

CLIMATE CHANGE AND FIRE ECOLOGY AS FACTORS IN THE QUATERNARY BIOGEOGRAPHY OF MADAGASCAR

David A. BURNEY

Department of Biological Sciences, Fordham University, Bronx, NY 10458 U.S.A.

ABSTRACT.- Palynological studies throughout Madagascar have demonstrated the importance of Quaternary climate variation and fire ecology in determining the character of prehuman vegetation in Madagascar. Although rain forest may have persisted along the eastern escarpment throughout the Cenozoic, dynamic shifts have occurred in other areas, forcing the biota of dry woodland, grassland, montane, and semi-desert regions to accommodate changes in temperature, precipitation, and seasonality. Some highland and western regions were influenced by drought and fire long before any known human inputs, and this is reflected in plant and animal adaptations and ranges. The probable effect of burning by humans has been to increase fire frequency and to spread pyrogenic communities into areas previously too wet or too dry to ordinarily support a natural fire regime. The emerging synthesis regarding presettlement vegetation and subsequent human-caused changes helps clarify some of the formerly puzzling aspects of species distributions.

KEY-WORDS.- Paleobiogeography, Palynology, Paleoecology, Climate change, Fire

RESUME.- Les recherches palynologiques à Madagascar ont montré l'importance de la variation du climat au Quaternaire et de l'écologie des feux pour déterminer le caractère de la végétation préhistorique de la Grande Île. Bien que la forêt dense humide ait pu persister le long de la côte est pendant tout le Cénozoïque, les changements dynamiques survenus dans d'autres régions, ont amené les milieux de forêt sèche, savanicole, montagnard et des régions semi-désertiques à s'adapter aux changements de température, de précipitation et de saisonnalité. Quelques aires des hauts plateaux et des régions de l'ouest ont été soumises à l'influence de la sécheresse et des feux bien avant l'influence de l'homme ce qui se traduit dans les adaptations et la distribution des plantes et des animaux. L'effet probable des feux humains a été d'accroître la fréquence du feu et de les étendre à des aires auparavant trop humides ou trop sèches pour supporter normalement un régime de feu naturel. La synthèse concernant la végétation avant l'arrivée de l'homme et les changements qu'il a entraînés, aide à clarifier certaines distributions d'espèces restées énigmatiques.

MOTS-CLES.- Paléobiogéographie, Palynologie, Paléoécologie, Changements de climat, Feu

INTRODUCTION

There has been an understandable tendency for biogeographers working in Madagascar to focus on historical factors operating on two quite different timescales. The island's isolation represents a profound influence on a scale of millions of years. Today, however, one sees everywhere in Madagascar the consequences of factors that have operated in a much more recent time frame -- that of human interaction with the biota in the last two millennia.

What of those events influencing the biogeography of Madagascar that function on intermediate temporal scales? Specifically, what roles have Quaternary climate change and other prehuman ecological variation played in Madagascar?

Studies throughout the world have demonstrated the importance of glacial-interglacial climate cycles on scales of thousands to hundreds of thousands of years. Other forms of ecological change, manifesting themselves on a wide range of temporal and spatial scales could also be considered, and this paper will address one of these - fire, a topic with obvious relevance to Madagascar.

Biogeographers have not talked much about these factors in the context of Madagascar because so little is known about their role there. Paleoecological research (reviewed in BURNEY, in press,a) has in recent years dispelled some mysteries regarding Madagascar's past, only to reveal others. Thinking about Madagascar as a dynamic biotic phenomenon that may always be changing on several temporal scales can have profound impact on how we interpret the island's paleobiogeography. Let us consider first, what sorts of empirical evidence there might be in the biostratigraphic record of the late Quaternary for significant environmental changes even before colonization by *Homo sapiens*, and second, what significance any observed trends of change might have for understanding the biogeographic patterns we observe today.

SITES AND METHODS

There are now about two dozen sites throughout Madagascar for which radiometrically-dated paleoecological information has been published or is in preparation. The majority of these studies have been in the central highlands, but information is also available from the SW, NW, N and E. We still have no results from the extreme S and SE, or the NE coast.

