated, the resulting plot of sediment depth vs age (solid circles in Fig. 2) produces a line almost identical to the uncalibrated dates, but slightly offset at the lower end in the direction of younger dates. A plausible explanation for the slight discordancy of this date is that a temporary increase in sedimentation rate and release of old carbon from the soil may have accompanied the sudden increase in charcoal noted at this level. This explanation is supported by the charcoal and pollen evidence presented below. The best fit with the radiocarbon data suggests a sedimentation rate for most of the period represented by the core of  $2.3 \text{ mm yr}^{-1}$  or  $4.3 \text{ yr cm}^{-1}$ , with the caveat that influx calculations derived from this parameter may be less reli-

able in the vicinity of 2.8–2.9 m, since sedimentation may have briefly accelerated around this level.

A fifth  $^{14}\text{C}$  date (Beta-11729), from the topmost 10 cm of the core, was rejected from the chronology. Abundant rounded silt grains and poorly preserved pollen grains in the top few centimeters of this section suggest that the anomalous age of  $710 \pm 100 \text{ yr B.P.}$  resulted from erosion and subsequent redeposition of older organic sediments situated on the lake margin. Wetland cultivation along the shore has produced a series of small, recent-looking gullies.

### Charcoal

Charcoal influx data for the Kavitaha core are shown in Figure 3. Also shown in this figure is a ratio developed in the North American studies of Swain (1980) and Cwynar (1978). The ratio is formed by dividing the projected area (number of grid squares) of charcoal by the number of terrestrial pollen grains seen in the same tran-

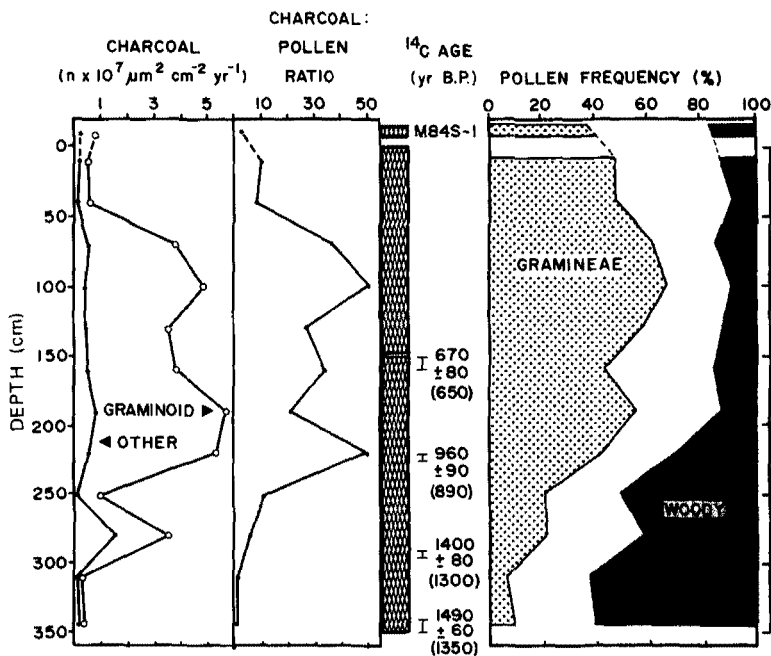


FIG. 3. Charcoal and synoptic pollen diagram for the Lake Kavitaha core. Dates in parentheses are calibrated ages from Stuiver and Pearson (1986) without SD's.

sects. The intent is to use the rate of pollen deposition as a check for sedimentation-rate changes that may occur when there is a sudden increase in burning. A plot of these ratio values for the Kavitaha core, on the appropriate scale, shows remarkably good agreement with charcoal influx values at all levels; an exception is at about 2.8 m, where the radiocarbon evidence likewise suggests a sedimentation anomaly.

The data from both approaches indicate the same pronounced trend: prior to about 1400 yr B.P. (perhaps as late as about 1300 yr B.P., as explained previously), charcoal was present in the sediment at relatively low values. Rather suddenly, it appears, charcoal values rise to some of the highest observed in the entire period covered by the core. For the next 1000 yr or more, charcoal values remain relatively high. Only within the last 2 or 3 centuries have charcoal levels in the sediments returned to approximately those of the earliest period.

