



# **Extinct Madagascar**

**Picturing the  
Island's Past**

Steven M. Goodman  
and William L. Jungers  
With plates by  
Velizar Simeonovski

## Extinct Madagascar



# **Extinct Madagascar: Picturing the Island's Past**

**Steven M. Goodman and  
William L. Jungers**  
Plates by Velizar Simeonovski

The University of Chicago Press  
*Chicago and London*

**Steven M. Goodman** is the MacArthur Field Biologist at the Field Museum, Chicago, and based in Antananarivo, Madagascar. **William L. Jungers** is distinguished teaching professor and chair of anatomical sciences at Stony Brook University School of Medicine. **Velizar Simeonovski** is an artist based in Chicago who specializes in reconstructions of extinct species and prehistoric landscapes.

The University of Chicago Press, Chicago 60637  
The University of Chicago Press, Ltd., London  
© 2014 by The University of Chicago  
Plates © 2014 by Velizar Simeonovski  
All rights reserved. Published 2014.  
Printed in the United States of America

23 22 21 20 19 18 17 16 15 14 1 2 3 4 5

The University of Chicago Press wishes to acknowledge gratefully the Critical Ecosystem Partnership Fund, the Ellis Goodman Family Foundation, the Field Museum of Natural History, and Association Vahatra for their generous contributions toward the publication of *Extinct Madagascar: Picturing the Island's Past*.

ISBN-13: 978-0-226-14397-2 (cloth)  
ISBN-13: 978-0-226-15694-1 (e-book)

DOI: 10.7208/chicago/9780226156941.001.0001

#### Library of Congress Cataloging-in-Publication Data

Goodman, Steven M., author.

Extinct Madagascar: picturing the island's past / Steven M. Goodman and William L. Jungers; plates by Velizar Simeonovski.  
pages cm

Includes bibliographical references and index.

ISBN 978-0-226-14397-2 (cloth) — ISBN 978-0-226-15694-1 (e-book) 1. Fossils—Madagascar. 2. Animals—Madagascar. 3. Geology—Madagascar. 4. Plants—Madagascar. 5. Natural history—Madagascar. I. Jungers, William L., 1948– author. II. Title.

QE757.M28G664 2014

560.691—dc23

2014016894

© This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

To our families (Asmina, Hesham, Vavizara, Mboty,  
Mahery, Mandresy, Matthew, and Jocelyn)

and

In memory of Madame Berthe Rakotosamimanana  
and Robert Dewar



# Contents

FOREWORD ix

ACKNOWLEDGMENTS xi

## **PART 1: Madagascar in Perspective: Past and Present**

### **Introduction 3**

General 3

Aspects of Format 3

The Artist 5

### **Geological Time, Dates, and Radiocarbon Dating 7**

What Is a Subfossil? 9

The Types of Subfossil Sites 10

### **An Overview of the Origins, Geology, Animal Colonization, and Modern Habitats of Madagascar 16**

Madagascar in Deep Time—Isolation and Origin  
of Its Plants and Animals 16

History of Animal Colonization 18

Geography 18

Geology 22

Vegetational Patterns 23

*Humid Forest* 25

*Dry Deciduous Forest* 26

*Spiny Bush* 27

*Savanna and Grassland Formations* 30

### **A Brief History of Climatic Change on Madagascar since the Late Pleistocene 36**

### **History of Human Colonization of Madagascar 38**

Considerations of Language and Different Types  
of Introductions 38

The Human Genetic Evidence 41

Evidence of Pre-Iron Age Colonization of  
Madagascar 42

The Archaeological Record of Occupation and  
Settlement 44

Paleontological and Paleoecological

Evidence 45

Summary 46

### **Human Interactions with Now-Extinct Land Vertebrates 47**

Reptiles 47

*Tortoise* 47

Birds 47

*Elephant Birds* 47

Mammals 48

*Lemurs* 48

*Hippos* 48

### **Hypotheses on What Caused the Extinctions during the Holocene 52**

### **Extinction, Conservation, and the Future 53**

## **PART 2: Case Studies**

### **Geographical Plates**

Plate 1: Cap Sainte Marie—the Ecology of Elephant  
Birds and Their Interface with Humans 59

Plate 2: Andrahomana I—the Ecology of Extreme  
Southeastern Madagascar and a Barometer of  
Change 65

Plate 3: Andrahomana II—Evidence of a Holocene  
Tsunami in the Southern Indian Ocean and  
Predator-Prey Relations 74

Plate 4: Tsimanampetsotsa—Rapid Ecological Shifts  
in the Face of Natural Climate Change 79

Plate 5: Taolambiby—Hypotheses Associated with  
Animal Extinction and Hunting by Humans:  
Physical Evidence and Interpretation 87

Plate 6: Ankilitelo—a Deep Pit Cave and  
Inferences on Recent Ecological and Faunal  
Change 94

Plate 7: Ampoza I—Reconstruction of the Ecology  
and Fauna in a Formerly Permanent Riverine  
Habitat in the Southwest 102



- Plate 8. Ampoza II—Ecological Change in a Forest Community and Connecting Humid Forest Corridors to the Eastern Portion of the Island 107
- Plate 9: Belo sur Mer—a Window into Different Hypotheses Associated with Environmental Change: Natural versus Human-Induced 112
- Plate 10: Mananjary—the Former Estuary System of Eastern Lowland Madagascar and Some Its Faunal Elements 120
- Plate 11: Antsirabe Region—Ecology of Highland Marsh and Forest Habitats as a Measure of Change through Time 125
- Plate 12: Ampasambazimba—Reconstruction of a Montane Woodland Habitat that No Longer Occurs on the Island 133
- Plate 13: Anjohibe I—Secrets of the Past Disclosed by Careful Study of Subfossil Bone and Pollen in a Cave 144
- Plate 14: Anjohibe II—Inferences Based on Cave Remains and Aspects of the Organisms Living in the Adjacent Ecosystem 150
- Plate 15: Anjajavy—a Trapdoor Cave, Ecology of an Extinct Lemur, and Untold Extinct and Extant Biodiversity 157
- Plate 16: Ankarana I—Ecological Change of a Forest Community, a View from the Ground Up 162
- Plate 17: Ankarana II—Ecological Change of a Forest Community, a Bird's-Eye View from the Forest Canopy 168
- Plate 18: Ankarana III—Tragedy and How the Bone Remains of an Extinct Lemur Can Help Piece Together How It Lived and the Former Local Forest Ecology 173

### **Species Plates**

- Plate 19: *Cryptoprocta spelea*—an Extinct Mega-Predator and Aspects of How It May Have Lived and Hunted 177
- Plate 20: *Stephanoaetus mahery*—a Presumed Primate Specialist and Its Role in the Evolution of Behavioral Aspects of Living and Extinct Lemurs 182

REFERENCES 187

INDEX TO MALAGASY PLACE-NAMES 201

INDEX TO SCIENTIFIC NAMES 203

A COLOR GALLERY OF PLATES 1–20 FOLLOWS  
P. 132.

# Foreword

Madagascar, like Africa, is not a place for the faint-hearted. If you are prone to complain a lot, you will find lots to complain about in this challenging land, with its climate extremes, bad roads, complex bureaucracy, and, for a foreigner, just plain strangeness. It is thus no surprise that, again like Africa, the kind of *vazaha* (foreigners) who take to Madagascar tend to be extraordinary people. Steve Goodman and Bill Jungers are two of the first examples to come to mind, and their remarkable resolve, thoroughness, and persistence is in evidence on every page of this book. These are not timid people, and I have never had a boring moment with either of them.

Steve was somebody whom I did not actually run into in Madagascar until well into my many years there. I was down in one of the most arid parts of southwest Madagascar, by that remarkable hypersaline playa lake with the unpronounceable name: Tsimanampetsotsa (for understandable reasons, it often turns up in the literature with alternate spellings).

I admit to having been a little skeptical at first. Here was this scrawny, hirsute white guy, like myself, but who also had, like me, plenty of training for Madagascar in Africa. He was traveling alone, checking out sites for what would eventually be a uniquely stellar career on this island nation. Steve was a neophyte on the island and lacked the reflex that comes through experience, but he had a certain something—a determination and quickness of wit—that is essential for success *en brousse* in a place like Madagascar. I came away from our first encounter, after hearing about his optimistic agenda, thinking: *This guy will go far in Madagascar—or die trying.*

Now, a quarter century later, Steve Goodman is the name on the lips of more Malagasy people out in every remote place in Madagascar than any other *vazaha* who has anything to do with nature. In this juncture, I remember visiting one particularly remote cave in Madagascar. At the nearest village, while doing my *visite de courtoisie*—showing my papers, finding out

what sort of stuff to watch out for around there, and hiring local camp help and guides—I asked the chief if any other *vazaha* had come out to see his cave in recent years. His answer was similar to one I have heard in other remote villages: “Yes, there was one a few years ago—he looked like Jesus.” Well, it would not be much hyperbole to say that if nature in Madagascar has a savior, Steve is probably it.

But I have never really worked much with Steve, except on a few papers about interesting fossils I have found that he took an interest in, and contributions to a couple of his excellent edited volumes. By the time he was hitting full stride there, I was looking at places with interesting similarities and differences elsewhere around the world. I sincerely wish we could have worked together more, and, in fact, we are making plans for an upcoming project in one of the most remote places in western Madagascar, where I really look forward to getting to know this “unforgettable character” better.

My recollections of early Steve Goodman are scant and perhaps tattered by too many hard decades in remote places and confused by too many other stories not yet written down. Bill Jungers, on the other hand, I know a lot better; I count him among my best friends, and on reflection he has probably saved my life indirectly at least once or twice, simply by being there with his always casual and friendly demeanor—and his imposing size. Tall and stocky, Billi-be, as Malagasy often call him (“Big Bill”), is a true giant of a man in every way. Like Steve, he has a CV full of enviable accomplishments that just go on and on, decade after decade. He is also truly full of what we out here in Hawai‘i call “*Aloha*,” a kind of radiant positive attitude that overpowers the negative forces so often arrayed on all sides in our kind of complicated endeavors. He is at once both a dead-serious academic administrator and a top-notch scientist in his several chosen fields. At the same time, he is more fun to be around than anybody of his academic stature whom I

have ever shared an expedition with, and we have had plenty of adventures in essentially every quarter of Madagascar, for a very long time. I got my start with Madagascar research in the early '80s, and he had been around the island for several years by then, so I learned a lot from him. Along with Elwyn Simons, he was one of the few Americans one had any chance of running into in the wilds of Madagascar in those years. Back then, if I encountered a Caucasian in Madagascar, I was just as likely to have to resort to my pitiful recollection of Russian as English or French.

Bill and I had many rewarding and enjoyable seasons in many of the wonderful but challenging places discussed in this book: Anjohibe, Andrahomana, Ampasambazimba, Antsirabe, Belo sur Mer, and many others. We found a lot of stuff you will read about in this excellent compendium, but we also befriended many truly memorable Malagasy characters and, more cheerfully than you might imagine, shared car breakdowns, close encounters with crooks, bureaucratic obstacles, rivers with no bridge, and bad weather. One night in particular I will never forget, when an unannounced windstorm of cyclone force struck our camp near Andrahomana, and our entire crew piled into Bill's tent—the only one left standing—then spent an arduous night hugging the ground as the tent collapsed on top of us, the wind howled, a lot of rain fell, and the lightning played above the aluminum framework of his big new tent that was ruined on its first outing. You need somebody like Bill around to be able to laugh it off the next morning.

I am so thrilled to see the manuscript for this book, one that has needed to be written for years and one that will be an important source for years to come. When I saw Velizar Simeonovski's illustrations, I was green with envy, I admit. I have worked with many artists over the years, in the hope of bringing to life the prehistoric scenes that play about in my mind as I piece together the paleoecology of a place. The prehistoric landscapes visualized in this book have done a remarkable job of bringing to the eye a world that some of us live in when we work in a museum, or look through a microscope at fossil pollen grains, or even measure in a test tube, but have trouble conjuring up for the general reader. Much of what has been in the heads of people like Steve, Bill, and me for decades regarding the remarkable scenes that have passed, presumably forever, from the landscapes of this unique mini-continent is recorded now, in this

volume. When I look at the spectacular illustration of a nesting colony of *Aepyornis*, the largest bird that ever lived, at Cap Sainte Marie, or see a plant community from Ampasambazimba that I first wrote about nearly thirty years ago, describing it as a world with no modern analogue—complete with one of the most diverse primate communities that ever lived and in a mosaic of different habitat types—I realize that a lifetime of research is not necessarily wasted if it opens for others a window into a world that may have passed away but that can still be shared in a sense with fellow members of my species through the magic of art dedicated to science. For Madagascar, this book is that window. Come with us now on a unique journey, one never taken by anyone before, perhaps as close to a real time machine as you will ever get.

David A. Burney  
February 2013  
Kalaheo, Kaua'i, Hawai'i

# Acknowledgments

We would like to present our grateful thanks to numerous Malagasy colleagues, without whom our combined sixty-plus years of experience working on Madagascar would not have been possible. From the University of Antananarivo, we are indebted to different heads of the Department of Animal Biology: Prof. Sylvère Rakotofiringa, Dr. Daniel Rakotondravony, the late Prof. Olga Ramilijaona, and the current head Dr. Hanta Razafindraibe; and from the Department of Paleontology and Biological Anthropology: the late Prof. Berthe Rakotosamimanana, Dr. Armand Rasoamiamanana, and current head Dr. Haingoson Andriamialison, who provided access to specimens and helped with numerous administrative details. Madame Berthe was our guardian angel for several decades and without her aid and help, advancements in the different fields of study by numerous researchers discussed in this book would have been notably less. For providing permits in Madagascar, we thank Madagascar National Parks (ex-ANGAP), the Ministry of Energy and Mines, and the Ministry of Environment, General Direction of the Environment and Forests.

Different aspects of our work have been graciously supported by Conservation International (CABS), Critical Ecosystem Partnership Fund (CEPF), Ellis Goodman Family Foundation, E. T. Smith Fund of the Field Museum of Natural History, John D. and Catherine T. MacArthur Foundation, National Geographic Society (6637-99, 7402-03), Margot Marsh Fund, National Science Foundation (BCS-0129185, BCS-0237388, DEB-0516276, SBR-0001420), Volkswagen Foundation, and WWF-Madagascar. The Critical Ecosystem Partnership Fund is a joint initiative of l'Agence Française de Développement, Conservation International, the European Union, the Global Environment Facility, the Government of Japan, the MacArthur Foundation and the World Bank. A fundamental goal is to ensure civil society is engaged in biodiversity conservation.

We have been actively involved over the past decades in different research programs with a number of colleagues associated with subjects discussed in this book and these include Chris Brochu, David Burney, Prithijit Chatrath, the late Robert Dewar, John Flynn, Jörg Ganzhorn, Laurie Godfrey, Mark Hamrick, Helen James, David Krause, Olivier Langrand, Pierre Lemelin, Pete Lowry, Kathleen Muldoon, the late Césaire Rabenoro, Chantal Radimilahy, Jean-Gervais Rafamantanantsoa, Lydia Raharivony, Marie Jeanne Raherilalao, Jean-Aimé Rakotoarisoa, Daniel Rakotondravony, Toussaint Rakotondrazafy, the late Berthe Rakotosamimanana, Lucien Rakotozafy, Mirya Ramarolahy, Ramilisonina, the late Gisèle Randria, Achille Raselimanana, Joelisoa Ratsirarson, Malalarisoa Razafimpahanana, Brian Richmond, Yves Rumpler, Karen Samonds, George Schatz, Elwyn Simons, Voahangy Soarimalala, Natalie Vasey, Henry Wright, Roshna Wunderlich, and Anne Yoder. These different interactions have been enlightening and important in formulating different sections of this book. Many collaborations have evolved into enduring friendships.

For help with bibliographic sources, we acknowledge Christine Giannoni at the Field Museum and Henry Wright. For access to images used in this book we are grateful to Fanja Andriamialisoa, Rich Baxter, David Burney, Woody Cotterill, Don DeBlieux, Manfred Eberle, Foiben-Taosarintanin'i Madagasikara, Laurie Godfrey, Paul Godfrey, Dominique Gommery (Mission Archéologique et Paléontologique dans la Province de Mahajanga—Centre National de la Recherche Scientifique), Hesham T. Goodman, Daniel Grossman, David Haring (Duke Lemur Center Division of Fossil Primates), Chris Hildreth, Olivier Langrand, Katsumi Matsumoto, Greg Middleton, Stephen Nash, Michael Parker Pearson, Ventura Perez, Chantal Radimilahy (Institut de Civilisations / Musée d'Art et d'Archéologie), Mbolatiana Rakotoniaina (Aca-

démie Malgache), Vavizara Patrica Ranaivo, Achille P. Raselimanana, Tim Ryan, Corrie Schoeman, Harald Schütz, Voahangy Soarimalala, William T. Stanley, Mark Teaford, Alan Walker, and Thomas Wesener.

We would be remiss not to give special thanks to David Burney for writing the foreword and Velizar Simeonovski for creating the twenty plates that grace this book. The insights of Velizar in the reconstruction of the different animals found in these plates, his openness to modify and adjust the images, and his friendly demeanor made it a delight to work with him. We also owe Herivololona Mbola Rakotondratsimba and Luci Betti-Nash a debt of gratitude for helping to prepare maps and the latter for some other charts and figures used in this volume. Malalarisoa Razafimpahanana helped in untold ways in different aspects in the completion of this project. We also offer our gratitude to Claude Allibert, William Bond, Chris Brochu, Brooke Crowley, Jack Frazier, Jörg Ganzhorn, Dominique Gommery, Owen Griffiths, Michael Parker Pearson, Chantal Radimilahy, Jean-Aimé Rakotoarisoa, Dabe Rakotonavalona, Achille Raselimanana, George Schatz, Elodie Van Lierde, Miguel Vences, and Henry Wright, all of whom provided information and ideas that have been incorporated in this book in many different manners—but we accept full responsibility for all interpretations presented here. For comments on the original book manuscript, we are grateful to Laurie Godfrey and Anne Yoder. Our friends and colleagues at the University of Chicago Press were a pleasure to work with, and we thank Christie Henry and Erin DeWitt for their help in producing this book.

Finally, we would like to thank our families for their patience and simply putting up with us. The current project was notably intensive during the northern summer of 2012 and winter of 2012–13, with early departures and long hours away from home. Our profound acknowledgments and enduring thanks to our wives, Asmina and Vavizara, and our kids, Hesham, Mboty, Mahery, Mandresy, Matt, and Jocie.

*Steve Goodman and Bill Jungers*  
July 2013

**Part 1:**

**Madagascar in  
Perspective:**

**Past and Present**



# Introduction

## General

It is important to mention at the onset that this book is not intended to be a technical summary of what we know about ecological change and animal extinction on Madagascar in recent geological history. Instead, given our own fascination in trying to understand and perhaps partially answer the question as to what happened to an extraordinary assortment of endemic Malagasy animals that no longer roam the Earth, we decided to bring to a general audience an overview of these subjects. Our own particular research interests, which accent different aspects of these questions, are presented in the text. While enormous strides have been made in the past decades to understand different facets of “what happened,” we still lack many of the critical details to properly weigh and put in balance factors induced by natural climate change versus those due to human modifications of the landscape. Critical for the latter “anthropogenic” aspect is the incomplete archaeological record of Madagascar, so that questions such as when humans originally arrived on the island remain controversial and uncertain. The complete story is like a puzzle, but several linking pieces are missing or insufficiently known to provide the complete window into what transpired. After the general opening sections in Part 1 to set the stage, Part 2 has twenty plates created by Velizar Simeonovski as centerpieces for reasonably well-known paleontological and archaeological localities. Discussing each individual plate, we unfold different pieces of the puzzle for a variety of sites and extinct species based on different sources of information. His plates, each of which acts as a separate “window into the past,” bring our narratives to life.

As we learn more about the island of Madagascar, which covers nearly 600,000 square kilometers—the size of California with a good portion of Oregon—it becomes clear that a single, unequivocal response to the question of what happened is a fleeting possibility. No panacea exists for several reasons. Given the

ecological, geological, topographical, meteorological, and cultural complexities and variation found across this massive landscape, multiple and different factors at the regional level have to be invoked to explain dramatic change during short periods of geological time, that is, on a scale of a few thousand years. As suggested by the late Robert Dewar some years back, if scientists working on Madagascar have come to understand one aspect, “it seems less and less appropriate to expect a single, uniform cause for the extinctions will be found” (83). Hence, in following this point, we suggest that an island-wide response as to what happened to the ecosystems and their constituent animals is inappropriate and implausible; there simply is no single “silver bullet.” The different biological regions and cultural aspects in various cases need to be examined individually. Many debates remain to be resolved concerning what factors are responsible for these changes. Our intent with this book has been to summarize and provide a glimpse into decades of detailed scientific studies for a general audience in order to help them discover the extraordinary island of Madagascar and appreciate all of the recent changes that have taken place.

## Aspects of Format

We have tried to write this book in a relatively non-technical style. Words and expressions are occasionally used that might not be familiar to a general audience, but at first use and sometimes deeper into the text, we have tried to explain such terms. Further, while it is important to provide a certain number of bibliographic references for critical points and information presented in the text, particularly for documentary purposes and for those wanting additional details, we have done this in a light-handed fashion. Rather than congesting the text with such citations, we have used a number system, with complete reference information at the end of the book. Finally, we have included two indexes, one to the scientific





names and another of Malagasy locality names used in the text.

We differentiate between two different types of illustrations used in this book. The term “plate” specifically refers to paintings by Velizar Simeonovski that are presented in Part 2; these twenty plates capture the different site-specific ecosystems and animals that occurred or still occur on the island. On the inside front cover is a map of the different localities for the twenty plates, providing the reader a key to their geographical position. In the text associated with these plates, different themes are discussed and considerable cross-references are made between them. In several cases, a small black-and-white figure and associated text are presented adjacent to a plate to provide a key to the identification of the animals depicted. The term “figure” refers to all of the other illustrations presented in this book. Associated with their often-complex names and considerable number of syllables, Malagasy locality names can be difficult for the non-initiated. In Figure 1, we present the placement for most localities mentioned in the text and distinguish between paleontological and archaeological sites.

Major advances have been made in the past few decades in our understanding of extinct and living animals of Madagascar. New insights are now available on their distribution, ecology, and classification (taxonomy). Given these diverse studies, various scientists maintain differing interpretations of certain types of data and, naturally, opinions vary. Hence, the systematics or classifications for different organisms presented in this book are in some cases in a state of flux. As a case in point, the giant extinct tortoises of Madagascar were classically placed in the genus *Geochelone*, with two recognized species: *Geochelone abrupta* and *Geochelone grandidieri*. Subsequently, it was proposed that these species should be placed in the genus *Dipsochelys*, and this in turn created more debate. Accordingly, a petition supported by numer-

ous scientists working on reptiles has been sent to the International Commission on Zoological Nomenclature in an effort to stabilize the taxonomy of these animals; in this case, for certain living and extinct giant tortoises, the generic name would be *Aldabrachelys*. Herein, we use this genus for the two extinct species of Madagascar, *Aldabrachelys abrupta* and *Aldabrachelys grandidieri*, as well as the extant Aldabra tortoise, *Aldabrachelys gigantea*. We have used the abbreviation “sp.” for species and “spp.” in its plural form.

### The Artist

Velizar Simeonovski is a native of Bulgaria. In 1987 he graduated from the Professional Art School of Applied Arts in Sofia, and in 1995 he received his MS in vertebrate zoology from the Sofia University (his thesis was on aspects of wild and feral cats). His current



Figure 2. Using his knowledge of animal anatomy, Velizar Simeonovski is able to reconstruct the physical appearance of extinct animals with considerable skill and precision. Here, starting with the skull of the extinct lemur *Megaladapis*, he layers on the soft tissue, and then adds the skin and fur. Aspects of coloration are largely based on artistic license, but in many cases using observations in nature. For example, virtually all of the large living primates in the world are dark. Hence, he drew upon a parallel palette of coloration for the animal reconstructed here. (Figure by Velizar Simeonovski.)

research interests are in the evolution of external mammal traits, such as spots, stripes, and different types of pelage patterns, including aspects of variation and development. Using his considerable knowledge of animal anatomy and careful observation of wild and captive animals, he has an extraordinary capacity to reconstruct and figure extinct animals. Starting with bony characters, he is able to layer on muscles and add skin and other ornamentation (Figure 2). His ability to bring his subjects to life distinguishes him from many other artists working in this domain.

In late 2002, Velizar was in contact with Tom Gnoske at the Field Museum in regard to Tom's recent discoveries on lion ecology. They formed an important bond over their common interests in Carnivora, and the following year Tom was able to organize Velizar's visit to Chicago so they could work on some joint projects. Subsequently, the word got around to scientific and exhibition members at the museum about Velizar's extraordinary talents, and he was engaged to illustrate a number of different scientific works, field guides, and general public exhibits. His work has now been incorporated into permanent museum exhibitions, as well as temporary shows around the world.

While his original training was in traditional art forms and techniques, which he used during the earlier portions of his career, he has also embraced rapidly changing digital technologies. In fact, all of the plates presented in this book are "computer art," that is, drafted and drawn on a computer. Given Velizar's profound curiosity of how the animal world functions, combined with his training in biology and unparalleled talents to create flesh from bone, his current work has helped to create a new genre of art.

# Geological Time, Dates, and Radiocarbon Dating

In this book, we focus on a very recent period of geological time, specifically the Holocene Epoch, which commenced slightly less than 12,000 years BP (see Figure 3). Most of the bone and pollen deposits discussed in this book are from the Holocene, although some are slightly older and date from the Late Pleistocene, about 40,000 years BP. These two epochs, Holocene and Pleistocene, form the period known as the Quaternary. Given that the Earth is over 4.5 billion years old, the period we are discussing is less than 0.0009 percent of its history! For a little more perspective, members of the genus *Homo*, to which we belong, evolved near the beginning of the Pleistocene approximately 2.3 million years ago in Africa, another blink of the eye in terms of deep geological time.

Scientists use several different time scales to gauge the date or period of past events. As most of the dating we employ in this book is based on radiocarbon analysis (see below), we employ the time scale known as “years before present,” which is abbreviated throughout the book as “years BP.” (The term “years BP” is equivalent to calendar years before present, or cal yr BP.) As the testing of nuclear weapons in the 1950s greatly changed the proportion of carbon isotopes in the atmosphere, the date of 1 January 1950, at the start of these activities, is used as the cutoff year of this system. Hence, using our modern calendar, a date of 150 years BP in the year 2014 is  $150 + 64$  (i.e.,  $2014 - 1950$ ) = 214 years ago.

The advent of radiocarbon techniques in the 1950s provided an important development for dating organic materials recovered from archaeological and recent paleontological sites. Carbon is found in nature in different isotope forms, with the dominant one being carbon-14 ( $^{14}\text{C}$ ). Physicists have been able to calculate with a high level of precision the rate that  $^{14}\text{C}$  degrades into its different isotopic forms. During the process of photosynthesis, when plants assimilate and fix carbon dioxide into their organic tissues, they incorporate  $^{14}\text{C}$  at levels largely equivalent to those

found in the atmosphere. As the system of photosynthesis is fundamental to most food chains, whether it involves a herbivorous animal such as a beetle or a gazelle that eats plants, carnivorous birds that consume beetles, or leopards that feed on gazelles, all have measurable levels of  $^{14}\text{C}$  in their tissues. Thus, in turn, based on the degradation of this isotope starting with the death of the plant or animal in question, the period it was living can be estimated with considerable precision. This technique—whether for wood, charcoal, or bone found at an archaeological site or a recent paleontological site—works for a variety of organisms that were alive within the past 60,000 years. Because of the manner in which  $^{14}\text{C}$  degrades, other dating techniques need to be employed for older plant and animal material.

The vast majority of dates reported in this book are from bone samples. In such cases, these dates are derived mostly from carbon isolated from the collagen portion of the bone, which includes both organic and inorganic portions. A critical step in this process is the separation of contaminated carbon, which is currently done in most labs with a special pre-treatment processing of the bone. Further, other artifacts can modify the accuracy of radiocarbon dates from chemical change or contamination, either natural or artificial. In any case, there are non-trivial technical hurdles in producing reliable dates, and not all published ones are necessarily accurate. Hence, this highlights the importance of having multiple dates from a given strata or horizon of a site that fall within the same immediate range. In cases when these are not available, other corroborative information needs to be marshaled. Further, the techniques used for radiocarbon dating pose other complications, such as how certain organisms stock or assimilate older  $^{14}\text{C}$ . Different calculations have been proposed to get around these problems, and they provide corrected estimates centered on calibrated maximum and minimum values for a given radiocarbon date. Herein

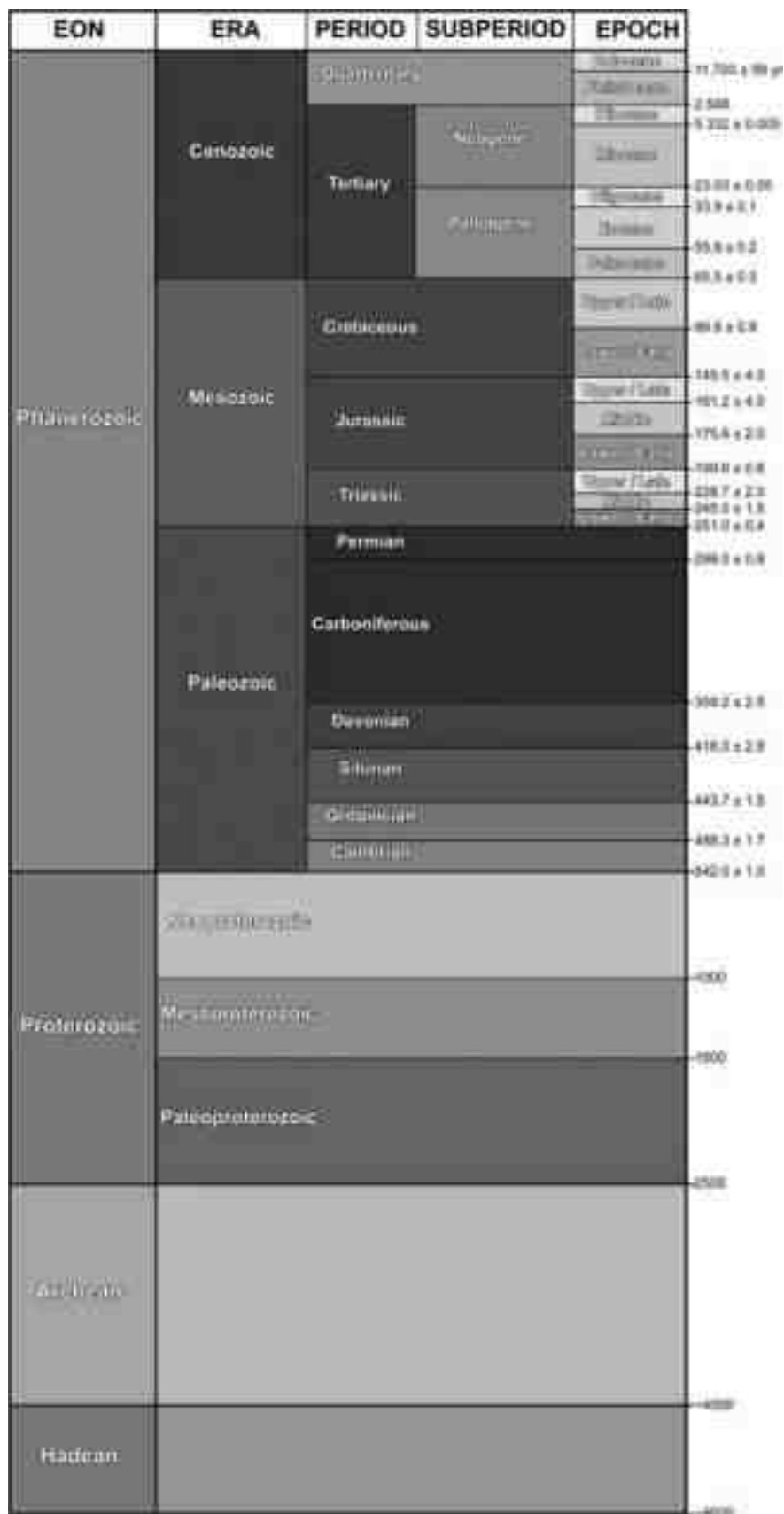


Figure 3. Divisions of geological time. Modified from U.S. Geological Survey Geologic Names Committee (366).

we also use the mean of these values, often cited in the text as “mean calibrated date,” which follows in parentheses the radiocarbon date in years BP. For example, the maximum and minimum  $^{14}\text{C}$  calibration dates for a lemur bone from a site yielded the dates of 2,360–3,450, with the mean of these values being 2,905, giving us the mean calibrated date. In virtually all cases, these different calibrated values are derived from the work of David Burney and colleagues or Brooke Crowley (54, 69).

Among plants, different systems exist when they convert light energy from the sun into chemical energy (photosynthesis) that is used to meet the plant’s nutritional needs. Photosynthesis is at the origin of all organic carbon within the tissues of a plant, invertebrates that eat plants, vertebrates that consume the invertebrates, and carnivores that feed on the vertebrates. In this regard, different aspects of the diet of an organism can be followed based on the types of carbon within them. There are three types of photosynthesis, and these three processes give rise to different carbon cycling. Without going into too much detail, plants that trap carbon dioxide based on a three-carbon compound are  $\text{C}_3$  plants, and those that use a four-carbon compound are  $\text{C}_4$  or CAM plants; the  $\text{C}_4$  or CAM types of photosynthesis are differentiated during the period (night or day) in which they fix carbon dioxide. Now an extraordinary aspect is that based on carbon isotope values from radiocarbon-dated organic material, inferences can be made as to the type of photosynthetic cycle that a given plant underwent, or for animal-eating organisms the types of plants entering into the food chain that formed the basis of their diet. In Part 2 of this book, on several occasions we discuss this type of information to provide insight into different life-history traits of extinct animals.

### What Is a Subfossil?

When most people think of a fossil, they envision some form of rock that holds traces of a formerly living organism, such as shell, bone, wood, coprolites, tracks, and so on. A number of different processes led to the creation of fossils, but one of the more common is the deposition of an organism or portions of it underwater and out of direct contact with the air; this anaerobic situation notably reduces the speed of tissue decomposition. Under certain conditions, remains can be rapidly buried in sediments, forming a mold. In such cases, the process of mineralization can commence, in which water heavily charged with

precipitates, such as silica or calcite, come out of solution, fill the mold cavity, and form a rock replicate of the organism that made up the cast.

Now subfossils, as we refer to them herein, are the physical remains of animals (bone) or plants (wood, seeds, and pollen) but without any significant degree of mineralization. In some cases, subfossil remains look like they just came out of the stew pot, in largely perfect shape and only slightly discolored, while in other cases they are fragmented and notably decomposed. The remains of animals recovered in caves can be covered and/or infiltrated with calcite from active formations, although minerals have not replaced the bone itself (Figure 4). One of the very useful assets of subfossils is that they are essentially unmodified remains of the former living organism and can yield DNA for molecular genetic studies, carbon for radiocarbon dating, or different types of stable isotopes to examine dietary preferences of the organism; the latter two aspects are discussed above. Regrettably, in some cases, the manner in which the material was deposited, or perhaps something chemical in the surrounding soils, can degrade the valuable organic molecules.

After deposition, animal carcasses, including bone and other organic material, decay, and different trans-



Figure 4. As frequently found in caves that have active dripping water and continuous deposition of minerals, subfossil remains can be covered with a calcite layer but internally still remain as bone. Here is an example of an *Archaeolemur* skull from Anjohibe, which was nicknamed “Old Crusty,” and excavated by David Burney and colleagues in 1996. In the matrix surrounding the skull, a considerable variety of bones were recovered including shrew-tenrecs (*Microgale*), carnivorans (*Galidia elegans*), bats (*Hipposideros* and *Triaenops*), native rodents (*Eliurus myoxinus*), primates (*Microcebus* and *Cheirogaleus*), and dwarf hippos (*Hippopotamus lemerlei*). (Photograph by David Burney.)

formations can happen to them over time. The study of these preservational aspects is the field known as taphonomy. Such alterations can include sedimentation and the start of the fossilization process, as described above, or a reordering of the material through tectonic action of the Earth. Because paleontologists need to pay close attention to the vertical position of material they excavate in order to decipher the periods and time sequences of the deposits (stratigraphy), very close consideration needs to be given to taphonomic processes. For example, in caves flooding can rearrange or mix deposits by stirring up and transporting the sediments containing organic remains, including bone. This is not uncommon with certain deposits on Madagascar, therefore close attention needs to be shown to this potentially confounding affect in interpreting the time sequence of remains, even in open-air sites, such as marsh and lake margin deposits (see below).

### The Types of Subfossil Sites

A number of sites on Madagascar, particularly in the west and more specifically in the southwest, have yielded numerous bones of a wide assortment of vertebrate animals (see Table 1) and pollen remains from plants (including wind-dispersed pollen). This material provides an important window into deciphering geologically recent ecological changes that have taken place on the island on one side and human-induced environmental transformations on the other. As mentioned earlier, the vast majority of these subfossil specimens date from the Holocene, but some earlier ones are from the Late Pleistocene.

Holocene subfossil sites and associated deposits can be divided into four different types (modified from 256):

- (1) *Caves found in different portions of the island:* These formations have yielded large quantities of bone, often representing numerous taxonomic groups. Bone remains at such sites can include animals that (a) have wandered through horizontal entrances into the cave or fallen through holes or “windows” in the cave ceiling (Figure 5, left); (b) small animal prey carried in by raptors to be dismantled and consumed, to feed to young at the nest, or regurgitated in the form of pellets (Figure 5, right); and (c) slightly larger prey carried in by Carnivora, deposited as uneaten portions or fecal remains. For the most part, organisms trapped in such caves are terrestrial, but in cases when aquatic ecosystems

**Table 1**

List of birds, mammals, and selected reptile remains recovered from sites on Madagascar dating from the Late Pleistocene to recent times. Extinct species are indicated with †, and the author(s) and description date are given, as well as scientific name synonyms used in the literature. (Note: In cases when a species was named in a genus in which it no longer remains, the author(s) and date are in parentheses.) For living taxa, the English common name is given. The higher taxonomy of certain groups, particularly birds (class Aves), is in a state of flux, and we have used an older classification. Introduced species are not included in this list. Bibliographic references for the different sources of information are listed after the higher taxonomic categories. In recent years, for different Malagasy vertebrate groups, a number of systematic changes have taken place and many new species have been described. This is particularly the case for lemurs, and a considerable proportion of these new taxa are not recognized here for different reasons (see 361), which includes those that were named based on molecular genetic differences rather than by their bones. We acknowledge the possibility of additional species by using the abbreviation “sp.” after selected genera.