What kinds of relevant data have been collected? Dated stratigraphies have been produced for fossil pollen and spores, microscopic charcoal particles, and diatom frustules. Coupled with many of these microfossil studies have been parallel investigations of subfossil faunal remains, plant macrofossils, sedimentological parameters, and human artifacts. More recently, high-resolution information has begun to accumulate from laminated sediments of deep crater lakes as well as from speleothems, and from tree rings.

RESULTS AND DISCUSSION

THE EVIDENCE FOR PREHUMAN ENVIRONMENTAL CHANGE

I wish to point out some key trends in these data that pertain to Quaternary paleobiogeography. The first of these relates to the mode, timing, and extent of climate and vegetation changes associated with Milankovich rhythms, the global sequence of glacial-interglacial cycles. Global climate records from deep-sea cores, ice cores, and

terrestrial microfossil stratigraphy have made it clear that, when ice has covered higher latitudes of the Northern Hemisphere every ca. 100,000 years, there have been a large array of consequences at all latitudes (IMBRIE & IMBRIE, 1986). Scientists are now realizing the profound impact of Pleistocene glaciations for the tropics: paleoecological data from East Africa (HAMILTON, 1982), Ghana (MALEY & LIVINGSTONE, 1983), Guatemala (LEYDEN *et al.*, 1993), Panama (BUSH & COLINVAUX, 1992), Colombia (VAN DER HAMMEN, 1974), Hawaii (PORTER, 1979), New Guinea (WALKER & FLENLEY, 1979) and other tropical areas have led to estimates of depression of the mean annual temperature at the localities of 3-6° C or more during the Last Glacial Maximum (LGM). These and other authors have concluded that tropical montane vegetation belts must have been vertically displaced 900-1500 m at LGM. Unless lapse rates showed a radically different relationship to elevation during the late Pleistocene, which is not likely and for which no mechanism is known (RIND & PETEET, 1985), this means that present snow lines, timber lines, and montane vegetation zones would have extended down tropical mountains roughly a kilometer or more below present levels. If Madagascar corresponded to this apparently pan-tropical trend, the biogeographic consequences would be profound.

Evidence for such late Pleistocene downward displacements of cold-adapted vegetation zones in Madagascar (BURNEY, 1987a; STRAKA, 1993; GASSE *et al.*, 1994) suggest that the ericoid, graminoid, and composite-dominated vegetation of Madagascar's highest mountain ranges may have flourished at times during the Pleistocene down to elevations of ca. 1000 m ASL (Fig. 1). Such a cold-driven displacement of vegetation zones would have confined the island's humid forest zones to the relatively small land areas along the east coast, with only isolated patches elsewhere (*e.g.*, river valleys in the Sambirano region of the NW, Nosy-Be, and similar low-elevation humid refugia). Much of the extensive central highlands might have been unsuitable for many rain forest species at this time.

The Pleistocene glacial climates would have posed another limitation on forest vegetation, as well. Evidence from pollen, sedimentology, paleo-lake levels, and diatom stratigraphy suggest that these cooler climates were also at times very dry. A 30,000-yr diatom record from a core from the depths of Lake Alaotra (REYES, 1993), suggests that Madagascar's largest lake, located today on the western edge of the eastern rain forest zone, was completely dry for several millennia around the LGM. Sediment cores from areas of the central highlands and N dating back 30 kyr or more (BURNEY, 1987b) show that the cold-adapted ericoid heathlands and grasslands of the interior were also subject to periodic desiccation and fires.

The pollen records indicate that early Holocene warming led to the gradual replacement of ericoid vegetation in the mid-elevations, with forests developing in wetter locations along the eastern escarpment (RAKOTONDRAZAFY, 1992; STRAKA, 1993), and a rise in the level of Lake Alaotra (REYES, 1993). The drier interior and W show a different but parallel trend. As in southern African arid-to-mesic sites at similar latitudes and elevations (*e.g.* SCOTT, 1989; BURNEY *et al.*, 1994) Madagascar's climates were relatively arid in the early Holocene. Many shallow lakes and marshes were probably dry at this time (BURNEY, 1993; MATSUMOTO & BURNEY, 1994). A highland site yielding a complete record of the Holocene (BURNEY, 1987a) shows a transition from montane shrubland to a woodland-grassland mosaic that was essentially complete by ca. 7-8 kyr BP. In the mid-Holocene, this dry trend is reversed: sites in the highlands, N, W, and even the dry SW show that the period from ca. 5-3 kyr BP was the wettest time so far identified in the late Quaternary of Madagascar (BURNEY, 1987a, 1993; MATSUMOTO &

BURNEY, 1994; BURNEY, in press,a). Beginning about 3 kyr BP, and peaking between 1-2 kyr BP, very dry conditions return, with dry forests and woodlands giving way in some areas to grasslands, bushlands, and semi-desert.