Progress has been made in recent years (Goldberg, 1986; Griffin and Goldberg, 1975, 1979; Smith *et al.*, 1973) in distinguishing various types of microscopic charcoal. By referring to SEM pictorial atlases of African Gramineae (Palmer and Tucker, 1981, 1983; Palmer *et al.*, 1985) and Cyperaceae (Haines and Lye, 1983), I classified charcoal fragments into two categories, graminoid and "other." Very small pieces of wood charcoal are difficult to distinguish by light microscopy from amorphous charcoal produced by burning tree leaves, plant resins, and other sources, and so all non-graminoid pieces were classified as "other." Analyses of charcoal produced in modern Malagasy environments (Burney, 1986) indicates that, as might be expected, grasslands produce primarily graminoid charcoal and extensive forests almost exclusively "other" (nongraminoid) charcoal. Wooded grasslands, bushlands, and other mixed ecotypes produce intermediate ratios of the two.

Prior to the first great increase in char-

coal influx, about twice as much graminoid charcoal as "other" charcoal was being deposited in the sediment. At the time of the charcoal increase (about 1300 yr B.P.) both types show a marked increase, followed in a few centuries by a decline in the "other" category. Graminoids remain high until the last few centuries.

### Pollen Analysis

The synoptic pollen data (on the far right in Fig. 3) summarize the changes in terrestrial pollen spectra at the site concurrent with the changes in charcoal influx during about the last 1500 yr. For the two levels prior to the rise in charcoal, grasses compose 9.7 and 6.4% of the pollen spectra and woody taxa 60.6 and 62.1%. Woody taxa decline slightly and grass percentages double in the next few samples, until, at the level dated  $960 \pm 90$  yr B.P., Gramineae have increased to 42.7% and woody taxa have decreased to 29.3%. From then until the present, Gramineae pollen values have ranged between about 40 and 70%. By  $670 \pm 80$  yr B.P. woody taxa declined to 15.6%.

The topmost sample (which is connected to the other values by dashed lines) is a surface sample scooped from the sediment-water interface at the coring site in order to get a pollen spectrum from the late 20th century A.D. This is the only pollen spectrum containing exotic tree pollen types introduced by European settlers to Madagascar about a century ago (*Pinus* and *Eucalyptus*). These have been excluded from the woody taxa percentage.

There are two distinct pollen zones in the Kavitaha core (Fig. 4). Prior to 1000 yr B.P. (Zone I), the pollen spectra include some tree taxa, such as *Celtis*, *Trema*, *Zizyphus*, *Eugenia*, *Uapaca*, *Ilex*, *Podocarpus*, and several Moraceae types, including *Ficus*. In Zone II, beginning with the level dated  $960 \pm 90$  yr B.P., a decline of these tree-pollen types began, and from  $670 \pm 80$  yr B.P. until the present century, most appear