#### Order Reptilia

Family Testudinidae (36)

†*Aldabrachelys abrupta* (A. Grandidier, 1866)

†*Aldabrachelys grandidieri* (Vaillant, 1885)

*Astrochelys radiata* radiated tortoise

Family Crocodylidae (39)

†*Voay robustus* (A. Grandidier & Vaillant, 1872)

*Crocodylus niloticus* Nile crocodile

#### Class Aves (55, 151, 276)

##### \*Order Aepyornithiformes

†Family Aepyornithidae

†*Aepyornis gracilis* Monnier, 1913

†*Aepyornis hildebrandti* Burckhardt, 1893  
syn. *Aepyornis mulleri* Milne-Edwards & A. Grandidier, 1894

†*Aepyornis maximus* I. Geoffroy-Saint-Hilaire, 1851  
syn. *Aepyornis modestus* Milne-Edwards & A. Grandidier, 1869

syn. *Aepyornis titan* Andrews, 1894

syn. *Aepyornis ingens* Milne-Edwards & A. Grandidier, 1894

†*Aepyornis medius* Milne-Edwards & A. Grandidier, 1866

syn. *Aepyornis grandidieri* Rowley, 1867

syn. *Aepyornis cursor* Milne-Edwards & A. Grandidier, 1894

syn. *Aepyornis lentus* Milne-Edwards & A. Grandidier, 1894

†*Mullerornis agilis* Milne-Edwards & A. Grandidier, 1894

†*Mullerornis betsilei* Milne-Edwards & A. Grandidier, 1894

†*Mullerornis grandis* Lamberton, 1934

\**Mullerornis rudis* Milne-Edwards & A. Grandidier,  
1894  
syn. *Flacourtia rudis* Andrews, 1894

#### Order Procellariiformes

Family Procellariidae  
*Puffinus* sp. shearwater

#### Order Pelecaniformes

Family Phalacrocoracidae  
\*? *Phalacrocorax* sp. (probably undescribed extinct species)  
*Phalacrocorax africanus* Reed Cormorant

#### Order Ardeiformes

Family Ardeidae  
*Bubulcus ibis* Cattle Egret  
*Egretta* sp. egret  
*Ardea purpurea* Purple Heron  
*Ardea cinerea* Gray Heron  
*Ardea humbloti* Humblot's Heron  
Family Ciconiidae  
*Mycteria ibis* Yellow-billed Stork  
*Anastomus lamelligerus* African Openbill Stork  
Family Threskiornithidae  
*Threskiornis bernieri* Madagascar Sacred Ibis  
*Lophotibis cristata* Madagascar Crested Ibis  
*Platalea alba* African Spoonbill  
Family Phoenicopteridae  
*Phoenicopterus ruber* Greater Flamingo  
*Phoeniconaias minor* Lesser Flamingo

#### Order Anseriformes

Family Anatidae  
\**Centronis majori* Andrews, 1897  
\**Alopochen sirabensis* (Andrews, 1897)  
syn. *Chenalopex sirabensis* Andrews, 1897  
*Dendrocygna* sp. whistling duck  
*Sarkidiornis melanotos* Knob-billed Duck  
*Anas bernieri* Bernier's Teal  
*Anas erythrorhyncha* Red-billed Teal  
*Anas melleri* Meller's Duck  
*Thalassornis leuconotus* White-backed Duck

#### Order Falconiformes

Family Accipitridae  
\**Stephanoaetus mahery* Goodman, 1994  
\*? *Aquila* sp. a (specific designation uncertain)  
\*? *Aquila* sp. b (specific designation uncertain)  
*Milvus aegyptius* Yellow-billed Kite  
*Haliaeetus vociferoides* Madagascar Fish Eagle  
*Polyboroides radiatus* Madagascar Harrier-Hawk  
*Accipiter francesii* Frances's Sparrowhawk  
*Buteo brachypterus* Madagascar Buzzard  
Family Falconidae  
*Falco newtoni* Madagascar Kestrel

#### Order Galliformes

Family Phasianidae  
*Margaroperdix madagarensis* Madagascar Partridge  
*Coturnix* sp. quail

#### Order Gruiformes

Family Mesitornithidae  
\*? *Monias* sp. (probably undescribed species)  
Family Turnicidae  
*Turnix nigricollis* Madagascar Buttonquail  
Family Rallidae  
\**Hovacrex roberti* (Andrews, 1897)  
syn. *Tribonyx roberti* Andrews, 1897  
*Rallus madagascariensis* Madagascar Rail  
*Dryolimnas cuvieri* White-throated Rail  
*Gallinula chloropus* Common Moorhen  
*Fulica cristata* Red-knobbed Coot  
*Porphyrio porphyrio* Purple Gallinule

#### Order Charadriiformes

Family Recurvirostridae  
*Himantopus himantopus* Black-winged Stilt  
Family Scolapaciidae  
*Numenius phaeopus* Whimbrel  
Family Charadriidae  
\**Vanellus madagascariensis* Goodman, 1996  
Family Laridae  
*Larus dominicanus* Kelp Gull  
*Larus cirrocephalus* Gray-headed Gull

#### Order Columbiformes

Family Pteroclididae  
*Pterocles personatus* Madagascar Sandgrouse  
Family Columbidae  
*Streptopelia picturata* Madagascar Turtle Dove

#### Order Psittaciformes

Family Psittacidae  
*Coracopsis vasa* Lesser Vasa Parrot  
*Agapornis cana* Gray-headed Lovebird

#### Order Cuculiformes

Family Cuculidae  
\**Coua berthae* Goodman & Ravoavy, 1993  
\**Coua primavea* Milne-Edwards & A. Grandidier,  
1895  
*Coua gigas* Giant Coua  
*Coua cursor* Running Coua  
*Coua cristata* Crested Coua  
*Cuculus rochii* Madagascar Lesser Cuckoo  
*Centropus toulou* Madagascar Coucal

#### Order Strigiformes

Family Tytonidae  
*Tyto alba* Barn Owl  
Family Strigidae  
*Otus rutilus* Madagascar Scops Owl  
*Ninox supercilialis* White-browed Owl  
*Asio madagascariensis* Madagascar  
Long-eared Owl

#### Order Apodiformes

Family Apodidae  
*Apus barbatus* African Black Swift



## Order Coraciiformes

- Family Alcedinidae
  - Alcedo vintsioides* Madagascar Malachite Kingfisher
- Family Meropidae
  - Merops superciliosus* Madagascar Bee-eater
- Family Upupidae
  - Upupa marginata* Madagascar Hoopoe
- Family Leptosomatidae
  - Leptosomus discolor* Madagascar Cuckoo-roller
- Family Coraciidae
  - Eurystomus glaucurus* Broad-billed Roller
- Family Brachypteraciidae
  - \**Brachypteracias langrandi* Goodman, 2000

## Order Passeriformes

- Family Alaudidae
  - Mirafra hova* Madagascar Bush Lark
- Family Hirundinidae
  - Phedina borbonica* Mascarene Martin
- Family Pycnonotidae
  - Hypsipetes madagascariensis* Madagascar Bulbul
- Family Sylviidae
  - Nesillas cf. lantzii* Lantz's Brush Warbler
- Family Bernieridae
  - Thamnornis chloropetoides* Sub-desert Tetraka
- Family Monarchidae
  - Terpsiphone mutata* Madagascar Paradise Flycatcher
- Family Zosteropidae
  - Zosterops maderaspatana* Madagascar White-eye
- Family Vangidae
  - Vanga curvirostris* Hook-billed Vanga
  - Leptopterus viridis* White-headed Vanga
  - Cyanolanius madagascarinus* Blue Vanga
  - Newtonia brunneicauda* Common Newtonia
- Family Corvidae
  - Corvus albus* Pied Crow
- Family Ploceidae
  - Ploceus sakalava* Sakalava Weaver
  - Foudia madagascariensis* Madagascar Fody

## Class Mammalia

### \*Order Bimymalagasias (250)

- \**Plesiorycteropus germainepetterae* MacPhee, 1994
- \**Plesiorycteropus madagascariensis* Filhol, 1895

### Order Afrosoricida (55, 281)

- Family Tenrecidae
  - Tenrec ecaudatus* common tenrec
  - Setifer setosus* greater hedgehog tenrec
  - Echinops telfairi* lesser hedgehog tenrec
  - Geogale aurita* large-eared tenrec
    - syn. *Cryptogale australis* Grandidier, 1928
  - \**Microgale macpheeii* Goodman, Vasey & Burney, 2007
  - Microgale brevicaudata* short-tailed shrew-tenrec
  - Microgale longicaudata* lesser long-tailed shrew-tenrec
  - Microgale cf. majori* Major's long-tailed shrew-tenrec
  - Microgale nasoloi* Nasolo's shrew-tenrec

- Microgale principula* greater long-tailed shrew-tenrec
  - syn. *Microgale decaryi* Grandidier, 1928
  - syn. *Paramicrogale decaryi* Grandidier & Petit, 1931
- Microgale pusilla* lesser shrew-tenrec

## Order Primates (52, 55, 121, 138, 281)

### Suborder Strepsirrhini E. Geoffroy, 1812

#### Infraorder Lemuriformes

- \*Family Archaeolemuridae G. Grandidier 1905
  - \**Archaeolemur edwardsi* Filhol, 1895
  - \**Archaeolemur majori* Filhol, 1895
  - \**Hadropithecus stenognathus* Lorenz von Liburnau, 1899
- \*Family Palaeopropithecidae Tattersall, 1973
  - \**Archaeoindris fontoynontii* Standing, 1909
  - \**Babakotia radofilai* Godfrey, Simons, Chatrath & Rakotosamimanana, 1990
  - \**Mesopropithecus dolichobrachion* Simons, Godfrey, Jungers, Chatrath & Ravaoarisoa, 1995
  - \**Mesopropithecus globiceps* Lamberton, 1936
  - \**Mesopropithecus pithecoideus* Standing, 1905
  - \**Palaeopropithecus ingens* G. Grandidier, 1899
  - \**Palaeopropithecus maximus* Standing, 1903
  - \**Palaeopropithecus kelyus* Gommery, Ramanivosoa, Tombomadiana-Raveloson, Randrianantenaina & Kerloc'h, 2009
- Family Lepilemuridae Stephan and Bauchot, 1965
  - Lepilemur* sp. sportive lemur
  - Lepilemur edwardsi* Milne-Edward's sportive lemur
  - Lepilemur leucopus* white-footed sportive lemur
  - Lepilemur mustelinus* weasel sportive lemur
  - Lepilemur dorsalis* gray-backed sportive lemur
  - Lepilemur septentrionalis* northern sportive lemur
  - Lepilemur ruficaudatus* red-tailed sportive lemur
- Family Daubentonidae Gray, 1863
  - \**Daubentonia robusta* Lamberton, 1934
  - Daubentonia madagascariensis* aye-aye
- Family Cheirogaleidae Gray, 1873
  - Microcebus* sp. mouse lemur
  - Microcebus griseorufus* gray-brown mouse lemur
  - Microcebus murinus* gray mouse lemur
  - Cheirogaleus* sp. dwarf lemur
  - Cheirogaleus major* greater dwarf lemur
  - Cheirogaleus medius* fat-tailed dwarf lemur
- Family Lemuridae Gray, 1821
  - \**Pachylemur insignis* Filhol, 1895
  - \**Pachylemur jullyi* G. Grandidier, 1899
  - Eulemur* sp. true lemur
  - Eulemur coronatus* crowned lemur
  - Eulemur fulvus* brown lemur
  - Eulemur mongoz* mongoose lemur
  - Hapalemur griseus* lesser bamboo lemur
  - Hapalemur simus* greater bamboo lemur
  - Lemur catta* ring-tailed lemur
  - Varecia variegata* ruffed lemur
- \*Family Megaladapidae Major, 1893
  - \**Megaladapis edwardsi* G. Grandidier, 1899
  - \**Megaladapis grandidieri* Standing, 1903
  - \**Megaladapis madagascariensis* Forsyth-Major, 1894

Family Indriidae Burnett, 1828  
*Avahi* sp. woolly lemur  
*Avahi laniger* eastern woolly lemur  
*Indri indri* indri  
*Propithecus* sp. sifaka  
*Propithecus diadema* diademed sifaka  
*Propithecus tattersalli* golden-crowned sifaka  
*Propithecus verreauxi* Verreaux's sifaka

## Order Chiroptera (55, 281, 333)

Family Pteropodidae  
*Eidolon dupreanum* Madagascar straw-colored fruit bat  
*Pteropus rufus* Madagascar flying fox  
*Rousettus madagascariensis* Madagascar rousette  
Family Hipposideridae  
<sup>†</sup>*Hipposideros besaoka* Samonds, 2007  
*Hipposideros commersoni* Commerson's leaf-nosed bat  
<sup>†</sup>*Triaenops goodmani* Samonds, 2007  
*Triaenops furculus* Trouessart's trident bat  
Family Emballonuridae  
*Paremballonura atrata* Peters' sheath-tailed bat  
*Paremballonura tiavato* rock-dwelling sheath-tailed bat  
Family Molossidae  
*Mormopterus jugularis* Peters' goblin bat  
*Mops leucostigma* Malagasy large white-bellied free-tailed bat  
*Otomops madagascariensis* Malagasy large-eared free-tailed bat  
Family Vespertilionidae  
*Myotis goudoti* Malagasy mouse-eared bat  
Family Miniopteridae  
*Miniopterus gleni* Glen's long-fingered bat

## Order Carnivora (165, 281)

Family Eupleridae  
<sup>†</sup>*Cryptoprocta spelea* G. Grandidier, 1902  
syn. *Cryptoprocta antamba* Lamberton, 1939  
*Cryptoprocta ferox* fossa  
*Fossa fossana* spotted fanaloka  
*Galidia elegans* ring-tailed vontsira  
*Galidictis grandidieri* Grandidier's vontsira  
*Mungotictis decemlineata* narrow-striped boky

## Order Artiodactyla (107, 358)

Family Hippopotamidae  
<sup>†</sup>*Hippopotamus guldbergi* Fovet, Faure & Guérin, 2011  
<sup>†</sup>*Hippopotamus laloumena* Faure & Guérin, 1990  
<sup>†</sup>*Hippopotamus lemerlei* A. Grandidier, 1868

## Order Rodentia (55, 268, 281)

Family Nesomyidae  
<sup>†</sup>*Brachytarsomys mahajambaensis* Mein, Sénégas, Gommery, Ramanivosoa, Randrianantenaina & Kerloc'h, 2010  
*Eliurus* sp. tuft-tailed rat  
*Eliurus myoxinus* western tuft-tailed rat

*Hypogeomys antimena* Malagasy giant jumping rat  
<sup>†</sup>*Hypogeomys australis* G. Grandidier, 1903  
*Macrotarsomys bastardi* western big-footed mouse  
*Macrotarsomys petteri* Petter's big-footed mouse  
<sup>†</sup>*Nesomys narindaensis* Mein, Sénégas, Gommery, Ramanivosoa, Randrianantenaina & Kerloc'h, 2010  
*Nesomys rufus* eastern red forest rat

1. According to Chris Brochu, who has extensively studied subfossil crocodile remains from Madagascar, all of the specimens he has examined of these animals are referable to *Voay robustus*. This calls into question the previous identifications presented in the literature of *Crocodylus niloticus*.

were in close proximity, different associated microorganisms (bacteria, diatoms, etc.) or bones of crocodiles, aquatic birds, and hippos can also be found, sometimes in abundance. The different cave types discussed in this book include the extensive systems of Ankarana (see Plates 16–18) and Anjohibe (see Plates 13 and 14), the deep vertical pit of Ankilitelô (see Plate 6), the smaller systems of Andrahomana (see Plates 2 and 3) and Anjajavy (see Plate 15), and rock shelters occupied by humans (84).

(2) *Marsh deposits in the lowland east and in the volcanic areas of the Central Highlands:* Several localities in formerly extensive marsh systems have been found that contain important concentrations of aquatic and forest-dwelling animals, as well as plant and other organic remains. In several cases, there is good evidence that forest ecosystems were in close proximity to these aquatic ecosystems (see, e.g., Plate 11). For the most part, animal remains excavated from such sites were probably from individuals that died of natural causes, and because of the nature of the drainage systems, their disassociated bones were on occasion concentrated in certain places. This type of site includes both shallow marsh areas with some open water and larger bodies of open water or basins associated with streams, for example, dammed by lava flows (Figure 6). Subsequent erosion and down-cutting of these dams resulted in the draining of the former water body. Examples from the Central Highlands, all above 1,100 m, are Ampasambazimba (see Plate 12) and several different deposits near Antsirabe (see Plate 11). To date, the only known bone-bearing marsh deposit from the lowland east is close to Mananjary (see Plate 10).



Figure 5. Caves on Madagascar have been an important source of subfossil remains. In numerous cases, the cave ceiling has holes of different sizes that open up to the ground surface and act as natural traps for animals that accidentally stepped in the wrong place and fell through them. Here we present an example from the ceiling of Andrahomana Cave (*left*). (Photograph by Thomas Wesener.) Frequent sources of small animal bones—particularly rodents, tenrecs, bats, and to a lesser extent birds—are the regurgitated pellets of birds of prey. Shown here is a dense deposit of bones derived from Barn Owl *Tyto alba* pellets accumulated over many years (*right*). (Photograph by Greg Middleton.)

- (3) *Western coastal marsh deposits:* Along the western coastal zone, numerous subfossil sites are known, which often occur in among different sand dunes (48). At such sites, the majority of deposited remains are probably of animals that succumbed to natural causes or were taken by predators in close vicinity to surface water and resurgent underground sources; at such localities the bone remains were then concentrated over time. The different types of vertebrates recovered at such sites can include those occurring in aquatic, woodland, and forest habitats. Further, different sorts of plants and microorganisms have been uncovered at such locations. This type of site can be complicated to excavate due to the rapid seepage of water into excavation pits that are at the level of or below the water table (Figure 7). Some of the more productive sites known to date include Lamboharana, Belo sur Mer (see Plate 9), and Itampolo. The coastal area of Cap Sainte Marie (see Plate 1) has considerable remains of elephant bird eggshell that are not necessarily associated with an old marsh system.

- (4) *Riverine deposits:* At several localities on the island, particularly in the southwest, concen-



Figure 6. An important source of subfossil material has been marsh deposits in the Central Highlands. Shown here is an excavation pit in organically rich and wet soils at Ampasambazimba, which was dammed during a past period by a lava flow. (Photograph by Laurie Godfrey.)

trated subfossil remains have been found in the sediments along deep-cut riverbanks (Figure 8). Given that in certain cases forest habitat formerly bordered these systems, bone remains of both aquatic and forest animals have been recovered from such deposits. In such cases animal bones were washed into the river system,



Figure 7. In certain deposits, the excavation of vertical holes at the level of the water table results in relentless seepage. Hence, a pumping system is needed to keep the pits as dry as possible in order to dig with careful stratigraphic control. Shown here are the excavations in 2000 of a site known as Ankilibeandry near Belo sur Mer (see Plate 9), with two participating Malagasy graduate students in and to the right of the trench. (Photograph by David Burney.)



Figure 8. Excavations of bone remains in riverine deposits, particularly in the southwest, have uncovered a considerable variety of both forest-dwelling and aquatic animals. In several known cases, the material remains in place within stratified or layered bank deposits and provides a window into different ecological or human-induced events. Shown here are David Burney and Laurie Godfrey working the bank at Taolambiby in 2004 to search for animal bone and plant remains. The name of the site translates from the Malagasy as “the place of animal bones,” and many such named localities are known in the southwestern portion of the island. (Photograph by Daniel Grossman.)

for example, following heavy rains, where they were buried within fluvial soils along sharp bends in the river or immediately below natural dams. Good examples of such deposits are known from Ampoza (see Plates 7 and 8) and Taolambiby (see Plate 5). In the southwest of the island, there are a number of localities known to local people as *taolambiby*, meaning in Malagasy “animal bones” or in a more interpretive manner “the place of animal bones.”

The subfossil sites discussed in this book can be divided into three general types:

- (1) *Paleontological*: the deposition of the bone or pollen material that was natural and without human intervention. However, this material remains as subfossil, as defined above (see “What Is a Subfossil?”). Sites treated in this book that are strictly or largely paleontological in origin include Cap Sainte Marie (see Plate 1), Tsimanampetsotsa (see Plate 4), Ankilitelô (see Plate 6), Ampoza (see Plates 7 and 8), Antsirabe (see Plate 11), Anjajavy (see Plate 15), and Ankarana (see Plates 16–18).
- (2) *Archaeological*: in such cases, humans were responsible for the deposition of the material, which can include remains of consumed food and associated refuse heaps, “kill” or “butcher” sites, and vestiges of domestic and introduced animals near occupation sites. Within this book, not one of the sites illustrated in the plates is purely archaeological in origin, but several with a clear human context are discussed, such as Taolambiby (see Plate 5).
- (3) *Mixed*: refers to sites for which during the early stages of subfossil deposition the process was natural (paleontological), and after human colonization of the zone, people left remains of animals and cultural artifacts (archaeological). In some cases, particularly during nineteenth- and twentieth-century excavations when the precise position of the bone and cultural remains were not sufficiently controlled (stratigraphy), it is often difficult to verify the direct association of certain subfossils and human artifacts. Mixed sites treated in this book include Andrahomana (see Plates 2 and 3), Taolambiby (see Plate 5), Mananjary (see Plate 10), Ampasambazimba (see Plate 12), and Anjohibe (see Plates 13 and 14).

# An Overview of the Origins, Geology, Animal Colonization, and Modern Habitats of Madagascar

For appropriate reasons, Madagascar is often referred to as an “island continent” and has a surface area of about 590,000 km<sup>2</sup>. Being the fourth largest island in the world, after Greenland (2,175,600 km<sup>2</sup>), New Guinea (785,750 km<sup>2</sup>), and Borneo (748,170 km<sup>2</sup>), Madagascar possesses numerous physical characteristics, such as mountains and rivers, that divide the island into natural sectors. These physical aspects combined with differences in weather, including temperature and rainfall, are directly related to the distribution of the island’s unique fauna and flora, as well as different adaptations to the local conditions encountered by these organisms. We will describe these aspects in more detail below, but the best place to start to explain why the island is so biologically unique, with a remarkable assortment of endemic organisms, is long ago in deep geological time.

## Madagascar in Deep Time—Isolation and Origin of Its Plants and Animals

About 165 million years ago, a massive landmass, known as Gondwana, split into two separate blocks, the first comprising Africa and South America, and the second, Madagascar, Seychelles, India, Antarctica, and Australia (2, 97) (Figure 9). During this period of active continental drift, the latter block pulled apart from the former, and a large basin was formed, the Mozambique Channel. In the early stages of the split, Madagascar and India were still attached, in a landmass often referred to as Indo-Madagascar; about 115 million years ago, this unit was fully separated from the other landmasses of Gondwana. Subsequently, about 88 million years ago, Indo-Madagascar split in two (269), with Madagascar remaining largely in its current position. The other section, which was to become the Indian subcontinent, moved north, and massive sections fell into the sea along the way, forming the granitic islands of the modern eastern Seychelles archipelago, before colliding with Eurasia and creating the Himalayas.

One crucial point to mention about the timing of the split between Indo-Madagascar and the balance of the former Gondwana continent is that 115 million years ago was a period when a considerable portion of living groups of plants and animals, such as modern mammals, had not yet evolved. Hence, their occurrence on Madagascar cannot be explained by them hitching a ride on Indo-Madagascar as it separated from the rest of Gondwana (sometimes referred to metaphorically as a “Noah’s Ark” scenario), but instead must be accounted for by some subsequent post-drift means for the ancestors of these groups to have made it to Madagascar (377). One of the most important exceptions to this is the elephant birds (family Aepyornithidae) (Figure 10; also see Plate 1), a group of large flightless birds that probably had their origins before the fragmentation of Gondwana.

The subsequent colonization by flying animals—such as bats, birds, and certain insects—or wind-dispersed pollen can be more easily imagined than non-flying organisms that would have been obliged to swim or float on vegetation (rafting) from Africa to Madagascar. Among the recent land (terrestrial and freshwater) mammals occurring on Madagascar—that is, the living and Holocene fauna, which represents something approaching 200 species—all of this diversity can be explained by seven different colonization events of the island. These seven groups of mammals, three of which are extinct (†), are represented by †Bibymalagasias (order Bibymalagasias), formerly referred to as the “Malagasy aardvark” (see Plate 14); three different extinct species of hippos, placed herein with the genus *Hippopotamus*, representing two apparent colonization events (see Plate 10); lemurs (superfamily Lemuroidea); rodents (subfamily Nesomyinae); Carnivora (family Eupleridae); and tenrecs (family Tenrecidae). For four of these groups, which are represented in the living fauna, estimations of when their ancestors colonized the island are based on molecular genetics, and the following dates

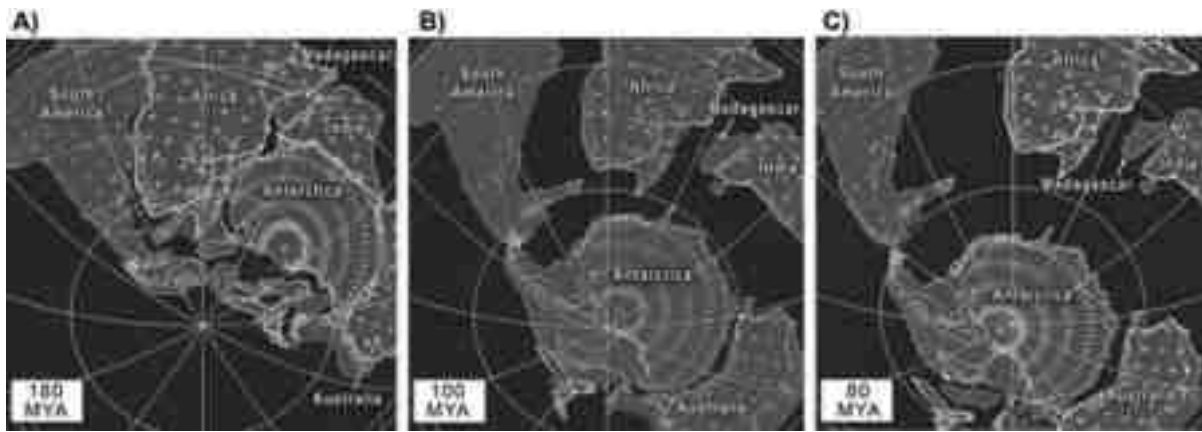


Figure 9. Over the past 150 million years, Madagascar's position relative to other landmasses has changed dramatically. About 88 million years ago, the island obtained its approximate current position, isolated in the western Indian Ocean. The sequence of major geological events leading to this were (a) the existence of the Gondwana supercontinent, which included South America, Africa, India and Madagascar (Indo-Madagascar), Antarctica, and Australia; (b) the subsequent splitting of Gondwana and the severance of land connections between, for example, Indo-Madagascar and other former portions of Gondwana; and (c) Madagascar reaching its current position and separated from India. (Modified by Luci Betti-Nash from [http://aast.my100megs.com/plate\\_tectonics/files/images.htm](http://aast.my100megs.com/plate_tectonics/files/images.htm).)

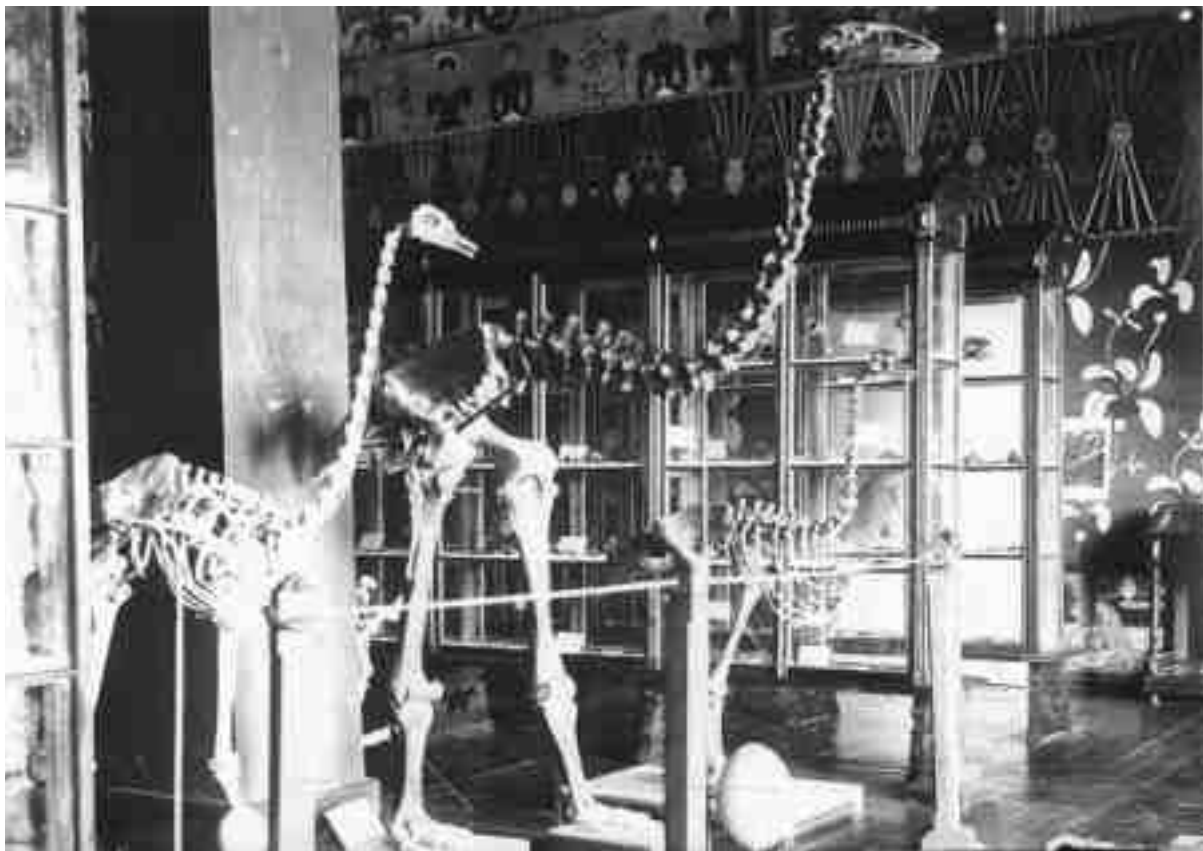


Figure 10. Photograph taken in the halls of the Académie Malgache sometime during the early portion of the twentieth century. In the foreground to the left is a mounted skeleton of a modern Ostrich *Struthio camelus*, in the middle an elephant bird of the genus *Aepyornis*, and to the far right another elephant bird of the genus *Mullerornis*. Eggs of the first two birds rest under their respective skeletons and provide a relative measure of the enormous size of the *Aepyornis* egg, which measured  $32 \times 24$  cm and based on volume held the equivalent of 150–170 chicken eggs. (Photograph from the archives of Foiben-Taosarintanin'i Madagasikara.)

have been proposed: during the Paleocene-Eocene, lemurs (77–55 million years ago); during the Eocene-Oligocene, tenrecs (47–29 million years ago); and during the Late Oligocene–Early Miocene, Carnivora (24–20 million years ago) and rodents (26–19 million years ago) (335). In other words, during the course of 58 million years, only four colonization events took place of terrestrial mammals that are still represented in the island’s living fauna; this underlines how rare such successful events were over extensive periods of geological time (377).

### History of Animal Colonization

The physical means that non-flying mammals used to make it out to Madagascar is of great interest, and at the same time of considerable debate. If we assume that these animals came from Africa, the over-water stretch they would have had to cross is the Mozambique Channel, slightly over 400 km at the narrowest point. As mentioned in the above section, the approximate colonization dates of the four living land-mammal groups (lemurs, tenrecs, carnivorans, and rodents) based on the genetic data are not during the same period, and, hence, this negates the idea that they synchronously navigated a sort of ephemeral land bridge or perhaps leap-frogged across a series of temporarily exposed islands. In any case, there is not good physical evidence that such a land connection or islands existed during the appropriate geological periods (4).

Another possibility is that non-flying organisms came across on floating vegetation or protected in hollows or holes of trees bobbing in the sea. George Gaylord Simpson presented this notion many years ago in a context of a “sweepstakes” dispersal, where animals were cast out to sea after torrential rains or tropical storms that caused flooding, and they rafted across bodies of water on floating vegetation (350). The rare “lucky” individuals subsequently washed up on some distant land and were in sufficiently good health to have successfully colonized the new area. For such an event to succeed, at least for sexually reproducing organisms, they would have had to reproduce once on the island, which translates to a colonization event by a pregnant female or a minimum of a male and female pair. As the wind direction across the Mozambique Channel is from the east to west and the current toward the south, this would have impeded movement of floating vegetation from Africa to Madagascar. However, a very interesting

and remarkable recent discovery has changed certain aspects of this scenario and its interpretation.

Using different forms of information to model ancient oceanographic patterns, Jason Ali and Matthew Huber suggested that the current east-west direction of surface water circulation is relatively recent (3). Before 20–15 million years ago and during the Miocene, the general pattern was in the opposite direction, which is to say from west to east. This would have been distinctly more conducive for the movement of floating vegetation—and the rare cast-aways they may have contained—between Africa and Madagascar. This shift during the Miocene, as compared to the modern pattern, has important bearing on how certain animal groups presumably made it to Madagascar, and only after the circulation direction changed was dispersal impeded by ocean currents. It is once again important to emphasize, given the small number of mammal groups represented in the living Malagasy fauna, that even with favorable currents, successful colonization was an extremely rare event in geological history. Based on calculations of probable current speed before the shift, during the height of the austral summer, floating objects jetted into the sea along the east African coast would have taken about 30 days to reach the west coast of Madagascar (335).

Another interesting twist in the story is that three of the four groups of modern Madagascar land mammals—lemurs, Carnivora, and tenrecs—have living species with adaptations to hibernate or reduce their metabolic systems in the form of torpor (Figure 11). Perhaps their founding ancestors did too. As explained by Peter Kappeler, under the right conditions this capacity might have allowed the ancestors of these animals to endure the long seafaring trip, presumably with little or nothing to eat or drink (213)—hence, providing a plausible mechanism for how they survived the month-long voyage.

### Geography

The island of Madagascar is naturally divided into several different geographic units. The central portion of the island, which we refer to herein as the Central Highlands, is a large elevated plateau that covers about 40 percent of the total land area of Madagascar. Generally, the 900 m elevation mark is defined as the lower limit of the Central Highlands (Figure 12), although some botanists use figures as low as 800 m. The eastern limit of the Central Highlands descends rather



Figure 11. How non-flying animals could have survived the long journey across the Mozambique Channel between Africa and Madagascar on floating vegetation is difficult to understand. Among several groups of Malagasy land mammals, such as certain lemurs, they have the ability to store significant amounts of fat that would help them through long periods of food shortage. Here, we show a lemur, *Cheirogaleus medius*, with massive tail fat. In addition, this primate is known to enter a state of dormancy (aestivate), with reduced body temperature and activity, which in turn would substantially reduce its energy expenditures and increase chances of reaching the other side in a relatively healthy state. (Photograph by Manfred Eberle.)

dramatically toward the Indian Ocean side of the island, often along a several hundred-meter escarpment, while the western side shows a more gradual reduction in elevation until the Mozambique Channel.

On the eastern side of the Central Highlands, there is a north-south-aligned mountain chain, which runs most of the length of Madagascar. In addition, in the north there is an area of appreciable elevational relief. Several large massifs on the island reach over 2,000 m, including the highest peak at 2,870 m (Tsaratanana). The eastern side of this north-south-oriented mountain chain forms the upper portions of eastern-draining watersheds, and the western side, the upper portions of western-draining watersheds. As this divide does not occur in the middle of the island, there is notable asymmetry, with about 70 percent of the island's land surface draining toward the west and into the Mozambique Channel. This in turn creates two distinct types of river systems. Most east-draining rivers abruptly descend the Central Highlands along a steep elevational gradient and in a

relatively short distance enter the Indian Ocean (Figure 13, left). In notable contrast, numerous western-drainage systems—such as the Onilahy, Mangoky, Tsiribihina, and Betsiboka—are long watercourses, and in the lower sections become wide and meandering rivers, sometimes with large deltas, before emptying into the Mozambique Channel (Figure 13, right).

These two different types of rivers have important potential effects on the dispersal of animals, specifically associated with their capacity to cross water barriers. For example, among lemurs, there are few species restricted to eastern lowland habitat (see section below, “Vegetational Patterns”), and the rivers for the most part in this portion of the island do not seem to present dispersal barriers for these animals. This is probably associated with the history of Pleistocene climatic change in this zone, specifically during periods of cooler and drier weather, when a large percentage of the lowland formations were replaced by montane vegetation (see section below, “A Brief History of Climatic Change on Madagascar since the Late Pleistocene”). Perhaps as a direct result of this, most lemur species in the east (Figure 14, left) have broad elevational ranges, with the upper limit often being higher than the headwaters of the large regional rivers. Hence, these animals are able to “cross over” river systems near their sources (150). In contrast, there is evidence that for members of the modern fauna the wider and meandering western rivers impose dispersal obstacles. In this portion of the island, numerous vertebrates have their distributions wedged between two large rivers (Figure 14, right).

Across the north-south-aligned eastern mountain range, there are pronounced climate differences between the eastern and western slopes. As most weather systems come off the Indian Ocean from a southeasterly direction, the windward side of these mountains receives notably more rainfall and has a less-marked dry season than the leeward side. The ecotone between these habitats can be very dramatic, with an 800–1,000 mm reduction in annual rainfall over about 10 km, as seen to the west of Tolagnaro (see Plate 2 for further discussion).

Another important ecological-geographical aspect is that there are several important clines set across the expansive landscape of Madagascar, which at its longest point is nearly 1,600 km and at the widest point, 570 km. Perhaps the most important of these is associated with rainfall. In the extreme northeast, on the Masoala Peninsula, annual precipitation can



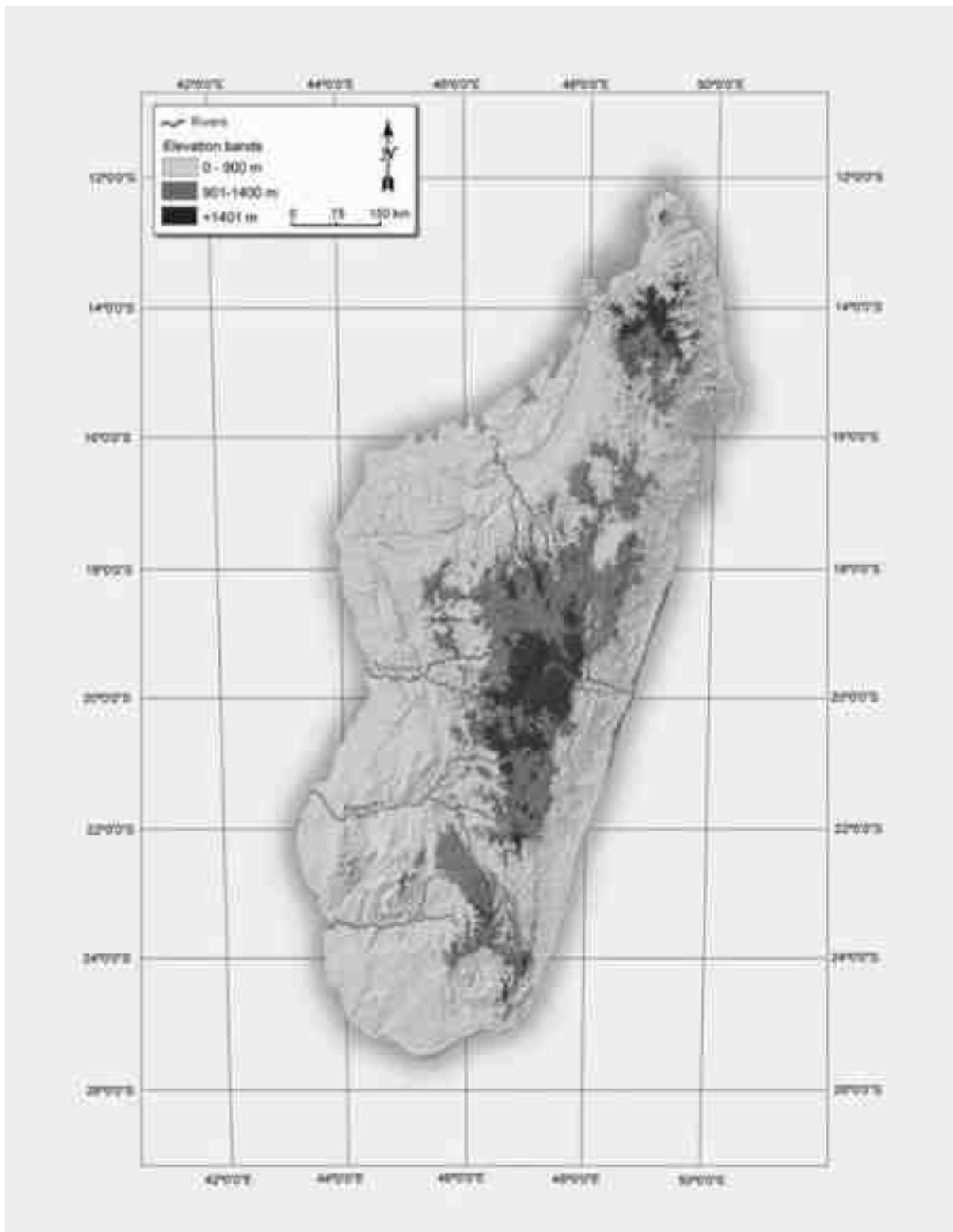


Figure 12. Map of Madagascar showing three different elevational zones. The area in the central portion of the island above 900 m is the Central Highlands and that in the northern portion the Northern Highlands. Some of the principal rivers with their headwaters in the Central Highlands are shown. (Map by Herivololona Mbola Rakotondratsimba and Luci Betti-Nash.)