Let us turn our attention for a moment to an ecological factor that often correlates in complex ways with climate change: fire. Evidence for fire in prehuman Madagascar is sufficient to dismiss any notions that fire was not a factor on the island before human arrival. This observation accords with the paleoecological evidence for prehuman fire on other tropical landmasses (e.g., CLARK, 1983; BURNEY *et al.*, 1995). The proper focus for discussion of prehuman fire belongs with the details: when, how much, in which regions and with what consequences? The prevalence of fires in the prehuman central highlands and west, and the scarcity of fires in the eastern, northern, and southwestern sites leads to two general observations (BURNEY, in press,b). First, litter conditions for fire are most favorable in areas of strong wet-dry seasonality (center and W) and least favorable in areas that are very wet (E) or very dry (S and SW) throughout the year. Second, ignition sources would have been most abundant in the central highlands, especially in the Itasy massif and Antsirabe region, where volcanic activity was prevalent in the late Pleistocene through mid-Holocene (BURNEY, 1987a,b). Both the highlands and the western region are also subject to dry-season and early wet-season lightning from powerful convection cells, a second major cause of natural fires (WRIGHT & BAILEY, 1982; PIANKA, 1992)

It thus follows, both from the paleoecological record and comparison with similar areas elsewhere in the world, that the primary and quite considerable effect of human activity on the island's fire ecology would take two forms: 1) fires in the human period are likely to have occurred with higher frequency, although individual natural fires may have often burned over larger areas (in the absence of roads and croplands to interrupt them) and with considerable intensity (owing to the longer time for litter to accumulate and the generally very dry conditions under which natural fires ignite); and, 2) the persistent, deliberate use of fire by humans to clear woody vegetation and tall grass, coupled with the introduction of exotic fire-prone species, probably has promoted the spread of pyrogenic communities and conditions to wetter and dryer areas where they would have been rare before.

BIOGEOGRAPHIC CONSEQUENCES OF ENVIRONMENTAL CHANGE IN MADAGASCAR

It is useful to ask whether the new information from paleoecological research has any explanatory power in the area of biogeography. Much remains to be worked out in the emerging regional syntheses concerning Madagascar's paleoenvironments, but it is already possible to make some testable predictions regarding the consequences of late Quaternary climate change and fire ecology for the island's biogeographic patterns. Let us first consider the potential impact of full-glacial cooling and consequent lowering of the elevational extent of the kinds of vegetation characteristic of the highest mountaintops today. This vegetation, in its most exposure-adapted form (generally from ca. 2000 m to the summits, the highest being Tsaratanana at 2876 m), is a kind of montane heathland dominated by shrubs, bushes and small trees in the Ericaceae (many species of *Philippia*, also *Erica* and *Agauria*). Also important are shrubby Compositae (Asteraceae) of such genera as *Psiadia*, *Helichrysum*, *Stoebe*, and *Stenocline*, the dwarfed gymnosperm *Podocarpus*, and several other genera of stunted woody vegetation, as well as distinctive grasses, including native bamboos (KOECHLIN *et al.*,

1974). The general biogeographic pattern is one of highly localized species-level endemism, representing variations on genera often found in all the high mountain areas of Madagascar and also on the mountains of East Africa and Réunion (GULLAUMET, 1984). In more sheltered areas at somewhat lower elevations (ca. 1800-2000 m), low woody formations often described as « lichen woodland » and « moss forest » are typical where they have not been destroyed by human encroachment. Patterns of local endemism are similar, with the tree *Symphonia* being a case in point. It has one species in Africa and South America (*S. globulifera*) and a multitude of species in the mountains of Madagascar. As with the Ericaceae and other high mountain forms, there are also species in the genus on the eastern escarpment at lower elevations (KOECHLIN *et al.*, 1974; GULLAUMET, 1984).