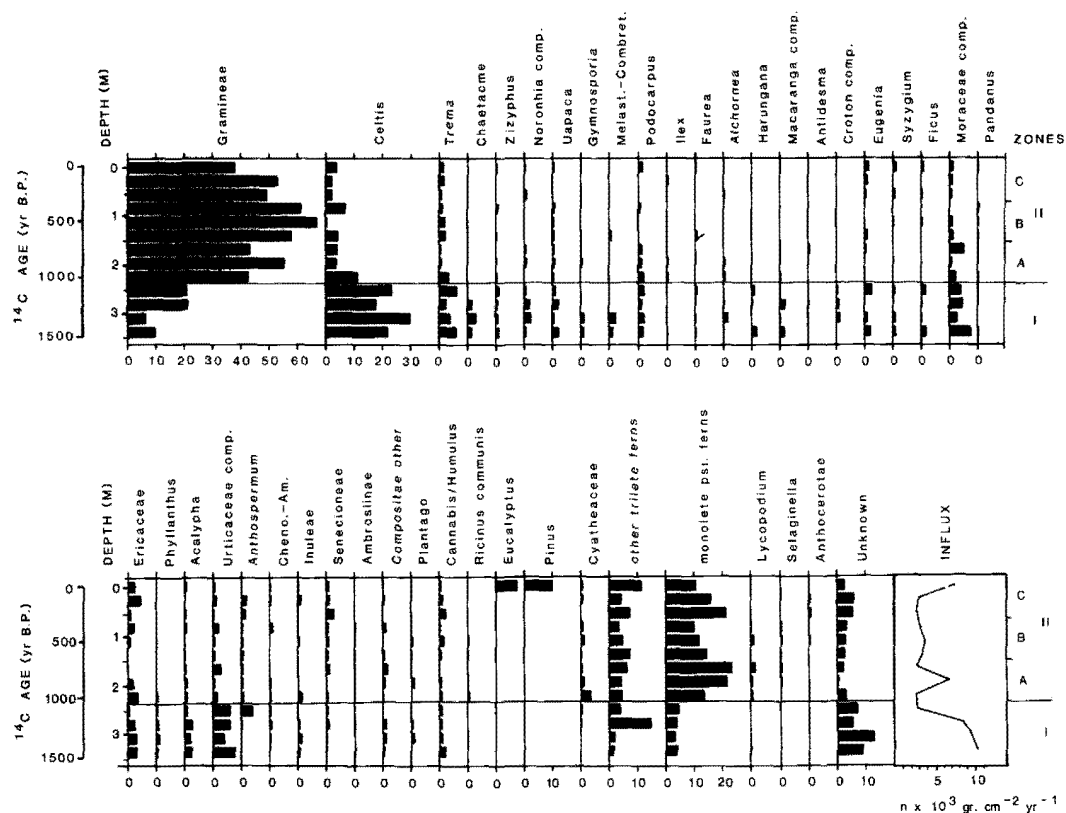


FIG. 4. Lake Kavitaha terrestrial pollen and spore diagram. About 300–600 grains were counted at each level. Thirty-three trace taxa are not shown, but were included in the pollen sum. Aquatic and paludal types (not shown) were excluded from the percentage calculations. Influx (lower right) calculated from total terrestrial pollen sum.

as a trace (<2%) only and are absent at some levels.

*Celtis* and *Trema* are by far the most numerically significant woody taxa in Zone I, ranging from 9 to 25% and 2.5 to 6%, respectively. The three Malagasy species of the former are primarily found in alluvial environments, and would therefore tend to be overrepresented in lake sediments. *Celtis gomphophylla* Bak. occurs along rivers of the central region at present (Leroy, 1952). *Trema orientalis* Bl. (= *T. guineensis* Ficalho), a very widespread and variable species in Madagascar, is characteristic of forest edges, disturbed forests, and pioneer communities (Koechlin *et al.*, 1974). Eggeling and Dale (1951, pp. 438–440) note that it is “a fast-growing,

light-demanding tree. . . . It is very short-lived. . . . A very common species in secondary forest and on forest edges, regenerating profusely in felling gaps, etc. especially on bare soil.” The other species in this genus in Madagascar, *T. humbertii* J.-F. Ler., is less widespread, but does occur in the center and southwest of the island in dry woodlands on soils derived from crystalline rocks. Its adaptation to dry seasonal environments is demonstrated by the fact that it has been collected on the Mahafaly plateau (Perrier No. 4409), the driest part of the island.

The major tree taxa can hardly be taken as evidence of the dense forest cover hypothesized by early botanists for the pre-settlement late Holocene, but the area may

have already been under human influence by 1500 yr B.P. However, a pollen diagram from another central Madagascar site, covering the entire Holocene, shows that the earliest pollen spectra from Kavitaha are almost identical to spectra from that site for the period about 4000–1200 yr B.P. (Burney, 1987). This comparison suggests that the earliest spectra from Kavitaha reflect presettlement conditions.