Figure 13. Two distinct types of rivers can be found on Madagascar, largely depending on if they are eastern- or western-draining watersheds. In general, toward the east, rivers drop quickly off the Central Highlands and in a relatively short distance enter the Indian Ocean, as represented here by the Namorona River above the village of Ranomafana (*left*). (Photograph by Hesham T. Goodman.) In contrast, many western-draining rivers are wide meandering bodies of water, as seen here with the Onilahy River, a short distance before it enters the Mozambique Channel (*right*). (Photograph by Harald Schütz.)



Figure 14. For different rivers on Madagascar, the source elevation and river length and width have important consequences on the dispersal ability and distribution of animals. For several lemur species in the east with broad elevational ranges, rivers in general do not pose a dispersal barrier, as is the case with this brown lemur *Eulemur fulvus*, which is broadly distributed across an altitudinal range from near sea level to over 1,850 m (*left*). (Photograph by Harald Schütz.) In contrast, there are animals whose complete distribution is wedged in between two rivers, which form dispersal barriers. A good example is the lizard *Zonosaurus quadrilineatus* (*right*), which is known to occur only between the Onilahy and Mangoky Rivers. (Photograph by Achille P. Raselimanana.)



Figure 15. The forests of Madagascar show considerable differences in structure and species composition, ranging from notably wet to dry. Several areas of the island receive heavy annual rainfall, and the local forests are distinctly tall, with a closed-canopy forest, and without a pronounced dry season, such as in the Masoala National Park (*left*). (Photograph by Harald Schütz.) In contrast, certain areas of the spiny bush in the southwest receive less than a few hundred millimeters of rainfall per year and experience long dry seasons, such as in the Tsimanampetsotsa National Park (*right*). Plant adaptations to drought include bulbous tree trunks to stock water. (Photograph by Voahangy Soarimalala.)

reach nearly 7 m (Figure 15, *left*), with generally no pronounced or extended dry season. In contrast, in portions of the arid extreme southwest, 400 mm of rainfall per year is exceptional, and the dry season can last ten months (Figure 15, *right*). In this latter region, there can be total drought over the course of several years. Natural vegetation ecosystems are closely tied to the amount of rainfall and physical aspects of the soil (see below), and these in turn shape animal and plant distributions.

### Geology

The geology of Madagascar is complex. The oldest rock on the island is the portion formerly attached to Africa (Gondwana) and dating from 3.2 billion years ago (88), which approaches the period when the Earth formed (see Figure 3). A good place to find this ancient rock today is the western face of the Andringitra Massif. This is rather extraordinary because Andringitra is found in the central-southeastern portion of the island, and all of the geological formations to the west of this area, a swath of over 350 km to the Mozambique Channel, have formed since the breakup of Gondwana some 165 million of years ago. These more recent western-lying geological formations include limestone forced up from the seafloor by the inner movements of the Earth (tectonics) and sandstone formed by the erosion of extensive mountains. These profound transformations provide fine examples as to how dynamic our Earth is through deep time. Things can really change!

A few points need to be mentioned about the mod-

ern geology of Madagascar. In the west, inland from the coastal sandy plain, there are different limestone deposits. In the extreme southwest, the principal limestone formations date from the Tertiary. Farther inland, there is a long band of Mesozoic limestone running discontinuously to the Ankarana area in the far north, and this includes several areas that have the distinct limestone pinnacles, which are referred to in Malagasy as *tsingy* (see Plate 16). In many of these areas, the rock has been heavily eroded by eons of infiltrating water, forming canyons, crevices, and, in some cases, extensive cave systems (Figure 16, *left*). Several of these limestone areas have subfossil sites that have been excavated by paleontologists, and these localities play a critical role in our understanding of Late Pleistocene to Holocene environmental change (e.g., see Plates 16–18 on the Ankarana).

The main central portion of the island, including the area extending to the east coast, is composed principally of metamorphic and igneous rock (Figure 16, *right*). In comparison to the limestone areas of the west, this zone is distinctly moister today, which leads to the deterioration of bone remains, and these rock formations possess fewer nooks and crannies. Hence, very few subfossil sites are known from this vast region. This may in part be related to the fact that it has been less explored by paleontologists because of logistic constraints (see Plate 10). The major exceptions are some riverine and marsh sites of the Central Highlands that until recently were volcanically active, such as the Antsirabe area (see Plate 11) and Ampasambazimba (see Plate 12).



Figure 16. Madagascar has a considerable range of geological formations and structures, which include western limestone formations deeply cut by water erosion (*tsingy*), as shown here from the Bemaraha Massif (*left*). The suspended bridge to the middle right is part of the Madagascar National Park's *tsingy* tourist walkway. (Photograph by Olivier Langrand.) Another very remarkable formation is the large domes made up of granitic rocks like those near Ambalavao (*right*). (Photograph by Voahangy Soarimalala.)

### **Vegetational Patterns**

As mentioned above, there are notable differences in the natural vegetational communities of Madagascar that are directly related to meteorological factors. Two pronounced gradients or clines of decreasing annual precipitation occur across the island—from east to west and from north to south. Areas with greater amounts of rainfall have distinctly lush vegetation and in most cases higher levels of biotic diversity. Traversing the various botanical communities, there are considerable differences in forest characteristics that have important implications for the types of organisms that inhabit these zones. Further, patterns of plant endemism and distribution are linked to different ecological factors, such as plant-animal interactions, which almost certainly were important for some of the animal species that have gone extinct over the past few millennia. For example, different extinct lemurs, giant land tortoises, and elephant birds were presumably important consumers of various seeds and fruits, in some cases responsible for the dispersal of some plants. Since the extinction of these animals, few or no extant species have the same capacity, and, as a result, populations of such plants have declined or there is little recruitment of trees into the adult breeding population.

Several systems have been proposed by botanists to classify the vegetation of Madagascar, which differ in the principal variables used, ranging, for example, from meteorological patterns to soil types and elevation. Rather than getting too bogged down in these

details, here we present a simplified version with three distinct forest types: humid forest, dry deciduous forest, and spiny bush (Figure 17). Also in this section, we consider the question of whether savanna or open grassland formations, dominated by the family Poaceae, are part of the natural vegetational communities of the island.

In recent years, there has been a tendency for ecologists and conservationists to utilize the terms “untouched,” “virgin,” or “primary” for different forested areas on Madagascar. In most cases, these terms are incorrect, as they at least implicitly indicate that the formations referred to have been spared the influence of human-induced degradation. Very few remaining forest blocks on the island have not fallen under the impact of people, and, thus, by definition, little primary forest remains (see section at end of Part 1, “Extinction, Conservation, and the Future”). For example, during an inventory of a remote zone of the Andohahela National Park, to the west of Tolagnaro, in an area without trails and where people in peripheral villages rarely venture, pottery and tombs dating from 500–600 years BP were found (152). People had abandoned this zone, and the natural vegetation was able to regenerate, but telltale indications of previous degradation were still visible many hundred years later. Across the island in remaining “intact” large forest blocks, clear signs of plant exploitation or animal hunting can still be seen deep into such formations. Hence, in the purest sense, little untouched forest actually occurs on Madagascar.

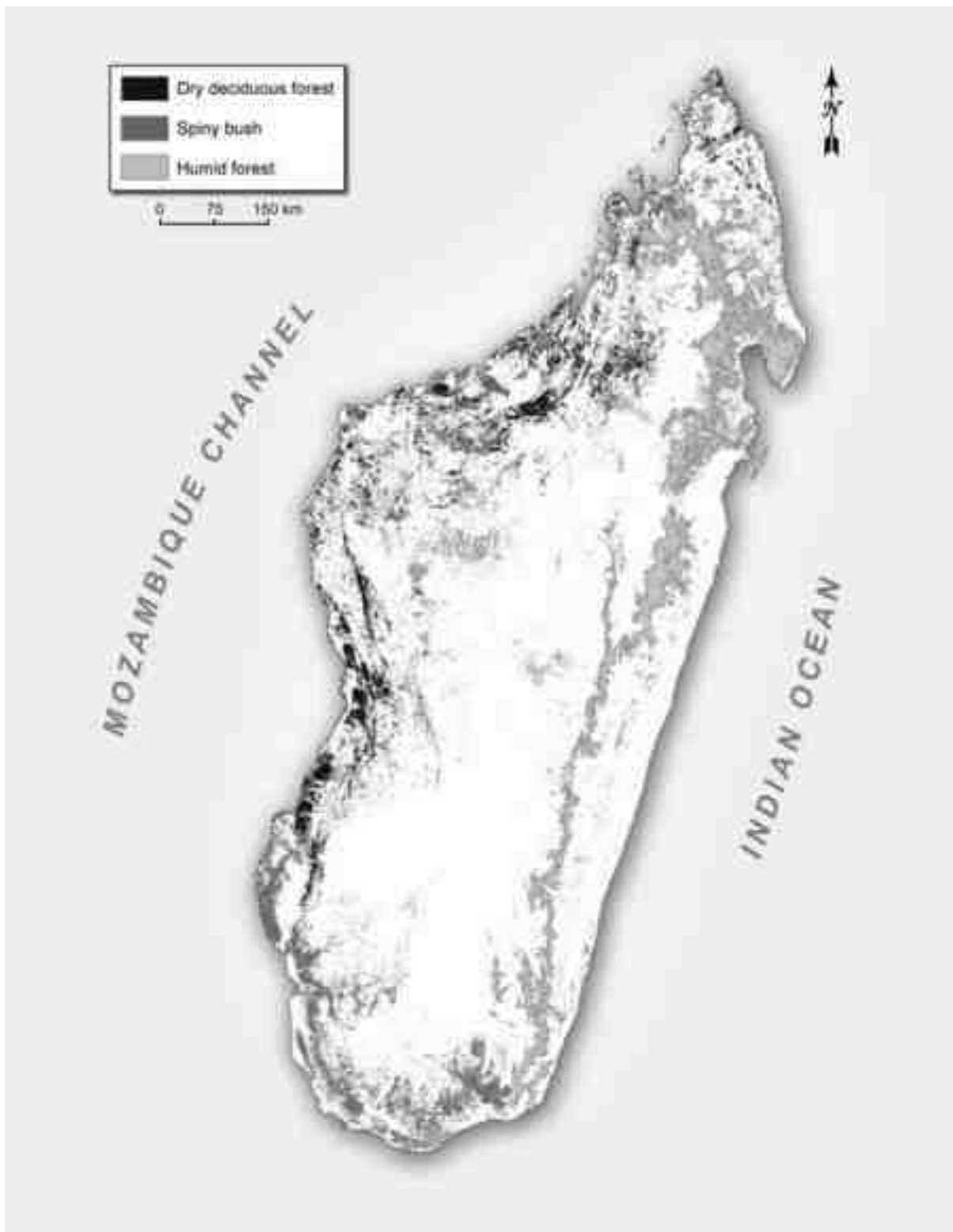


Figure 17. In a simplified model of the natural vegetation cover of Madagascar, three different types can be recognized: humid forest found along most of the eastern half and into the northwest, dry deciduous forest from the north and then south along the lowland west to the south-central zone, and spiny bush in the extreme southwest and south. (Map by Herivololona Mbola Rakotondratsimba and Luci Betti-Nash.)

### Humid Forest

The eastern portions of the country, as well as parts of the Central Highlands and the northwest, are under the influence of the southeastern winds. These promote cloud formation and provide appreciable rainfall throughout much of the year due to rising humid air masses along an important elevational gradient. In general, these areas experience a distinct warm and rainy season, the timing of which varies based on altitude and to a lesser extent latitude, but generally between December and March. Thereafter, there is a transition into the cold and dry season, which continues to September, followed by the transition to the rainy and warm season. During the wet season, Madagascar can experience strong cyclonic systems that can locally bring more than 1 m of rainfall within 24 hours along with winds reaching 200–300 km/hour.

The stable stage (climax) of this vegetation type is mainly dense humid forest (see Figure 17), which shows noteworthy changes in structure and floristic composition associated with elevation. Several authors have noted that the transition between these different vegetational zones is gradual, and specific delineations between them are difficult to define (116, 277). However, to better explain certain patterns described in other portions of this book, and specifically shifts in vegetation associated with climate change, we have maintained the distinction of these zones: lowland forest (near sea level to 800–900 m), mid-elevational or montane forest (800–900 to about 1,800 m), and Ericaceae or sclerophyllous montane forest (about 1,800 m to the upper limit of vegetation).

In general, the lowland formation has tall forest, with trees reaching 25–30 m in height, often with

several strata, closed canopy, and a diffuse understory. It is floristically very rich, but generally with reduced epiphytic growth of lichens, moss, and orchids (Figure 18, *left*). Annual rainfall is generally in excess of 2 m, although the extreme of nearly 7 m has been documented in portions of the Masoala Peninsula in the northeast. Precipitation decreases rapidly from the Masoala area toward the northern tip of the island and more gradually southward along the eastern coast to the extreme southeast. Mean minimum temperature in the lowland forest zone during the coldest month ranges from more than 18°C at sea level to about 12°C at the base of the Central Highlands escarpment. Former lowland forest areas cleared for slash-and-burn agriculture (in Malagasy, *tavy*) regenerate slowly, and introduced invasive plants at these sites can become dominant, further inhibiting the recolonization by native plants (Figure 18, *right*).

The next habitat type with increasing altitude is montane forest, which shows important shifts in structure and appearance along its nearly 1,000 m elevational swath. At the lower end (slightly above 900 m), this forest type has a canopy that can reach up to a height of about 25 m and toward the upper end (about 1,800 m), less than 15 m, where it is often composed of contorted and low-branched trees. Across this gradient, there is an augmentation of epiphytes growing on the ground and woody vegetation, and the understory often has thick herbaceous growth (Figure 19). The climate of this zone is more seasonal than that of the lowland formation, and annual rainfall is between 1.2 and 2.5 m. This may be an underestimate as no permanent weather stations are in place within forest toward the upper end of this vegetational type.



Figure 18. The lowland forests of eastern Madagascar are notably tall, with a closed canopy and little epiphytic plant growth. Here we show an example of this forest type from the Masoala Peninsula (*left*). This is a habitat type where slash-and-burn agricultural activities have resulted in a large percentage of the remaining forest cover being cleared, as shown here on the lower slopes of the Manongarivo Massif (*right*). (Photographs by Harald Schütz.)



Figure 19. Along the nearly 1,000 m elevational band of montane vegetation, from 900 to about 1,800 m, there are pronounced changes in vegetation structure. At the lower end of the zone, the forest is similar to the upper end of lowland forest, although shorter in stature and with more epiphytic plants. In contrast, at the upper end of this zone, the forest is distinctly shorter, with an upper understory and notably heavy epiphytic growth. For example, the upper portion of the montane forest of the Andringitra Massif, here slightly below 1,800 m, really characterizes “mossy forest.” (Photograph by Harald Schütz.)

Across much of this zone, frequent mists provide moisture, rather than direct rainfall, which probably acts as an important buffer against desiccation. Mean minimum temperature in the coldest month depends heavily on altitude, ranging from more than 13°C to less than 5°C in the higher zones.

Toward the upper limit of the montane forest, there is an abrupt shift to the Ericaceae formation. This forest type is distinctly low in stature, generally no more than 10 m tall, with contorted tree trunks and branches, and heavy epiphytic growth. It is similar to the upper montane forest shown in Figure 19, but it is even more diminutive and heavily covered with different epiphytes. The understory is open, and the soil and vegetation are often blanketed with a thick layer of mosses and lichens. The upper limit of this formation is often dominated by species of *Erica* (family Ericaceae) bush, also known as heather, which has a distinct appearance (Figure 20, left).

Weather data from stations in this zone are not

published, but we estimate that there is considerable seasonality in rainfall, which at least is partially buffered by cold and dry season mists. Mean minimum temperature in the coldest month depends again on altitude, ranging from less than 6°C in the lower zones to nights below freezing in the upper elevations. On the Andringitra Massif, which is at about 22° south latitude and reaches 2,658 m in elevation, snow has been recorded. In the higher zones of this massif, temperatures can drop to –11°C, and daily differences between highs and lows span almost 40°C. Toward the summit zone of Andringitra and several other mountains on Madagascar, there is little vegetation and the landscape is mostly exposed rock (Figure 20, right).

#### *Dry Deciduous Forest*

Today, somewhere between the western edge of the Central Highlands, where the remaining natural habitat is best considered humid forest, and farther west,



Figure 20. The upper portions of the higher mountains in the humid forest zone possess some rather pronounced habitats. At the upper limit of the montane forest, there is an abrupt transition to an area dominated by members of the family Ericaceae, predominantly members of the genus *Erica* (heather) and *Vaccinium* (blueberries). This transitional zone is shown here from the upper portion of the Andringitra Massif, where the higher slope exhibits the distinct Ericaceae formation, the middle section is upper montane forest, and the lower section Ericaceae habitat (*left*). This type of interdigitation is probably associated with differences in soil or the history of regeneration after the passage of fire. (Photograph by Harald Schütz.) Toward the summit of Andringitra, the upper section reaching almost 2,700 m, there is little in the way of vegetation (*right*). The deep vertical cuts in the upper section of the massif are associated with Pleistocene glaciation. (Photograph by Voahangy Soarimalala.)

starting at about 800 m, there is a change in the vegetation toward a dry deciduous formation. This shift is closely associated with decreasing rainfall. In dry deciduous forest, a substantial portion of the vegetation loses their leaves during the dry season. In the central west and northwestern portions of the island, where dry deciduous forest is the principal forest formation (see Figure 17), different exposed rock types have an important influence on the structure of local plant communities. A good example is the limestone areas with *tsingy* formations, which include Ankarana (see Plate 16) and Bemaraha. As this zone of Madagascar falls within the rain shadow of more easterly portions, precipitation is generally limited, and there is a notable gradient in annual rainfall, decreasing from north to south. The northwestern portion of the island has a tropical climate with a dry season of about five months per year. Farther to the south, the dry season is notably longer. In the area near the Mangoky River that forms the transitional zone between dry deciduous forest and spiny bush, the dry season can be ten months per year. In comparing images from the dry season (Figure 21, *left*) and the wet season (Figure 21, *right*), it is clear the profound effect that seasonality has on the vegetation.

In general, the upper canopy of intact dry deciduous forest reaches 10 to 15 m high, sometimes up to 20 m, with a relatively open middle section and understory. As these formations experience a signifi-

cant dry season, epiphytic plants, lichens, and moss are largely not present. Along river margins in the western and southern portion of the island, there is another vegetational formation referred to as riverine or gallery forest. In some cases, these courses contain flowing water throughout the year or at least isolated pools or subterranean moisture during the dry season. Hence, gallery forests tend to be notably taller than the adjacent dry deciduous forest, sometimes reaching 15 to nearly 20 m, and with some differences in plant composition (Figure 22). Further, in areas of broad alluvial plains, marsh formations occur and in many cases are associated with areas of *Raphia* palms.

#### Spiny Bush

The dominant natural vegetation of the extreme southern and southwestern portions of Madagascar is spiny bush (see Figure 17). The transitional zone toward the north, giving rise to dry deciduous forest, is near the Mangoky River, and toward the east, shifting to humid forest, along the slopes of the Anosyenne Mountains to the west of Tolagnaro. The spiny bush zone is the driest and hottest portion of the island, with average yearly rainfall generally being less than 700 mm. In the extreme southwest, it can approach 350 mm in the best of years. Average annual temperatures range between maximums of 30–33°C and minimums of 15–21°C.





Figure 21. The dry deciduous forests of western Madagascar are highly seasonal concerning their vegetational structure, and during the dry season most trees lose their leaves. This can be clearly seen in the following images with little leaf cover during the dry season in the Beanka Forest to the east of Maintirano (*left*) (photograph by Achille P. Raselimanana) and considerable greenery during the wet season in the Ankarafantsika Forest to the east of Mahajanga (*right*) (photograph by Voahangy Soarimalala).

---



Figure 22. In portions of western Madagascar, there is a distinct vegetational community, often referred to as riverine or gallery forest, which occurs along the edge of river systems. The example presented here is along the Ihazoara near Beza Mahafaly, which is a seasonal river that stops flowing during the dry season, although the ground remains humid. (Photograph by Harald Schütz.)

---

Different formations make up the natural vegetation of the spiny bush, which are related to substrate (sandy soils as compared to growing on exposed rock) and exposure (partially shaded in canyons or in direct sun in open areas or on cliff faces). In general, this formation is less than 5–10 m in height and dominated by plants of two families (Didiereaceae and Euphorbiaceae) (Figure 23). Baobabs (family Malvaceae) and *Pachypodium* (family Apocynaceae) are also characteristic groups of this vegetation type. Given the



Figure 23. The spiny bush of southern and southwestern Madagascar is a very particular formation, with a notably high percentage of micro-endemic plants and considerable species diversity. Here in the area near Ranobe, to the north of Toliara, cactus-like members of the family Didiereaceae and bulbous trunk baobabs of the family Malvaceae dominate this plant community, which at this site has been heavily modified by different forms of human exploitation. This photo was taken during the height of the rainy season when plants have leaves and the foliage is notably verdant. During the dry season, which can last for at least 10 months, most plants drop their leaves. (Photograph by Harald Schütz.)

pronounced local dry season, many spiny bush plants have adaptations to store what little annual moisture is available and to minimize water loss; these include tiny leaves and bulbous trunks or large underground tubers as storage vessels (see Figure 15, right). These plants also have adaptations to their foliage, trunks, and branches, such as spines, to inhibit leaf-eating animals (folivores). Spiny bush plants have several different adaptations for their dissemination, ranging from seeds with fishhook spines that get tangled in the fur of mammals, to brightly colored fruits, often with considerable sugar content that would be nutritionally important, to attract different frugivores. In the modern spiny bush ecosystem, there are few dispersal agents of such seeds and fruits, and it has been proposed that different extinct large mammals and birds were probably responsible for such dispersal in the not-too-distant past (132, 271).

Another very particular aspect of the local flora is the considerable number of endemics, but more specifically those restricted to the spiny bush (micro-endemics). A study published in 1996 indicated that nearly 90 percent of the plants of this region are locally endemic (304). Given the considerable work conducted over the past two decades on this flora and the description of many new species, the level of endemism is certainly even higher than the previous estimate. In fact, the spiny bush has one of the highest levels of micro-endemism of any forest type in the world.

As in the dry deciduous forest, some remnant gallery forests remain along the margins of the larger rivers in the southwest and south (see Figure 22). In most cases, these rivers are seasonal, with running water limited to less than four to six months per year, but some moisture does persist. One of the dominant trees in these gallery forests is *Tamarindus indica* (family Fabaceae), which is widely consumed by several endemic vertebrates, including the ring-tailed lemur *Lemur catta*, and was previously thought to be introduced to Madagascar from the Indian subcontinent. Recent research has shown that this is not the case, and this tree is actually native (89). Hence, the endemic animals feeding on this tree have not adapted to consume an introduced plant, but rather to something native, and this fact gives a different perspective on aspects of their feeding ecology. This is an important example of how new studies provide important windows into understanding the island's past and current biota.

### *Savanna and Grassland Formations*

Across a considerable portion of Madagascar, savanna grasslands cover vast expanses (Figure 24), which have been previously interpreted as the direct result of human degradation of the landscape (297). A slightly outdated estimate of 72 percent of Madagascar's total surface area is composed of grasslands, mostly at lower and middle elevations (245). Over the past few years, researchers have questioned the interpretation that these grasslands are anthropogenic in nature and have proposed instead that they are at least in part natural and not the result of human modification of former forested areas (35). The debate on this topic is in part associated with semantics, and it is useful to clarify this section with a clear definition of what comprises savanna habitat.

For many people, when they think of savanna, they have the image of the vast grassland zone of eastern Africa, specifically the Serengeti, with the landscape dominated by continuous grassland and some occasional trees. In his definition of grassland associated

with a vegetation classification of Africa, the late Frank White used the following, "Land covered with grasses and other herbs, either without woody plants or the latter not covering more than 10 per cent of the ground" (385). In the African context or elsewhere in the world, many grassland animals are adapted to this ecosystem. The mechanism for the maintenance of such savanna is a combination of a large biomass of grass-eating animals (herbivores) and natural fires. It is important to highlight that many ecosystems today referred to as "savanna" have varying densities of trees, from grasslands with scattered acacia (family Fabaceae) as in the Serengeti, to densely vegetated *Brachystegia* (family Fabaceae) or Miombo woodlands as in portions of southern Africa (Figure 25). By definition, all of these formations are savannas (323). White's characterization of woodland is "an open stand of trees at least 8 m tall with a canopy cover of 40 per cent or more. The field [= ground] layer is usually dominated by grasses" (385).

On the basis of structural and functional aspects



Figure 24. A considerable percentage of Madagascar is covered by savanna grassland, and an important question is if such formations are natural. These grassland areas are frequently set on fire to stimulate new growth of grasses for cattle pasture, as shown here with the Horombe Plateau to the east of Ranohira. (Photograph by Harald Schütz.)



Figure 25. In portions of southern Africa, there is a natural vegetation formation known as Miombo woodland dominated by the genus *Brachystegia* (family Fabaceae). This habitat has variable cover, ranging from areas that have dense trees with a closed canopy to other areas with dispersed trees and open canopy. Here we show Miombo woodland to the east of Lake Mweru, Zambia. Note the variable canopy cover in this extensive formation. On the basis of different reconstructions of animals recovered from different subfossil sites on Madagascar, it would appear that a parallel type of wooded savanna once occurred on the island. (Photograph by Woody Cotterill.)

of subfossil lemur bones excavated at different locations on Madagascar, such as the Central Highlands site of Ampasambazimba (see Plate 12), certain species were largely or exclusively arboreal, using mid- and upper-canopy lianas and branches to navigate, while others were largely terrestrial. Further, mixed among the lemur bones were those of animals such as elephant birds and giant tortoises, which almost certainly lived in open woodland, as compared to closed-canopy habitat. Hence, we propose that a structurally similar ecosystem to Miombo woodlands existed on Madagascar until a few thousand years ago. While by definition this is a form of savanna, it would have had a very different structure than African grassland savanna. These Miombo-like woodlands could easily have been the preferred habitat of numerous organisms occurring today on Madagascar that seem to thrive in modern open, non-forested habitats, such as larks, sandgrouse, and other “savanna” species. Now

that we have proposed the presence of Miombo-like woodlands on Madagascar, at least in the sense of the vegetation structure, we can turn to the question of open grassland savannas as a natural formation on the island.

Without going into too much detail in the debate over whether or not open grasslands are largely man-made formations, a few points need to be mentioned in this regard. Excluding high-elevation habitats—specifically montane and Ericaceae formations, where numerous endemic grasses occur and are clearly part of the native flora of Madagascar—little research has been conducted on the taxonomy of grasses in open lowland areas. The assumption that many of these grasses were introduced to Madagascar from Africa needs to be properly tested, particularly with molecular genetic studies. This would provide a much clearer idea on the probable origin(s) of lowland grasses found on the island today. If indeed

a large percentage of grasses were introduced from Africa, this would explain several issues, such as the particular photosynthesis aspects ( $C_4$ ) for the species found today on the island and typical of African grassland savannas. In turn, this would negate one line of evidence that open savannas are a natural formation on Madagascar. In this regard, it is important to point out that  $C_4$  grasses dominate African Miombo woodlands and that recent work has demonstrated that the evolution of  $C_4$  plants is not directly associated with the emergence of open grassland formations (100).

In the northwest of Madagascar, a region where some of the first relatively large settlements occurred and human perturbation of the natural forest habitats is rather pronounced, a study was conducted to assess the dietary preferences of extinct and introduced animals (71). Based on carbon isotope values from radiocarbon-dated bones mostly from lemurs, one of which is extinct, as well as other animals, certain inferences could be made. For the species that are now extinct with bone remains dated to before 1,500 years BP, little preference was found in the consumption of  $C_4$  plants. Subsequently and particularly for introduced species, there is a distinct shift toward the consumption of  $C_4$  plants. We interpret this to mean that  $C_4$  resources were not an important part of

the natural environment until after habitat changes occurred in association with human disturbances. A similar study was conducted on lemur subfossils from different sites in the southwest and extreme south, and in most cases the results were similar to those from the northwest—the now-extinct species did not favor  $C_4$  plants (72).

Another critical finding from field research on the vegetational dynamics at the ecotone between forest and grassland is that under stable natural conditions, at least in the Central Highlands (Figure 26, *left*), the normal dynamic is for forest to take over grasslands, rather than the opposite (190, 291). This provides evidence that forest, probably including Miombo-like woodland formations in the recent past, is the climax vegetation in portions of the Central Highlands.

A number of modern studies associated with the impacts of forest fragmentation on Madagascar have shown that the ecotone between open grassland areas and forest has been stable for many decades, for example, in the Daraina region (Figure 26, *right*) (306). This observation has been interpreted as the grassland being a natural formation and as fragmentation not necessarily being a human-induced process. However, given current information that forest or woodland is probably the climax vegetation in these settings, we would maintain that over the period that the grassland-forest ecotone remained stable, a better explanation is that certain human factors have impeded forest colonization of the grasslands. Regeneration is a very slow process. Further, if these grasslands were indeed a natural formation, one would



Figure 26. Critical to deciding if current forested islands are a natural formation is an understanding of vegetational dynamics. At least in the Central Highlands, at Ambohitantely, recent research indicates that under stable conditions the forest takes over grassland (*above*). (Photograph by Olivier Langrand.) Many of the forest fragments at sites such as the Daraina (Loky-Manambato) region in the northeast are in topographic situations where they might be more protected by fires. Hence, the forest limits at such sites show certain stability over the past decades (*right*). (Photograph by Harald Schütz.)





Figure 27. The Serengeti is well known for its considerable biomass of grass-eating ungulates, such as the hartebeest, zebras, and gazelles shown in this image. There is no evidence, at least among the bird and mammalian fauna that recently occurred on Madagascar, of a comparable level of herbivorous animals that could have helped maintain reputed savanna grasslands. (Photograph by William T. Stanley.)

expect a higher level of plant species richness and endemism at these sites, particularly among members of the family Poaceae, than current data indicate. For example, African savanna formations have a notable percentage of endemic grasses (220). At numerous lowland sites, however, the grasslands of Madagascar hold only a few species of grasses and, based on current taxonomy, are widespread, often pantropical, perennial, and fire-resistant species (245).

As mentioned earlier, the maintenance of open grasslands—for example, in east Africa—is associated with natural fires and a huge biomass of herbivores feeding on grasses generated after the seasonal rains. On the basis of microscopic charcoal particles found in pollen cores taken from lake deposits at different places on Madagascar (e.g., see Plate 9), it is clear that fire was a natural aspect of certain vegetational communities before human arrival (48). The critical question is whether these natural fires, based on their frequency and intensity, were sufficient to maintain this habitat as they do in undisputedly

natural grassland savannas outside of Madagascar. For the moment, we cannot unequivocally answer this question. However, there is no evidence of any naturally occurring ungulates on Madagascar, in contrast to those occurring in the Serengeti, such as antelopes, gazelles, giraffes, and so on (Figure 27). While it is true that the different species of hippos that occurred on the island (see Plate 10) would have been important grass consumers, these would have been limited to marshlands or riverine habitats that would have covered a fraction of the surface area of modern open grasslands. It remains unclear what the different species of elephant birds (family Aepyornithidae) ate, and at least for now they cannot be cited with any confidence as prominent consumers of grasses (see 34).

On the other hand and rather extraordinarily, the current density of herbivorous Aldabra giant tortoises *Aldabrachelys gigantea* on the Aldabra Atoll (see Plate 4 for more details) reaches a biomass of between 3.5 and 58 tons per square kilometer (Figure 28). This



Figure 28. On the Aldabra Atoll, a few hundred kilometers to the north of Madagascar and in the western portion of the Seychelles Archipelago, an important population of giant tortoise (*Aldabrachelys gigantea*) remains today, closely related to the species that went extinct on Madagascar. The biomass of these herbivorous animals on Aldabra is notably greater than that of mammals in the Serengeti savanna grasslands. The extinct giant tortoises of Madagascar were probably important grazers in different vegetational formations, including Miombo-like woodlands. Shown here is a group of Aldabra tortoises on Picard Island coming down to freshwater pools after a heavy rain. Although slightly concentrated because of the ephemeral water resource, this still gives an idea as to their relative density. (Photograph by Rich Baxter.)

is more than the combined biomass of various species of mammalian herbivores in any African landscape (65)! Given that recently extinct Malagasy members of this tortoise genus were the same size as *Aldabrachelys gigantea*, and presumably reached important natural densities, this might indicate that their disappearance had considerable consequences for different aspects of ecosystem functioning. This notion is often referred to as an “evolutionary anachronism,” where a critical former ecological component, such as a large herbivore, is now extinct and consequently an important interaction has vanished with them. Remains of the extinct Malagasy tortoises have been found at subfossil sites interpreted as having Miombo-like woodlands, which span a considerable elevational and latitudinal range, such as Tsimanampetsotsa (see Plate 4), Belo sur Mer (see Plate 9), and Ampasambazimba (see Plate 12). Accordingly, they were probably important herbivores across their

former broad distribution, but the question remains if they were sufficient to regulate and maintain grasslands.

As mentioned above, there are several endemic organisms occurring on Madagascar today that are clearly adapted to open habitats, as compared to closed-canopy forest formations. Based on this observation, as well as other ecological aspects, it is reasonable to assume that the pre-human island vegetation was not closed-canopy forest formations from coast to coast. As echoed by early botanists such as Henri Perrier de la Bâthie (297), the natural Holocene vegetation of the island was a montage of habitats, which we propose would have included different types of closed-canopy forests, Miombo-like woodlands, and various forms of dry deciduous forest, spiny bush, and open marshland habitats. The recent animal subfossil record echoes and corroborates this inference of notably varied vegetational formations

on the island. Given that among the animal remains of certain paleontological sites, such as Ampasambazimba (see Plate 12), there is good evidence of animals adapted to arboreal lifestyles and others to more terrestrial modes, this would necessarily indicate varied habitats within the same ecosystem.

A worthwhile question to ask would be if Miombo-like woodlands were indeed a natural feature of the recent Malagasy landscape, then what would have been the most common plants in such a formation? Certainly, the fire-resistant *Uapaca bojeri* (family Phyllanthaceae), which today forms a near monoculture in the remnant *tapia* forest in different areas of the Central Highlands, would be a prime candidate. In addition, a wide variety of woody trees and shrubs in the endemic families Sarcolaenaceae and Asteropeiaceae are likely members of this former community. This type of woodland would have been subjected to natural fires set, for example, by lightning storms. A number of woody species would have had fire-related adaptations, such as thickened or corky bark, to protect the plant from quick-passing fires and, in general, to preserve the local vegetation's capacity for regrowth.

In summary, several lines of evidence indicate that there is little evidence that open lowland grasslands are part of the natural ecosystems of modern Madagascar or that they were in the recent geological past. However, the idea that savanna formations occurred on the island that were structurally similar to existing southern African Miombo woodlands is consistent with different anatomical inferences as to the types of habitats used by the subfossil fauna. Today certain portions of the central and drier western portions of the island show some vegetationally distinct habitats, such as a "wooded grassland-bushland mosaic," "plateau grassland-wooded grassland mosaic," or "tapia forest" (277). We suggest that these are either highly degraded forest formations or remnants of former Miombo-like woodlands. Finally, different habitats in the Central Highlands have experienced dramatic changes in the past 50 or so years, and particularly significant is the loss of wetlands and gallery forest (223), further emphasizing the role of human modifications in their modern configuration.



# A Brief History of Climatic Change on Madagascar since the Late Pleistocene

Recall that the Pleistocene geological epoch that began over 2 million years BP transitioned into another epoch called the Holocene just after 12,000 years BP (see Figure 3). The Pleistocene was a period with many colder and warmer cycles, referred to as “glacial” and “interglacial” periods, respectively. The last cold episode is referred to as the Last Glacial Maximum (LGM), occurring about 20,000 years BP. The known climatic record on Madagascar is not a very long one, with direct evidence reaching only as far back as the Late Pleistocene (but beyond the LGM). Information on climate change on the island is not only shallow, but is also quite limited geographically.

The best evidence currently comes from long cores drilled from the crater Lake Tritrivakely (Figure 29) in the Central Highlands (43, 113, 115) (see Plate 11). This site and others in the same region reveal that cold and dry full-glacial conditions were in place from about 40,000 years ago through the LGM. The identification of pollen from these cores show that an Ericaceae formation of heath and shrubs, which today in humid forest habitats tends to be found at high elevations (see section above “Humid Forest”), mixed with some grasses, occurred during this period, about 1,000 m lower than it does today. With the expansion of this montane vegetation toward lower elevation, it has been suggested that during this period lowland forest, which today occurs from sea level to about 900 m, may have been compressed into relatively limited pockets along the eastern and northwestern coasts.

Responses to these profound climatic cycles apparently varied from region to region in Madagascar, at least based on the limited information in hand, and certain areas appear to have been more stable. Pollen has also been extracted from limestone cave ornaments known as speleothems at Anjohibe (see Plates 13 and 14), not far from present-day Mahajanga in the northwest. It appears that the palm savanna vegetation, which is characteristic of that area today, was already in place rather early on, perhaps punctu-

ated later and briefly by less dry-adapted plants during the warmer and wetter mid-Holocene. The more recent portion of a 40,000-year-BP pollen spectrum is said to be “remarkably similar” to that of the modern pollen sample, with moderate values reported for palms (*Medemia*), high values for grasses (Gramineae), and traces of various savanna and woodland tree pollen types (52). However, the datation for the upper portion of this core is not clearly defined.