Modern pollen spectra from the high mountains show a dominance of Ericaceae, Compositae, Gramineae, and *Podocarpus* pollen (BURNEY, 1988). Eastern rain forest spectra, however, are dramatically different from this, because these genera, although present, share the environment with a multitude of other plant families that contribute to the pollen spectra there. It thus follows that the late Pleistocene and very early Holocene pollen spectra from sites in the 1000-2000 m range, showing essentially identical spectra to those collected from higher elevations today, indicate that the globally-observed cooling effects were also occurring in Madagascar at that time.

If that is the case, we could predict from the vast area of land encompassed by the 1000 m elevational contour (Fig. 1), that this spectacular high-mountain vegetation of Madagascar represents the last remnants of a kind of vegetation that may have been widespread in the highlands during cooler times of the Pleistocene. Even if the montane heaths generally reached only the 1500 m contour, this would still greatly expand the area it covered in the highlands. Such a pattern should manifest some characteristic patterns that might be used to formulate a testable hypothesis: those high peaks and massifs of Madagascar that are linked by intervening areas of moderately high elevation (*i.e.*, > ca. 1000 m) should show more similarity in their native flora and poorly dispersed faunal elements than more isolated peaks. This is a subject worth investigation, and vicariance data for reptiles and amphibians already bears this out remarkably well. Raxworthy (*pers. comm.*) suggests that the evidence for vicariance in these taxa between the Andringitra and Ankaratra Massifs, but lack of herp vicariance between Ankaratra and Tsaratanana, suggests that heathland may indeed have extended down 500 m or more below its present level at some time, allowing dispersal between the former two, but not the latter two, which are separated by lowland areas (see Fig. 1).

If montane vegetation has been much more widespread in Madagascar in the Pleistocene, this would explain the apparent high incidence of generic and even species-level plant disjunctions between the high mountains and eastern escarpment of Madagascar, which are linked along a broad front at 1000 m contours and above. It would also suggest an explanation for the wider array of montane disjunctions in the western Indian Ocean region as well. Such formerly extensive vegetation in the cool Pleistocene highlands of Madagascar and East Africa (HAMILTON, 1982) would have formed a large « target » for migrants and accidental dispersers moving between East Africa and Madagascar and, by extension, from Madagascar to Réunion. Thus we could think of the high peaks of Madagascar, East Africa, and Réunion as « interglacial refugia, » supporting many cold-adapted, formerly widespread taxa through the warm Holocene. This idea deserves testing in Madagascar with other taxa, such as invertebrates and lichens.