Many of the other woody taxa occurring at lower percentages in the lowest levels of the Kavitaha core are likewise associated with open uplands or riparian conditions (Koechlin *et al.*, 1974). *Zizyphus*, *Gymnosporia*, and *Chaetacme* are small trees or shrubs found on forest edge or in wooded grasslands. *Syzygium* grows in riparian habitats throughout Madagascar, including areas where grassland completely dominates the area away from the river banks and lake shores where it primarily occurs. *Croton* and most of the Combretaceae are dry-adapted trees and shrubs of open woodlands and wooded grasslands of the western region, but there are enough exceptions to cast doubt on their value as indicator species in the present analysis. In particular, the Melastomataceae, which are difficult to distinguish from the Combretaceae and have therefore been grouped with the latter, as is often done by palynologists, do not conform to this pattern. *Eugenia* is a diverse and ubiquitous genus in Madagascar, with species in nearly every terrestrial habitat. *Podocarpus* and *Ilex* are characteristic of montane forests and woodlands, but these pollen types disperse over long distances in East Africa (Hamilton, 1982) and are not useful in trace amounts as firm indicators of the character of nearby vegetation. Likewise *Faurea*, Urticaceae, *Alchornea*, and *Phyllanthus* suggest that some forest or woodland was present, but how much and how near the site is difficult to assess. The decline of Urticaceae from about 9% at 1500 yr B.P. to <1% in many samples from Zone II suggests a decline in

woody vegetation, since most species in this family grow as an understory in forests and woodlands, especially along edges and in openings (Leandri, 1965).

Some arboreal pollen types, such as Moraceae (many of which are riparian species) show the general trend only weakly. *Upaca* persists through the zonal change right up to the present. *Upaca bojeri* Baill. is a markedly fire-resistant sclerophyll tree that presently thrives in the *tapia* woodlands and wooded grasslands of the interior highlands. Although some predominantly shrub taxa, such as *Acalypha*, show the same declining trend as most trees, ericoid bushes do not conform to the trend. *Phillippia* spp. and *Agauria salicifolia* (Comm. ex Lam.) Hook. f. ex Oliv. are locally common ericoids that often survive the grass fires that are common at present in central Madagascar during the dry winter season (June–September). The Cyatheaceae, or tree ferns, show a pattern that is opposite to that of most woody taxa, being essentially absent from Zone I. Perhaps this is because they often grow as pioneers on riparian habitats from which the taller trees have been removed.

Figure 5 shows the results of a computer program used to zone the spectra from the Kavitaha core. Not surprisingly, Zones I and II are clearly delineated as the two highest-order clusters. Also, a high degree of similarity, with a second-order separa-

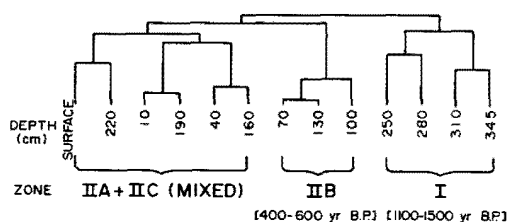


FIG. 5. Ward's Minimum Variance Hierarchical Cluster Analysis of Lake Kavitaha pollen spectra. This technique groups pollen samples according to similarity in composition. Pollen Zone I and Subzone IIB form distinct groups, but the dendrogram indicates a high degree of similarity between Subzones IIA and IIC.

tion from the rest of Zone II, is indicated for the contiguous samples at 70, 100, and 130 cm. These samples, hereafter referred to as Subzone IIB, are estimated to range in age between about 375–625 yr B.P. Subzone IIA, which comes between IIB and Zone I, is the period of decline in woody pollen taxa; many taxa represented in Zone I occur at lower levels in IIA. During IIB, however, many woody taxa fail to appear in the pollen sum, only to reappear in IIC, the period from about 300 yr B.P. until the present. Thus, the dendrogram shows mid-level similarity between IIC and IIA, with the modern surface sample from the coring site grouping most closely with the 220-cm sample, which comes just after the decline in woody taxa and dates to  $960 \pm 90$  yr B.P. It would therefore appear that the modern environment of the site represents a "recovery" of woody taxa from less-favorable conditions that had persisted for about 1000 yr. This may be merely the result of entirely local conditions arising from the occupation of one side of the lake in the present century by persons with fairly large land holdings. These properties have been managed for residential and recreational use, with the consequence that cattle and wildfires have been largely excluded and the growth of indigenous woody plants encouraged.