The LGM’s cold and dryness almost certainly influenced other parts of the island, including the Andringitra Massif in the central southeast, and evidence for desiccation ranges from Lake Alaotra in humid eastern Madagascar to the extreme north on Montagne d’Ambre. Post-LGM conditions are signaled from the pollen records at Lake Tritrivakely as deglaciation, and warming began. In association with this climatic shift, there was a distinct reduction in Ericaceae pollen around the lake area. Temperature fluctuations continued, but by just after 10,000 years BP, the Ericaceae vegetation appeared to be gone and was replaced by wooded grasslands. Somewhat wetter conditions existed briefly in the mid-Holocene in the southwest too, with dry forest expanding at the expense of other dry-adapted plants and palms. Desiccation then reappeared, and brief droughts were reconstructed in various regions of the island until moister conditions return. Even with higher effective moisture, cooler conditions returned to the Central Highlands, and trees may have spread into the higher elevations as woodlands. However, roughly 3,000 years BP aridification set in again more or less island-wide and then persisted, but the southwestern area was especially hard hit.

It has been suggested that a severe island-wide drought occurred as recently as 950 years BP, and that this severe desiccation was coupled in some areas with elevated frequencies of fire and the introduction of domestic livestock (374). One might expect that this toxic combination would have profound



Figure 29. Important for studying aspects of pollen, cores—microscopic particles of charcoal, spores, and diatoms—are made by sinking piping into the lake sediments from floating rafts. This image was made in late July 1991 at Lake Mitsinjo. From left to right are Jean-Gervais Rafamantanantsoa (kneeling), David Burney, and Toussaint Rakotondrazafy. (Photograph by Katsumi Matsumoto.)

---

implications for landscape transformation and the ultimate extinction of many land vertebrate species, and perhaps it did in some locations. However, even in the face of the numerous climatic oscillations discussed above, it is noteworthy that the majority of the extinct vertebrates currently known to science weathered these sometimes extreme fluctuations, and many persisted beyond the severe drought until quite recently, even in the southwest (54).

# History of Human Colonization of Madagascar

Anyone who visits Madagascar today will be impressed by the great physical variation among its people. There are citizens who could easily be misidentified as Southeast Asians, perhaps from Indonesia or the Philippines, and others who are distinguished by decidedly mainland African features. These differences are readily apparent in skin color and hair texture, and in many ways they represent the extremes of variation within the Malagasy populace. There are also imperfect geographical correlates of these two extremes, with the more Asian-looking people typically associated with the Central Highlands (Figure 30, left), whereas the more African-appearing people are regarded as primarily coastal denizens (Figure 30, right). These are clearly oversimplifications concerning contemporary Madagascar, and there is obviously much blending and a continuum between these two extremes. Nevertheless, they serve as reminders of the complex colonization history of the island by different cultural groups.

Precisely who the original founders were (sometimes referred to as the “Proto-Malagasy”), and when and how they arrived on Madagascar, remains a topic of intense research and considerable debate. Every few years or so, researchers present new evidence and the date of initial colonization recedes deeper into history. Scientists have language, genetic, archaeological, and paleontological clues as to the probable origins of the Malagasy people, and some aspects of the story are clearer than other parts. Arab traders, European pirates of the Indian Ocean, European colonialists, and Indo-Pakistani and Chinese merchants all arrived much later in successive waves of immigration, and they, too, have added their genetic and physical signatures to the impressive mix evident in today’s population. European contact and subsequent colonization are usually dated to the beginning of the sixteenth century with the discovery of the island by the Portuguese explorer Diogo Dias. Different schools of thought as to the origins of the

Malagasy have waxed and waned in influence as new evidence and interpretations have been presented, and we offer our synthesis and assessment below.

Madagascar has a rich tradition of archaeology and paleontology research. Generations of national and foreign researchers have devoted their careers to understanding different aspects of how and from where different organisms (including people) colonized the island. Much is now known about human dispersal and settlement across the landscape, phases of different foreign invasions and occupations, and the development and expansion of state societies into the modern era. Researchers and collaborators associated with the Institut de Civilisations / Musée d’Art et d’Archéologie of the University of Antananarivo, created in 1970, have conducted numerous missions to different areas of the island to excavate archaeological sites. In many cases, these outings include university students and form an important component in capacity building (Figure 31). Among paleontologists, several active groups involve young university students in their education and advancement (Figure 32). Researchers in a variety of domains have advanced our knowledge of Madagascar before and after human colonization, and thanks to the myriad themes that have been investigated, we are able to formulate the following sections.

## **Considerations of Language and Different Types of Introductions**

Although there are several different dialects spoken around the island, which for the most part are understandable to the majority of Malagasy-speaking people, it has been known for a long time that the language is part of the Austronesian family. The Merina tribal dialect of the Central Highlands is apparently the one most similar to the Western Malayo-Polynesian branch of this linguistic family. Otto Christian Dahl is usually given scholarly credit for identifying an especially close relationship between



Figure 30. The facial features and complexion of people from different portions of Madagascar can be notably different. People from the Central Highlands, specifically the region of Antananarivo, tend to have lighter skin and straight hair, as seen by the group of three full sisters (*left*). (Photograph by Olivier Langrand.) This is in contrast to people from the coast, excluding the extreme southwest, who generally have darker skin color and distinctly more frizzled hair, as shown by these two half-sisters coming from the north (*right*). (Photograph by Vavizara Patrica Ranaivo.)



Figure 31. In this photograph, the late Pierre Vérin is figured (standing to the upper left). He was a faculty member at the University of Antananarivo between 1962 and 1973, a major figure in Malagasy archaeology, and conducted numerous field excursions around the island, often using these opportunities to train upcoming generations of Malagasy scholars. This particular image was taken during a 1970 mission to Ambariotelo Island, in the far north. Among the accompanying students is Jean-Aimé Rakotoarisoa (seated on the ground between an older man with a hat and a young woman, Vikye, who would subsequently become Jean-Aimé's wife), the future director of the Institut de Civilisations / Musée d'Art et d'Archéologie (see 310). Standing at the far right is Claude Chanudet, who worked on Malagasy subfossils (62). (Photograph courtesy of the Institut de Civilisations / Musée d'Art et d'Archéologie.)



Figure 32. Direct experience is primordial for the development of young Malagasy scholars. Shown here is a field school of students sorting through debris at Belobaka, a few kilometers east of Mahajanga, from the Geology-Paleontology-Museum Science Department at the University of Mahajanga. Seated to the left and with a light brown hat is Beby Ramanivosoa, professor in that department. She is a collaborator with Dominique Gommery, who is associated with a French-Malagasy team of paleontologists and archaeologists working in the greater Mahajanga region. (Photograph courtesy of Mission Archéologique et Paléontologique dans la Province de Mahajanga—Centre National de la Recherche Scientifique.)

Malagasy and the language spoken in the region of the Barito River in southeast Borneo (75). Because today the Barito people lack seafaring technology, it has also been speculated that these Barito-speaking people were probably laborers or enslaved crew members of boats commanded by the maritime Malayan Srivijaya Empire, which was expanding sometime in the sixth and seventh centuries (31).

Dahl also correctly recognized an African Bantu “substratum” to the Malagasy language, but precisely when Bantu words (and other cultural elements) were introduced and assimilated is not yet settled. Philippe Beaujard (26) suggests that these Bantu-Austronesian contacts might have first occurred in the Comoros Islands, just to the northwest of Madagascar. Again, based largely upon linguistic evidence,

Beaujard also infers that the first Austronesians in Madagascar brought rice, the greater yam, coconuts, and Indian saffron with them; only later were sorghum, bananas, and various other crops introduced from Africa.

The first metal in the form of iron could have come to Madagascar from either Africa or Asia; the archaeological record indicates that iron was known in both east Africa and Southeast Asia more than 2,000 years BP. Debate also exists over whether African cattle might have preceded and were subsequently replaced by the current island-wide, hump-backed zebu (Figure 33, *left*), which are most likely of Asian origin (354). Another physical cultural aspect found today on Madagascar that points to Asian origin includes outriggers on canoes (Figure 33, *right*); these



Figure 33. The hump-backed zebu, which occurs across most of Madagascar, is thought to be of Asian origin (*left*). This scene is from the Central Highlands near Ambalavao. (Photograph by Olivier Langrand.) Seagoing canoes on Madagascar often have outriggers, which were apparently developed by Austronesian-speaking people (*right*). This image was taken in the Morondava area. (Photograph by Fanja Andriamialisoa.)

were apparently developed by Austronesian-speaking peoples living on islands specifically for greater boat stability during sea travel.

Another interesting example that can be presented to infer the cultural origins of different tools and handicrafts is the Malagasy word *tefy*, which is derived from a proto-Indonesian word for both the making of pottery and the forging of iron (372). This etymology implies that the early Austronesians who arrived on Madagascar knew about iron. Further evidence for this is that many modern Malagasy words associated with iron technology are also derived from Austronesian, while those used for pottery fabrication have Bantu roots. Hence, based on linguistic evidence, the origins of these two handicrafts are different, iron working from the Austronesians and pottery from the Bantus.

Roger Blench has revived the idea that Austronesians may have arrived on mainland Africa before Madagascar, possibly incorporating African genes and words prior to departing from east Africa and arriving on the shores of Madagascar (31). This theory is sometimes referred to as an “anteroom” scenario in mainland Africa and begs for concrete archaeological evidence (but see below with respect to genetics). Blench also suggests that the first human pioneers to arrive on Madagascar may not have been Austronesians at all, but early African hunters and gatherers (see below, “Paleontological and Paleoecological Evidence”).

In addition to the Bantu impact on its Austronesian foundation, wherever and whenever that first

occurred, additional words have been borrowed and incorporated more recently into Malagasy, including Kiswahili, Arabic, English, and French. In fact, the first example of written Malagasy was in Arabic script from the late sixteenth century in the southeast. As late as the seventeenth century in the west, people in some villages spoke an African dialect not unlike that from Mozambique, and this is said to persist today in isolated pockets (85). Until a few years ago, older people in remote villages in the northwest, such as at Marodoka on Nosy Be, spoke Kiswahili but were eventually integrated into Malagasy culture. The name of the village, with *maro* coming from the Malagasy and meaning “many” and *doka* from the Kiswahili and meaning “shops,” provides a trace of cultural mixing. Today in the northern dialects of Malagasy, the word *dokana* signifies shops or stores.

### The Human Genetic Evidence

The dual origin of the Malagasy people, African and Asian (coastal versus Central Highlands), was supported by early analysis of blood-typing. Other genetic data subsequently corroborated this fundamental two-group evidence, and a small but variable amount of Eurasian admixture was found in some Malagasy cultural groups (Figure 34). Although lacking among the modern Barito people of Borneo, almost 20 percent of Malagasy people in one study were found to carry a well-defined “Polynesian motif” of mutations in maternal mitochondrial DNA. This result was also supported by simultaneous analysis of both maternal and paternal genomes (200), which pinpointed Bor-

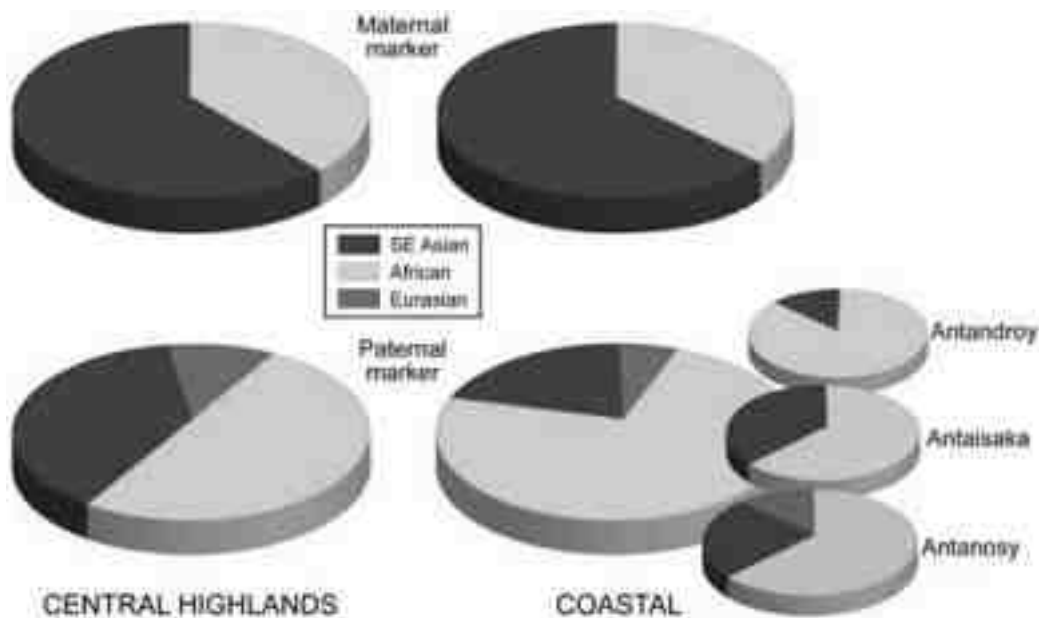


Figure 34. Diagrams showing the proportions of the Malagasy population from the Central Highlands and coast divided into their ancestral genetic components, specifically from southeastern Asia, sub-Saharan Africa, and Eurasia. Two different markers were used, those inherited from the mother (maternal) and from the father (paternal). For ethnic groups in the southeast and south of Madagascar, separate pie diagrams are presented for the paternal marker. (Adapted from 363.)

neo again as the most likely origin of the Asian component of the Malagasy people. When reexamined by Sergio Tofanelli and Stefania Bertoni (363), the same genetic markers provided a more subtle conclusion: Austronesian ancestry was more conserved in females than in males and, in general, more in people from the Central Highlands; a pre-Malayan Srivijaya Empire spread of Austronesians was also inferred. Importantly, the newer results were compatible with a first contact of Bantu and Austronesians over 2,000 years BP. A new genetic “Malagasy motif,” present in 20 percent of the modern Malagasy, has also been more recently identified that distinguishes itself from the aforementioned “Polynesian motif” by a handful of additional mutations, and has yet to be found in Southeast Asia. These same authors also believe that the anteroom scenario mentioned above is still viable and merits deeper investigation.

A very recent analysis (68) of the Malagasy mitochondrial genome is provocative in several ways. Using a different set of models, they conclude that the “main episode” of African-Asian admixture occurred very early during colonization, and that the founding Indonesian female group lineages were limited, and these individuals may have reached Madagascar by chance in a single wayward vessel, approximately

1,200 years BP. Although the authors of this paper acknowledge that sporadic early arrivals on the island cannot be ruled out based on other evidence, their best estimate for actual settlement was placed in the early part of the ninth century, consistent with some of the linguistic-based assessments and again possibly implicating the maritime Malay Empire of that period. However, this estimated date, which does not take into account any archaeological evidence from Madagascar, has an enormous confidence interval (255–4,721 years BP); this level of imprecision overlaps temporally with almost all other colonization scenarios.

### Evidence of Pre-Iron Age Colonization of Madagascar

Over 40 years ago, Marimari Kellum-Ottino published a paper citing the discovery of apparent Neolithic tools near the village of Tambozo, about 180 km inland from Morondava (217). Two proposed implements were found on the surface along a riverbank and were described as an unfinished adze and a small hammer stone; both were composed of chalcedony or a form of crystalline silica and quartz. This is the classic type of rock material that stone tools were made from by Neolithic people in other portions of the Old



Figure 35. Recent excavations in the rock shelter known as Lakaton'i Anja in the Montagne des Français in the far north have found evidence of microlithic flakes. Here is a portion of the excavation team including Chantal Radimilahy, to the left and replacing her glasses, and Henry Wright, in the foreground to the right. The third principal member of the group, Robert Dewar, is not shown in this photo. These researchers have made fundamental discoveries in understanding human history on Madagascar. Henry Wright started working on Madagascar in 1975, the late Robert Dewar in 1978, and they have collaborated with Chantal Radimilahy since 1980. (Photograph courtesy of the Institut de Civilisations / Musée d'Art et d'Archéologie.)

World. Kellum-Ottino was of the opinion that these two objects were shaped by humans via flaking and chipping. Importantly, these were the first reputed Neolithic tools reported from Madagascar. Perhaps associated with the nature and the conditions of the discovery, combined with being so radically different from the archaeological evidence of that period, these details were largely lost and not mentioned in the subsequent literature on the history of colonization of Madagascar (54, 86).

Recently, the archaeological team composed of Chantal Radimilahy, Henry Wright, the late Robert Dewar, and several other colleagues reopened excavations at a northern site known as Lakaton'i Anja in a gorge of the Montagne des Français, which had already produced the earliest known human occupation site on Madagascar (Figure 35; and see next section). Under a large sandy area below the overhang of a rock shelter, they excavated two pits to a depth of less than 1 m with stratified deposits and painstakingly washed and sorted the sediment under magnification to recover fine material (87). Within these deposits, they found chert flakes associated with stone tools,

which is a type of stone that does not occur naturally near the site. Members of this team concluded that these flakes are evidence of a human-manufactured stone industry. Using a dating technique known as optically stimulated luminescence, which measures exposure of certain sediments to sunlight, the lower levels associated with the stone tools yielded dates of 3,470 and 4,380 years BP. Radiocarbon dates from the deposits were notably more recent. The proof that these microlithic flakes were human-made is solid, but ambiguity remains as to the period from which they date. Similar-styled tools were also recovered from the site of Ambohiposa, near Vohémar in the northeast, but their dating context was largely unresolved (87). In any case, on the basis of the Lakaton'i Anja and Ambohiposa excavations, there is strong evidence that humans certainly arrived on Madagascar before the fourth- to sixth-century date indicated by archaeological evidence (see below, "The Archaeological Record of Occupation and Settlement") and perhaps even before the 2,350 years BP date based on paleontological information (see below, "Paleontological and Paleoecological Evidence").





Figure 36. Recent archaeological research in extreme southern Madagascar at Enijo on the west bank of the Menarandra River by Michael Parker Pearson and colleagues has found a distinct type of pottery. The pottery is not that of any Malagasy tradition and is closely comparable to Triangular Incised Ware (TIW) dated from 1,100 to 1,400 years BP along the Swahili coast of Tanzania and Kenya. Although it is of an east African style, the pottery's constituent portions are consistent with local manufacture within the limestone and coastal dunes of this portion of Madagascar. This provides good evidence that human movements from east Africa to Madagascar occurred notably earlier than previous thought and that the south was colonized by groups from the Swahili coast. (Photograph by Michael Parker Pearson.)

### The Archaeological Record of Occupation and Settlement

Direct evidence from *in situ* human artifacts for an unequivocal occupation site, as opposed to longer-term settlement, comes from a rock shelter in northern Madagascar not far from Antsiranana. The aforementioned Lakaton'i Anja is a cave in the Montagne des Français with "debris from coastal and forest foraging" and charcoal dated to the fourth to sixth centuries (84, 85). The home base for whoever occupied this temporary encampment remains unknown. Other northern sites appear more residential in nature and date from 1,200 years BP (Irodo) to 1,250 years BP (Nosy Mangabe in the Bay of Antongil). A number of archaeologists have been conducting research on apparently early human occupation sites (see section above), and it is almost certain that the "first" date will be substantially pushed back in time in the near future. Hence, as in the case in any field of active scientific inquiry, amelioration and further precision can be anticipated with new finds associated with the initial human colonization of Madagascar.

Another early archaeological site was documented in the southwest at Sarodrano; this was a settlement on a sandbar, now washed away by a cyclone, which

was dated to 1,460 years BP (293). There are also three settlement sites in the south at the mouth of the Menarandra River that evidence suggests were inhabited 1,100–1,400 years BP. These sites are especially interesting in that they have pottery identified as stylistically east African (Figure 36) and not mixed with typical Malagasy pottery of this same period. Most importantly, the pottery was made from local soils and, hence, not imported to the island. This suggests "that colonization of the south might have been initiated by Swahili communities" or Swahili traders (293). Taken together, these dates suggest that relatively early colonization and settlement may have occurred at roughly the same time in the southwest and north from separate African and Austronesian populations, respectively. This scenario is not at odds with some of the linguistic and genetic evidence for early mixing reported above. Further, given this mixing at an early stage of human colonization, this might explain the relatively homogenous and single modern language on Madagascar today, Malagasy. Population growth in the interior in the Central Highlands is evident by approximately 1,400 years BP (52), but larger, more urban-scale archaeological sites are more recent still, such as the eleventh- to

fourteenth-century Islamic port of Mahilaka on the northwest coast.

Occupation sites from the southeast are also relatively recent, and it appears that more expansive and intensive occupation of the southwest did not occur until around 500–600 years BP (69). State formation in the Central Highlands was based economically on slaves and rice, and does not occur until the end of the eighteenth century (see contributions in 393). The archaeological record is therefore consistent with regional colonization sometime around 1,680–1,300 years BP in the north, but other evidence in the southwest and elsewhere suggests that human arrival and impact began even earlier.

### **Paleontological and Paleoecological Evidence**

The accumulated data from modified bones of now-extinct animals, charcoal particles, pollen from introduced plants and other proxies for human presence and the impact of these different variables on the Madagascar landscape coalesce around a date for human arrival between 2,000–2,350 years BP. These data are referred to as “proxies” because they do not concern human artifacts in the archaeological sense of pottery or tools, but taken together they tell a consistent story of human arrival on the island (49, 54, 69).

Currently, the earliest date for human presence comes from an interior southwestern site called Taolambiby (see Plate 5). A radius, one of the bones of the forearm, from a giant extinct lemur (*Palaeopropithecus ingens*) bears cut marks; this signals intentional human activity to deflesh the carcass using a sharp object. This specimen is radiocarbon dated to 2,325 years BP. Given potential problems with radiocarbon-dating techniques, comparable dates from other modified bone material from the site are needed to corroborate this apparently initial moment on Madagascar in the history of human–extinct animal interactions.

Pollen from introduced plants (*Cannabis*/*Humulus*, family Cannabaceae) was found in a core from Lake Tritrivakely in the Central Highlands (see Plate 11) and has been dated to a similar age of 2,200 years BP. In this case, the pollen morphology of *Cannabis*, used for hemp rope or perhaps smoked for its narcotic effects, and *Humulus*, an important ingredient in the brewing of beer, are morphologically similar and difficult to tell apart. Over the next centuries, many different plants were introduced to the island for a variety of reasons (224).

While discussed in detail below in a section entitled “Human Interactions with Now-Extinct Land Vertebrates,” a few points are important to present here to highlight other proxies between humans and extinct animals. The femur of an extinct pygmy hippo *Hippopotamus lemerlei* from the southwest coastal site of Ambolisatra was found to be modified by humans (in other words, chop marks and butchery) and was dated to roughly 2,000 years BP. A modified leg bone of the extinct elephant bird from another southwestern site (Itampolo) was dated to 1,880 years BP. While these dates are notably similar to one another, given potential problems with radiocarbon dating, singleton dates per site for such proxies are by no means well-supported proof. Further, there is no known archaeological occupation site from this period in southwestern Madagascar. However, if these proxies are used as hypotheses, people do appear to have been on the scene and hunting now-extinct “megafauna.” It is not clear if these early people were Africans or Austronesians, but they were sufficiently numerous to begin altering the local natural landscape.

If the early record of introduced pollen in the Central Highlands mentioned above was indeed of *Cannabis*, this can be interpreted as associated with originally seafaring people (Austronesians perhaps), who needed renewable resources, such as hemp, for the manufacture of sails and ropes. As a complicating side note, the predominant winds over the past millennia in the southwestern Indian Ocean are easterlies, and it is distinctly easier to navigate small sailing vessels from east to west than west to east.

Early evidence for human-induced landscape transformation also comes from the southwest. *Sporormiella* is a fungus that produced recognizable spores and has been associated with the dung of extinct megafauna from North America to New Zealand (53). It has also left its dung fungus signature in Madagascar. The first marked decline in *Sporormiella* abundance from soil deposits comes from records at Andolononby, north of Toliara, dating to AD 230–410 years, and slightly older but less securely dated dung fungus decline comes from the west coastal site of Belo sur Mer (see Plate 9). Such a decrease suggests a decline in the populations of local megafauna—elephant birds, hippos, giant tortoises—but such a decline does not necessarily translate into a rapid extinction. In fact, the evidence in hand indicates that some of the now-extinct large terrestrial vertebrates held on to relatively recent times in the southwest. The drop in population densities of these animals

in certain portions of the island can probably be attributed directly to successful hunting of naive animals and/or shifts in climate that negatively affected them. There is a correlation between their decline and increased abundance of charcoal particles. This might be explained by fewer herbivores consuming vegetation, resulting in an increase in combustible matter, and associated augmentation in the ferocity and frequency of fires. This sequence of cumulative events might well precipitate a downward spiral of habitat change and animal extinction.

### Summary

To date, evidence from Madagascar of Neolithic cultures, as known from nearby portions of Africa and offshore islands, needs further verification. It is with little doubt that the archaeological record underestimates the antiquity of human arrival and occupation of Madagascar. Proxies for human presence indicate that people were on the scene in the southwest well over 2,000 years ago. It remains possible that different populations colonized Madagascar quite early and perhaps synchronously from different directions, such as Africans in the southwest and Austronesians in the north. Genetic information indicates that the contact and admixture of these two groups occurred very early on in the history of the Malagasy people. The linguistic (and to a lesser degree, cultural) dominance of the Austronesian language group that is shared by all Malagasy today should not be misinterpreted as evidence that Madagascar was first populated exclusively by people from Southeast Asia. It is clear that the early Proto-Malagasy overlapped in time and space with many of the now-extinct and endemic birds, reptiles, and mammals of Madagascar.

In any case, an important point is the uniqueness of Malagasy culture, which is nicely summarized in the following quote from Jean-Aimé Rakotoarisoa (Figure 31), one of the doyens of the study of Malagasy culture and archaeology (311):

*The Malagasy are from Madagascar. This statement may seem a truism, but it actually represents a departure from most scholarship about the island and its people. Past studies have tried to explain and define the Malagasy largely in terms of their overseas origins in East Africa, Asia, and the Near East. The unique culture of the Malagasy, however, has developed in place, on the island, during the nearly two thousand years since the first settlers arrived from those distant points. It is an autochthonous culture that has selectively appropriated and combined elements—linguistic,*

*material, and cultural—from sources scattered across the vast Indian Ocean and turned them into something new. Though a consuming mystery for scholars, overseas origins play no part in the lore or identity of most rural Malagasy. The only “ancestral land” (tanin-drazana) they know and recognize is the island of Madagascar itself; their only ancestors are those residing in the tombs that conspicuously dot the landscape.*

# Human Interactions with Now-Extinct Land Vertebrates

During the course of excavations of archaeological and mixed paleontological/archaeological sites, a number of bone and tooth remains have been found that show evidence of human modifications. The assumption associated with these types of marks is that the animal lived contemporaneously with humans and, at least in certain cases, the death of the animal was associated with human persecution, such as hunting. On the basis of these proxies, particularly the form and nature of the cut marks when examined at a magnified level, it can be inferred that they were made with tools fashioned from metal, presumably iron (251, 296). It has been widely assumed that the first people to colonize Madagascar arrived (see previous section) with iron technology. Another important aspect is the nature of the cut marks. Without excessive force, cut marks in fresh bone normally have notably smooth edges (Figure 37), while in older and at least partially dried bone the marks are distinctly jagged. From two sites discussed below, the cut marks appear to have been made in fresh bone, lending further support that these animals were dismantled by humans with metal knife-like objects directly after they were killed. In other cases of the modification to bone or teeth, it is certainly possible that people were not implicated in the death of the animal and simply found the remains and modified them. This maybe the case, for example, of the drilled *Daubentonia robusta* teeth mentioned below.

As pointed out by Robert Dewar and Alison Richard, there are two different manners to address the question “When did people first arrive on Madagascar?”

- (1) Based on archeological evidence of human settlements and physical remains at sites, which has been covered in the previous section, and
- (2) first evidence of human impact on elements in the environment(85).

In this section, we address the second aspect, and in order to give these details in a more digestible fashion, they are presented by taxonomic group.

## Reptiles

### Tortoise

In the mid-1960s when Alan Walker and the late Paul Martin visited Taolambiby (see Plate 5), they collected a portion of a tortoise carapace that was artificially perforated (308). There appears to be some ambiguity as to what species of tortoise the carapace represented, but it was probably *Aldabrachelys grandidieri* (36). No further details to our knowledge have been published about this find.

## Birds

### Elephant Birds

A human-modified bone of *Aepyornis* from Itampolo yielded a radiocarbon date of 1,880 years BP (69). No details are available on the manner in which the bone was modified (48). During the excavations conducted at Ampasambazimba (see Plate 12) in the early twentieth century, it was reported that a modified *Mullerornis* leg bone was recovered among cultural remains (82, 105). Based on subsequent deliberations, the evidence was deemed insufficient to implicate humans in the deposition or reworking of this bone (21, 255).

Eggshell fragments of elephant birds have been found at a number of mixed sites (see Plate 1). Whether these remains are the remnants of people feeding on the eggs for food or eggs that were slightly modified to carry liquids is difficult to establish (82, 293). As whole eggs are still found today in the lowland and coastal sandy areas of the south, long after the extinction of these birds, previous utilization of eggs to transport liquids could have been those taken either from active nests or from discoveries of old buried specimens.

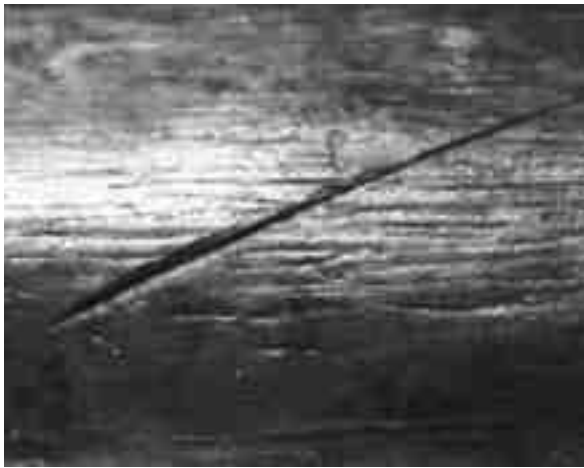


Figure 37. A number of animal remains recovered from archaeological sites show signs of bone cut marks. A cut mark was identified on the femur of a *Propithecus verreauxi* recovered from Taolambiby (see Plate 5). As one can see in this close-up image, the mark is a smooth V-shaped cut, which is characteristic of a metal object passing across fresh bone. (Photograph by Laurie Godfrey.)

## Mammals

### Lemurs

Different lemur remains have been found in archaeological or mixed sites, which show signs of human reworking of bone and teeth. These modifications include apparent use as hand tools, ornaments, or with cut and fracture marks associated with the manner in which the animal was dispatched or butchered. In most cases, there is a lack of stratigraphic context for these remains, and to date not one site has yielded cultural artifacts clearly associated with the modified bones that would provide direct evidence of a contemporaneously human presence. Hence, in a pure archaeological sense, these are also proxies, and critical links between signs of human interaction with animals and cultural artifacts are lacking. This is perplexing, as one would assume that remnants of the objects used to cut up the animals or other cultural remains—for example, pottery—would be found in association with modified bones.

Incisors almost certainly excavated by Guillaume Grandidier at Lamboharana have the proximal portions of the roots drilled out in a small and symmetric hole. These teeth have been allocated to the extinct species *Daubentonia robusta* (253). In his report of the excavation of Lamboharana, Grandidier proposed that the perforation was the means to attach the teeth to an ornament, such as an amulet or necklace, worn

by people (183). Hence, if this was the case, some aesthetic or magical properties would have been associated with these objects. It is important to note that there is no obvious way to know if the animal was killed for the tooth (and presumably meat) or if the tooth was found and modified long after the animal's demise.

The detailed study of lemur bone remains has provided some extraordinary windows into aspects of their morphology, distribution, and natural history (Figure 38). For example, the first recognized evidence of a site where people hunted, dispatched, and butchered animals at an important scale is Taolambiby (see Plate 5 for detailed information on this site). Among the bones of extinct lemurs recovered and examined in detail from Taolambiby, both *Palaeopropithecus maximus* and *Pachylemur insignis* showed evidence of dismantling with a metal tool (296). Bones of two living species, *Propithecus verreauxi* and *Lemur catta*, were also recovered from Taolambiby, but only the bones of the sifakas exhibited butcher marks (Figure 37). Interestingly, a couple of *Megaladapis madagascariensis* bones were also examined from the site, and neither showed butchering signs. As the Taolambiby bone remains were not excavated with stratigraphic control, it is difficult to know if *Megaladapis* was an unpreferred meat to the people that hunted and consumed other lemur species, or if the *Megaladapis* bones date from an earlier pre-human hunter period (or if this is just a simple case of sampling error in not-extensive samples).

Other remains of modified extinct lemur bones have been cited in the literature, for which the cultural context is vague. At Andrahomana (see Plate 2), the skull of an *Archaeolemur* showed signs of being fractured with an ax-like tool, and burned bones of this genus have also been recovered (82, 379); however, a radiocarbon date derived from this specimen falls during a period before current estimates of human colonization of the island (see Plate 2). Other purportedly pierced skulls of *Archaeolemur* have been excavated from Ampasambazimba (see Plate 12) and Beloha (23).

### Hippos

Ross MacPhee and David Burney examined some *Hippopotamus lemerlei* material held in the Muséum national d'Histoire naturelle in Paris that was excavated by Alfred Grandidier from two different sites north of Toliara, Lamboharana, and Ambolisatra (251) (Figure 39). It has recently been suggested that hippo



Figure 38. For several decades Laurie Godfrey, together with several colleagues, has been studying lemur subfossils from many different facets. In this photo, taken in 1971 in the former Académie Malgache laboratory in Antananarivo, she is shown examining and measuring excavated bone remains. (Photograph by Paul Godfrey.)

material from these two sites might be referable to *Hippopotamus guldbergi* (107). In any case, these bones had cut marks, the origin of which could best be explained by a metal object passing across the surface immediately following the hippo's death. Three of the four radiocarbon dates they obtained from different modified hippo bones spanned the range from

about 2,020 to 1,740 years BP, and these dates, when published, represented the earliest known animal-human interactions on the island. Subsequently, other evidence has been found that pushes this date further back in time (see Plate 5). The fourth hippo specimen, showing a knife mark, yielded a radiocarbon date of 3,495 years BP.



Figure 39. A historical photograph taken by Guillaume Grandidier at the subfossil site of Ambolisatra during the 1898–99 excavations. (Photograph courtesy of the Académie Malgache.)

A few different points need to be mentioned about the MacPhee and Burney hippo samples. The oldest of these radiocarbon dates was deemed unreliable. A second sample from the same original bone was resubmitted for radiocarbon dating and yielded a date of around 2,020 years BP. Hence, there is a discrepancy of nearly 1,500 years between samples from the same specimen, with contamination or the low level of recovered bone collagen creating important analytical problems in producing accurate dates. The important message here is that reported radiocarbon dates are not always accurate and, when possible, multiple dates from the same stratum or individual are important for corroboration and correct documentation of the timing of an event. Another quandary is that most of the cut marks are centered on the bone mid-shaft. This is not intuitive, as it can be assumed that someone dismantling a hippo would have sufficient anatomical insight to know that cuts should be made at the ends of the bones rather than toward the center.

As mentioned in the introduction to this section,

a dilemma for archaeologists is reconciling often important temporal differences between physical remains, such as pottery or other cultural objects, as compared to inferred human proxies, such as cut marks in bone. This problem is exemplified by the MacPhee and Burney hippo radiocarbon dates, which at that time pushed back by several hundred years the period when humans first colonized the island, as the previous archaeological evidence indicated a date of about 1,500 years BP (24).

More recently Dominique Gommery and colleagues (139), based on hippo material from Anjoihibe (see Plates 13 and 14), have presented even older dates of about 3,950 years BP for cave deposits associated with reported human-modified bone remains. Three different hippo bones were recovered from the site, which had distinctive marks on the surface that were interpreted as having been caused by an undefined object when the animals were butchered. However, based on the illustrations provided, the cut marks in certain cases appear similar to gnawing marks of smaller mammals and do not show parallel structure

to the previously reported straight and non-serrated traces left in the bone remains such as, for example, at Taolambiby (see Plate 5) (296). In addition, the marks are often not concentrated toward the ends of the bone, which would normally be the case when dismantling an animal with a sharp object. Most critically, Gommery and his colleagues were unable to use these hippo bones in the radiocarbon dating, but relied instead on other bone material in the same deposits. As these tantalizing dates are notably before previous published evidence of people on the island, in order for them to be widely accepted, the hippo bones need to be dated and the marks reexamined in detail by forensic specialists.



# Hypotheses on What Caused the Extinctions during the Holocene

Over the course of the past century, numerous ideas have been presented on the potential causes associated with habitat and ecosystem changes and the extinction of different land animals on Madagascar. David Burney (48) has distilled many of the ideas into five distinct hypotheses, which are summarized here.

- (1) *Massive fire*: The idea that a considerable portion of the island was transformed by large-scale fires set by humans during a short period was formulated by Henri Humbert (197). The principal notion here is that as humans colonized the island from the coast inland, they employed fire to clear forests and forested woodlands, which resulted in the loss of habitat and subsequently the extinction of a considerable number of animal species.
- (2) *Climate change and extensive drought*: Joël Mahé and Michel Sourdat proposed that the southwestern portion of Madagascar went through a drastic climatic change, toward increasingly dry conditions and a critical disappearance of permanent wetlands (257). Subsequent extinctions of terrestrial and aquatic organisms were associated with natural habitat changes directly linked to aridity.
- (3) *Pleistocene overkill*: Quickly after people arrived on Madagascar and spread from the coastal to highland areas, they hunted and over-exploited locally occurring animal species that were naive to humans, and this led to massive extinction. This “blitzkrieg” hypothesis was formulated by Paul Martin and has been applied to different areas of the world (260, 262). It implies an inexorable, wave-like extirpation process that proceeds very rapidly and can be distinguished from a longer lasting or “protracted overkill” model (49).
- (4) *Hypervirulent disease*: A relatively recent hypothesis was proposed that pathogenic organisms

introduced by humans or their commensal animals were lethal to mammals as well as possibly to other organisms (252). The pathogen(s) quickly spread across the island, leaving a wake of extinction behind.

- (5) *Synergy*: Recognizing the complex ecological and cultural landscapes of Madagascar, this hypothesis proposes that different factors worked in a synergistic manner and were not necessarily the same in various areas of the island (48). Climate change as a background factor was subsequently amplified by different anthropogenic impacts.

In Part 2 of this book, we discuss the finer details of these hypotheses associated with the narratives that accompany the different plates, and we weigh the pros and cons of evidence at hand to support or reject these explanations of what has transpired on Madagascar over the past millennia. The various sites examined in detail in Part 2 provide distinctly different insights into these questions. As will become apparent, in many cases the “jury is still out,” and current information only provides partial clarification as to the changes that took place. However, in several cases, the evidence allows the rejection of some of the above hypotheses.

# Extinction, Conservation, and the Future

Over the past few thousand years, Madagascar has experienced the extinction of a wide assortment of extraordinary animals, ranging from giant elephant birds, small hippos, large Carnivora, massive eagles, lemurs the size of gorillas, a bizarre “aardvark-like” beast, and other assorted creatures. To quote from a review of the culture history of Madagascar by Robert Dewar and Henry Wright, “Madagascar’s Holocene natural history has been portrayed as a one-act morality play: a paradise of wonders destroyed by the cupidity and folly of men” (83). We now know that what transpired was distinctly more complicated. As explained in detail in Part 2 of this book, based on site and regional case studies of subfossil bone and pollen and charcoal deposits, no single island-wide cause can be invoked to explain the disappearance of the extinct fauna, as well as the considerable modifications of the natural ecosystems, which have occurred in the recent geological past. In some cases, climate change seems to be the principal reason for decline leading toward extinction, whereas in others human-induced factors or a synergistic combination of climate and human sources are more plausible.