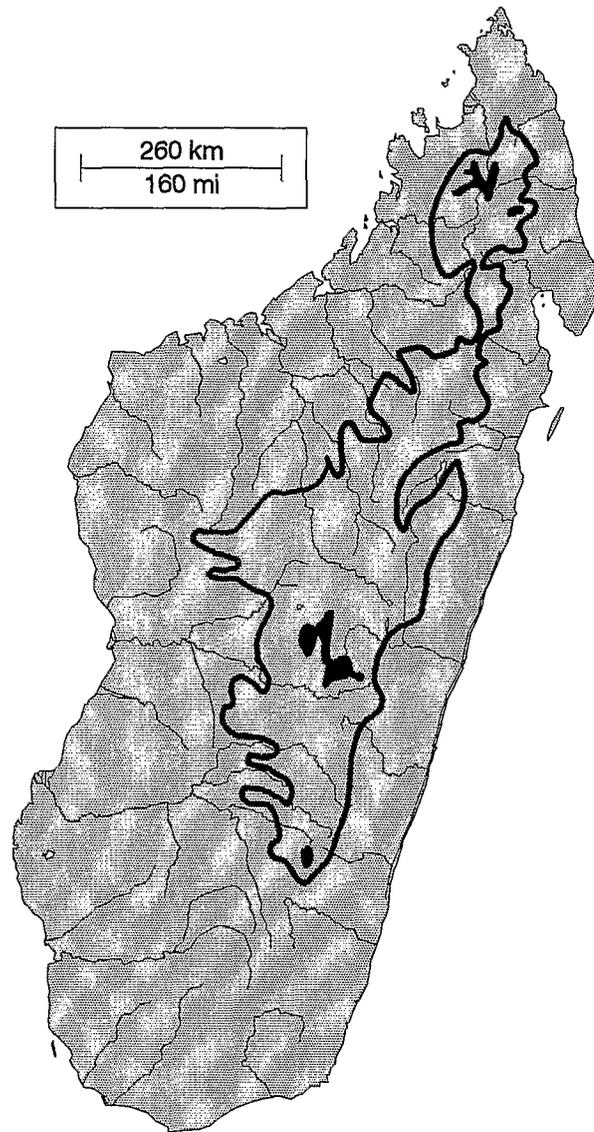


Fig. 1. Map of Madagascar showing the present distribution of montane ericoid vegetation (solid black) and the contiguous area above *ca.* 1000 m (dark outline) that is the postulated lower extent of this type of vegetation during the Last Glacial Maximum. There are also several non-contiguous areas reaching elevations > 1000 m in the southern, western, and extreme northern parts of the island.

The arid and semi-arid regions of Madagascar also show striking endemism and peculiar disjunctions. Perhaps the paleoclimatic evidence for alternate wet and dry episodes, such as those documented above for the late Pleistocene and Holocene,

could help dispel some mysteries and generate testable hypotheses. GUILLAUMET (1984), among others has remarked that it seems peculiar that the baobabs (*Adansonia*), for instance, are represented by one species in Africa, one or two in Australia, and at least eight in Madagascar, seven of them endemics. Some of these have very small ranges, others grow sympatrically in areas of the far N and SW. Similar striking diversity, narrow endemism, and peculiar disjunctions and sympatries are typical of other diverse dry-adapted groups, such as the Euphorbiaceae, which are well-represented in eastern and southern Africa but also reach remarkable diversity in western and southern Madagascar. It stands to reason that, if Madagascar has experienced many phases of dry climate interspersed by occasional wetter periods, several biogeographic trends could be predicted: arid-zone taxa would be diverse, and show a wide array of patterns of endemism and sympatry, owing to the frequent opportunities to disperse during extreme dry phases across areas otherwise too wet, and to occasional periods of severe local isolation enforced by wetter conditions. Likewise, one could predict that endemic wetland taxa might be rather rare and not particularly diverse in the western and southern regions today, but that many other species may have colonized these areas during wet phases only to become rare or locally extirpated later on as surface water dried up. Just such a pattern has been recently documented for aquatic birds in southwestern subfossil sites by GOODMAN and RAKOTOZAFY (in press). This pattern would also help explain why, among native freshwater fishes, endemism seems to be largely restricted in the W to deep crater lakes and cave ichthyofaunas, the only persistent aquatic habitats likely to retain permanent fresh water through the severe dry phases of the late Quaternary (Paul LOISELLE, pers. comm.).

Finally, let us ask whether the paleoecological information presented concerning prehuman fire ecology might tell us anything about biogeographic patterns. While it is true that there are many endemic plants in Madagascar that appear to have little or no resistance to fire, it is perhaps equally perplexing that there are a number of widespread endemic species that actually fare rather well in spite of burning activities. Among these are such familiar species as the satra palm (*Medemia* [*Bismarckia*] *nobilis*), the traveller's tree (*Ravenala madagascariensis*), the tapia (*Uapaca bojeri*) and various savanna shrubs and grasses. It is no longer so mysterious that these endemics could have evolved strategies for resisting fire, if we allow that fires might have been present to select for these features before the recent arrival of humans.