Prehistoric plant introductions and ruderals are an interesting feature of the pollen spectra. *Cannabis/Humulus* and *Plantago* pollen occur frequently in the spectra, but it is not clear whether these are early introductions or indigenous ruderals. They could have been introduced prior to actual settlement on the island by earlier sea voyagers (Vavilov, 1949). *Ricinus communis* L., which was probably introduced from Africa (Candolle, 1885), appears in the pollen spectra for the first time about 1000 yr B.P., and its increasing frequency in IIB perhaps 4 centuries later, along with an increase in Compositae and a decline in woody taxa, suggests a possible

increase in sedentary agriculture about this time (about 625 yr B.P.).

### Principal Component Analysis

Analyses have been completed for modern pollen spectra collected from 13 lakes and bogs in northern, eastern, and central Madagascar. A comparison has been made between these data and the phytogeography of the pollen source areas (Burney, 1986). In order to make some statistical comparisons between modern and fossil pollen spectra, these modern pollen data have been merged with pollen results from the Kavitaha core and the early Holocene pollen spectra published previously (MacPhee *et al.*, 1985) from Ampasambazimba. Principal component analysis (SAS Institute, Inc., 1982) was performed on the pollen percentages. Major terrestrial taxa were entered individually, and minor terrestrial taxa were entered under general categories such as "woody," "herbaceous," and "variable life form." The program was run under three different criteria for defining "major" and "minor": (1) individually entering all taxa that occurred in any one sample at 5% or more, (2) the same but at 2%, and (3) individually entering any taxon with a mean for all samples  $>1\%$ . Because 2 yielded a list of taxa that contained about twice as many variables as observations, a statistically undesirable condition for PCA, it was rejected. Criteria 1 and 3 yielded very similar lists of taxa, with the first four principle components explaining 67 and 68% of the variance, respectively. Factor loadings and eigenvalues for criterion 3 are shown in Table 1. No strong correspondence was observed between any of the axes and a simple environmental variable, although p.c. 1 shows a general "woody vs Gramineae" trend. Since a cumulative eigenvalue of 90% is not reached until p.c. 8, an arbitrary cutoff of four axes was chosen for use in the bivariate plots of pairwise combinations of principle components shown in Figure 6. Inter-



TABLE 1. FACTOR LOADINGS FROM PRINCIPAL COMPONENT ANALYSIS OF FOSSIL AND MODERN POLLEN SPECTRA

Variable	Eigenvectors			
	Prin 1	Prin 2	Prin 3	Prin 4
<i>Celtis</i>	0.406	-0.151	0.172	-0.134
<i>Trema</i>	0.370	-0.174	0.256	-0.058
<i>Eugenia</i>	0.134	0.215	-0.506	0.256
<i>Podocarpus</i>	0.091	-0.036	0.120	-0.011
Moraceae	0.374	-0.081	-0.055	0.015
Ericaceae	-0.110	-0.063	-0.168	-0.650
Cyatheaceae	-0.092	0.418	0.300	-0.023
Other woody taxa <sup>a</sup>	0.325	0.401	-0.112	0.072
Urticaceae	0.396	-0.158	0.191	-0.127
Compositae <sup>b</sup>	-0.114	0.288	-0.185	-0.234
Other terr. herbs <sup>c</sup>	0.118	-0.116	-0.166	0.530
Gramineae	-0.314	-0.345	-0.015	0.246
Variable life form <sup>d</sup>	0.321	0.290	-0.190	-0.007
Trilete ferns	-0.014	0.033	0.391	0.192
Monolet ferns <sup>e</sup>	-0.082	0.208	0.376	0.179
Other lower plants <sup>f</sup>	-0.100	0.426	0.260	0.018
Eigenvalue	4.5	2.6	2.3	1.5
% Variance explained	28.3	16.2	14.4	9.2
Cumulative %	28.3	44.5	58.9	68.1

<sup>a</sup> *Zizyphus*, *Noronhia*, *Ilex*, *Uapaca*, and 60 other less prevalent pollen types from trees, shrubs, and woody vines. Each taxon in this group has a mean occurrence for all samples <1%.