Regardless of the origins of these extinctions dating from the past millennia, massive modifications of the remaining natural environments have taken place during periods that are more recent. This includes very substantial reduction in forest cover over the past 100 years (Figure 40, *left*) and large-scale conversion of former wetlands to rice paddies (Figure 40, *right*). For example, from 1950 to 1985, the eastern humid forests of Madagascar were reduced in surface area by 50 percent, and the zone of heaviest human impact was the lowland formations (185). Over the past three decades, since 1985, this portion of the island has been degraded even further, and the very high level of deforestation has resulted in the destruction of considerable natural habitats, negatively affecting the locally occurring plants and animals.

Large-scale erosion across deforested portions of

the island has had a considerable impact on siltation and productivity in agricultural bottomlands (Figure 41, *left*). In portions of the island, up to 250 tons per hectare of topsoil are eroded away per year (315). A particular form of erosion gully occurs on Madagascar, known locally as *lavaka* (Figure 41, *right*), a Malagasy word that has been incorporated as a technical term in the international geological literature. Recent work indicates that certain *lavaka* formations probably predate human arrival and landscape transformation. Even though these are natural formations associated with certain aspects of Malagasy soils, human degradation of the landscape has intensified their extent on the island, particularly in portions of the east.

A more recent study of existing forest cover on Madagascar, with a greater variety of images and including the different forest types, found a similar pattern (191). On an island-wide scale, forest cover between about 1953 and 2000 was decreased by 40 percent, with the specific rate for humid forest being 47.5 percent and dry forests 57.8 percent; the spiny bush suffered less. During this period, nearly four-fifths of the remaining forest blocks were reduced in size, leading to very substantial fragmentation and isolation (Figure 26, *left*). Regardless of debates concerning the original habitat types and extent of forest on the island during the period that humans originally colonized, these figures are associated with changes within the past decades, and, in the simplest of terms, human-induced habitat degradation was the cause. As a further indication of these trends, even what we consider anthropogenic habitats in the Central Highlands have experienced transformation in the past half-century, particularly the conversion of wetlands to rice paddies and the disappearance of significant areas of gallery forest (223).

As a significant proportion of the island’s endemic land vertebrates are forest-dwelling and will not cross non-forested areas—for example, to search for food



Figure 40. Regardless of the manner in which evidence from the paleontological and archaeological records of climate change and human modification of the environment are interpreted, there is undisputable documentation of the impact that people have had on the island in the past few centuries. This includes the clearance of large areas of forest for slash-and-burn agriculture, as shown here in the hills south of the Andasibe forest (*left*) and the large-scale modification of former wetlands into rice paddies, as found, for example, across areas of the Central Highlands such as near the Andringitra Massif (*right*). (Photographs by Olivier Langrand.)



Figure 41. Large-scale ecological problems on Madagascar are associated with deforestation and the extraordinary levels of erosion that follow. This is a particularly serious problem with the siltation of productive agriculture lands and vast quantities of sediments flowing into the sea and suffocating marine ecosystems. In some portions of the island, such as in this section of the Makira Forest near Maroantsetra, the landscape has been severely scarred by erosion (*left*). A particular form of erosion gully occurs on Madagascar, known in Malagasy as *lavaka* (*right*), and this word has been incorporated into the international technical geology literature. Shown here is an aerial view of a massive *lavaka*. (Photographs by Olivier Langrand.)

and mates or disperse—the impact of deforestation has very ominous implications for the long-term future of the island’s biodiversity. Studies on the consequence of forest fragmentation at sites such as Ambohitantely in the Central Highlands have shown a direct relationship between fragment size and species diversity (154, 235, 367). Specifically, as forest blocks become smaller, measurable numbers of the land vertebrates become locally extinct.

The critical point for this discussion is that the modern biological crisis facing Madagascar is rooted

in socioeconomic factors. A significant proportion of Malagasy living in the countryside lead subsistence or nearly subsistence lifestyles as agriculturalists, and deforestation to obtain short-term agriculturally productive lands is part of their tradition. With high levels of population growth and ever-decreasing forest areas, this system is simply not viable for the short-term ecological future of the country. In part related to inflation, political strife in 2009 leading to a military coup, and the associated mismanagement, corruption, and stagnant economy, Madagas-



Figure 42. Unique and biologically important areas of forest remain on Madagascar, such as this dry deciduous *tsingy* forest of the Bemaraha Massif. Here toward the southern end of the massif, the Manambolo River forms a deep canyon, and exposed areas of limestone, as well as human-cleared areas, can be seen. The conservation of sites such as Bemaraha holds enormous importance for safeguarding the extraordinary natural patrimony of Madagascar and for that matter that of our planet. (Photograph by Olivier Langrand.)

of Madagascar's biodiversity and the maintenance of certain aspects of Malagasy culture and the island's natural patrimony are simply bleak. To quote a very poignant summary by David Burney, "The message from the past, sent clearly to conservationists concerned for the future of Madagascar, is that the extinction spasm that eliminated the . . . megafauna is working its way down through smaller organisms. . . . The fossil record provides mute testimony that a great deal can be lost rapidly and irretrievably" (47).

As an important closing statement to Part 1, while putting together this book, we have learned that generalizations cannot be applied across the complete island. This conclusion came to us as a bit of a surprise, but in our opinion it follows logical assessment of existing data. What happened in a given region in recent geological history associated with the disappearance of habitat and extinction events needs to be logically separated into two separate periods during the Holocene, that is, between pre- and post-human colonization, rather than stringing all of these events across a time continuum.

car was chosen as the country with the world's worst economy in the first half of 2011 (103). Until elemental land-management issues coupled with economic growth and education advancement are properly addressed, the precarious future of the country will remain in an indeterminate state.

Given the high level of biological diversity and human-induced threat to the remaining natural habitats, such as the extraordinary *tsingy* formations of the west (Figure 42), Madagascar is considered one of the world's conservation hotspots. Both national and international biologists, conservationists, and social scientists have considered these critical questions in detail, and numerous programs have been proposed and advanced to address the future of the island's social development and unique biodiversity. While there have been many positive developments, current political strife, the lack of a properly functioning judicial system, and irrational utilization of natural resources—including massive exploitation of precious wood in existing protected areas—continue to reduce the little remaining forest cover. Recent estimates of the extant natural forest cover indicate that somewhere between 10–15 percent of the island retains forest, and through time the remaining habitat decreases in size and becomes more fragmented.

With continued loss of natural habitat, the future



# Part 2:

# Case Studies



# Geographical Plates

## Plate 1: Cap Sainte Marie—the Ecology of Elephant Birds and Their Interface with Humans

As discussed in Part 1, Madagascar has an extraordinary extant flora and fauna, with one of the highest levels of unique organisms (endemic) anywhere in the world. One of the principal reasons why the biota of Madagascar is so exceptional is directly related to its geological history, specifically its isolation from other large landmasses deep in geological time. In order to understand how this uniqueness came about, it is necessary to start millions of years ago. Here we briefly discuss the geological history of the island to provide the background needed to understand the chronicle of vertebrate colonization of the island, in this case an exemplary group of recently extinct birds, the elephant birds of the family Aepyornithidae. (For further details, see “Madagascar in Deep Time—Isolation and Origin of Its Plants and Animals,” in Part 1.)

Certain areas of bedrock on the island are some of the oldest in the world, dating to more than 3.2 billion years (88). Today Madagascar is slightly more than 400 km to the east of Mozambique and southern Tanzania, in the western portion of the Indian Ocean, but its position has changed over many millions of years, and it was not always isolated in the Mozambique Channel. The best place to start to explain the geological history of the island is with the supercontinent of Gondwana, which was composed of Africa,

---

On the basis of the density of eggshell remains of elephant birds, specifically *Aepyornis maximus*, recovered at Cap Sainte Marie, the southernmost point on Madagascar, it is inferred that this species nested in relatively dense colonies. The factors that led to the extinction of this species, the largest bird that is known to have lived on Earth, remain vague. (Plate by Velizar Simeonovski.)





South America, Australia, Antarctica, Madagascar, and India. This massive continent was stable until about 165 million years ago, when deep movements in the Earth (tectonics) started. When Madagascar detached from Gondwana, India was still connected to it, forming Indo-Madagascar, which reached the current position of Madagascar about 130–120 million years ago. Subsequently, about 88 million years ago, India separated from Madagascar and started moving toward the north. It eventually collided with the landmass that is today Asia.

To help put things in perspective, 165 million years ago is the middle portion of the Mesozoic (see Figure 3), more precisely the Jurassic, which was the age of dinosaurs. Note that this ancient period is long before the evolution of the majority of animal groups that exist today. Hence, the presence of most living land vertebrates on Madagascar cannot be explained by their ancestors having been on Indo-Madagascar when it detached and moved away from the Gondwana continent (vicariance). The “Noah’s Ark” metaphor just does not work here. The colonizing ancestors, in more recent geological time, would have instead had to find another manner to find their way to Madagascar. For flying organisms such as bats, certain insects, and birds, it is easy to imagine how they might have colonized the island, as compared to non-flying land mammals such as lemurs, tenrecs, and rodents, who would have had to transverse a considerable area of oceanic water or arrive by some other means.

The first known fossils of a modern bird lineage date from the end of the Cretaceous, or about 70 million years ago (63). It is important to keep in mind that at this date Madagascar was already completely isolated from Gondwana and, for that matter, any other landmass. Among the living birds of Madagascar, two groups have been shown, based on molecular genetic inferences, to be older than the end of the Cretaceous and may have their origin before the breakup of Gondwana. These include the flightless elephant birds of the family Aepyornithidae and the weakly flying mesites of the family Mesitornithidae (67, 196, 335). Hence, given the fact that the elephant birds are flightless and their origin is notably deep in geological time, the working assumption is that they represent an ancient group that was on the Madagascar landmass before the breakup of Gondwana. Although we accept this vicariance scenario as the more plausible one, alternative hypotheses have been presented, such as their swimming or rafting on

flotsam across the Mozambique Channel to Madagascar sometime after the separation of Madagascar or Indo-Madagascar from Gondwana. With this as the prelude, we can now turn to the amazing elephant birds, one species of which represents the largest known bird to have ever existed on our planet.

In 1851 the world scientific community was astounded by a communication by Etienne Geoffroy Saint-Hilaire, announcing to the Académie des Sciences of Paris the discovery of a giant extinct bird he called *Aepyornis maximus*. The generic name is derived from the Greek *aipus* (high) and *ornis* (bird), and the species name comes from the Latin meaning “great or enormous.” This discovery was based on three massive intact eggs purchased by a merchant marine along the southwest coast of Madagascar and brought back to France. This bird is estimated to have reached 3–4 m in height and approached 440 kg in body mass (7, 61); more recent estimates indicate that these body-size estimates might be too large (391). In any case, these measurements are much larger than the living ostrich, *Struthio camelus* (order Struthioniformes), of Africa and the Middle East (Figure 43) (38). Eggs of *Aepyornis maximus* measured about 32 by 24 cm and based on volume held the equivalent of 150–170 chicken eggs, or 7.5 liters—which would be sufficient to make an omelet to feed about seventy-five people! The egg of this bird is the largest single cell known in the animal world. Whole eggs can still be found today, particularly in the Androy region between Marovato and Cap Sainte Marie, including those that contain embryonic remains (16).

Elephant birds were flightless, with very small and rudimentary wings and no keel on the breastbone (sternum) for the attachment of flight muscles. These birds had distinctly long legs, with the tibiotarsus (leg bone) being longer than the tarsometatarsus (ankle-bone). They were clearly capable of marching and running, perhaps at considerable speeds for at least short bursts. The bill was long and relatively broad, and bore a sharp cutting edge. It has been suggested that they may have been forest-dwelling, similar to cassowaries, *Casuarius* sp. (order Struthioniformes) of Australia (199).

Over the course of the subsequent eighty years after the description of *Aepyornis maximus*, at least fourteen other taxa belonging to the genus *Aepyornis*, as well as a smaller genus *Mullerornis*, were described. Remains of these birds are known from the western side of the island from the southern to the northern tips and from several localities in the Cen-



Figure 43. Elephant birds were massive birds. Shown here is a composite skeleton of the largest species, *Aepyornis maximus* (in the middle of this photo taken in the galleries of the Académie Malgache probably at the turn of the twentieth century), which produced eggs approximately 7.5 liters in volume. In comparison, to the left is a skeleton and egg of a living ostrich, which is notably smaller than *Aepyornis maximus*. (Photograph from the Archives of Foiben-Taosarintanin'i Madagasikara.)

tral Highlands, such as Antsirabe (see Plate 11) and Ampasambazimba (see Plate 12). Interestingly, they are largely unknown from the lower-lying areas of the east, but this may be associated with the lack of subfossil sites from this region (see Plate 10).

The problem in discerning how many species of elephant birds existed on Madagascar is that some were diagnosed and described based on isolated bone remains or eggshell fragments. Thus, for example, *Aepyornis cursor* was named using a leg bone, and *Aepyornis grandidieri* was proposed from eggshell fragments. Based on morphology, or the lack thereof, it is simply not possible to determine whether these two names represent the same species or not. With the advent of sophisticated ancient DNA techniques, this should provide important insight to the number of species of elephant birds that existed. However, in general, osteological and eggshell material of these

birds has yielded low-quality DNA to date (67), but advances have been made in obtaining DNA from eggshell fragments (201, 287). The use of ancient DNA techniques with the extinct New Zealand moas (order Dinornithiformes)—in many ways a parallel group of large flightless birds, which are often referred to collectively as ratites (superorder Palaeognathae)—has provided extraordinary insight into their systematics, ecology, and species diversity. These techniques provide remarkably fine details, from picking apart the ratio of males to females in different bone deposits down to specific details on their diet based on fecal contents (5, 389). Once the techniques are worked out, comparable ancient DNA studies on elephant birds would certainly provide an important window into their natural history and perhaps the cause(s) of extinctions.

Following older morphological comparisons of elephant bird material, it would appear that about seven species, three in the genus *Mullerornis* and four in the genus *Aepyornis*, are recognizable (40); however, these figures are tentative at best. If these species showed pronounced differences in body size between adult males and females (sexual dimorphism), as has been shown in the New Zealand moas, the number of species could be cut in half. The eggshells of these two genera are generally differentiated based on thickness, with those of *Aepyornis* being more substantial than *Mullerornis*. In the south, remains of the latter genus are rare and represent roughly 1 percent of the eggshell found in the context of paleontological and archaeological sites (293).

Étienne de Flacourt (1607–1660) was named commandant of Madagascar in 1649 by the king of France and was based in the region of Fort Dauphin, which is today known as Tolagnaro. He was a chronicler of culture and nature during the period he was in the southeast, and extraordinary details are presented in his book *Histoire de la Grande Isle Madagascar* (104). Although he did not see elephant birds firsthand, he was able to obtain information on these animals and used the Malagasy name “vouron patra” in his book. While it is tempting to assume that these animals were still alive during the period of Flacourt’s tenure on Madagascar, this might not have been the case, and as discussed below, oral tradition associated with details of these animals has lasted much longer than their residence on Earth. The Malagasy name of this bird cited by Flacourt is derived from *vorona* for “bird” and *patra* for the geographical region of the “Ampatres,” which corresponds on a map produced by Fla-

court to the Mandrare Basin and the zone referred to today as Androy, that is, the home of the Antandroy. Today elephant birds remain in local folklore have many different names, which in the Antandroy dialect of Malagasy include *vorombe* or *vorom-bey* (large bird), *vazoho* (to look at), and *vorombazoho* (the bird with keen vision).

In modern times among the Antandroy, some elements remain in their oral tradition on the natural history of the *vorom-bey*, which include “*Vorom-bey mahilala ty agnombe, mahilala feie tsy mivolagne,*” or “the zebu are like giant birds, they are very wise, even though they do not communicate this wisdom to one another” (364). In the Central Highlands and coastal sites in the south and western portions of the island, remains of elephant birds have been found at different paleontological and archaeological sites close to watering points such as rivers, marshes, artesian wells, and open caves with freshwater sources. Isotope analyses conducted on elephant bird eggshells seem to indicate that they browsed predominantly on  $C_3$  vegetation, and in comparison to African ostriches, their oxygen isotopes suggest that they may have relied on groundwater-fed coastal wetlands for drinking water (64). However, with the current state of information on these birds, including these isotope analyses, little can be directly gleaned about basic aspects of their natural history, such as diet and breeding systems, and the best strategy to piece together what happened to them is to draw parallels to other large ratites, such as ostrich and New World rheas (order Rheiformes) or extinct moas.

It has been recently proposed that elephant birds were responsible for the dispersion of the seeds of *Uncarina* (family Pedaliaceae) (271), a genus restricted to the dry forests of Madagascar. This plant has very spiny burr-like fruits, with fishhook-like attachments. Once ripe, these fruits fall to the ground and could easily attach to the feet of large vertebrates, such as *Aepyornis* or *Mullerornis*. However, as several giant lemurs, such as *Archaeolemur* and *Hadropithecus*, were also at least partially terrestrial, there is no compelling reason to postulate that there was a direct co-evolution between *Uncarina* and elephant birds.

It is also rather likely that elephant birds, as well as some of the larger extinct lemurs, were responsible for opening the large fruits of baobabs (*Adansonia*, family Malvaceae), which can reach the size of a coconut (294). Six of the eight species of baobabs in the world are endemic to Madagascar, and their biomass in certain forests is notably important. Hence, given

this resource, it can be presumed that elephant birds and different extinct lemur species cracked open fallen fruits and consumed baobab seeds. Whether these seeds passed intact through the digestive systems of elephant birds is a difficult question to answer without the recovery of their subfossil feces and the study of their contents. As noted above, recent analysis based on carbon isotope values from radiocarbon-dated *Aepyornis* eggshell seems to indicate that these birds were feeding predominantly on  $C_3$  plants (70).

Another paper was recently published relevant to possible plants consumed by elephant birds, with particular attention to plant defensive adaptations against their foliage or other parts targeted for consumption by herbivores (37); this study made numerous comparisons to an inferred plant defensive system against extinct New Zealand moas. The idea behind this comparison is as follows: plants can maintain certain structural defenses to reduce consumption of their vegetative parts long after the extinction of browsing animals. In New Zealand, a number of plants have wide-angle or zigzag branching patterns, often with spines in places that would diminish the interest of herbivores feeding on the leaves. These adaptations have been interpreted as evolved defenses specifically against feeding by moas, which have been extinct for at least 600 years. These researchers have identified similar types of adaptations in certain Malagasy plants and by analogy have inferred that a parallel defense system against large browsing birds also evolved there.

Excluding aquatic habitats, where at least three extinct species of hippos occurred until very recently, elephant birds almost certainly made up an important biomass of herbivores on Madagascar, perhaps second only to giant tortoises (see Plate 4), before the introduction of cattle only a few centuries ago. William Bond and John Silander’s line of reasoning is plausible and certainly tantalizing, but requires some caveats; an important difference on Madagascar is the sizable number of other terrestrial herbivores, including extinct and extant lemurs and tortoises, while on New Zealand moas were the principal herbivores. Hence, these plant adaptations on Madagascar, if correctly identified, are not necessarily specifically or exclusively against elephant birds.

Another good example of trying to draw parallels between living and extinct species of ratites is the considerable elephant bird eggshell remains found on terraces above the beach level at Cap Sainte Marie

at the southern tip of Madagascar. What is the origin of these remains? Along a 12 km portion of this part of the island's coast, twenty-two different clusters of often dense elephant bird eggshells were located, most within a relatively short distance of dry valleys passing between the coastal dunes and the coastal sandstone cliff (293). At a few sites, there is an extraordinary concentration of eggshell remains covering something approaching just under a hectare of what is presumed, based on the shell thickness, to be mostly eggshells of *Aepyornis maximus*. The quantity and density is reminiscent of an archaeological site, but in this case eggshell fragments replace the pottery sherds. These high concentrations have been interpreted as ancient colonial nesting sites of *Aepyornis* (23, 364); based on this supposition, we have composed Plate 1. Ostriches and rheas, both probably phylogenetically closely related to elephant birds, have communal nests with eggs laid by a broad assortment of females, including a dominant or major female, and the territory-holding male incubates the eggs and provides parental care to the young (28). These types of nests, particularly when in high concentration, generate lots of egg debris. Hence, by further extrapolation, it is possible that the birds that occupied the presumed former colony at Cap Sainte Marie had ancestral breeding systems found in certain living ratites, although we cannot rule out the alternative that this behavior evolved in parallel.

Now we can turn to the question of what happened to elephant birds. Was their disappearance associated with natural climatic change, the direct result of human intervention, or the interactions between these two factors? The eggs of elephant birds have been found in different archaeological contexts such as at Talaky in the extreme south near Tsihombe (25, 371). Several potential problems arise in interpreting some of the archaeological data, specifically if the elephant bird remains were found within the archaeological layers and, if so, for what reason did humans exploit these animals? Were the eggs consumed or used as 10-liter "jerry-cans" to transport liquids such as water? In the latter case, association is not necessarily causality. Relevant here and rather extraordinarily, there are cases of Malagasy using eggs of enormous size, with little doubt those of elephant birds, to transport liquids until the mid-nineteenth century (25).

Several ratites such as Australian cassowaries, which will violently lash out with their long straight claws, would be formidable protectors of their nests from pilfering egg predators, including humans.

Even if humans could easily locate the occupied nests, such as in the case of the proposed *Aepyornis maximus* colony at Cap Sainte Marie, a kick from a several hundred-kilogram bird would be a clear hazard. For a well-known and amusing science-fictional account of such a hypothetical encounter, we refer you to the marvelous short story by H. G. Wells titled "Aepyornis Island." Therefore, with this information as a slight tangent, we now return to the question as to what happened to the elephant birds. There are several lines of evidence, often pointing in different directions, that we can enlist in order to try to piece together a coherent response to this question.

As noted above, a recent study on the amino acids and stable isotope contents of elephant bird eggshell concluded that they had notably lower oxygen isotope values as compared to those of living African ostriches, which live in a semi-arid habitat (64). On the basis of different lines of evidence, these authors suggested that elephant birds fed extensively on coastal plants tapping local groundwater sources. If this is correct, as southern Madagascar became more arid (see Plate 4 for a discussion of this point), the reduction or complete drying out of certain sources would have certainly impacted local populations. Following this logic, birds would have been concentrated around the remaining seasonal or permanent freshwater habitat, particularly along river margins or zones of resurgent water such as coastal lagoons. Strikingly, these are indeed places where elephant bird eggshell remains are abundant (293). However, concentrations of eggshells, such as found at Cap Sainte Marie, are also known from coastal sites without any freshwater sources. Therefore, even though these isotope findings are noteworthy, they cannot explain broad patterns of extinction of elephant birds across their vast former range.

During their extensive archaeological survey of southern Madagascar, specifically within the Androy area, Michael Parker Pearson and colleagues investigated different questions associated with the extinction of elephant birds (293). Appreciable concentrations of eggshell remains of these birds have been identified from different human coastal settlements dating from the last 1,000 years, but no unequivocal evidence of human predation has been found. One important result of this study was that elephant eggshell remains found in stratified deposits yielded radiocarbon dates notably older than associated wood remains. It would appear that these birds assimilated older carbon through their diet, which was deposited

in the eggshells during their formation and thereby yielded these seemingly discordant dates. Based on these results, this would indicate that radiocarbon dates derived from eggshell remains provide inaccurate and older dates than when the eggs were actually laid. Hence, this casts some doubt on the precision of dates, without a date adjustment, for these birds derived from eggshells; perhaps this problem is limited to populations that inhabited coastal areas. In light of this point, two dates are available for elephant birds based on bone samples: a *Mullerornis* sp. tibiotarsus obtained at Ankilibeandry, near Belo sur Mer, at 1,280 years BP (mean calibrated date of 1,135) and an *Aepyornis* sp. from Itampolo at 1,880 years BP (mean calibrated date of 1,730) (69). What is important about the specimen that produced the last date is that humans modified the bone (48).

Michael Parker Pearson and colleagues revisited the Talaky site, which represents the only archaeological site they excavated that produced elephant bird eggshell remains in a clear human context. This is the site mentioned earlier that was worked by René Battistini and colleagues some years ago that had been previously invoked as providing evidence that people had fed upon elephant birds. In the new excavations, the Parker Pearson field team found intact human occupation layers with some remains of elephant bird eggshell (293). On the basis of radiocarbon dates, including an adjustment for the old carbon reservoir problem mentioned above, the dates span the range from the ninth to fourteenth centuries. This range of dates overlaps with when Talaky was occupied by humans. Parker Pearson and colleagues make the very valid point that if indeed humans were responsible for the local demise of elephant birds, the quantity of eggshell remains would be expected to be much greater than the current evidence indicates. As ancient intact eggs are still recovered today from the coastal sandy areas, it is possible that at least a portion of eggs used to transport liquids were not necessarily fresh. Perhaps some of these were broken and made their way into the human debris. To offer further credence to this speculation, recall that we mentioned earlier that there are several nineteenth-century accounts of people using what could only be elephant bird eggs as “jerry-cans” or organic jugs to transport liquids (193).

One other interesting element in the history of elephant birds is that several Middle Age travelers brought home stories of a legendary bird, often referred to as the *rokh*. These include the tales from

*The Voyage of Sinbad and A Thousand and One Nights*, where Madagascar could be construed as the place where the *rokh* lived. Certain naturalists have interpreted this celebrated creature to be the elephant bird of the family Aepyornithidae, while others have equated it with a large bird of prey. Further discussion is provided under Plate 20 as to the possible identity of the *rokh*.

When elephant birds went extinct is unclear, but at least in the Androy region, combining accounts from Flacourt and different information from archaeological excavations (293), they probably disappeared about 750 years BP and hence locally overlapped in time with humans. However, there is little evidence to date of extensive human hunting of these birds or their eggs in this region; nevertheless, the later pressure has been cited as a probable cause of their extinction (23). Climate change toward increasing aridity is well documented in the south, starting about 3,000 years BP, which certainly had a profound impact on the local populations. The factors in other portions of the geographical range of members of this family, which ranged to the far north and across portions of the Central Highlands (278, 388), may be radically different from the south. As Pierre Vérin succinctly stated more than fifty years ago, “We believe that the question associated with the extinction of this large ratite cannot be resolved without the direct collaboration of geologists, zoologists, and archeologists” (25). We propose that once tangible data are available to address this question, the critical factors will probably be a synergy between natural climate change and human intervention (54). We also imagine that across the former range of this extraordinary group of birds, there will also be geographical and cultural differences in the causes of their extinction.

## Plate 2: Andrahomana I—the Ecology of Extreme Southeastern Madagascar and a Barometer of Change

The Andrahomana Cave, in southeastern Madagascar, has been excavated on several occasions by different paleontologists and archaeologists, spanning the period from 1899 to 2003. The cave and its contents

are interesting for several reasons. The ceiling of the main portion of the cave has collapsed and, together with some remaining holes in the upper portion (or “skylights”), natural pitfall traps have formed, captur-

---

A scene at dusk in the forest above Andrahomana Cave. A Madagascar Long-eared Owl *Asio madagascariensis* begins hunting, and its first prey of the evening is an individual of the now-extinct shrew-tenrec *Microgale macpheei*, held in its talons. Below the perched owl is the changing of the guard, with the smaller and slightly crepuscular red forest rat *Nesomys rufus* finding its last food before retiring for the night, and the now-extinct, notably larger, and presumed nocturnal *Hypogeomys australis* starting up its activities. Two species of the large extinct lemur genus *Megaladapis* (dubbed “koala-lemurs” by some) have been identified from the site: *Megaladapis madagascariensis*, which was the smaller of the two, meandering below the owl and about to accidentally fall through one of the “trapdoor” skylights in the cave ceiling; and *Megaladapis edwardsi*, which was much larger and more frequently preserved in the cave sediments, seen here grasping the base of a short tree, perhaps feeding on strips of bark. The extinct giant tortoise *Aldabrachelys abrupta* in the background has “closed down” for the night, retreating into its shell. For a key to the different animals, see black-and-white inset for Plate 2 in color gallery. (Plate by Velizar Simeonovski.)



ing a variety of organisms (see Figure 5, left). Hence, the cave has served as a filter over time, preserving an assortment of remains that provide insight into regional climatic and biotic changes. Further, the cave is at the western foothills of the Anosyenne Mountains and close to one of the more dramatic ecotones in the world, at the divide between humid forests to the east and the dry spiny bush to the west. The natural plant community remaining near the cave is transitional and retains elements of these two vegetational types. With the waning and waxing of wetter and drier periods in recent geological time, the cave's subfossil remains provide a barometer to measure these shifts. To give a better sense of this ecotone, we present a quote from Steve Goodman's field notes at a site north of the cave and at the western limit of parcel 1 of the Andohahela National Park (145):

*In the early afternoon after climbing over the Col d'Ambatmaniha . . . we came to the final ridge before the descent down the western slopes of the Anosyenne Mountains. . . . Here we were surrounded by large trees and terrestrial leeches. Just below us, we could see to the west a dramatic shift in vegetation. Large baobabs were within a kilometer . . . and with binoculars, the characteristic . . . Didiereaceae of the spiny bush . . . could be seen. . . . The calls of humid forest birds were around us, while those characteristic of the spiny bush could be heard below. The shift was so abrupt that it seemed possible to stand in the humid forest and throw a rock into the spiny bush.*

The early excavations of Andrahomana Cave conducted by Franz Sikora in 1899 (Figure 44) and over the following three years by Charles Alluaud, together with Guillaume Grandidier and then Martin François Geay in 1906, produced remarkable collections of animal bones (55). Some of the more notable material from these early years included several splendid skulls of *Megaladapis edwardsi*, partially complete skeletons of *Archaeolemur majori* and *Hadropithecus stenognathus*, as well as remains of a very large rodent of the genus *Hypogeomys*. The material that these different paleontologists removed from the cave would be subsequently studied by generations of researchers. As typical of the era, these early excavators were keen to find bone remains of large animals and hence concentrated their efforts on the megafauna, paying little attention to questions of the position of the subfossil material in the sediments (stratigraphy) and largely ignored the smaller bones present in the cave deposits.



Figure 44. Over the past century, Andrahomana Cave has been visited and subfossil material excavated by numerous researchers. In 1899 Franz Sikora visited the site and obtained important material that has been subsequently studied by numerous scientists. Here we present a historical photograph of the cave entrance taken by Franz Sikora. (Courtesy of the Académie Malgache.)

In 1926, the renowned French naturalist and colonial administrator Raymond Decary visited the cave (78). He sent a collection of small mammal remains, probably at least in part derived from raptor pellets that are common in the cave (see Figure 5, right), and other small vertebrates to Guillaume Grandidier, who subsequently named two small insectivorous animals from the remains as new to science and belonging to the endemic family Tenrecidae. In both cases, the two animals described by Grandidier (182), *Cryptogale australis* and *Paramicrogale decaryi*, were subsequently found to have already been named by earlier taxonomists, and hence became synonyms of scientific names already in usage.

Perhaps the next most important visit to the cave was by Paul Martin and Alan Walker in 1966. This is the year that Martin published a landmark paper setting the stage for his Pleistocene overkill hypothesis



Figure 45. The most recent paleontological team to visit Andrahomana Cave was in 2003 under the direction of David Burney. Here the group is shown trekking back to base camp along a zebu trail after a long day in the cave (*left*). Bill Jungers is in the foreground, and the Indian Ocean can be seen in the distance. The coastline in this image was employed to configure portions of Plate 2. (Photograph by Laurie Godfrey.) The seaside entrance to the cave, specifically during medium to high tide, can be treacherous. Here the entrance is shown during the period of low tide (*right*). During the 2003 field season, a cable ladder and ropes were used via holes in the cave ceiling (see Figure 5, *left*) to get people in and out of the cave. (Photograph by Thomas Wesener.)



(see Part 1, “Hypotheses on What Caused the Extinctions during the Holocene”) to explain the observation that after the colonization of a given area by humans, the large animals quickly go extinct (260). Martin and Walker reminisce about their adventure together in an anthology of short stories celebrating the life of the daredevil pilot, Ike Russell, who delivered them to Madagascar via Tanzania and Mozambique in a very small airplane (381). Walker described it as “the trip of a lifetime” that contributed greatly to his dissertation on giant extinct lemurs, and Martin acknowledged it as an experience that strengthened his then-unconventional ideas about the role of humans in megafaunal extinctions. During this trip, Martin and Walker first visited and excavated paleontological sites in the southwest, including Ampoza (see Plates 7 and 8), but then turned their attention to Andrahomana. Russell dropped them off about 6.5 km from the cave after landing on dried-up Lake Erombo. Time in the cave was limited, but they recovered a few fragments of the giant “koala-lemur” *Megaladapis edwardsi* and part of a giant tortoise carapace.

During about three weeks in the southern winter of 2003, David Burney and several colleagues, including Bill Jungers (Figure 45, *left*), excavated portions of

the cave, using more modern techniques than previously employed at the site. This included screening of sediments, which allowed fine bone to be recovered, and close attention to aspects of stratigraphy. On the basis of nearly thirty radiocarbon dates, the excavated deposits span the time period from about 7,810 years BP (mean calibrated date of 8,700) to modern times (55, 69). Certain species, such as the ring-tailed lemur *Lemur catta*, span the complete period represented by the radiocarbon dates. This research group recovered a considerable quantity of bone material, and based on their identifications and material from previous collections, a diversity of vertebrates has been identified from the cave (see Table 2): 29 different types of birds, including 2 genera of extinct elephant birds (*Mullerornis* and *Aepyornis*) and a massive waterbird (*Centrornis*); 9 species of the family Tenrecidae, including the extinct *Microgale macpheei*; 8 species of bats, all of which still occur in the general area today; 11 species of primates, 6 of which are extinct; 5 species of rodents, including the extinct *Hypogeomys australis*; as well as an assortment of carnivorans, reptiles, amphibians, an extinct dwarf hippo, and introduced animals (55).

There are several different ways that animals can enter the cave. At the base of the cliff, facing the sea, there is an opening that is “accessible” during low tide, where it is necessary to cross some coral and then climb over some rocks into a relatively large entrance (Figure 45, *right*). During medium or high tide, such an exit or entrance is treacherous at the very least. Otherwise, the only manner to enter safely, excluding a person on a short rappel, is for a flying animal to pass over the principal sinkhole, which is accessible from the upper portion of the cliff face. The remaining portion of the cave ceiling, often



**Table 2**

List of land vertebrates identified from Andrahomana sub-fossil remains (36, 55, 276). Extinct animals are denoted with †, and the author(s) and description date are given. For living taxa, the English common names are given. Listing does not include introduced species.

**Order Reptilia**

Family Testudinidae

†*Aldabrachelys abrupta* (A. Grandidier, 1866)

*Astrochelys radiata* radiated tortoise

Family Crocodylidae

†*Voay robustus* (A. Grandidier & Vaillant, 1872)<sup>1</sup>

*Crocodylus niloticus* Nile crocodile

**Class Aves****†Order Aepyornithiformes**

†Family Aepyornithidae

†*Aepyornis* sp.

†*Mullerornis* sp.

**Order Procellariiformes**

Family Procellariidae

*Puffinus* sp. shearwater

**Order Anseriformes**

Family Anatidae

†*Centronis majori* Andrews, 1897

**Order Falconiformes**

Family Accipitridae

*Accipiter francesii* Frances's Sparrowhawk

Family Falconidae

*Falco newtoni* Madagascar Kestrel

**Order Gruiformes**

Family Turnicidae

*Turnix nigricollis* Madagascar Buttonquail

*Gallinula chloropus* Common Moorhen

*Fulica cristata* Red-knobbed Coot

**Order Columbiformes**

Family Columbidae

*Streptopelia picturata* Madagascar Turtle Dove

**Order Psittaciformes**

Family Psittacidae

*Coracopsis vasa* Lesser Vasa Parrot

**Order Cuculiformes**

Family Cuculidae

*Cooua* cf. *gigas* Giant Coua

*Cooua cristata* Crested Coua

*Cooua cursor* Running Coua

**Order Strigiformes**

Family Tytonidae

*Tyto alba* Barn Owl

Family Strigidae

*Otus rutilus* Madagascar Scops Owl

**Order Apodiformes**

Family Apodidae

*Apus* sp. swift

**Order Coraciiformes**

Family Upupidae

*Upupa marginata* Madagascar Hoopoe

**Order Passeriformes**

Family Alaudidae

*Mirafra hova* Madagascar Bush Lark

Family Sylviidae

*Nesillas* cf. *lantzii* Lantz's Brush Warbler

Family Bernieridae

*Thamnornis chloropetoides* Sub-desert Tetraka

Family Monarchidae

cf. *Terpsiphone mutata* Madagascar Paradise

Flycatcher

Family Zosteropidae

*Zosterops maderaspatana* Madagascar White-eye

Family Vangidae

*Vanga curvirostris* Hook-billed Vanga

*Leptopterus viridis* White-headed Vanga

*Cyanolanius madagascarinus* Blue Vanga

Family Corvidae

*Corvus albus* Pied Crow

Family Ploceidae

*Ploceus sakalava* Sakalava Weaver

*Foudia madagascariensis* Madagascar Fody

**Class Mammalia****Order Afrosoricida**

Family Tenrecidae

*Tenrec ecaudatus* common tenrec

*Setifer setosus* greater hedgehog tenrec

*Echinops telfairi* lesser hedgehog tenrec

*Geogale aurita* large-eared tenrec

†*Microgale macpheeii* Goodman, Vasey & Burney, 2007

*Microgale longicaudata* lesser long-tailed shrew-tenrec

*Microgale nasoloi* Nasolo's shrew-tenrec

*Microgale principula* greater long-tailed shrew-tenrec

*Microgale pusilla* lesser shrew-tenrec

**Order Primates****Suborder Strepsirrhini****Infraorder Lemuriformes**

†Family Archaeolemuridae

†*Archaeolemur edwardsi* Filhol, 1895

†*Archaeolemur majori* Filhol, 1895

†*Hadropithecus stenognathus* Lorenz von Liburnau, 1899

Family Cheirogaleidae

*Microcebus* cf. *griseorufus* gray-brown mouse lemur

*Cheirogaleus medius* fat-tailed dwarf lemur

Family Lemuridae

†*Pachylemur insignis* Filhol, 1895

*Lemur catta* ring-tailed lemur

- \*Family Megaladapidae
  - \**Megaladapis edwardsi* G. Grandidier, 1899
  - \**Megaladapis madagascariensis* Forsyth-Major, 1894
- Family Indriidae
  - Avahi laniger* eastern woolly lemur
  - Propithecus verreauxi* Verreaux's sifaka

#### Order Chiroptera

- Family Pteropodidae
  - Eidolon dupreanum* Madagascar straw-colored fruit bat
  - Pteropus rufus* Madagascar flying fox
  - Rousettus madagascariensis* Madagascar rousette
- Family Hipposideridae
  - Hipposideros commersoni* Commerson's leaf-nosed bat
  - Triaenops furculus* Trouessart's trident bat
- Family Molossidae
  - Mormopterus jugularis* Peters' goblin bat
  - Mops leucostigma* Malagasy large white-bellied free-tailed bat
- Family Miniopteridae
  - Miniopterus gleni* Glen's long-fingered bat

#### Order Carnivora

- Family Eupleridae
  - \**Cryptoprocta spelea* G. Grandidier, 1902
  - Fossa fossana* spotted fanaloka

#### Order Artiodactyla

- Family Hippopotamidae
  - \**Hippopotamus lemerlei* A. Grandidier, 1868

#### Order Rodentia

- Family Nesomyidae
  - \**Hypogeomys australis* G. Grandidier, 1903
  - Eliurus* sp. tuft-tailed rat
  - Eliurus myoxinus* western tuft-tailed rat
  - Macrotarsomys bastardi* western big-footed mouse
  - Macrotarsomys petteri* Petter's big-footed mouse
  - Nesomys rufus* eastern red forest rat

1. The crocodile remains found in the cave need to be re-evaluated associated with their generic designation.

reaching at least 3 m in height, has a series of open holes or “skylights” (see Figure 5, left) that can act as trapdoors for land vertebrates walking on the ground surface above the cave (Plate 2). Animals “falling” into the cave by this means would have incurred important injuries or met with death. During the 2003 excavation at the site, after one member of the Burney team, Laurie Godfrey, received a head wound and nearly drowned in a bore-like tidal wave while trying to access the seaside entrance on foot, entry to the cave by the expedition members was subsequently limited to descent through skylights via ropes and

ladders. Sediment was lifted out by bucket and then dry-screened above, a tedious but much safer alternative to the unpredictable coastal route.