The paleoecological record shows that open vegetation types were present in prehuman central and western Madagascar and at times expanded their aerial extent in response to the frequent dry periods. If we allow for this possibility, it also could explain how many African species of grasses and other savanna plants could have reached Madagascar on their own well before human arrival. A number of grassland bird species, including two species of quail, the Madagascar Pratincole, and the Broad-billed Roller, for instance, migrate seasonally between the island and the African coast (LANGRAND, 1990). The opportunity for transfer of well-dispersed plant seeds (e.g. grasses and savanna trees and shrubs) in the gut of birds and on their feathers is sufficient to explain the presence of many of the same savanna species on both landmasses. CARLQUIST (1974) has observed that bird dispersal as a mechanism of plant propagation has been quite effective for colonizing even the most remote islands such as Hawaii, an order of magnitude more spatially isolated than Madagascar. It might be predicted that the preponderance of savanna species common to Africa and Madagascar (and not known with certainty to have been deliberately introduced by humans) may in fact be those types capable of dispersal by birds (e.g., small-seeded monocots, woody plants with edible

fruits and small seeds, and plants with clinging devices on their seeds). Such possibilities become entirely plausible if we allow for the existence of suitable open habitats for these colonizations over the last several million years.

Regarding the generally uniform and depauperate character of many interior grasslands today, we must also allow for the likelihood that their diversity has been reduced since human arrival by the postulated increase in fire frequency. Experimental and observational studies in other areas of the world show that quite different pyrogenic communities may be generated under different fire return intervals. Typically, diversity is lowest when fire frequency is highest (WRIGHT & BAILEY, 1982), as all but the most fire-resistant species are eliminated. One might also expect that, as humans spread fire into areas ordinarily too wet or too dry to burn naturally, the resulting communities would be quite species-poor, since few of the local native species are likely to have fire adaptations.

I would not be surprised to find some disagreement with some of the ideas related in this paper. I have merely attempted to suggest that, now that we have abundant empirical evidence from paleoecology showing the dynamism of the climates and prehuman ecosystems of Madagascar over various time-scales, new explanations may be proposed for some of Madagascar's biogeographic mysteries. As always, new evidence may dispel some questions, and raise many others. I will have succeeded in my task today if I have prodded biogeographers working in Madagascar to generate and test some new hypotheses, and to reconsider some old beliefs about the island that may be less compelling now that we have some applicable paleoecological data.

ACKNOWLEDGEMENTS

Work by the author and his students and collaborators described in this paper was supported primarily by the National Science Foundation (USA), NOAA Global Change Program, the National Geographic Society, and the Smithsonian Institution. This contribution was prepared with the support of NOAA Human Dimensions of Global Change grant #NA46GP0465.

REFERENCES

- BURNEY, D.A., 1987a. Pre-settlement vegetation changes at Lake Tritrivakely, Madagascar. *Palaeoecology of Africa*, 18: 357-381.
- BURNEY, D.A., 1987b. Late Quaternary stratigraphic charcoal records from Madagascar. *Quat. Res.*, 28: 274-280.
- BURNEY, D.A., 1988. Modern pollen spectra from Madagascar. *Palaeogeogr., Palaeoclimat., Palaeoecol.*, 66: 63-75.
- BURNEY, D.A., 1993. Late Holocene environmental changes in arid southwestern Madagascar. *Quat. Res.*, 40: 98-106.