<sup>b</sup> Excludes *Brachylaena*, a tree composite placed with woody taxa.

<sup>c</sup> *Anthospermum*, Chenopodiaceae—Amaranthaceae, *Restio*, *Plantago*, Periplocaceae, Labiatae, Aizoaceae, *Crassula*, and *Kalanchoe*.

<sup>d</sup> Anacardiaceae, Acanthaceae, *Pachypodium*, *Euphorbia*, Passifloraceae, Pedaliaceae, Papilionoideae, Solanaceae, Rubiaceae, and *Phyllanthus*.

<sup>e</sup> Psilate types only.

<sup>f</sup> *Lycopodium*, *Selaginella*, Anthocerotae, Davalliaceae, and Polypodiaceae.

esting features of these plots concern the relation between the fossil and modern spectra and among various subgroups of these two data sets:

(1) The early Holocene pollen spectra from Ampasambazimba form a distinct cluster on all plots, which implies that no modern analog has been found for these spectra and that they are very similar to each other despite being separated by about 700 radiocarbon years.

(2) The Kavitaha core Zone I spectra cluster loosely on p.c. axes 2 vs 1, 3 vs 1, and 4 vs 1 and are quite far from any modern spectra on these plots. This is entirely a result of the high factor scores for

these samples on PC1. In the other three plots they are scattered over the diagram, with some samples in proximity to various modern wooded grassland and shrub grassland spectra from the central part of the island. The broad scatter of these samples on most plots suggests that rapid changes in the vegetation may have been occurring during Zone I (about 1500–1000 yr B.P.).

(3) On none of the six plots do Ampasambazimba or Kavitaha Zone I spectra cluster with the modern spectra from humid forests (Perinet Reserve and Montagne d'Ambre), although these two modern spectra cluster together with wide separation from other modern and fossil