The vast majority of bird taxa identified from the remains are species that still occur in this portion of southeastern Madagascar. There are a few exceptions. The two elephant bird genera, *Mullerornis* and *Aepyornis*, are now extinct and were once widespread across different portions of the island (see Plate 1). A radiocarbon date from eggshell remains recovered in close proximity to the cave yielded a date of 1,000 years BP (mean calibrated date of 895) (69); however, as discussed under Plate 1, there are potential accuracy problems with such dates based on eggshells of elephant birds coming from coastal areas. It is unclear if these very large birds were forest-dwelling or tended to live in more open habitat, and little can be interpreted about their diets. However, if they had feeding preferences similar to other large flightless birds, such as the forest-inhabiting Dwarf Cassowary *Casuarius bennetti* (family Casuariidae) of New Zealand, they would have been largely fruit-eating (frugivorous) (248) or to the more open-country Emu *Dromaius novaehollandiae* (family Dromaiidae) of Australia, which feeds on a wide variety of fruits, seeds, flowers, insects, and green herbs (76).

One of the other extinct birds identified from the Andrahomana deposits is *Centronis*, which was a massive waterbird related to living ducks, with long legs and spurs on its wings, a bit like the screamers (family Anhimidae) of South America (see Plate 11). Based on the inferred habits of this bird, it would be reasonable to assume that there was a body of water, small lake or flooded area, nearby the cave. However, how such a bird would have entered into the cave is unclear, but perhaps it was brought there by a large carnivoran, such as *Cryptoprocta spelea* (see Plates 3 and 19), while the remains of the elephant birds were probably the result of skylight accidents.

Among the small mammal remains, which include tenrecs of the family Tenrecidae and rodents of the subfamily Nesomyinae, a number of species warrant comment. The presumably extinct shrew-tenrec *Microgale macpheei*—named in honor of Ross MacPhee for his contributions to the study of Malagasy small mammals and paleoecology—was described from bone material recovered from Andrahomana Cave (171). This species is closely related to the living *Microgale brevicaudata*, which occurs in the dry deciduous forests of central western and northern portions of the island. Hence, by inference, the presence of

*Microgale macphee* in the cave deposits provides evidence of moister conditions in the Andrahomana area in the recent geological past.

The *Microgale macphee* bones in the cave also provide insight into another important point. The extinction events that occurred on Madagascar over the past few thousand years are often referred to as the disappearance of the megafauna or large-bodied animals. Given that most early paleontologists seeking subfossils from Holocene deposits on Madagascar only collected the bigger bones, this provided a biased window into what actually disappeared. With the screening of sediments by David Burney and colleagues during the past decades, considerable small mammal remains have been recovered. This has led to the description of numerous extinct small animals new to science, such as *Microgale macphee*, which weighed about 10 g, as well as several species of extinct bats from Anjohibe (see Plate 13). Hence, it is now clear that the wave of extinctions and the associated ecological causes touched a broad range of animals of different sizes, and not just the megafauna.

The genus *Microgale* is the most speciose of the living mammals of Madagascar, with twenty-three species (353). More than 70 percent of these species live in the humid eastern forest, and the balance occur in different habitats, including spiny bush and dry deciduous forest; importantly, most tend to be habitat specific. Among the remains identified from Andrahomana Cave, there are represented non-extinct species typical of humid forests (*Microgale principula* and *Microgale pusilla*) and dry deciduous forests (*Microgale nasoloi*). Hence, the presence of these different species in the cave deposits is a good measure of shifts between dry and wet forest conditions in the immediate vicinity of the cave over the past few millennia. The forests to the west of Andrahomana, specifically the region of the Ambatotsirongorongo Massif, still maintain some vertebrates typical of humid forest, rather than spiny bush formations (9); this mountain can be considered a vestige of the habitat types that once occurred in this portion of extreme southern and southeastern Madagascar. The remains of the rodent *Nesomys rufus* in the cave deposits provide another clear sign of formerly moister conditions. This species is typical of humid forests and still occurs in the eastern and southern foothills of the Anosyenne Mountains (353).

Another interesting case among the small mammals is the presence of *Macrotarsomys petteri*, a terrestrial rodent only described in 2005 from the Mikea

Forest north of Toliara (160), over 400 km to the northwest of Andrahomana Cave. If the subfossils of this notably large kangaroo-like rodent had been found before the living animal, it would almost certainly have been described as an extinct species (170). Radiocarbon dates from *Macrotarsomys petteri* bone recovered from the cave include one of 2,480 years BP and another of 1,760 years BP (mean calibrated dates of 2,525 and 1,620) (55, 69). Another species of small mammal mentioned above, *Microgale nasoloi*, was identified from the cave bone remains, and it has a history rather similar to that of *Macrotarsomys petteri*. It was only recently described and is known today from a few localities in the transitional forests near Sakaraha and the dry deciduous forests of the Central Menabe, north of Morondava (352). Given the quantity of *Microgale* spp. and *Macrotarsomys* spp. skeletal remains found at Andrahomana, often concentrated in a particular section of the cave, we suspect that these mammals were preyed upon by raptors, such as owls, which subsequently regurgitated undigested bones in the form of pellets, thereby producing abundant deposits of small mammal remains below the predator roost sites (see Figure 5, right).

The last “small” mammal of note is *Hypogeomys australis*, a large extinct rodent, named from Andrahomana Cave by Guillaume Grandidier (179), that probably weighed something approaching 2 kg. Bones allocated to this species are also known from a Central Highlands site near Antsirabe (153) (see Plate 11). The only known species in the same genus is the smaller *Hypogeomys antimena*, which today is found only in the dry deciduous forests north of Morondava and has the conservation status of Endangered. In the not-too-distant past, *Hypogeomys antimena* had a substantially broader distribution in the southwestern portion of Madagascar. For example, a radiocarbon analysis of bone remains referred to this species from Ampoza (see Plate 7), at least 250 km southeast of its current known distribution, yielded a date of 1,350 years BP (mean calibrated date of 1,190). This is quite recent, and this species’ dramatic range retraction is probably related firstly to natural habitat shifts associated with climate change and secondly to human-induced factors (153). *Hypogeomys antimena* occurs today in areas with sandy soils, where it digs out extensive burrow systems. If *Hypogeomys australis* had similar life-history traits, it most likely occurred away from the immediate vicinity of Andrahomana Cave, which has little in the way of sandy soils and is mostly composed of exposed rock. Hence,

the presence of remains of this species in the cave deposits may best be explained by transport to the cave by predators. Two radiocarbon dates from Andrahomana of *Hypogeomys australis* ranged from 4,440 to 1,536 years BP (mean calibrated dates of 5,060 and 1,400) (55, 153).

Several species of introduced mammals to Madagascar have been identified from the cave remains, which include bones of domestic dogs and cattle. Among the rodents (family Muridae), these include *Mus musculus* and *Rattus* sp., and among the shrews (family Soricidae), a minuscule species of less than 2 g, *Suncus etruscus*, that was previously thought to be endemic to Madagascar under the name *Suncus madagascariensis* (285). Based on the stratigraphic position in the excavated deposits and the minimum number of individuals unearthed, notable changes through time were recorded for several rodent species. Between the lower to upper layers, *Rattus* increased from 14 to 67 percent of the rodent bones excavated and *Mus musculus* from 7 to 45 percent (368). The opposite relationship was found in three endemic rodents with values decreasing for *Eliurus myoxinus* from 50 to 2 percent, for *Macrotarsomys bastardi* from 21 to 4 percent, and for *Macrotarsomys petteri*, locally extirpated, from 7 to 1 percent. This might indicate some competition between introduced and native species, or some other cause, such as the introduction of infectious diseases transmitted from the introduced to the endemic species.

The Andrahomana faunal list includes eleven lemur species, five still extant and six lost to extinction. In other words, more than half of the local primate community has disappeared, and it is assumed that all lived contemporaneously during the Holocene. Mouse lemurs (*Microcebus* sp., probably *Microcebus griseorufus*) and ring-tailed lemurs (*Lemur catta*) are relatively common in the deposits; the Verreaux's sifaka (*Propithecus verreauxi*), the woolly lemur (*Avahi laniger*), and the fat-tailed dwarf lemur (*Cheirogaleus medius*) are less abundant. *Avahi laniger*, a species typical of humid forest, is no longer found in the immediate region, another indication of oscillating climates in the immediate area of the cave; the nearest known localities are in the southern and eastern foothills of the Anosyenne Mountains. Twelve specimens of *Lemur catta* from the cave deposits have been radiocarbon dated, and all but one are very recent, mostly from the last two centuries (69). This lemur is still plentiful in the region today and often visited the cave during the excavations in 2003.

Six extinct species of lemurs have been identified from the deposits, and all are larger—some much larger—than any living lemur: *Archaeolemur majori* (~18 kg), *Archaeolemur edwardsi* (~25+ kg), *Hadropithecus stenognathus* (~30+ kg), *Megaladapis madagascariensis* (~45+ kg), *Megaladapis edwardsi* (~85 kg), and *Pachylemur insignis* (11+ kg) (212). Most specimens of *Archaeolemur* from here fit comfortably within the known range of *Archaeolemur majori*, the smaller “monkey-lemur” species collected from many sites in the south and southwest. However, several specimens from Andrahomana seem to be too large to belong to this species and are referred instead to *Archaeolemur edwardsi*. There is currently no way to know for sure if these two morphologically similar congeners overlapped in time at the cave, and, if they did so, whether or not they competed with each other for the same food resources. Unlike most living lemurs and the majority of extinct lemurs, both were well adapted for life on the ground. They were probably most active during the day (diurnal). Their skulls and teeth indicate that they could generate high bite forces and probably were trophic generalists, including some animal protein in their mixed diets (129).

The only dated specimen of *Archaeolemur* from Andrahomana is a skull fragment of *Archaeolemur majori* at 3,975 years BP (mean calibrated date of 4,340) (69). This specimen was once thought to exhibit a fatal wound from an ax or similar implement (see Part 1, “Human Interactions with Now-Extinct Land Vertebrates”); its early date, almost two millennia before humans probably arrived on the island, essentially precludes humans as the likely agent of this animal's demise. *Hadropithecus stenognathus* is another closely related monkey-lemur that is well represented in the collections from Andrahomana. It was also a large-bodied quadruped that was at least semi-terrestrial and perhaps more at ease on the ground than any living or extinct lemur. We defer further discussion of *Hadropithecus* to Plate 3.

The three other subfossil species from Andrahomana are more closely related to each other than to monkey-lemurs (archaeolemurids). The *Pachylemur* from here is identified as *Pachylemur insignis* largely on biogeographic criteria; *Pachylemur jullyi* is very similar in anatomy but is slightly larger on average, and is usually identified as the species from the Central Highlands. Genetic and anatomical information combine to indicate that *Pachylemur* is closely related to the living ruffed lemur *Varecia*, the largest of the living true lemurs; in fact, *Pachylemur* has in the past

been viewed as a junior synonym of *Varecia*. *Pachylemur insignis* was a large-bodied, robustly built, fruit-eating lemur that lived in the trees. Two radiocarbon dates are available for this beast from Andrahomana, ranging from 2,300 to 1,940 years BP (mean calibrated dates of 2,245 and 1,805) (69). Additional aspects of the paleobiology of this genus can be found in the discussion of Plate 19.

Of the two species of *Megaladapis* from Andrahomana, the smaller *Megaladapis madagascariensis* is very rare, represented by a single bone from the forearm recovered long ago by Sikora and kept in the paleontological collections of Vienna. The larger species, *Megaladapis edwardsi*, is much better represented, including several magnificent skulls also found by Sikora and described soon thereafter with exquisite illustrations by Ludwig Lorenz von Liburnau (242). Lorenz von Liburnau erected separate subspecies or varieties for some of these skulls, but they clearly are just minor variations accommodated easily within a single species. Importantly, and unfortunately overlooked by some of his scientific contemporaries (see Plate 12), postcranial bones were found in reasonable association with these crania. One fragment of *Megaladapis edwardsi* has been dated to 4,566 years BP (mean calibrated date of 5,150) (55, 69). Although these two species of koala-lemurs were very different in body size, locomotor and feeding adaptations appear to be very similar—both were arboreal folivores. They both lacked upper incisor teeth and sported odd noses, long upper canines, and elongated koala-like crania. Their forelimbs were longer than their lower limbs, although both sets of limbs were short relative to body size; their hands and feet were large, powerful, and pincer-like. By virtue of their considerable bulk, they no doubt frequented the ground, if only to move from one tree to the next. During these terrestrial saunters, it appears that individuals of both species fell though sinkholes into the cave.

These two members of the genus *Megaladapis* are found together at many localities in the south and southwest, so it appears that despite many similarities in trophic adaptations and arboreal-terrestrial lifestyles, they somehow managed to have reduced competition between them and sufficiently divided resources to allow coexistence. In view of how rare *Megaladapis madagascariensis* appears to have been at Andrahomana, a possible alternative is that *Megaladapis edwardsi* was successful in competitively excluding its close relative, at least in this region of the

island. It might also be interesting in this regard to have dates on multiple individuals found in the cave deposits.

A few other noteworthy species have been recovered from the cave. The first is the pygmy hippo *Hippopotamus lemerlei*, which by its presence implicitly means that there was freshwater within a few kilometers of the cave and presumably associated with a riverine or marsh ecosystem. A direct corollary to this is the presence of *Crocodylus* bones in the cave. It is unclear if they represented what is now called *Voay robustus*, which is extinct, or *Crocodylus niloticus*, which is extant. Remains of giant tortoises have been recovered from the cave, which had been previously identified as *Geochelone grandidieri* (55), now placed in the genus *Aldabrachelys*. Two dates are available for this giant tortoise, 6,450 and 1,755 years BP (mean calibrated dates of 7,260 and 1,600). Roger Bour, a specialist on this group, has examined the older Andrahomana material and determined it is best referred to as *Aldabrachelys abrupta* (36). He also considers the Andrahomana Cave as the possible eastern limit of giant tortoises on Madagascar, further emphasizing the important ecotonal barrier of the Anosyenne Mountains. Three different turtles are known from the cave remains: the giant tortoise described above; another tortoise, *Astrochelys radiata*, which still occurs in the general region; and the aquatic turtle *Pelomedusa subrufa*, which was recently shown to have been introduced to Madagascar (108).

As we have tried to present in this account on Andrahomana Cave, the remains recovered from the site provide an extraordinary window into the animals that lived or still live in this portion of southeastern Madagascar. Among the birds known from the site, 3 of 27 (11 percent) are extinct; for the Tenrecidae, 1 of 8 (13 percent) are extinct, with 3 (*Microgale nasoloi*, *Microgale pusilla*, and *Microgale principula*) no longer occurring in the immediate region; for the endemic rodents, 1 of 5 (20 percent) are extinct, with 1 (*Macrotalesomys petteri*) no longer occurring in the area; and for lemurs, 6 of 11 (55 percent) are extinct. Most of these changes took place over the past few millennia and before pronounced human perturbations of the local natural environment, which, based on current evidence, commenced in the ninth century (309). This underscores the critical point that extinction events and their underlying causes (and timing) differed from region to region across the island. What happened at Andrahomana and environs may repre-

sent an important exception to what Ross MacPhee has called the “deadly syncopation”—people arrive, then animals go extinct. Recent information has been uncovered indicating that an extraordinary event might have taken place in the region during the Holocene, about 6,000 years ago, a major tsunami that is discussed in the next narrative (Plate 3). Such a catastrophe, if it did indeed occur, could have resulted in rather severe local extirpations long before people arrived on the island, but with some taxa locally replenished over time by immigration back into the coastal area.

## Plate 3: Andrahomana II—Evidence of a Holocene Tsunami in the Southern Indian Ocean and Predator-Prey Relations

There is evidence that a tsunami event took place in the Indian Ocean several millennia ago. The origin of the hypothesized wave was not the same as the earthquake that triggered the devastating tsunami of

26 December 2004 in southern Asia, but instead from a meteorite that crashed to Earth, entered the Indian Ocean, and set in motion a massive wave. In fact, the collision and associated wave are projected to have

---

Geologists have recently hypothesized that a major tsunami event took place approximately 6,000 years ago as the result of a meteorite plummeting to Earth's surface and entering the Indian Ocean to the southeast of Madagascar. Even though there is verification of the meteor, the jury is still out about if it caused a major tsunami, awaiting corroborative evidence related to the timing and, if indeed, such a tsunami event happened. Here we depict a large *Cryptoprocta spelea* attacking its prey *Hadropithecus stenognathus*; both of these animals are extinct and are part of the cave's Holocene fauna. The *Cryptoprocta* is shown in poor physical condition, weak from not eating, and injured after falling through a "trapdoor" in the Andrahomana Cave ceiling. A subadult *Hadropithecus*, now in the grip of the injured carnivore, has also suffered the misfortune of tumbling from above to the floor of the cave. This attack occurs at the precise moment that the coastal portion of southern Madagascar is struck with a massive wave. (Plate by Velizar Simeonovski.).



been so monumental that it is referred to as a “mega-tsunami.” If indeed correct, this massive wave would have resulted in large-scale environmental changes to the terrestrial landscape (264). The data supporting the physical evidence for its potential impact in southern Madagascar are threefold and include (1) massive inland sediment deposits in the form of dunes, (2) the presence of a large oceanic crater to the southeast of Madagascar, and (3) exceptional composition of some terrestrial sediment (188).

Along the southern coast of Madagascar, there are large dunes, reaching up to 200 m in height, that show evidence of being deposited by large-scale flooding (but see 37, 305). These formations, because of their directional “wedge shape,” are referred to as chevron dunes. Examples of this type of chevron can be found at Cap Sainte Marie, Fenambosy, and Faux Cap, along the far southern coast. Directly inland from the dunes, there is evidence of massive transport of sediments, referred to as “run-ups,” that can reach nearly 50 km inland. The Faux Cap chevron, for example, in the portion facing the sea contains marine shells mixed with sand, as well as large rocks of up to 15 cm in diameter. At the distant end of the chevron—that is, the farthest point from the sea—the sand layer is not consistent in thickness and comprises rocks of up to 23 cm in diameter mixed in with the sand; these formations have been postulated as “tsunami dump deposits.” The Fenambosy chevron is one of the largest and along its east-west axis nearly 26 km in length. The layer that corresponds with the marine section contains coarse sand and fragments of carbonate rock, and other sections contain rock oyster and mollusks. The reputed tsunami layer at the top of the 170 m tall escarpment has large carbonate rocks of 50 cm in diameter.

The hypothesis is that when the massive wave hit the southern portion of Madagascar, it traveled up to about 45 km inland and reached a height of over 200 m above sea level. If this reconstruction is accurate, it is hard to fathom the force of such a wave. For comparison, the wave height of the infamous 2004 tsunami was approximately 30 m tall. Hence, the hypothesized mega-tsunami wave that hit southern Madagascar would have been about seven times the height and, presumably, many times the force of the devastation witnessed in late 2004.

The second line of evidence is a massive crater in the Indian Ocean about 1,500 km southeast of Madagascar, which has been given the name Burckle Crater (264). The crater is estimated to be about 30 km

in diameter, nearly 4 km deep, and apparently was formed in recent geological time by the impact of a meteorite. The crater rim is high on three sides, one side is partially broken, and the deepest point within the crater is toward the southeast. By consequence, the material expelled from the collision would have been toward the northwest, which is the direction of Madagascar. No measured date is available on when the crater formed, but it has been proposed to be about 6,000 years BP. A physical dating of the actual Burckle Crater would be an important piece of data to place this reputed mega-tsunami event in a greater—and for us, a more relevant—context. It is important to mention that this event with its associated crater is but one of nearly thirty projected to have taken place on our planet during the Quaternary (264).

The third aspect used as proof of the mega-tsunami event is the physical composition of the chevron sediments (265). These “ejecta” are apparently composed of deep-ocean microfossils, fused with different types of metals, and are associated with the physical impact of a meteorite. The upper surface of deep-sea sediments collected in proximity to the Burckle Crater contains layers with high magnetic properties. Further, based on fine structure analysis, they contain “impact spherules,” which are the result of cooling vapor from the large plume or fireball that condenses into molten glass droplets (206). In the case of sediments from the southern Madagascar chevrons, the “ejecta” are composed of glasses, to which are adhered particles of iron, chromium, and nickel, and considered remnant fragments of the meteorite and oceanic mantle.

In any case, the notion of mega-tsunami events in recent geological history has come under scrutiny, and a number of geologists are doubtful about the ideas presented by Dallas H. Abbott, W. Bruce Masse, Viacheslav K. Gusiakov, and colleagues (305). For example, these skeptical scientists claim that the chevrons of southern Madagascar are aligned with the dominant wind direction and are the result of the carving force of the air current over geological time. In their rebuttal to these criticisms, the pro-mega-tsunami group notes that dune orientation in southeastern Madagascar is in fact not aligned along prevailing winds, and they also raise the pertinent question as to how fist-size rocks could be part of wind-generated sediments, as these would be too large to be transported (1, 188).

While we do not intend to weigh the pros and cons of these different arguments, and more data would



clearly be helpful, we regard the mega-tsunami hypothesis as intriguing and plausible. There is evidence from the 2003 excavations based on radiocarbon dates that the deposits are not in sequential order (55), but it is hard to imagine that the above-described tsunami event would have been responsible for this disturbance. Given the force and size of this hypothesized wave, it is assumed that the cave would have been scoured and completely cleansed of its contents. Only three published radiocarbon-dated specimens—out of many—from Andrahomana are older than 6,000 years (one giant lemur, one *Lemur catta*, and one tortoise) (69), so the more recent dates from there all postdate the hypothesized 6,000 years BP mega-tsunami. It is also possible that the impact of the tsunami was less than projected or perhaps occurred slightly earlier. Further, it cannot be excluded that other waves of much smaller magnitude also entered the cave's opening over the years and contributed to some degree of reworking and mixing of deposits.

If this mega-tsunami actually happened, imagine the impact it would have had on Madagascar and the world, no doubt producing a global deluge of sorts (264). The heat generated from such a collision would have also produced a massive amount of water vapor, which would have resulted in a net increase in rainfall and cyclonic activity across the globe. At the same time, the high temperatures produced by the shock would have baked the southern portion of Madagascar. The proponents of this meteorite-impact theory have been able to find numerous cases in oral and mythological tradition of cultures around the world to support that humans have recorded such events. Tsunami or no tsunami, now back to Andrahomana Cave.

In Plate 3, we have depicted a *Cryptoprocta spelea*, a large Carnivora, in rather poor condition, being emaciated from not having eaten much after accidentally falling through a “trapdoor” in the cave ceiling (see Figure 5, left) and injuring itself. This predator is notably larger and presumably more powerful than any carnivoran occurring on Madagascar today. It is shown about to take a giant lemur, *Hadropithecus stenognathus*, now extinct, also trapped in the cave after falling through a hole in the ceiling. This act of predation coincides with the moment that a massive wave hits the southern coast of Madagascar, associated with the reputed mega-tsunami event discussed above. The *Cryptoprocta* had tried to exit the cave via the seaward opening (see Figure 45, right), but because of its bum leg, it was unable to negotiate

the different levels of rocks and coral. Simultaneous with this, it heard the calls of the trapped lemur from within the cave and as quickly as it could returned to attack the animal.

The name *spelea* is derived from the Latin word *speleum* for cave. The first bone remains of this extinct *Cryptoprocta* were identified from Andrahomana Cave by Guillaume Grandidier, who concluded that the excavated material represented a new form larger than extant *Cryptoprocta ferox* for which he proposed the name “*C. ferox* var. *spelea*” (178, 180) (see Plate 19 for further details). Subsequent studies have verified that this “variety” should be considered a full species (165).

Now the prey animal depicted in this scene is an extraordinary beast known as *Hadropithecus stenognathus*, another “monkey-lemur,” related to the more common *Archaeolemur* but with a restricted range and relatively enigmatic. The genus name of *Hadropithecus* is derived from the Greek *hadros*, meaning “stout” or “large,” and *pithekos*, meaning “ape.” The species name derives from the Greek *steno-*, meaning “narrow,” and *gnathos*, meaning “jaw” or “mouth.” The type specimen of this species comes from Andrahomana Cave via Franz Sikora's 1899 excavations (see Plate 2) and Lorenz von Liburnau's diagnosis of a right lower jaw in 1899 (240; also see 360). One of only two known skulls and a few postcranial bones of *Hadropithecus* from the same cave were described shortly thereafter by the same author, and they revealed a bizarre creature with a surprisingly flattened snout, bony crests on the back of the skull (neurocranium), and very unusual teeth (241). A second skull was found in 1931 at the southwestern site of Tsirave by Charles Lamberton, who later that decade summarized everything then known about *Hadropithecus* (229), including the allocation of hindlimb bones to the species for the first time. Unfortunately, Lamberton's long-bone attributions turned out to be wrong (125), and new material from the 2003 excavations at Andrahomana led by David Burney have proven invaluable in clarifying the likely locomotor adaptations of this species (130). As an historical side note, Giuseppe Sera's eccentric reconstruction of *Hadropithecus* in 1950 as “aquatic” was widely, and justifiably, ignored (343). Sera viewed much of primate and human evolution through an aquatic prism, but Lamberton (232) tactfully demolished these fanciful scenarios, at least for subfossil lemurs.

The skull and teeth of *Hadropithecus* have long fascinated paleontologists and anthropologists. The



Figure 46. A computer reconstruction of the Vienna Museum of Natural History's *Hadropithecus stenognathus* skull from Andrahomana Cave. The cranium (described in 1902) is seen in the top left in white. Missing parts are mirror-imaged in blue just below and to the right, and the brow ridges discovered in 2003 at the same site are joined digitally to complete the orbits. The right jawbone found in 1899 is also mirror-imaged and then articulated with the cranium (*below right*), and the missing fragment of the frontal bone is created in gray in order to complete the reconstruction. The final "*in silico*" subadult skull is seen below left in white. For more details on the reconstruction, see reference 331. (Image courtesy of Tim Ryan.)

comparison of *Hadropithecus* to *Archaeolemur* skulls was used effectively as an adaptive analogy for craniodental differences between African geladas (*Theropithecus*) and baboons (*Papio*) and, ultimately, differences in the trophic food chain between robust and gracile australopithecines (early Plio-Pleistocene human ancestors from Africa) (207). The monkey-like analogy was pushed further still by Alan Walker (380), but this time for the limb bones and bodily proportions. *Hadropithecus* was described as having longer, slimmer limbs than *Archaeolemur*, but this inference was influenced by Lamberton's aforementioned misattributions. Although both *Archaeolemur* and *Hadropithecus* do exhibit some skeletal convergences with terrestrial monkeys (e.g., in details of the

elbow), there are real limits to this analogy. Overall, the monkey-lemurs are decidedly more lemur-like than monkey-like.

*Hadropithecus* was a stout, large-bodied (up to 30+ kg) quadruped that was well adapted for life on the ground (terrestrial). The forelimbs are longer than the hindlimbs, but all limb bones are robust and relatively short. *Hadropithecus* was no doubt strong and agile but not built for speed. It sported a long tail along with small, almost paw-like hands and feet (as also seen in *Archaeolemur*), and peculiar features of its short fingers are simply difficult to understand as to how they functioned (239). It is likely that it was less of a tree climber in comparison to most other living and extinct lemurs.

The skull of *Hadropithecus* is remarkable for a lemur in many ways. Its small orbits indicate a diurnal activity cycle, and its brain is relatively large and approaches “higher primates” in this regard. Its upper canine teeth are reduced in size, and stout, slanting-forward (procumbent) lower teeth replace the typical lemur “toothcomb.” The premolar teeth are huge, and the chewing surfaces of the post-canine teeth are complex and tend to be heavily worn. Attachment sites for chewing muscles are well developed, with both halves of the lower jaw firmly fused together, and it was once believed to be a powerful nut-cracking machine (“hard object feeder”). Recent biomechanical analyses indicate that this last picture is wrong and suggest instead that *Hadropithecus* probably consumed large quantities of vegetation with relative low-quality nutritional value (95). Repetitive chewing, as in a cow, was more important than generation of high bite forces. This species’ carbon isotopic signature is also unique among living and extinct lemurs (72), with decidedly C<sub>4</sub> values that implicate grass bulbs and corms and, perhaps, sedges in the diet; succulent leaves of CAM plants common in southern Madagascar (e.g., *Alluau-dia* of the family Didiereaceae) were another possible dietary staple for *Hadropithecus* (70).

Sometimes fossils collected long ago can be reunited in a novel, high-tech manner with those collected more recently in the digital age, and *Hadropithecus* provides an instructive and fun example of these new imaging capabilities. Frontal bone fragments (“brow ridges”) were discovered in the 2003 excavations at Andrahomana that appeared to match the missing parts of the first skull of *Hadropithecus* described by Lorenz von Liburnau over a century ago, which is housed in Vienna’s Natural History Museum. When the paleontological team was at the site in 2003, their hunch was that they had rediscovered part of Franz Sikora’s original excavation and were picking up bones of some of the same individuals. High-resolution CT scans were obtained for both the new and old bones of *Hadropithecus*, and a new *in silico* reconstruction was created by putting the different pieces together digitally (331). The bones matched perfectly (Figure 46). The newly restored skull, although a subadult, bears a striking similarity to the more complete fully adult skull found by Charles Lamberton from Tsirave now on display at the Académie Malgache in the Madagascar capitol of Antananarivo. For further information of predator-prey relationships of extinct Holocene large animals from Madagascar, see Plate 19.

## Plate 4: Tsimanampetsotsa—Rapid Ecological Shifts in the Face of Natural Climate Change

One of the more stark natural landscapes on Madagascar today is the Mahafaly Plateau region in the extreme southwest (Figure 47). This area has a distinct vegetation, known as spiny bush (see Part 1, “Spiny Bush”), which is composed mostly of plants adapted to notably dry conditions (xerophytic). The local flora is species rich and populated by many endemics that have very restricted distributions (micro-endemics).

In most years, the region receives less than 500 mm of rainfall, with a pronounced 10-month dry season; although in some years, there is no recorded precipitation at all. The period between December and February is the principal “rainy season,” with on average only 7–9 days of rain per year! This is a zone where most local organisms have adaptations for the arid conditions. These evolutionary strategies range, for

---

A view looking toward the east from the edge of the ancient Lake Tsimanampetsotsa and toward the Mahafaly Plateau. Today this area has annual rainfall of less than 500 mm, virtually no freshwater, a distinct arid spiny bush formation, and a very pronounced dry season (see Figure 47). However, a consideration of subfossil remains reveals that just a few millennia ago this zone was notably more mesic, with extensive areas of probably permanent freshwater, and home to a considerable number of animal species that no longer occur locally or are now extinct. The habitat between the lake edge and the foot of the Mahafaly Plateau may have been a variety of wooded savanna, with areas containing largely closed-canopy forest and others more open, structurally similar to Miombo woodlands of southern Africa (see Figure 25). For a key to the different animals, see black-and-white inset for Plate 4 in color gallery. (Plate by Velizar Simeonovski.)





Figure 47. A view looking eastward from what would have been the eastern edge of the ancient Tsimanampetsotsa fresh-water lake and toward the Mahafaly Plateau. This image was used in the composition of Plate 4. Note the exposed limestone along the face of the Mahafaly Plateau and distinct spiny bush (see Figure 15, *right*). At the base of the plateau is a narrow band of low-growing *Salvadora* (family Salvadoraceae) trees, which have distinctly bright light green leaves. The area in the foreground is largely devoid of woody vegetation, and toward the east, in the area behind the photographer, is a large area of salt pan, which continues to the edge of the highly saline Tsimanampetsotsa Lake. (Photograph by Achille P. Raselimanana.)

example, from trees that have bottle-trunks to store water (see Figure 15, *right*), few leaves to reduce surface area and associated water loss, or large underground tubers for stocking water. On the animal side, certain vertebrates, such as tenrecs (*Tenrec ecaudatus*) and mouse lemurs (*Microcebus griseorufus*), hibernate or go into a sort of torpor; some show dramatic changes in their diet and feed on whatever is available, while others are obliged to disperse considerable distances to find needed resources.

One region that is typical of the Mahafaly Plateau ecosystem and that has been studied in detail is the Tsimanampetsotsa National Park, to the south of the Onilahy River. This site was established in late 1927 with the statute of a Strict Nature Reserve (Réserve Naturelle Intégrale), and was one of the first protected areas to be named on the island. During the period when Madagascar was still a French colony, protected areas were under the scientific control of

the Muséum national d'Histoire naturelle in Paris, and, as a result, scientists associated with that institution conducted inventories, such as at Tsimanampetsotsa. This survey provided the first window into the faunistic and floristic particularities of this unique region (301). The reserve was originally about 17,500 ha and in 1966 was augmented to 43,200 ha. Further, the status was changed in 2001 to a national park, and, more recently, the surface area extended to nearly 300,000 ha.

While the zone has many unique organisms, several of which have only recently been found and described (e.g., 283, 392, to list only a few), terrestrial vertebrate diversity is not particularly high. For example, a recent biological inventory within the park found 39 species of reptiles, 2 amphibians, 74 birds, 3 lemurs, 5 bats, 2 native Carnivora, and 6 native small mammals (163). However, regardless of its relatively low vertebrate diversity, after a visit to the park,

one is very impressed with the beauty of the site and the extreme nature of the environment. Based on this latter point, one might assume that the adaptations of the local plants and animals “must” have evolved locally over extensive periods in their evolutionary history.

Certainly, one of the limiting factors for the regional biota is the combined lack of permanent exposed freshwater and the notably long dry season. Some underground water drains from the east and under the Mahafaly Plateau; this comes to the surface in caves and artesian wells at the foot of the plateau. At such sites, there is a greater concentration of biological life than in areas without such water sources. One example within the national park is Mitoho Cave, which has a permanent underground lake that holds blind cavefish and shrimp, with the former feeding on the latter (195, 300). Tsimanampetsotsa still has a large lake, which today is notably saline and relatively uninviting except to certain organisms such as flamingos and other waterbirds that have special feeding and foraging habits. The lake is within a few kilometers of the Mozambique Channel. What is extraordinary is that the subfossil record of the immediate region tells us that this extreme environment was notably different just a few millennia ago.

Perhaps a good place to start is with some details on the modern floral communities found between the edge of Lake Tsimanampetsotsa, which is on the west side of the park, passing toward the east, including the foot of the Mahafaly Plateau and then on to the higher tableland. The lake sits in a low-lying area, and the amount of brackish water is variable between the height of the rainy season and the low of the dry season. Some reeds and other aquatic vegetation occur at the lake edge, including a fern adapted to the saline conditions. Moving toward the east and the plateau, there is a broad open plain that can be partially inundated during the rainy season. This zone is largely salt pan, and local plants include *Salicornia* (family Salicorniaceae) and some small groves of *Casuarina* (family Casuarinaceae); the latter may not be native to the island. Farther to the east and at the edge of the spiny bush (see Figure 47), the habitat is dominated by a narrow band of low-growing *Salvadora* (family Salvadoraceae) trees, and then by two distinct spiny bush plant communities. The first of these occurs at the base of the plateau with roots firmly growing in soil, whereas the second grows on the limestone massif, often with the roots wedged between rocks or in notably thinner soils. There are many organisms

endemic to the plateau, never venturing out or successfully dispersing toward the plain and lake.

Recent work on the periods of flowering and fruiting (phenology) of the local spiny bush flora of Tsimanampetsotsa indicates that day length, rather than rainfall, triggers fruiting and flowering (324). What is important about this observation is that plants have adapted their periods of reproduction to long-term climatic averages. Given the erratic periods of rainfall observed today, this weather signal would not necessarily be useful to prompt flowering, but rather would be a good adaptive strategy only during a geologically recent period when the zone was wetter and presumably with rainfall that was more regular.

Henri Perrier de la Bâthie was a botanist who traveled extensively around Madagascar, helped to build the early protected areas system, and was responsible for several important syntheses concerning Madagascar botany. In the 1930s, he visited Mitoho Cave and found on the surface, or in the soil at shallow levels, the subfossil remains of giant tortoises and crocodiles, as well as eggshell fragments of elephant birds (298, 301). Other animal bones were recovered from these deposits and sent back to the Paris museum. This included a portion of the leg bone of a large eagle belonging to the genus *Aquila*, which no longer occurs on Madagascar (142).

Over the course of several field seasons in the first half of the twentieth century, Charles Lamberton conducted paleontological excavations in caves along the Mahafaly Plateau and uncovered bones of extraordinary creatures. These included, for example, from Ankazoabo Cave, near Itampolo and less than 75 km south of Mitoho Cave, subfossils of three extinct large lemurs (*Palaeopropithecus ingens*, *Mesopropithecus globiceps*, and *Archaeolemur majori*), pygmy hippos (*Hippopotamus lemerlei*), giant tortoises (*Aldabrachelys abrupta*), a large Carnivora (*Cryptoprocta spelea*), and elephant birds (*Aepyornis* and *Mullerornis*) (165, 228).

Many years later, Ross MacPhee from the American Museum of Natural History visited several caves along the Mahafaly Plateau and, in particular, the immediate vicinity of Tsimanampetsotsa. Among the bone remains he found in Mitoho Cave were the giant lemur *Megaladapis edwardsi*; the large endemic rodent *Hypogeomys antimena*, now only known from the area north of Morondava; carapace pieces of the giant tortoise *Aldabrachelys abrupta*; and eggshell fragments of elephant birds allocated to the genus *Mullerornis* based on their thickness. Given the va-

riety of animals recovered from these deposits and those of Ankazoabo Cave, including species that depend on freshwater habitat, it is clear that major changes have taken place in the ecosystem of the Tsimanampetsotsa area.

Another collection of subfossils was obtained in 1981 in a cave on the Mahafaly Plateau near Tsimanampetsotsa, which has yet to be studied in detail (332). The tentative identification of remains of the rodent *Brachytarsomys* is rather exceptional, as this genus is known today from eastern and northern humid forests. Almost certainly, the preliminary assignment of these subfossils to the period of the Pliocene-Pleistocene is incorrect, and these bones presumably date from a more recent geological period unsupported by geological evidence or any form of dating. In any case, a considerable diversity of taxa have been identified from regional subfossil sites in the vicinity of Tsimanampetsotsa, and these reveal an expanded faunal community ecologically quite different from that seen today (see Table 3).