- BURNEY, D.A. (in press,a). Theories and facts regarding Holocene environmental change before and after human colonization. *In*: S.M. Goodman & B.D. Patterson (eds.), *Natural and Human induced Change in Madagascar*. Smithsonian Inst., Press, Washington.
- BURNEY, D.A.(in press,b). Tropical islands as paleoecological laboratories: Gauging the consequences of human arrival. *Hum. Ecol.*
- BURNEY, D.A., G.A. BROOK & J.B. COWART, 1994. A Holocene pollen record for the Kalahari Desert of Botswana from a U-series dated speleothem. *The Holocene*, 4: 225-232.
- BURNEY, D.A., R.V. DECANDIDO, L.P. BURNEY, F.N. KOSTEL-HUGHES, T.W. STAFFORD & H.F. JAMES, 1995. A Holocene record of climate change, fire ecology and human activity from montane Flat Top Bog, Maui. *J. Paleolimnol.*, 13: 209-217.
- BUSH, M.B., & P.A. COLINVAUX, 1990. A pollen record of a complete glacial cycle from lowland Panama. *J. Vegetation Sci.*, 1: 105-118.
- CARLQUIST, S., 1974. *Island Biology*. Columbia Univ. Press, New York.
- CLARK, R.L., 1983. Pollen and charcoal evidence for the effects of Aboriginal burning on the vegetation of Australia. *Archaeol. Oceania*, 18: 32-37.
- GASSE, F., E. CORTIJO, J.-R. DISNAR, L. FERRY, E. GIBERT, C. KISSEL, F. LAGGOUN-DEFARGE, E. LALLIER-VERGES, J.-C. MISKOVSKY, B. RATSIMBAZAFY, F. RANAIVO, L. ROBISON, P. TUCHOLKA, J.-L. SAOS, A. SIFFEDINE, M. TAIEB, E. VAN CAMPO & D. WILLIAMSON, 1994. A 36 ka environmental record in the southern tropics: Lake Tritrivakely (Madagascar). *C.R. Acad. Sci. Paris*, 318: 1513-1519.
- GOODMAN, S.M., & L.M.A. RAKOTOZAFY. (in press). Bird subfossils from south-western Madagascar: Inferences about environmental change. *In*: S.M. Goodman & B.P. Patterson (eds.) *Natural and Human-induced Changes in Madagascar*. Smithsonian Inst., Press, Washington.
- GUILLAUMET, J.-L., 1984. The vegetation: An extraordinary diversity. *In*: A. Jolly *et al.*, (eds.), *Madagascar: Key Environments*. pp. 27-54. Pergamon Press, Oxford.
- HAMILTON, A.C., 1982. *Environmental History of East Africa*. Academic Press, New York.
- IMBRIE, J., & K.P. IMBRIE, 1986. *Ice Ages: Solving the Mystery*. Harvard Univ. Press, Cambridge.
- KOECHLIN, J., J.-L. GUILLAUMET & P. MORAT, 1974. *Flore et Végétation de Madagascar*. Cramer Press, Vaduz.
- LANGRAND, O., 1990. *Guide to the Birds of Madagascar*. Yale Univ. Press, New Haven.
- LEYDEN, B.W., M. BRENNER, D.A. HODELL & J.H. CURTIS, 1993. Late Pleistocene climate in the Central American lowlands. *Geophysical Monograph*, 78: 165-178.
- MALEY, J., & D.A. LIVINGSTONE, 1983. Extension d'un élément montagnard dans le sud du Ghana (Afrique de l'Ouest) au Pléistocène supérieur et à l'Holocène inférieur: premières données polliniques. *C.R. Acad. Sc. Paris*, 296: 1287-1292.
- MATSUMOTO, K., & D.A. BURNEY, 1994. Late Holocene environments at Lake Mitsinjo, northwestern Madagascar. *The Holocene*, 4: 16-24.
- PIANKA, E., 1992. Fire ecology. *Nat. Geogr. Res. Expl.*, 8: 352-371.
- PORTER, S.C., 1979. Hawaiian glacial ages. *Quat. Res.*, 12: 161-187.

- RAKOTONDRAZAFY, T., 1992: Dynamique des environnements quaternaires de Madagascar par l'étude sédimentologique, l'analyse palynologique et la diatomologie de quelques bassins lacustres. Thèse de Doctorat de 3e Cycle, Univ. Antananarivo.
- REYES, N.E., 1993. The modern diatom spectra of Madagascar and diatom-inferred Late Quaternary climatic changes in northeastern and central Madagascar. Ph.D. Dissertation, Fordham University, New York.
- RIND, D., & D. PETEET, 1985. Terrestrial conditions at the Last Glacial Maximum and CLIMAP sea-surface temperature estimates: Are they consistent? *Quat. Res.*, 24: 1-22.
- SCOTT, L., 1989. Climatic conditions in southern Africa since the Last Glacial Maximum, inferred from pollen analysis. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 70: 345-353.
- STRAKA, H., 1993. Beiträge zur Kenntnis der Vegetationsgeschichte von Madagaskar. Festschrift Zoller, *Dissertationes Botanicae*, 196: 439-449.
- VAN DER HAMMEN, T., 1974. The Pleistocene changes of vegetation and climate in tropical South America. *J. Biogeogr.*, 1: 3-26.
- WALKER, D., & J. FLENLEY, 1979. Late Quaternary history of the Enga Province of upland Papua New Guinea. *Phil. Trans. R. Soc. Lond.*, 286: 265-344.
- WRIGHT, H.A., & A.W. BAILEY, 1982. *Fire Ecology*. Wiley, New York.