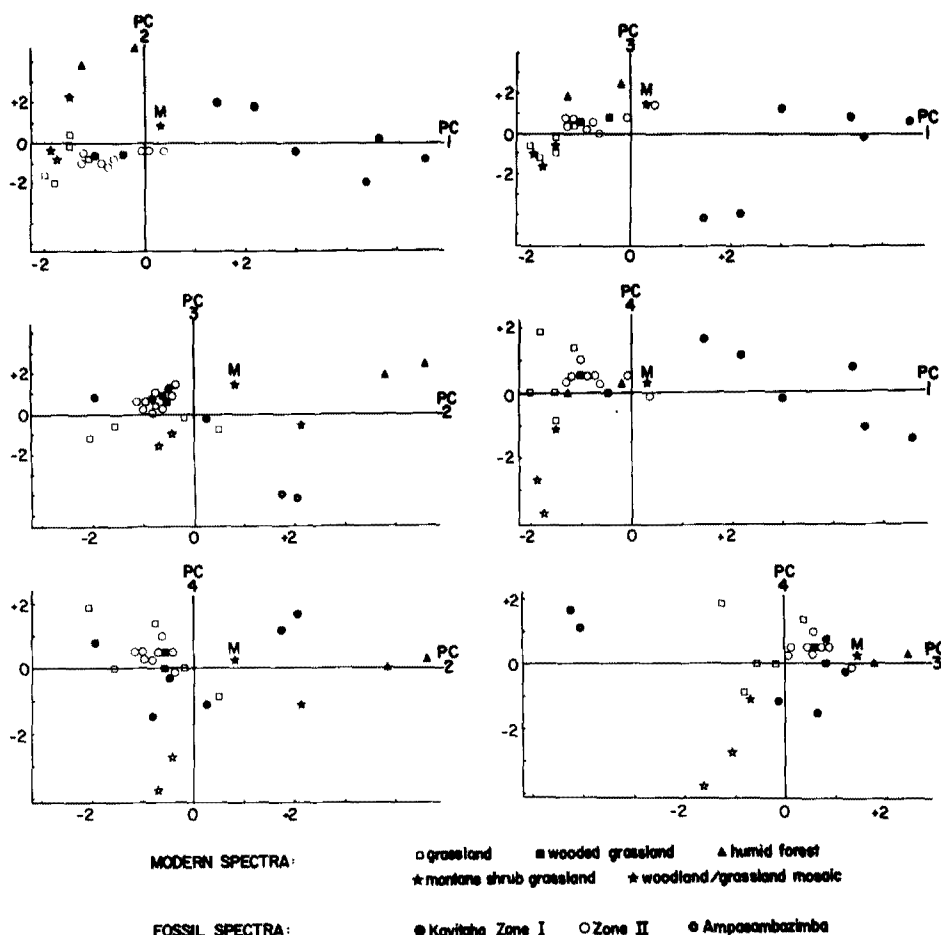


FIG. 6. PCA clustering of modern and fossil pollen spectra from Madagascar. Bivariate plots of pairwise combinations of the first four axes suggest that the modern spectrum from Lake Mahery (M) is the most similar to fossil spectra that predate the present millennium. However, no close analog has been found.

spectra on most plots. Contrary to the view of Humbert and Perrier de la Bathie cited earlier, the pollen data suggest no great similarity between the presettlement formations of the Itasy region (the Ampasambazimba early Holocene spectra) and the closed forest formations investigated.

(4) In five of the six plots, the pollen spectrum from Lake Mahery near Antsiranana (Diego-Suarez) was the closest outlier to the Kavitaha Zone I and Ampasambazimba fossil spectra. On the one exceptional plot (4 vs 3), it is still the closest to some of the Kavitaha Zone I spectra.

(5) In five of the six plots, the 220-cm

sample from the Kavitaha core (the earliest spectrum in Zone II) clusters very near the L. Mahery spectrum. This is the  $960 \pm 90$  yr B.P. sample that marks the decline of the Zone I formation.

It thus appears from the principal component analysis submitted that no close modern analogs have been found for Kavitaha Zone I, but that the closest is Lake Mahery in northern Madagascar.

Rain forest and montane forest habitats that were sampled generally lacked pollen of *Celtis*, *Trema*, and many of the other important tree taxa from Kavitaha. These pollen types occur as traces in many

modern spectra from the interior where grasslands and cultivation now predominate. The modern spectrum from Lake Mahery has the highest percentages of these taxa of any modern sample, although they are only about half the *Celtis* and *Trema* percentages in the earliest spectra from Kavitaha. The area around Mahery is predominantly grassland, with patches of open woodland on the rolling uplands, swamp forest around the lake, and ecotones containing bushes, vines, pteridophytes, and tree saplings. Flat uplands are predominantly grassed, with scattered shrubs and trees. The vegetation is physiognomically varied, with most of the large trees and dense woody growth in locations favored by wet soil, shelter from wind or fire, or a combination of these factors. Human population density in the vicinity is low, with economic activity centered around small-scale farming and pastoralism.

### DISCUSSION

The ideas developed in this study concerning the possible nature of late Holocene environments in central Madagascar bear comparison to the types of vegetation that exist over a wide area in comparable latitudes on the African continent. The relatively open *miombo* woodlands constitute the largest single vegetation type in southern Africa (Trapnell and Langdale-Brown, 1962). Grasses in these woodlands often catch fire, ordinarily with little or no damage to the woodlands, but Trapnell (1959) has shown that the trees can be destroyed by regular late-season burning. Rangeland managers in eastern and southern Africa have demonstrated that a vegetation composed of grasses, shrubs, and trees, whether in a coarse- or fine-grained mosaic, is generally in a state of flux with respect to species composition and prevailing physiognomy. A rapidly shifting balance often exists between the vegetation elements that depends, to a great extent, on the timing and frequency

of fires (Pratt and Gwynne, 1977). Modern ranchers and traditional pastoralists have long capitalized on this fact in order to facilitate the rapid spread of grassland in bush and woodland areas.