To help place these changes in a temporal context, some radiocarbon dates are available for a handful of the extinct animals. From Lamberton's excavations at Ankazoabo Cave, remains of *Cryptoprocta spelea* yielded a date of 1,865 years BP (mean calibrated date of 1,740); *Mesopropithecus globiceps* was dated to 2,148 and 1,555 years BP (mean calibrated dates of 2,120 and 1,410); and *Palaeopropithecus ingens* provided the most recent dates at 1,450, 1,269, and 1,148 years BP (mean calibrated dates of 1,315, 1,125, and 1,010) (69, 214). For elephant bird eggshell remains from Mitoho Cave, a date falls out much earlier at 4,030 years BP (mean calibrated date of 4,480) (69). Most extraordinary and informative for providing a window into how recent some of these animals lived—and the ecological changes implied thereby—there is a radiocarbon date from Itampolo of a dwarf hippo from 980 years BP (mean calibrated date of 905) (257). (We should note parenthetically that this date is derived from older and less precise radiocarbon techniques and needs to be verified with modern methods.) Hence, based on these dates, not only have major changes taken place in the regional fauna and the ecosystems that these animals occupied, but this major shift has also unfolded over the course of just a few millennia or less.

So what happened? Based on the existing archaeological record, this area of the island was never heavily populated by people, particularly inland at places such as Tsimanampetsotsa (54). Today a tract

**Table 3**

List of land vertebrates identified based on subfossil remains from Tsimanampetsotsa and surrounding areas. As few animals have been identified from the site, the list of local subfossil lemurs is derived in part from the nearby Ankazoabo Cave and certain birds from Beavoha, Bernafandry, Tsiandroina, Ambolisatra, and Lamboharana (36, 156, 159, 165, 176, 228, 250, 298, 332). Extinct species are indicated with †, and the author(s) and description date are also given. For living taxa, the English common names are given. Listing does not include introduced species.

#### Order Reptilia

Family Testudinidae

†*Aldabrachelys abrupta*<sup>1</sup> (A. Grandidier, 1866)

*Astrochelys radiata* radiated tortoise

Family Crocodylidae

*Crocodylus* sp. crocodile<sup>2</sup>

#### Class Aves

##### †Order Aepyornithiformes

†Family Aepyornithidae

†*Aepyornis maximus* I. Geoffroy-Saint-Hilaire, 1851

†*Mullerornis agilis* Milne-Edwards & Grandidier, 1894

##### Order Pelecaniformes

Family Phalacrocoracidae

†*Phalacrocorax* sp. (probably undescribed extinct species)

*Phalacrocorax africanus* Reed Cormorant

##### Order Ardeiformes

Family Ardeidae

*Egretta* spp. egret

*Ardea purpurea* Purple Heron

*Ardea humbloti* Humblot's Heron

Family Ciconiidae

*Mycteria ibis* Yellow-billed Stork

*Anastomus lamelligerus* African Openbill Stork

Family Threskiornithidae

*Threskiornis bernieri* Madagascar Sacred Ibis

*Lophotibis cristata* Madagascar Crested Ibis

*Platalea alba* African Spoonbill

Family Phoenicopteridae

*Phoenicopterus ruber* Greater Flamingo

*Phoeniconaias minor* Lesser Flamingo

##### Order Anseriformes

Family Anatidae

†*Centronis majori* Andrews, 1897

†*Alopochen sirabensis* (Andrews, 1897)

*Dendrocygna* sp. whistling duck

*Anas bernieri* Bernier's Teal

*Anas erythrorhyncha* Red-billed Teal

*Anas melleri* Meller's Duck

*Thalassornis leuconotus* White-backed Duck

##### Order Falconiformes

Family Accipitridae

†*Stephanoaetus mahery* Goodman, 1994

\*? *Aquila* sp. (specific designation uncertain)  
*Milvus aegyptius* Yellow-billed Kite  
*Haliaeetus vociferoides* Madagascar Fish Eagle  
*Polyboroides radiatus* Madagascar Harrier-Hawk  
*Buteo brachypterus* Madagascar Buzzard

#### Order Gruiformes

Family Rallidae  
 \**Hovacrex roberti*? (Andrews, 1897)  
*Rallus madagascariensis* Madagascar Rail  
*Dryolimnas cuvieri* White-throated Rail  
*Gallinula chloropus* Common Moorhen  
*Fulica cristata* Red-knobbed Coot  
*Porphyrio porphyrio* Purple Gallinule

#### Order Charadriiformes

Family Recurvirostridae  
*Himantopus himantopus* Black-winged Stilt  
 Family Scolapaciidae  
*Numenius phaeopus* Whimbrel  
 Family Charadriidae  
 \**Vanellus madagascariensis* Goodman, 1996  
 Family Laridae  
*Larus dominicanus* Kelp Gull  
*Larus cirrocephalus* Gray-headed Gull

#### Order Columbiformes

Family Pteroclididae  
*Pterocles personatus* Madagascar Sandgrouse  
 Family Columbidae  
*Streptopelia picturata* Madagascar Turtle Dove

#### Order Psittaciformes

Family Psittacidae  
*Coracopsis vasa* Lesser Vasa Parrot

#### Order Cuculiformes

Family Cuculidae  
 \**Coua primavea* Milne-Edwards & A. Grandidier, 1895

#### Order Coraciiformes

Family Coraciidae  
*Eurystomus glaucurus* Broad-billed Roller

#### Class Mammalia

##### \*Order Bibymalagasia

\**Plesiorycteropus* sp.

##### Order Afrosoricida

Family Tenrecidae  
*Tenrec ecaudatus* common tenrec  
*Setifer setosus* greater hedgehog tenrec  
*Geogale aurita* large-eared tenrec  
*Microgale pusilla* lesser shrew-tenrec<sup>3</sup>

##### Order Primates

##### Suborder Strepsirrhini

##### Infraorder Lemuriformes

\*Family Archaeolemuridae  
 \**Archaeolemur majori* Filhol, 1895  
 \*Family Palaeopropithecidae

\**Mesopropithecus globiceps* Lamberton, 1936

\**Palaeopropithecus ingens* G. Grandidier, 1899

##### Family Cheirogaleidae

*Microcebus* spp. mouse lemur

*Cheirogaleus* sp. dwarf lemur

##### Family Lemuridae

*Lemur catta* ring-tailed lemur

\**Pachylemur insignis* Filhol, 1895

##### \*Family Megaladapidae

\**Megaladapis edwardsi* G. Grandidier, 1899

\**Megaladapis madagascariensis* Forsyth-Major, 1894

##### Family Indriidae

*Propithecus verreauxi* Verreaux's sifaka

#### Order Chiroptera

##### Family Hipposideridae

*Hipposideros commersoni* Commerson's leaf-nosed bat

*Trienops furculus* Trouessart's trident bat

##### Family Emballonuridae

*Paremballonura atrata* Peters' sheath-tailed bat<sup>4</sup>

##### Family Molossidae

*Mormopterus jugularis* Peters' goblin bat

#### Order Carnivora

##### Family Eupleridae

\**Cryptoprocta spelea*<sup>5</sup> G. Grandidier, 1902

*Cryptoprocta ferox* fossa<sup>6</sup>

#### Order Artiodactyla

##### Family Hippopotamidae

\**Hippopotamus lemerlei* A. Grandidier, 1868

#### Order Rodentia

##### Family Nesomyidae

*Hypogeomys antimena* Malagasy giant jumping rat

*Macrotrichomys bastardi* western big-footed mouse

*Macrotrichomys petteri* Petter's big-footed mouse

*Brachytarsomys* sp.

1. This species identification is based on material from the nearby Itampolove. There are reports of *Aldabrachelys grandidieri* from the Tsimanampetsotsa region, which warrant further verification.

2. It is possible that these remains are best allocated to the extinct *Voay robustus*.

3. It has been proposed that the *Microgale pusilla* remains recovered from the Tsimanampetsotsa area might be best allocated to a recently described species *Microgale jenkinsae* (159).

4. Remains of an animal resembling *Emballonura atrata* have been reported from the area (332). After recent taxonomic changes, this would almost certainly be referable to *Paremballonura tiavato*, which no longer occurs in this portion of Madagascar.

5. Remains of this species have been identified from the regional site of Ankazoabo Cave.

6. Remains of this species have been identified from the regional site of Lelia.



of relatively intact forest occurs at the base of and on the Mahafaly Plateau for well over 100 km in a north-south direction, although some areas within are now notably disturbed. Hence, large-scale human-induced modifications of forest cannot explain the disappearance of certain habitats and extinct animals. On the basis of freshwater aquatic birds and mammals recovered from the subfossil deposits, a wetter habitat existed in the immediate region up to about a millennium ago. This is in complete contrast to the situation today, where in the Tsimanampetsotsa area the remaining freshwater sources are subterranean and surface in caves at the foot of the Mahafaly Plateau, or farther to the west are saline sources, running across the salt pan to the lake and then toward the coast. Certain of these modern water sources have more than 20 g of minerals per liter of water (91), approaching that of seawater. Further, given the extensive cave systems (karst) along the western flank of the Mahafaly Plateau, which were undoubtedly dissolved out of the rock by underground water activity, this implies that sometime in the recent geological past significant quantities of water drained through this area. Today most of the caves on the plateau are dry, which indicates a major drop in the water table since they formed.

In his description of the geology and topography of Lake Tsimanampetsotsa, Perrier de la Bâthie noted that the dune system just to the west of the modern limit of the lake showed clear signs of a more extensive freshwater aquatic ecosystem, where the remains of freshwater mollusks and elephant bird eggshells were abundant (298, 301). Using this observation and other aspects of the local topography, he proposed a hypothesis to explain what happened to the area in recent geological time. In his reconstruction, the source of the former freshwater ecosystem would have been a resurgent stream flowing out of the Mahafaly Plateau and then into a valley that carried water toward the Mozambique Channel. Along the length of this river, freshwater habitat and probably gallery forest would have existed, providing appropriate niches for numerous organisms that are now extinct or no longer occurring in this area of Madagascar. Through shifting movements of the coastal dunes, the river was at least on occasion blocked, forming an estuary system. Because this water flowed through the limestone of the Mahafaly Plateau, it would have had an important charge of calcium carbonate and other minerals. With the shift toward a drier climate, the freshwater source became seasonal and at some

point ceased to flow, and then with greater water evaporation rates, as compared to intake, the aquatic system turned increasingly saline.

In other regions of Madagascar, oral histories remain today that recount observations in nature by earlier generations of people, and in some cases the animals that are discussed are certainly among those that are now extinct (see Plate 9). In such cases, direct observations by early generations of modern scientists of these almost “mythological” animals are largely unknown. One curious account by Perrier de la Bâthie is worth mentioning. He writes after a visit to the underground lake in Mitoho Cave:

*We glimpse once under conditions of poor visibility, emerging to the surface of the water, a large turtle head, belonging to a species definitely not known to be currently living. The lack of equipment and depth of the water prevented us from further exploring the cave to clarify what we observed. However, the presence of blind fish, the characters of the cave which appeared to extend far beyond the lake, the extent of the limestone plateau to the east of Mitoho, the deep chasms observed at its surface, lead us to believe that there is a network of underground rivers, where perhaps the last examples of Testudo Grandidieri [= Aldabrachelys grandidieri, but see comments below] may have found refuge. Further, the rubble at the cave entrance contains numerous fragments of this tortoise's carapace (our translation; 298).*

Given the dramatic and extraordinary nature of Perrier de la Bâthie's observation, several explanatory comments have been presented in the literature. For example, perhaps the animal observed was a crocodile, but given the difference in head shape between a tortoise and a crocodile, this seems unlikely. Another possibility is the beast was a very large eel, which indeed do occur in caves with sea connections. Finally, maybe it was some large freshwater turtle. Members of the genus *Aldabrachelys* are able to swim, but what a tortoise would be doing in the Mitoho Cave lake is another question. The most recent radiocarbon date for a member of this genus is 750 years BP (mean calibrated date of 635) from north of Toliara (69), centuries before Perrier de la Bâthie's observation. In any case, it is unclear what he observed in the cave.

Two species of giant tortoises have been reported from the Mahafaly Plateau subfossil deposits—*Aldabrachelys grandidieri* and *Aldabrachelys abrupta* (see Table 3)—which show differences in their shell (plastron and carapace) characteristics (14, 36). Members of this genus are known to show considerable variability

in aspects of their external form, particularly in shell shape, and observed shape differences do not always reflect recognized genetic differences between different morphological types (289, 290). Whether two species actually occurred on Madagascar or not will need further investigation, including the isolation of DNA from *Aldabrachelys abrupta* and its comparison to sequences of *Aldabrachelys grandidieri*, DNA for which has already been successfully obtained (15). On Aldabra Island, in the western portion of the Seychelles and in close proximity to northern Madagascar, a large tortoise, *Aldabrachelys gigantea*, occurs that shows some genetic differentiation from *Aldabrachelys grandidieri*, but determining if *Aldabrachelys abrupta* is genetically distinct from these other two species will also require further investigation.

Recent research on the dispersal capacity of giant tortoises in the Galápagos has shown that they are able to carry seeds over a considerable distance and are responsible for prodigious diffusion of several different types of plants (30). On Aldabra *Aldabrachelys gigantea* reach an herbivore biomass of between 3.5 and 58 tons per km<sup>2</sup>, which is more than the combined biomass of various species of large mammalian herbivores in any given African landscape, such as the Serengeti (65). Hence, their disappearance from Madagascar would have considerable consequences for aspects of ecosystem functioning (see Part 1, “Savanna and Grassland Formations”). The void created by the extinction of these animals is often referred to as an “evolutionary anachronism,” as the former trophic role in keeping the ecological machine moving no longer exists. There is good evidence that such a role for *Aldabrachelys* on Madagascar was notably important. Hence, for modern ecological restoration of degraded native habitats on the island to develop in a correct manner, a surrogate herbivore, in this case the closely related *Aldabrachelys gigantea*, should be introduced to different sites (294).

In our reconstruction of the habitat and animals that occurred from the edge of Lake Tsimanampetsotsa to the Mahafaly Plateau (Plate 4), particularly the zone that is today salt pan, we have emphasized that it was probably similar to Miombo woodlands of southern Africa: that is, wooded but not with a continuous canopy, and in several areas, out from under tree shadows, with herbaceous plants perhaps dominated by grasses. Such zones would have provided herbage for grazers such as giant tortoises and elephant birds, and open habitat for lemurs such as the monkey-like *Archaeolemur*. Both genera of elephant

birds, the smaller *Mullerornis* and the larger *Aepyornis*, are known from the Tsimanampetsotsa region (see Table 3). The large “koala-lemur” *Megaladapis edwardsi* was a slow-moving, primarily arboreal animal that would have come down to the ground to travel between trees in areas where the canopy cover was not complete, as well as frequently walking down to the lake to consume water, as all extant lemurs are obligate drinkers.

On the basis of carbon and nitrogen isotope values from radiocarbon-dated bones of giant tortoises in the southwest, certain inferences could be made about the types of foods they utilized (72). A comparison between the values obtained from coastal sites and an inland site found notable differences in the types of plants consumed in these two different zones, and, in general, they did not show a preference for the consumption of C<sub>4</sub> grasses. Today in the spiny bush, a transect across forested zones from the coast to inland areas, there are distinct differences in the plant communities, which are closely related to soil types (312). Hence, variation in the diet of giant tortoises could be explained by such patterns.

Within the freshwater area of the lake, birds would have been plentiful, such as a cormorant of the genus *Phalacrocorax* known from southwestern Madagascar subfossil deposits and representing a species that no longer occurs on the island. We do not know if it is extinct or if populations remain today on Africa (156). Other waterbirds would have included the Bernier’s Teal *Anas bernieri*; this species is now very rare and known mostly from western and northwestern Madagascar. In the same fashion, the Madagascar Fish Eagle *Haliaeetus vociferoides*, shown perched in the dead tree to the upper right, would have fed largely on fish, which are completely absent from the saline waters of Tsimanampetsotsa Lake today.

One of the other freshwater habitat-specific animals would have been the pygmy hippo *Hippopotamus lemerlei*. Rich oral histories of these semi-aquatic animals refer to them variably as *laloumena*, *lalimena*, *kilopilopitsofy* (with supposedly floppy ears), *ndrimo*, *tsy-aomby-aomby*, or the variant *tsoungaomby* in different dialects of Malagasy (50, 119). The last “dated” observation of a hippo on Madagascar based on oral history is the middle of the twentieth century (see Plate 9). Whether this proposed date is a miscalculation of how long such tales remain part of active oral history or something approaching reality is unclear. Just as a side note, Steve Goodman has observed subfossil hippo remains at the base of a “trapdoor” verti-

cal cave opening on the Mahafaly Plateau, about 3 km from the modern edge of Lake Tsimanampetsotsa, which gives the impression that these animals on occasion climbed and dispersed considerable distances across non-aquatic habitat. The intriguing possibility exists that they were more terrestrial than the living hippos of Africa.

Considerable information is now available to show that dramatic ecological changes took place in the southwestern portion of Madagascar in recent geological time. On the basis of a pollen core taken at Ranobe, north of Toliara (see Plate 6), it is clear that shifts in climate, toward desiccation, can at least partially explain these rapid modifications. According to the archaeological evidence that human populations have probably always been low in this portion of Madagascar and in view of the fact that large areas of forest remain today, there is little evidence to implicate humans as primary agents in the ecological changes. Local people almost certainly hunted animals, including those that are now extirpated from the region or extinct. However, in this portion of the island, we propose that the overriding factor driving extinction was ecological change.

The very appropriate question can be asked, given the level of habitat change that we have described above in the region over only a few millennia: Why does the region have so many micro-endemic organisms adapted to the modern local arid conditions? This includes, for example, a multitude of plants, such as the endemic family *Didiereaceae*, and numerous vertebrates. We cannot really address this question in a definitive manner, but we propose the following. There is good evidence that the southwestern region has become increasingly arid, with freshwater habitats and different forested habitats having disappeared in very recent geological time. These different habitats provided a refuge for a wide variety of organisms. The drying up of the interior water sources, as well as a presumed decrease in local precipitation, which nourished these habitats, had devastating affects on the local biota, including those taxa living in the Miombo-like woodlands. Many animals, for example, went locally extinct because of these changes, and others adapted to the changing conditions. Hence, many endemic organisms were maintained, but notably less than a few thousand years ago. What role the proposed mega-tsunami and associated increase in temperatures (see Plate 3) may have had on these changes remains to be unraveled. In any case, it can be imagined that the spiny bush at

the foot of and on the Mahafaly Plateau was similar in many ways as today, but with more mesic elements. In a more general manner, perhaps the unique habitats and associated fauna and flora have moved about the island as sort of ecosystem plates, waxing, waning, and shifting position as ecological conditions changed through time.

## Plate 5: Taolambiby—Hypotheses Associated with Animal Extinction and Hunting by Humans: Physical Evidence and Interpretation

There is information from the late Pleistocene that shows that soon after human arrival in different regions of our Earth, large animals, often referred to as the “megafauna,” disappear—the aforementioned

“dreaded syncopation.” The actual cause of these extinctions has been a source of considerable debate, and numerous hypotheses have been proposed (see Part 1, “Hypotheses on What Caused the Extinctions

---

Recently a team of researchers found lemur bones in different museum collections previously excavated at Taolambiby and bearing “cut marks.” Based on different lines of evidence, it was proposed that Taolambiby was a site where humans, at least on occasion, hunted and butchered lemurs. Nothing is known about the cultural context of these people, with the exception that they had the technology to make metal cutting utensils that were used to dismember medium- and large-bodied animals. Presumably, they did not live in permanent settlements, or at least to date such sites have not been found by archaeologists. Here we illustrate three different lemur species being processed in a makeshift hunting camp: the extant species *Propithecus verreauxi*, with one individual hanging upside down by its hind legs in the upper right; and two extinct species, *Palaeopropithecus ingens*, lying on its back in the foreground, and *Pachylemur insignis*, being carried into the camp in the right foreground. In the middle section of the image, people are roasting lemur meat over an open fire, and in the back section, a returning hunting party is bringing in some additional animals. (Plate by Velizar Simeonovski.)



during the Holocene”). One of these was formulated by the late Paul Martin nearly four decades ago as the “overkill” hypothesis (260), the extreme version of which was also referred to as the “blitzkrieg” hypothesis, which translates from the German as “lightning war,” an indication of how quickly things passed. Martin’s suggestion was that after human colonization of an area, rapid extinction of the large animal fauna followed in causal association with hunting and habitat transformation pressures.

During the year that Paul Martin published this landmark paper, he visited Madagascar. Certainly, little was known then, at least compared to today, about the extinction of the island’s large animals, but in-

formation from that era entered into the refinement of this influential hypothesis (also see Plate 2). As an important caveat, the timing of initial human colonization of Madagascar, which may have led to the disappearance of numerous organisms, was notably later than in Martin’s continental Africa and North American examples. This temporal complication may have deemphasized Madagascar in the research and writings of Martin over his long and productive career. However, he encouraged several people—notably René Battistini, the late Pierre Vérin, Alan Walker, and David Burney (Figure 48)—to pursue research on what unfolded on the island after humans arrived. Numerous articles, chapters, and books have

Figure 48. Several different researchers have been active in different fields to understand what changes took place in the natural environments on Madagascar before and after human arrival. These include (A) the late Pierre Vérin during a field school trip to Itasy Lake with university students in 1963 (photograph courtesy of the Institut de Civilisations / Musée d’Art et d’Archéologie); (B) the late Paul Martin at the “shell site” near Ankazoabo-Sud in 1966 (photograph by Alan Walker); (C) David Burney at Taolambiby in 2004 (photograph by Daniel Grossman); (D) René Battistini on a field trip to the southwest in 1970 (photograph courtesy of the Institut de Civilisations / Musée d’Art et d’Archéologie); and (E) Alan Walker during a mission to the Kaswanga Primate Site on Rusinga Island, Kenya, in 1985 (photograph by Mark Teaford).



been written weighing the pros and cons of these different hypotheses to explain the largely synchronized extinctions of animals with human arrival in different areas of the world. It is now clear that no single hypothesis can explain what happened in the diverse geographical, cultural, and ecological regions that experienced such events.

With this as a brief introduction, we now turn back to Madagascar, to ask the question: What are the factors that correlate with the disappearance of different animal species over the past few millennia? These included a fantastic array of beasts, which ranged from lemurs greater in body size than any living species (culminating in the giant gorilla-size *Archaeoindris* of the Central Highlands; see Plate 12), a radiation of giant flightless birds (family Aepyornithidae; see Plate 1), three species of hippos (see Plate 10), and an assortment of odd beasts such as the aardvark-like *Plesiorycteropus* (order Bibymalagasia) (see Plate 14). On the basis of current paleontological and archaeological evidence, these extinction events took place within the past few thousand years, which is notably later than in Australia, for example, which date to about 46,000 years ago (328). An important aspect concerning the temporal framework, based on current information, is that after New Zealand, Madagascar was the last large island mass in the world colonized by humans. Hence, if there is indeed a causal relationship between human colonization of an area and extinction patterns, a late date from Madagascar is expected.

Until recently, little direct evidence existed from Madagascar for the hunting by people of vanished animals. In the older literature, there are several reported cases of human-modified bones of large and now-extinct species (e.g. 82, 181, 308). Subsequently, Ross MacPhee and David Burney examined some *Hippopotamus lemerlei* material held in the Paris museum and excavated by Alfred Grandidier between 1898 and 1901 at the sites of Ambolisatra and Lamboharana, north of Toliara (251). It has recently been suggested that two sympatric dwarfed hippos co-occurred at numerous localities across the island, and material from these two southwestern sites might be referable to *Hippopotamus guldbergi* (107). As had been previously recognized (181), several bones from these sites had marks deep into the bone that could best be explained by metal knife cuts. Based on several lines of evidence, they concluded that the modifications were made soon after the hippos' death, when the bone was still fresh, and the marks were the result of

butchering. While the find in itself was important, what was extraordinary is that three of the four radiocarbon dates they obtained from different modified hippo bones spanned the range from about 2,020 to 1,740 years BP (mean calibrated dates of 2,005 and 1,565) (69), which, at that point, represented the earliest known direct interactions between humans and animals on Madagascar. Even more important, these radiocarbon dates pushed back by several hundred years the projected date when humans first colonized the island, as the previous archaeological evidence had implicated the period of 1,500 years BP (24). Other points associated with these hippo bones and the interpretation of this important find are discussed in Part 1 (see "Human Interactions with Now-Extinct Land Vertebrates").

Although different references have been made in the literature to human-modified remains of extinct animals from the site of Taolambiby, close to Beza Mahafaly in the southwest, no precise details were available until a few years ago. Subsequently, a research team examined older subfossil collections held in different museums and obtained at Taolambiby by Paul Ayshford Methuen, Charles Lamberton, and Alan Walker, as well as material from Tsirave, near Beroroha, by Charles Lamberton (296). It is important to emphasize that at Taolambiby neither Methuen nor Lamberton recorded information on the relative position of the excavated bone remains, which were dominated by now-extinct lemurs. In the case of the Walker material, some information on the stratigraphic position of the bone was noted, and his collections contain mostly extant species, which may imply that this material represents more recently deposited bone. Various extrapolations from this site about human interactions with animals have been criticized because of the lack of stratigraphic precision placing different events in a time line of sorts, and the fact that no cultural objects, such as a knife, have been recovered (85). We will return to these aspects below.

The subfossil deposit of Taolambiby is along an exposed alluvial terrace with signs of water erosion (see Figure 8) (308). Some water seepage in the deposit still occurs, and at some point in time, during a period with greater rainfall, it may have been an important water source. Hence, this would have been an attractive locality for animals to drink and, in turn, an ideal place for humans to hunt. Further, given the local topography, it is possible that during periods of heavier rainfall, the formation funneled water, and

a stream flowed toward the Sakamena River, several kilometers to the east. Today the region of Taolambiby falls with the arid vegetational type known as spiny bush (see Part 1, “Vegetational Patterns”). This zone receives on average less than 650 mm of rainfall per year, with an 8- to 10-month dry season, and temperatures can rise to 49°C (316). Of considerable importance to our discussion concerning the modern fauna and flora of the region is the observation that free-flowing water is notably rare and highly seasonal (see Figure 22).

Among the collections from Taolambiby, the following extinct primates have been identified: *Palaeopropithecus ingens*, *Mesopropithecus globiceps*, *Archaeolemur majori*, *Megaladapis madagascariensis*, *Megaladapis edwardsi*, and *Pachylemur insignis* (see Table 4). Three extant species—*Propithecus verreauxi*, *Lemur catta*, and *Lepilemur leucopus*—are also part of the faunal list and still occur in the local forest formations. Among the Methuen material, *Palaeopropithecus* is the most common lemur, followed by *Pachylemur*. The material from Tsirave holds a similar assortment of taxa, but with the addition of *Hadropithecus stenognathus* and *Daubentonia robusta*, and with *Pachylemur* being the most common species represented in that sample. In total, nearly 300 bones were closely examined in the study of Ventura Perez and colleagues for surface modifications using a standardized microscopic procedure and strict definitions of what constitutes “butchering marks” or “chop marks.” This analytical protocol allowed the features associated with intentional cutting up of the lemurs to be differentiated from those more likely a result of sedimentation abrasion and non-human scavengers (rodents, Carnivora, etc.) (Figure 49).

Among the extinct species examined, 40 percent of the *Palaeopropithecus* bones showed evidence of butchering, 33 percent of the *Pachylemur*, and not one of the *Megaladapis*. In the case of the extant species, particularly from the Walker collection, 29 percent of the *Propithecus* material, but not one *Lemur* bone, showed signs of humans dismantling with knife-like objects. Hence, it can be surmised that at least a portion of the bone deposits at Taolambiby and Tsirave were associated with human hunting, and this may have taken place in the context of some social organization, such as hunting camps, at different points in time. This likely scenario for Taolambiby is depicted in Plate 5, which is considered the first known “kill site” on Madagascar.

We do not know how the various animals that



Figure 49. A considerable proportion of the lemur bones recovered from Taolambiby showed distinct marks associated with butchering and defleshing. For example, among the examined *Palaeopropithecus* bones, as shown here, nearly 40 percent had such marks, which are concentrated at the extremities (see arrows). This is construed as evidence that the marks are associated with dismantling of the presumably hunted animal. (Photograph by Ventura Perez.)

ended up as bush meat were hunted, but given the wide range of body sizes and different locomotor adaptations, we can speculate that several strategies were probably employed. Perhaps traps or snares were set. It is also possible that slings, spears, or bow and arrows were used to topple arboreal species off their branches and tree trunks. Large tree-dwelling species like *Palaeopropithecus* may have been clumsy and slow moving, and therefore vulnerable to clubs and stones when discovered on the ground. In fact, it seems likely that all species, including *Pachylemur* and *Propithecus*, may have been relatively naive when encountering an alien primate like a human being for the first time. Unaccustomed to this new and lethal predator, the native animals may have been relatively easy pickings. In any case, based on detailed genetic analyses and despite a probable history of human predation, modern populations of *Propithecus verreauxi* from the nearby Beza Mahafaly Special Reserve show no sign of passing through a genetic bottleneck in the past 2,000 years, whether the result of human predation or natural climatic change as discussed below (237).

**Table 4**

List of land vertebrates identified from Taolambiby sub-fossil remains (23, 36, 308, 379). Extinct species are indicated with †, and the author(s) and description date are given. For living taxa, the English common names are given. Listing does not include introduced species.

**Order Reptilia**

Family Testudinidae

†*Aldabrachelys abrupta* (A. Grandidier, 1866)

†*Aldabrachelys grandidieri* (Vaillant, 1885)<sup>1</sup>

*Astrochelys radiata* radiated tortoise

Family Crocodylidae

†*Voay robustus* (A. Grandidier & Vaillant, 1872)

*Crocodylus niloticus* Nile crocodile<sup>2</sup>

**Class Aves****†Order Aepyornithiformes**

†Family Aepyornithidae

†*Aepyornis* sp.

**Class Mammalia****†Order Bitymalagasia**

†*Plesiorycteropus madagascariensis* Filhol, 1895

**Order Afrosoricida**

Family Tenrecidae

*Tenrec ecaudatus* common tenrec

**Order Primates****Suborder Strepsirrhini****Infraorder Lemuriformes**

†Family Archaeolemuridae

†*Archaeolemur majori* Filhol, 1895

†Family Palaeopropithecidae

†*Mesopropithecus globiceps* Lamberton, 1936

†*Palaeopropithecus ingens* G. Grandidier, 1899

Family Indriidae

*Propithecus verreauxi* Verreaux's sifaka

Family Lepilemuridae

*Lepilemur leucopus* white-footed sportive lemur

Family Cheirogaleidae

*Cheirogaleus* sp.

Family Lemuridae

†*Pachylemur insignis* Filhol, 1895

*Lemur catta* ring-tailed lemur

†Family Megaladapidae

†*Megaladapis edwardsi* G. Grandidier, 1899

†*Megaladapis madagascariensis* Forsyth-Major, 1894

**Order Carnivora**

Family Eupleridae

†*Cryptoprocta spelea* G. Grandidier, 1902

**Order Artiodactyla**

Family Hippopotamidae

†*Hippopotamus lemerlei* A. Grandidier, 1868

1. Both species of *Aldabrachelys* have been reported from the site and their co-occurrence needs to be verified.

2. The remains identified as the genus *Crocodylus* need to be reevaluated to verify that they are not referable to the extinct *Voay robustus*.

As far as we can discern from published data, only a single radiocarbon date is available from a human-modified extinct lemur bone from Taolambiby; this is a forearm bone of *Palaeopropithecus ingens* dated to 2,325 years BP (122) (mean calibrated date of 2,250) (69). The only other lemur bone exhibiting cut marks from this site to undergo radiocarbon testing was a shinbone of *Propithecus verreauxi*, which yielded a date of 1,045 years BP (mean calibrated date of 885). Given the importance of the site in interpreting the human colonization history of Madagascar, as well as human interactions with the native fauna, we look forward to more dates on human-modified bones from here. However, without further radiocarbon dates little can be extrapolated other than, based on current information, that lemurs were hunted during two periods separated by about 1,300 years. For people who have experience in the dismantling of animals with sharp objects, such as metal knives, the anatomical positions of where to cut are learned quickly and become intuitive. Even for such practiced individuals, perhaps associated with a lack of attention or a mistake, the knife-like object may have occasionally fallen in the incorrect position and left marks on the central bone shaft. However, one would suspect that butchered animal bones would infrequently show such random signs when dismantled by experienced hunters. Defleshing marks away from joints, as opposed to dismembering ones, are more common on the giant extinct lemurs than on the smaller living species, which no doubt required more effort—and a bigger payoff.

If one accepts the marks in the forearm of the *Palaeopropithecus* to have been induced by a human-fabricated knife-like object, this single radiocarbon date represents the earliest documented presence of humans on the island (54, 69). Recently older dates associated with human-modified hippo bones have been proposed for elsewhere on Madagascar (99, 139), but as discussed in Part 1 (see “Human Interactions with Now-Extinct Land Vertebrates”), there are complicating factors in their interpretation (85), and we do not accept this earlier date.

There is an important quandary associated with human-modified bones recovered at Taolambiby and the interpretation presented above. Older dates are known from the site, such as *Megaladapis* bone dated to 3,025 years BP and 3,005 years BP (mean calibrated dates of 3,165 and 3,125) (69). Dates for tortoises and hippos from there are also almost this old, and not one, to our knowledge, has been associated with cut



marks or evidence of defleshing. One unmodified bone of *Archaeolemur majori* and another of *Crypto-procta spelea* are also older than 2,325 years BP. Given the complete lack of human context, these dates obviously cannot be used as evidence that people had already landed on the island. More parsimoniously, they simply represent animals that died of natural causes, and their remains were fortuitously deposited. Numerous bone remains of different extant animals have yielded largely modern radiocarbon dates, and it is clear that the site has acted as a natural deposition trap for many millennia. It is quite likely that the site was a watering spot, and over time many animals died in close vicinity. At some point or perhaps during different periods, humans also used the locality for hunting and dismantling prey, which in some cases may have been cooked and consumed in close proximity. The presence of a local water source would have facilitated the preparation of hunted animals. Hence, these different factors might explain the mixed contexts (human modified and non-modified) of how the different bone remains were deposited. Critically, until finer stratigraphic information and, very importantly, a greater number of radiocarbon dates from the bones with cut marks are available, questions will remain unanswered on the chronology of events related to human interactions with the local fauna.

So who were the people that occupied Taolambiby? No archaeological information is available from 2,300 years BP on the inhabitants of this site or for this general area of Madagascar (86, 308). It would be reasonable to presume that they did not live in permanent settlements, or at least the remains of these settlements have yet to be found. In 1966, when the late Paul Martin visited Taolambiby, he noticed pottery sherds in the upper portion of the bone deposits and collected a portion of a tortoise carapace that seemed to have been artificially perforated (308). Specialists did not examine the pottery, and it is undocumented concerning style and inferred date; no other similar finds have been reported from the site. What appears to be the case is that these people had metal technology and access to considerable protein in the form of lemur meat (296). If the context of a transient butchery site of Taolambiby is correct, what is the possibility of finding an archaeological site documenting something approaching the first unequivocal material evidence of humans to corroborate inferences drawn from these cut marks? Slim, we suspect. On the other hand, if the water source provided a

recurring magnet for human activities, ranging from a site for drinking or hunting, over a period ranging from decades to centuries, it is rather odd that, other than the pottery reported by Martin, no cultural objects have been reported from the site. Perhaps in a more fundamental context, major holes exist in what is known about the history of initial human colonization of Madagascar; only with new discoveries will the details of when this happened become clearer.

Returning to the question of what happened to the large animals that once occurred in this portion of Madagascar, does Martin's overkill hypothesis help explain their disappearance? Two points would be critically important to show support for this hypothesis (261), especially the blitzkrieg version: (1) the megafauna disappeared *rapidly* in association with hunting pressure, and ecological transformation followed quickly after human colonization; and (2) widespread ecological collapse was associated with the extinction events.

With respect to the first prediction, Taolambiby provides some evidence of local hunting pressure on animals that are no longer with us, as well as a certain number that are still extant. Given that we really do not completely understand when humans colonized this portion of Madagascar, it is difficult to set the time frame to measure if the extinction process passed rapidly or not. In any case, further radiocarbon dates from modified bone are needed to define properly the period of human interactions with the now-extinct fauna. Most critically, given that many of the extinct animals had relatively broad distributions and persisted until quite recently, at least in southern and southwestern Madagascar, and few kill sites are known and correctly documented in a temporal sense, current information does not suggest population-wide hunting pressure. Further, and working against the first postulate of the overkill hypothesis, many of the animals co-occurred with people for at least one millennium after the currently recognized period of initial human colonization (54). Hence, there is no support for their rapid disappearance as implied by this temporal aspect of the hypothesis.

For the second portion of the hypothesis, rapid ecological collapse, this seems to have happened, but more plausibly represents ecological change accelerated by climatic shifts rather than direct human modification of the environment. As discussed in detail for Tsimanampetsotsa (see Plate 4) and Ankililolo (see Plate 6), portions of southern and southwestern Madagascar experienced notable aridifica-

tion, which implicates natural climate change as the likely trigger leading ultimately to notable landscape alteration. As mentioned above, today in the immediate vicinity of Taolambiby, there is no permanently flowing freshwater to support aquatic ecosystems and marsh habitat. The principal river of the area, the Sakamena, flows only periodically during the rainy season. The presence of hippos and crocodiles in the Taolambiby subfossil deposits, both requiring freshwater, clearly signals significant ecological change in the region, presumably associated with a broad regional aridification that occurred between 3,500 and 2,500 years BP (47).

The Sakamena River has its headwaters in the Isalo Massif, to the north. As discussed in detail for the site of Ampoza (see Plates 7 and 8), which is in the western watershed of Isalo, this region has undergone a considerable decline in available permanent surface water over the past few millennia, as well as a presumed increase in the length of the dry season. As at Ampoza, these factors would have also important implications for the Taolambiby area, and desiccation associated with climatic change might be the best explanation for the principal disappearance of the local megafauna. For certain taxa, local hunting pressure by humans could have been the *coup de grâce*, but given the lack of such a context for other species that have gone extinct, shifts in the local ecology and weather regimes remain the best explanation for now.

A possible example of such an ecological shift comes from a recent study employing carbon isotope values from radiocarbon-dated subfossils of extinct and extant lemurs at Taolambiby (72). The study found that lemurs that have died out showed a preference for  $C_3$  plants in their diet, while the species still in existence showed a greater tendency to consume CAM or  $C_4$  plants; the latter two floral groups are relatively abundant in the regional flora of today. These isotopic differences may be associated with shifts in lemur feeding ecology and plant ecology tied to climatic change over the past few millennia.

Until this point, we have implicitly treated Taolambiby in the context of an archaeological site. However, given the nearly complete lack of cultural artifacts recovered from its deposits and only a couple of radiocarbon dates of human-modified bones, this is not correct in a technical sense. It is best to consider the site as largely paleontological, with an indeterminate period of bone deposition associated with humans. A considerable number of vertebrates are known

from the Taolambiby deposits (see Table 4), but not recognized among the species butchered by humans; these include, for example, *Megaladapis edwardsi*, *Megaladapis madagascariensis*, *Archaeolemur majori*, dwarf hippos, giant tortoises, and elephant birds (62, 69, 122). Radiocarbon dates of a giant extinct tortoise (*Aldabrachelys*) indicate that this genus still occurred in this portion of Madagascar until about 750 years BP (mean calibrated date of 635) (69). A similar situation exists for the extinct dwarf hippo (*Hippopotamus lemerlei*), but no signs of butchering marks have been found. Based on current data, there is no evidence of coinciding, punctuated shifts in the ecological conditions of Taolambiby and human-imposed modifications of the environment. Humans may have been a contributing factor, but, in short, Martin's overkill hypothesis does not seem sufficient to account for the changes and extinction events that took place at Taolambiby.