Based on these observations from Africa, if the environment of Kavitaha Zone I was an open mosaic somewhat similar to the modern environment around Lake Mahery, the closest spectral analog, then a sudden increase in the background level of fires (previously caused by lightning and volcanism) could favor the rapid expansion of grassland. This is especially plausible if the environment were becoming more arid in the late Holocene, as is believed to be the case in Africa and South America (Livingstone and Van der Hammen, 1978). It is not possible to distinguish in our results between human-induced and climatically induced causes for the increasing charcoal influx of the late Holocene.

As Dewar (1984) points out, the "mosiac" idea is generally more compatible with the kind of sudden, drastic environmental changes that could have led to the transformation of the interior of the island (and perhaps a megafaunal extinction event) than is the classic "continuous forest" idea. There is abundant empirical evidence from many tropical locales that a closed humid forest is, under normal circumstances, not very flammable (Phillips, 1974; Richards, 1952). Tropical forests do not generally accumulate a thick litter layer, because of the high moisture content and subsequent rapid bacterial decay of dead plant material. The thin litter that does cover the forest floor is shaded throughout the day in a dense forest, so it seldom dries out enough to catch fire easily. More-open savanna formations, however, generally have ideal conditions for the accumulation of dry litter. Empirical evidence for the importance of this distinction can be seen in the common case in which a grass fire reaches the edge of a

tropical forest: ordinarily the fire will burn only a short distance into the shrubby ecotone, and then it will go out underneath the big trees. In many cases the effect of repeated fires of this type is for the forest to retreat very gradually along the affected margin (Phillips, 1974).

If the late Holocene climate of central Madagascar suddenly became extremely arid, the balance could have shifted against large tracts of forest in marginal areas so that they were eliminated by fires and replaced by grassland. The present highly seasonal character of the precipitation in the Itasy region also points to the feasibility of changing the vegetation with well-timed fires. One of the more compelling reasons to believe the classic notion of a continuous, dense forest in the Itasy region during preanthropogenic times was that annual precipitation in recent years has ranged between 1750 and 1900 mm. However, a critical fact that has been generally unstressed is that the dry season is 7 months long, with only 10–11% of the precipitation falling between April and October (Ravet, 1952; Donque, 1972). One can thus imagine that a fire set (by humans or otherwise) under suitable fuel and humidity conditions could have burned, in the absence of large tracts of closed humid forest or such modern firebreaks as roads and plowed fields, over a very large area.

Discussion of environmental change in prehistoric Madagascar must for the present remain highly speculative. The geographic and temporal limitations of the present study preclude any more definitive interpretation of the data. One of the most serious limitations is that the Kavitaha core does not reach back far enough in time. By 1500 yr B.P., the radiocarbon age of the oldest sample, humans may have already affected the environment. This could mean that the open character of the presumably presettlement environment was merely a reflection of early disturbance. This problem could also be invoked to explain

the fact that some charcoal does occur in the sediments from this period. However, in a related study (Burney, 1986), I present charcoal data from cores recently taken in Madagascar that have been radiocarbon dated to as early as  $35,750 \pm 1360$  yr B.P. (Beta-14853). These show very high charcoal values during the late Pleistocene. An exceptionally complete Holocene record from Lake Tritrivakely near Betafo in central Madagascar shows that charcoal levels were relatively high in the early Holocene, declined to low levels about 4000 yr B.P. and then rose again very rapidly to levels similar to those of the earlier period about 1200 yr B.P. This was presumably at the time of the arrival of humans in this mountainous area, about 150 km south of the Itasy region.

The role of climatic change cannot be assessed from the Kavitaha core. It is conceivable that the seemingly severe impact of human arrival may in fact be a coincidence of the arrival of man at a time when the vegetation of Madagascar was under climatic stress. Firmer conclusions await more detailed pollen and diatom analysis of longer cores already collected. Climatic cycles of the glacial and interglacial intervals could prove to be as significant in explaining vegetation distributions and evolutionary patterns in Madagascar as they have elsewhere in the tropics and throughout the world. The Lake Kavitaha core demonstrates, however, that late Holocene vegetation changes at the site were contemporaneous with an increase in fire frequency or intensity. These changes, likewise, are approximately contemporaneous with the latest  $^{14}\text{C}$  dates for some of the extinct megafauna and the earliest dates for human occupation.

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