## Plate 6: Ankilitelo—a Deep Pit Cave and Inferences about Recent Ecological and Faunal Change

The vast majority of the subfossil sites discussed up to this point contain material that was deposited during a period before or soon after human colonization of Madagascar. In most cases, the material is old enough that current archaeological information indicates that people had not yet colonized the island (see Plate 4, for example). Even if people had

arrived without leaving a detectable trace, human density was probably still low, and different types of pressures such as deforestation and hunting are presumed to have been relatively minor. In the summer of 1994, Elwyn Simons and colleagues, including several professional cave explorers (speleologists), commenced excavations at a pitfall cave northeast of

---

The entrance to Ankilitelo Cave is rather dramatic, with a vertical shaft dropping 145 m in depth. Any terrestrial animal falling into the cave would have certainly met its doom at the bottom. Accordingly, at the base of the shaft a large quantity of bone material was recovered resting in a massive tangle on a large dome of rock debris. The scene presented here is at the upper edge of the vertical entrance, at night during a full moon. The centerpiece is a large extinct aye-aye *Daubentonia robusta*, about three to four times more massive than the extant species *Daubentonia madagascariensis*, shown about to pilfer eggs in a bird's nest. Also depicted is a hunting Carnivora *Galidictis grandidieri*, having turned over a log and about to feed on hissing cockroaches. In the background, the kangaroo-rat *Macrotarsomys petteri* can be seen moving on the ground. For a key to the different animals, see black-and-white inset for Plate 6 in color gallery. (Plate by Velizar Simeonovski.)





Toliara that yielded considerable quantities of subfossils (Figure 50). This cave, known as Ankilitelo, provides a much more recent window into the animals that lived in this region and demonstrates just how quickly things can change.

Ankilitelo Cave is found on the limestone Mikoboka Plateau and in close proximity to the village of Manamby (345, 349). The name of the site is derived from the Malagasy and means “the place of three tamarind trees” (*Tamarindus indica*, family Fabaceae), a plant that was thought to be introduced to Madagascar from India, but recent molecular evidence indicates that it is in fact native to the island (89). The entrance of the cave is a relatively narrow vertical shaft, 10 m in diameter and 145 m deep (281, 349)! Directly below the shaft, a pile of bones from terrestrial animals, about 1 m tall, was found. At the shaft’s bottom, the cave opens into a large room, with a sloping floor (Figure 51), and then continues to the true end of the cave, approximately 230 m vertical distance from ground level. Other than this vertical shaft, no other entrance into the cave is known.



Figure 50. Ankilitelo Cave area in 1997. Elwyn Simons next to skulls, limb bones, and miscellaneous bone fragments from deep in the cave, laid out to dry before being sorted and prepared for analysis and transport (left). Note the relatively dry scrubland in the background. Nice specimens of *Megaladapis madagascariensis* (skull in round container in center, limb bones to lower right) and *Palaeopropithecus ingens* (palate with all the upper teeth at lower left, limb bones to immediate right) removed from the cave and in the process of being sorted (right). (Photographs by Don DeBlieux.)

The vast majority of the approximately 5,000 subfossil bones collected to date come from the large pile of bones directly below the shaft, recovered by skilled speleologists who on a daily basis climbed in and out of the cave on long ropes, carrying the new finds to the surface in buckets. Much of the material, composed of a wide assortment of vertebrates, is well preserved, and rare skeletal elements of certain species were recovered for the very first time, like hand and foot bones of giant lemurs (189). This latter aspect has been very important in efforts to properly reconstruct the anatomy of these extinct animals and provide insight into aspects of their natural history (see Plate 18).

The cave entrance acted as a pitfall trap: animals walking along the rim of the shaft occasionally lost their footing and fell into the cave. It is easy to imagine when hitting bottom that they immediately perished due to the shock, and, over time, this resulted in the large concentration of bone material. This might have happened in several different ways, for example, at night or dusk when diurnal animals might move less adeptly and simply slipped, or perhaps in other cases the fall took place associated with the hot pursuit by a predator. One can imagine that large-bodied, arboreal lemurs were a bit clumsy when moving on the ground, and animals such as the “sloth-lemur”



Figure 51. Time-lapse image of the large lower room of Ankilitelo Cave below the trapdoor entrance (*upper left*), with a distinctly sloping floor. With the human images as points of perspective, it is possible to appreciate the size of this room, which is at the bottom of the 145 m deep vertical opening to the cave. This room leads to the end of the cave, about 230 m vertical distance from ground level. (Photograph by Chris Hildreth.)

*Palaeopropithecus ingens*, which was not designed for a terrestrial manner of locomotion, might be disproportionately represented in the bone remains. This is indeed the case. Birds of prey, such as nocturnal owls or diurnal hawks and eagles, may have also carried smaller animals to the rim edge or vertical tunnel ledge, and these dropped to the bottom of the shaft. As can happen on occasion, raptors when dispatching and manipulating prey can accidentally drop certain bits, or alternatively, after digestion of the animal, regurgitate remaining fur and bone remains in the form of pellets. At least one human also had the misfortune of falling into the shaft.

There is another extraordinary aspect of the cave. The bone remains that have been radiocarbon dated are remarkably recent. These include dates from two extinct lemurs: *Megaladapis madagascariensis* at 630 years BP (mean calibrated date of 585) and *Palaeopropithecus ingens* at 510 years BP (mean calibrated date of 475) (69, 280, 345). In the case of animals that are still living today (extant), a single date is available: *Cryptoprocta ferox* at 560 years BP (mean cali-

brated date of 560) (69, 281). Hence, all of these dates are quite close to one another and within the period after European colonization of the island, currently set at 500 years ago when Diogo Dias, a Portuguese merchant marine, was the first person known to have caught sight of the island (325). Why older remains have yet to be identified from the cave is difficult to say, but perhaps this is best explained by the small number of radiocarbon samples analyzed to date, or the fact that the collectors did not get down to the oldest remains at the bottom of the bone pile, or, most likely, the relatively recent period that the cave ceiling collapsed, thereby creating the vertical shaft pitfall trap.

In total, thirty-two species of mammals have been identified from the bone remains recovered in Ankilitelo Cave, not including two introduced to Madagascar (281) (see Table 5). In comparison, from the nearby forest of Zombitse-Vohibasia, which was surveyed in recent years, twenty-four species of native mammals have been documented, not including four introduced species. The Zombitse-Vohibasia forest has a distinct dry season, probably lasting about

**Table 5**

List of land vertebrates identified from Ankilitelo subfossil remains (121, 126, 281). Extinct species are indicated with †, and the author(s) and description date are given. For living taxa, the English common names are given. Listing does not include introduced species. A large collection of bird bones collected at Ankilitelo is currently under study.

---

**Class Mammalia**
**Order Afrosoricida**

## Family Tenrecidae

- Tenrec ecaudatus* common tenrec
- Setifer setosus* greater hedgehog tenrec
- Echinops telfairi* lesser hedgehog tenrec
- Geogale aurita* large-eared tenrec
- Microgale brevicaudata* short-tailed shrew-tenrec
- Microgale cf. majori* Major's long-tailed shrew-tenrec
- Microgale nasoloi* Nasolo's shrew-tenrec

**Order Primates****Suborder Strepsirrhini****Infraorder Lemuriformes**

- †Family Archaeolemuridae
  - †*Archaeolemur majori* Filhol, 1895
- †Family Palaeopropithecidae
  - †*Palaeopropithecus ingens* G. Grandidier, 1899
- Family Lepilemuridae
  - Lepilemur leucopus* white-footed sportive lemur
- Family Daubentoniidae
  - †*Daubentonia robusta* Lamberton, 1934
- Family Cheirogaleidae
  - Microcebus griseorufus* gray-brown mouse lemur
  - Microcebus murinus* gray mouse lemur
  - Cheirogaleus medius* fat-tailed dwarf lemur
- Family Lemuridae
  - †*Pachylemur insignis* Filhol, 1895
  - Eulemur fulvus* brown lemur
  - Lemur catta* ring-tailed lemur
- †Family Megaladapidae
  - †*Megaladapis madagascariensis* Forsyth-Major, 1894
- Family Indriidae
  - Propithecus verreauxi* Verreaux's sifaka

**Order Chiroptera**

- Family Molossidae
  - Mormopterus jugularis* Peters' goblin bat
  - Otomops madagascariensis* Malagasy large-eared free-tailed bat
- Family Miniopteridae
  - Miniopterus gleni* Glen's long-fingered bat

**Order Carnivora**

- Family Eupleridae
  - Cryptoprocta ferox* fossa
  - Galidia elegans* ring-tailed vontsira
  - Galidictis grandidieri* Grandidier's vontsira
  - Mungotictis decemlineata* narrow-striped boky

**Order Artiodactyla**

- Family Hippopotamidae
  - Hippopotamus* sp.

**Order Rodentia**

- Family Nesomyidae
    - Eliurus* sp. tuft-tailed rat
    - Eliurus myoxinus* western tuft-tailed rat
    - Hypogeomys antimena* Malagasy giant jumping rat
    - Macrotarsomys bastardi* western big-footed mouse
    - Macrotarsomys petteri* Petter's big-footed mouse
- 

nine months per year; as one might expect, this has a profound influence on the plants and animals of the region and their ecology. The species identified from Ankilitelo include three species of bats that still occur in this region of Madagascar and make their day-roost sites in caves (148). Also included in the remains are seven species of tenrecs (family Tenrecidae), three of these are relatively large in body size and hedgehog-like, and the other four are more shrew-like, including the shrew-tenrec species *Microgale nasoloi*. This species was described only a few years ago and is known from just a handful of specimens, all coming from dry deciduous forest or transitional deciduous formations (353); two of these sites are within 100 km of the cave. If the subfossil remains had been examined before the living animal was captured and studied, *Microgale nasoloi* probably would have been described as extinct.

Among the Carnivora, four endemic species belonging to the uniquely Malagasy family Eupleridae have been identified from the cave. These include one still known from the area (*Cryptoprocta ferox*), one occurring in lowland forest to the west of Ankilitelo but very rare (*Mungotictis decemlineata*), and two that no longer occur in this portion of Madagascar (*Galidictis grandidieri* and *Galidia elegans*). *Galidictis grandidieri* is known today only from the spiny bush habitat of the Mahafaly Plateau, in the general vicinity of Tsimanampetsotsa (see Plate 4), south of the Onilahy River. Based on current information, this species is adapted to live in one of the most extreme and arid portions of Madagascar (149). As Ankilitelo Cave is 125 km to the north of Tsimanampetsotsa and on the other side of the Onilahy River, this demonstrates that the river was not a barrier for dispersal of this species. The other Carnivora of note, *Galidia elegans*, is widespread in eastern humid forest and to a lesser extent in dry deciduous forest. Today the southern limit of this species in the west is the Bemaraha Massif, which is about 440 km north of Ankilitelo. Hence,

for these two Carnivora, it is clear that significant changes have taken place in their distributions, presumably linked to habitat shifts that occurred in just a few hundred years. It is interesting to point out that remains of two introduced carnivorans, dogs *Canis lupus* and cats *Felis silvestris*, are not known from the cave; this may indicate low densities of human and their commensals in this area of the island over the past few centuries.

Seven species of rodents were identified from the bone remains, which include five of the endemic subfamily Nesomyinae (*Macrotarsomys bastardi*, *Macrotarsomys petteri*, *Eliurus* sp., *Eliurus myoxinus*, and *Hypogeomys antimena*) and two introduced species of the family Muridae (*Rattus rattus* and *Mus musculus*). All of the endemic nesomyine rodents are forest-dwelling, with *Macrotarsomys* spp. and *Hypogeomys* being largely ground-dwelling (terrestrial) and the *Eliurus* spp. living in trees (arboreal). As discussed under Plate 2, *Hypogeomys antimena* is known today only from the region north of Morondava, about 325 km north of Ankilitelo. Given the presence of this species in remains dated to about 500 years ago, the rapid contraction of its range is clear and noteworthy; a radiocarbon date from the *Hypogeomys* remains would be informative about its range contraction.

Another interesting rodent in the deposits is *Macrotarsomys petteri*, which was described a few years back from the Mikea Forest, about 50 km to the west of the cave. Even after extensive faunal inventories in the Mikea Forest, as well as in many localities in the southern and southwestern portion of the island, only a single individual has ever been captured, and this represents the only modern specimen of this species. Subsequently, in Andrahomana Cave (see Plate 2), in the extreme southeast and about 380 km southeast of the Mikea Forest type locality, numerous bones of this rare rodent were found, and subsequently it was also identified from Ankilitelo Cave. Accordingly, we assume that it too has experienced a similarly massive retraction of its range in a short period. In contrast to the point mentioned above about introduced dogs and cats, the presence of non-native rodents in the cave is a clear sign of human intervention in the general region, and heralds that some sort of habitation must have occurred within a few kilometers of the cave.

Twelve species of lemurs have been identified from the cave, including seven still known from the area and ranging in body mass from 60 g to 3.5 kg, and five that are extinct, ranging in body mass from just over

10 kg to just less than 50 kg. Hence, it is clear that extinction differentially affected the larger lemurs, a phenomenon that appears across the island repeatedly. Lower reproductive rates and the slower life histories of large species appear to make them especially vulnerable. A local primate community of twelve species is considerable, particularly for what is presumed to have been a transitional dry-humid forest. For example, today in the nearby Zombitse-Vohibasia Forest to the east of the cave, only eight species are known, and in the Mikea Forest to the west, nine species (110, 111, 112). It follows, therefore, that based on comparisons to these modern faunas, the Ankilitelo primate community was notably richer, and the most important difference is the presence of the five species of large extinct lemurs.

Two species of lemurs are known today from the general region of Ankilitelo Cave, *Mirza coquereli* and *Phaner furcifer*, but have not been identified from the bone remains. This emphasizes two different points concerning our extrapolations from Ankilitelo Cave. If one includes *Mirza* and *Phaner*, the local primate community 500 years ago probably had fifteen species. Further, Ankilitelo Cave—or any subfossil site for that matter—probably does not hold a record of all of the mammals that occurred in the immediate region. There are sure to be holes in the record, with certain animals not having been deposited or excavated from the site. Hence, the absence of a species from a subfossil locality cannot be used as conclusive evidence that it did not occur locally in the past.

So what do the identified mammals tell us about what happened in the Ankilitelo region associated with potential changes to the ecological community over a relatively short duration? It is important to add here that the work of Kathleen Muldoon, who studied the Ankilitelo material in considerable detail, reveals that extinct pygmy hippo remains are especially rare in the cave, which probably means that some 500 years ago the site was not in very close proximity to marshland or permanently running water. Bones of dwarf hippos are known from other pitfall-style vertical caves, such as Tsimanampetsotsa (see Plate 4). Of the thirty-two native mammals found in the Ankilitelo remains, every species of large body size, and specifically the giant lemurs, are extinct, and several Carnivora and rodents of moderate-size no longer occur in this portion of Madagascar. With the exception of *Galidictis grandidieri*, extant animals absent in the immediate area today comprise species that are restricted to more humid forest sites on the island.

In turn, most of the balance of taxa identified to the level of species, excluding animals like *Eliurus* sp., still occurs in the remaining regional forests. Clearly, this unbalanced representation of extinct animals is not a coincidence and something very particular has taken place.

After an analysis of the forest types used today by the extant mammals identified from Ankilitelo Cave, it was concluded that the ecological structure of about 500 years surrounding the cave was similar to the “succulent woodlands of modern southwestern Madagascar” (280). Further, it was suggested that until about 500 years ago these transitional humid-dry habitats supported a subfossil lemur community that would have been highly vulnerable to increasing human pressure, which by inference somehow pushed them to extinction. Although several lines of evidence indicate that there may have been important ecological change tied to the disappearance of these animals, the analysis was not sufficiently sensitive to pick up specific ecological subtleties in the region and other aspects of change that might have played an important role in the faunal collapse.

For example, the reasons for the very pronounced shifts in the range of two rodents, *Macrotarsomys petteri* and *Hypogeomys antimena*, over the course of the past 500 years need to be examined more carefully. Evidence from subfossil sites clearly indicates that they had extensive distributions across central west to southeastern Madagascar (153, 170). *Macrotarsomys petteri* is currently restricted to the last remaining slightly mesic forest block in the Mikea, and *Hypogeomys antimena* is now limited to a distinctly moister forested area north of Morondava. There is no evidence that the massive range restriction of these rodents is tied to human pressures, specifically hunting for bush meat.

In contrast, no parallel subfossil data exists for the two Carnivora, *Galidictis grandidieri* and *Galidia elegans*, recovered from the deposits and locally extirpated in the Ankilitelo Cave area. If the remains of these animals are from the same period, as can be inferred by the few radiocarbon dates currently available from the cave, both have witnessed range contractions in the past few hundred years. However, their responses were different, with *Galidictis grandidieri* withdrawing its range into the notably arid spiny bush and *Galidia elegans* going in the opposite direction toward the remnant, relatively moist humid forests of the Bemaraha.

Another relevant and important line of evidence is

the obvious habitat shifts that took place in the Ampoza area (Plates 7 and 8), which is less than 110 km to the northeast of Ankilitelo Cave. At Ampoza, we can clearly see a notable drying up of the environment, including the disappearance of extensive freshwater wetlands, occurring at least a millennium before the animals fell to their death in Ankilitelo Cave. Further, biogeographic evidence from the distribution of remnant populations of different plants and animals occurring in Isalo indicates that in the recent geological past a broad corridor of humid forest stretched from eastern to southwestern Madagascar. Hence, we propose that the forest structure near Ankilitelo may not have been ecologically similar to the remnant forested areas on the Mikoboka Plateau today, but distinctly moister and with a less pronounced dry season; the humid forest elements of the local flora have disappeared along with animals linked to such habitats.

The nearby Analavelona Massif rising to nearly 1,350 m, just a few kilometers from Ankilitelo Cave, is an excellent point for comparison (see Plate 8 for further details). The upper portion of the mountain is a mist-oasis of sorts. This is associated with the “inverse foehn” effect, where hot rising air is forced to cool down as it moves up the mountain, forcing humid vapor to become liquid water (322). In turn, the vegetation along the upper reaches of Analavelona is distinctly more humid than surrounding formations. Even with relatively subtle changes in local climate in the past millennia, it is easy to imagine important ecological changes to the forest structure and vegetation that once surrounded Ankilitelo Cave.

Another window into the level of change that has taken place in southwestern Madagascar is from lake sediment cores that often provide a detailed sequential history of wind-dispersed plant pollen occurring in close proximity to the water body. Also from these cores, data obtained on the frequency and relative intensity of fires, both based on measures of minute charcoal particles in the sediments, are very informative. Over the past few decades, David Burney and colleagues have cored a number of sites around the island, and the accumulated data provide an extraordinary view of ecological change through recent geological time. The closest analyzed core sample to the Ankilitelo Cave is from Ranobe, a near coastal site slightly more than 30 km north of Toliara and about 30 km northwest of Ankilitelo (46). From the Ranobe Lake core, a detailed record of the pollen over the past 5,000 years was obtained, and by extrapolation



the local habitats were revealed. Without going into too much detail, some important points are worth highlighting:

- (1) Between 3,000 and 2,000 years BP, the zone become more arid, and by the latter portion of this temporal range, the majority of dry deciduous forest and wooded savanna habitats had disappeared.
- (2) Starting at about 1,900 years BP, the *Medemia* palm (family Arecaceae) formation largely disappeared and grasses increased dramatically, and other spiny bush plants such as *Didierea* (family Didiereaceae), which is common around the lake today, became distinctly more prevalent.
- (3) Somewhere toward 2,000 years BP, there was a dramatic increase in charcoal in the core, with levels increasing ten times from presumed natural levels, and, at the same time, an increase was recorded of disturbed area plant pollen. This almost certainly marks the beginning of human disturbance of the region.

One of the first known archaeological sites in southwestern Madagascar is at Sarodrano, just south of Toliara, with a radiocarbon date of 1,460 years BP (24). However, the context and cultural aspects of these people are unknown. In any case, this date provides support for the presence of humans in the southwest, which might be associated with the local habitat disturbance as measured in Burney's Ranobe pollen core from just a few tens of kilometers to the north of Sarodrano. Farther south, there is evidence of human colonization dating from about 600–900 years BP (see Part 1, "The Archaeological Record of Occupation and Settlement").

Now shifting to the regional archaeological record, two established settlement sites are known, Rezoky and Asambalahy, the former about 115 km northeast of Ankilitelô and dating from about 1,200–1,500 years AD (86). This jump in time is nearly 1,500 years after the Ranobe cores showed signs of human intervention in the natural environment, and we interpret this as a hole in the archaeological record of this region. It is also worth considering that this gap may be partially explained by people living largely a nomadic lifestyle during the intervening years, and cultural signs and material remnants of their existence would therefore be difficult to identify in an archaeological context. At these two relatively recent

sites, there are some of the first dog remains known from the island, animals that could have easily been trained to hunt wild fauna. Accordingly, it is perhaps no coincidence that in the same deposits, bones of tenrecs, Carnivora such as *Cryptoprocta*, and a range of extant lemur species have been recovered (314). Most importantly, remains of extinct dwarf hippos have been found in an archaeological context at both of these sites. So even though no extinct lemur bones were identified from these deposits, it is clear that people were hunting large and now-extinct animals. As mentioned above, dog remains are unknown from Ankilitelô Cave, although they have been identified from the general region during a period contemporary with dated remains from the cave.

So in conclusion, in weighing the evidence for the disappearance of a certain number of locally extirpated or extinct animals found in the Ankilitelô Cave remains, specifically natural change versus human-induced change, we agree with Kathleen Muldoon that human intervention was probably the *coup de grâce* for much of the extinct fauna of the region. However, we suggest that animal populations were already declining, associated with large-scale climatic change, specifically aridification, that gave rise to notable ecological shifts. Sitting at about 540 m above sea level, the vicinity of Ankilitelô may have been slightly buffered from the immediate ecological changes measured in Burney's nearly coastal pollen core from Ranobe. This idea is supported by the distinctly humid local climate of the nearby Analavelona Massif discussed above. If this was the case, shifts in habitat may have taken place several hundred years after they manifested themselves along the coastal plain, which in turn would have been closer to the period of the radiocarbon dates currently available from Ankilitelô Cave.

Now we turn to explaining the different details depicted in Plate 6. The scene takes place at night during the full moon, which lights up the landscape, and the rim of the vertical shaft of Ankilitelô Cave. The forest is a mixture of humid and deciduous vegetation, with a few trees already shedding their leaves and marking the start of a not-too-severe dry season. A few examples of aloes (family Xanthorrhoeaceae) occur in the areas with little soil and exposed rock. The centerpiece is the extinct aye-aye *Daubentonia robusta*, which was about three to four times more massive than is the extant member of this genus, *Daubentonia madagascariensis*. Here the giant aye-aye is shown pilfering the nest of a bird and will use

its elongated, pipe-cleaner-like third finger and claw to pierce the egg and then consume the contents. The giant aye-aye had ever-growing, rodent-like incisors like its living congener. Other than eggs and insect larvae, it probably had an assortment of hard seeds, fruits, and other items in its diet. On the basis of carbon isotope values from radiocarbon-dated bones, this species seems to have consumed a diet that included animal as well as  $C_3$  plant matter (72). It was restricted to southwestern Madagascar, where across portions of its former range it appears to have replaced its smaller living relative. We reconstruct it as a slow-moving quadruped that frequented both the trees and the ground during its nightly foraging rounds.

On the ground to the right is a Carnivora *Gali-dictis grandidieri*, which no longer occurs in this area of Madagascar, having just flipped over a rotten log that is teeming with hissing cockroaches. At Tsimanampetsotsa, within the area this species still occurs, these insects make up a significant portion of this carnivore's diet (10). In the background, an endemic rodent of Madagascar, *Macrotarsomys petteri*, can be seen moving on the ground with a kangaroo-like locomotion and searching for food. This rodent is only known to exist today in the Mikea Forest, about 50 km to the west of the cave.

## Plate 7: Ampoza I—Reconstruction of the Ecology and Fauna in a Formerly Permanent Riverine Habitat in the Southwest

As discussed in Part I, Madagascar is divided into three distinct biomes: (1) the eastern humid forest to the montane formations of the Central Highlands, (2) the dry deciduous forests of the northwest and central west, and (3) the spiny bush of the extreme south and southwest. In general, the transitional zones (ecotones) between these habitats, particularly between humid (east) and dry forest (west and southwest) types are rather abrupt. In 1997 Chris Raxworthy and Ron Nussbaum published a study based on new inventory data from different sites around the

island (326), indicating that the reptiles and amphibians of the Isalo and Analavelona Massifs, both zones of transitional dry deciduous forest, included species found in humid forests. What was striking about these results is the eastern limit of the humid forest today is at least 150 km to the east of these massifs.

Their study had several important implications. It clearly showed that the classical interpretations of plant geographic patterns (phytogeography)—specifically those of Henri Humbert (198), which for several decades have been axiomatic for scientists—did not

---

On the basis of the rich bone deposits of different animal species found by paleontologists at Ampoza, it is possible to reconstruct aspects of the local surroundings that existed locally a few millennia ago. Even though today the immediate region around the site approaches being arid, and the remaining natural forest formations are transitional between dry deciduous and partially humid forest, in relatively recent times the environment was notably different. Permanent water systems occurred, directly associated with river plains and marsh systems. The local animals living in these aquatic ecosystems included a crocodile *Voay robustus*, a lapwing *Vanellus madagascariensis*, a shelduck *Alopochen sirabensis*, and a dwarf hippo *Hippopotamus lemerlei*, all of which are now extinct. Further, several extinct terrestrial and largely forest-dwelling animals, such as *Megaladapis edwardsi* and *Archaeolemur edwardsi*, would have visited this habitat for obtaining water and perhaps foraging. For a key to the different animals, see black-and-white inset for Plate 7 in color gallery. (Plate by Velizar Simeonovski.)



necessarily fit the distributional patterns of animals (zoogeography). Based on these results, it is reasonable to conclude that the factors predominantly influencing the geographic distribution of plants and animals are not necessarily the same. Further, this study and others subsequently published on the flora and fauna of the southwestern region showed that the previously implied biotic divisions between the wet and dry habitats of the island were not as clearly delineated as previously thought. In recent geological time, considerable shifts in habitats, as well as biotic exchanges, took place between these zones. Support for this pattern of east-west exchange has also been found in numerous recent molecular genetic studies of living animals. We will now turn to the literature on the subfossil fauna to document the level of change that has taken place in inland southwestern Madagascar and to interpret these observations in the context what happened in the region during recent geological history.

A number of different paleontologists have exca-

vated the subfossil site of Ampoza, located a short distance north of the Analavelona Massif, to the west of the Isalo Massif, and not far from the village of Ankazoabo-Sud. In 1929 Errol I. White, a paleontologist associated with what was then called the British Museum (Natural History), conducted excavations at Ampoza. Before and after the work of White, a number of other paleontologists visited the site and obtained subfossil material (126, 205, 227, 360, 388). White's dig was a large-scale one and involved several local sites, employing a considerable number of local people (Figure 52). He noted, "The first locality was in the valley of a small stream. . . . Here a trial pit had already been dug, and fortunately the overburden, consisting of about 8 feet [= 2.4 m] of black earth, had been removed from a considerable area" (384). A couple of Scandinavian paleontologists, Mr. and Mrs. Ljungqvist, had previously cleared this section. White continues, "Underneath the limestone was the fossiliferous layers consisting of two or three feet [less than 1 m] of black mud and finally barren light-

Figure 52. Archival photograph of the excavations conducted by Errol I. White in 1930 at Ampoza. With the assistance of local people, notably large amounts of earth were removed from the former riverbanks of the site and a considerable number of subfossils recovered. In the foreground, just in front of first group of men, is a large collection of bones, mostly of an extinct species of dwarf hippo *Hippopotamus lemerlei*. (Photograph courtesy of the American Museum of Natural History.)



coloured sands.” Nearby to a second site he excavated was a freshwater stream that was a short distance from the Ampoza River.

With this description as the setting and taking into consideration all of the different subfossil animals identified from the site, we have tried to reconstruct what the riverine habitat would have been like (Plate 7), as well as the immediate forest habitat (Plate 8). In the narrative associated with the next plate, we will return to the question of what the subfossil fauna tells us about habitat change in central southwestern Madagascar and how this is associated with the observations of Raxworthy and Nussbaum about humid forest connections in the local reptile and amphibian fauna.

About sixteen species of aquatic birds were identified from the Ampoza bone deposits (144) (see Table 6), which include species found in moving water, such as the Gray Heron *Ardea cinerea*, Humblot’s Heron *Ardea humbloti*, and Bernier’s Teal *Anas bernieri*; as well as those found in slow or stagnant water, such as the Madagascar Sacred Ibis *Threskiornis bernieri*, African Openbill Stork *Anastomus lamelligerus*, Greater Flamingo *Phoenicopterus ruber*, and Purple Swampphen *Porphyrio porphyrio*. In addition, among the bird remains, there are some exceptional finds. Throughout much of the southern hemisphere, as well as portions of Eurasia, a common group of open-country and riverine habitat birds is the lapwings (subfamily Vanellinae), many species of which are adaptable to notable levels of human habitat perturbation. Lapwings are unknown from the modern avifauna of Madagascar but have been recorded on other islands in the Old World. In the Ampoza subfossil deposits, bones of a previously unknown and now-extinct species of lapwing, *Vanellus madagascariensis*, were identified and named (143). Here we have depicted this bird living in riverine habitat, often resting and feeding on sandbars in the river and along the banks. With the discovery of this species on Madagascar, the question “Why are there no lapwings on Madagascar?” has changed to “Why do lapwings no longer exist on the island?”

A common bird in the Ampoza deposits is a type of shelduck (subfamily Tadorninae), which is morphologically similar to the shelduck *Alopochen aegyptiacus*, which occurs today in portions of sub-Saharan Africa, such as the Nile River system. The Malagasy subfossil species, *Alopochen sirabensis*, is known from several other sites on the island, including the Central Highlands near Antsirabe (see Plate 11) and

**Table 6**

List of land vertebrates identified from Ampoza subfossil remains (36, 107, 144, 358). Extinct species are indicated with †, and the author(s) and description date are given. For living taxa, the English common names are given. Listing does not include introduced species.

#### Order Reptilia

Family Testudinidae

†*Aldabrachelys abrupta* (A. Grandidier, 1866)

Family Crocodylidae

†*Voay robustus* (A. Grandidier & Vaillant, 1872)

*Crocodylus niloticus* Nile crocodile<sup>1</sup>

#### Class Aves

##### †Order Aepyornithiformes

†Family Aepyornithidae

†*Aepyornis* sp.

†*Mullerornis* sp.

##### Order Ardeiformes

Family Ardeidae

*Ardea purpurea* Purple Heron

*Ardea cinerea* Gray Heron

*Ardea humbloti* Humblot’s Heron

Family Ciconiidae

*Anastomus lamelligerus* African Openbill

Stork

Family Threskiornithidae

*Threskiornis bernieri* Madagascar Sacred Ibis

*Lophotibis cristata* Madagascar Crested Ibis

*Platalea alba* African Spoonbill

Family Phoenicopteridae

*Phoenicopterus ruber* Greater Flamingo

##### Order Anseriformes

Family Anatidae

†*Alopochen sirabensis* (Andrews, 1897)

*Dendrocygna* sp. whistling duck

*Anas bernieri* Bernier’s Teal

##### Order Gruiformes

Family Rallidae

*Fulica cristata* Red-knobbed Coot

*Porphyrio porphyrio* Purple Gallinule

##### Order Charadriiformes

Family Charadriidae

†*Vanellus madagascariensis* Goodman, 1996

Family Laridae

*Larus* sp. gull

##### Order Columbiformes

Family Pteroclididae

*Pterocles personatus* Madagascar Sandgrouse

##### Order Coraciiformes

Family Brachypteraciidae

†*Brachypteracias langrandi* Goodman, 2000

## Class Mammalia

### †Order Bibymalagasia

†*Plesiorycteropus madagascariensis* Filhol, 1895

### Order Primates

#### Suborder Strepsirrhini

##### Infraorder Lemuriformes

†Family Archaeolemuridae

†*Archaeolemur edwardsi* Filhol 1895

†*Archaeolemur majori*<sup>2</sup> Filhol 1895

†Family Palaeopropithecidae

†*Palaeopropithecus ingens* G. Grandidier 1899

Family Lemuridae

†*Pachylemur insignis* Filhol 1895

*Lemur catta* ring-tailed lemur

†Family Megaladapidae

†*Megaladapis edwardsi* G. Grandidier 1899

†*Megaladapis madagascariensis* Forsyth-Major 1894

Family Indriidae

*Indri* cf. *indri* indri

*Propithecus verreauxi* Verreaux's sifaka

### Order Artiodactyla

Family Hippopotamidae

†*Hippopotamus lemerlei*<sup>3</sup> A. Grandidier, 1868

### Order Rodentia

Family Nesomyidae

*Hypogeomys antimena* Malagasy giant jumping rat

1. Remains of *Crocodylus niloticus* have been reported from this site, but with the recent recognition of the genus *Voay*, the identification of these remains needs to be reassessed.
2. There is extensive variation in *Archaeolemur* at Ampoza, and *Archaeolemur majori* may be represented in the subfossil deposits.
3. It would appear that *Hippopotamus guldbergi* may have also occurred at this site.

Ampasambazimba (see Plate 12). Interestingly, on other islands in the western Indian Ocean, specifically Mauritius and La Réunion, different species of *Alopochen* once occurred, but these too are extinct.

Another important denizen of this riverine environment would have been the endemic and now-extinct crocodile *Voay robustus* (39). This is an animal estimated to have reached up to 5 m in length and tipped the scales at roughly 170 kg in body mass. It was previously placed in the same genus as the Nile crocodile, *Crocodylus*, but based on several different characters, Chris Brochu created the genus *Voay* for this Madagascar endemic; *voay* is the Malagasy word for crocodile. Given its size, *Voay robustus* would have been a formidable predator and one of the largest in the Holocene fauna of the island. As is typical of croc-

odiles around the world, it almost certainly occupied riverine systems, presumably sunbathing along the banks and preying upon land animals coming down to the water to drink, such as the case of the *Archaeolemur edwardsi* shown in this plate. At Ampasambazimba (see Plate 12), there is evidence of croc teeth marks in the recovered subfossil bones of *Palaeopropithecus maximus*, providing independent, concrete evidence for this type of predation event (356); however, see Plate 20 for further discussion on this point.

The bone remains of dwarf hippos *Hippopotamus lemerlei* are abundant in the Ampoza deposits. It has recently been suggested that hippo material from this site might be referable to a different species, *Hippopotamus guldbergi* (107), but this remains to be determined. Four radiocarbon dates are available of hippos from Ampoza, which span a range of dates from 2,760 to 2,370 years BP (mean calibrated dates of 2,846 and 2,315) (69); these dates set the minimum period when extensive permanent aquatic habitats still occurred in this portion of Madagascar. Further, the presence of these animals would lend considerable support for an extensive riverine system, probably with backwater marshes. It is easy to imagine these dwarf hippos lazily spending much of their day wallowing in the mud, often in close contact with other members of their pod, and then at night passing onto land or the edge of the backwater marshes to feed on terrestrial or aquatic vegetation. On the basis of carbon isotope values from radiocarbon-dated bones of hippos from southern Madagascar, it would appear that at least a portion of their diet was composed of C<sub>4</sub> plants (72), perhaps sedges and marsh grasses. It has been suggested that adult males of this species were distinctly larger than adult females (358), which would support male-dominated female harems, as found in other living hippos.

In the riverine scene depicted here, we have tried to capture aspects of the fauna that several thousand years ago occupied this habitat around Ampoza. Herons and storks resting or actively feeding, animals such as the *Megaladapis edwardsi* coming down to the river to drink—or the group of *Archaeolemur edwardsi* doing the same, but one individual being the unlucky subject of predation by a *Voay* crocodile. One can imagine the moment the crocodile came out of the water and grabbed the big lemur, the mayhem that followed, including the strident honking of the shelducks and the loud piercing shrill cries of the lapwings. Such punctuated episodes of chaos were no

doubt common occurrences in the lives of the waterway vertebrate community of Ampoza.

Above the river margins would have been gallery or riverine forest, and on slightly higher ground a different forest formation, almost certainly composed of plants requiring more humid conditions than those generally occurring today in this portion of the island. The ecosystem of the adjacent forest, which is the subject of the next plate, would have probably been mostly closed canopy in structure and, at least in part, with different organisms than the aquatic habitat. Certainly, forest animals would have come down to the river margin to drink. Here we have depicted the river scene during the dry season, with water levels lower and the banks largely exposed. With the onset of the rainy season, the water level would have risen, washing cadavers and bones of dead animals to bends in the river, where they would have been deposited and by chance unearthed by different generations of paleontologists several centuries or millennia later. Further, with the advanced dry season, certain deciduous forest species have lost their leaves, while in stark contrast other tree species have evergreen leaves. Telltale signs of the mixed nature of the flora, between wet and dry forests, can still be found today in the remaining natural habitats of the region (see Plate 8 for further details).

Lemurs are obligate drinkers, so even the most drought-tolerant species have to find sources of freshwater, and we suspect that the subfossil forms were no different in this respect. There is some variation in tolerance to drought among living species, and it is possible that some giant extinct lemurs were more resistant than others (72). On the basis of the size of different bone remains, *Megaladapis edwardsi* has been estimated to have weighed on average about 85 kg and *Archaeolemur edwardsi* about 27 kg (212). The inferred habits and diet of *Megaladapis edwardsi* are that of a diurnal consumer of leaves; based on orbit size, *Archaeolemur edwardsi* was also diurnal, but its teeth and jaws indicated that it probably specialized on harder fruits and seeds (120). Despite differences in degree and anatomical details of their adaptations to terrestrial lifestyles, with *Archaeolemur* more fundamentally terrestrial than *Megaladapis*, members of these two genera have both been reconstructed with quite large home ranges, based on their large body sizes and inferred diets. It is very probable that riverine habitats, like that pictured in Plate 7, were incorporated into their normal territorial rounds near what was to become the subfossil site of Ampoza.

## Plate 8: Ampoza II—Ecological Change in a Forest Community and Connecting Humid Forest Corridors to the Eastern Portion of the Island

In the previous plate, we presented information on the former riverine ecosystem of the Ampoza subfossil site and highlighted some of the different organisms known from bone remains. Here we continue with

the same theme but pick up on the forest community. We end this section with a summary of what the inferences that are drawn from the subfossil deposits, as well as from other ancillary types of information,

On the basis of subfossil evidence, it is clear that the forest structure in the general region of Ampoza was notably different until a few thousand years ago. Here we present a reconstruction of the former forest habitat that we interpret was largely closed canopy, with some epiphytic plants, and an assortment of different animals. Those that are extinct include a ground-roller *Brachypteracias langrandi* and a “sloth-lemur” *Palaeopropithecus ingens*. Several existing species have also been identified from the remains. These include ring-tailed lemurs *Lemur catta*, a troop of which is coming down to the water to drink with a few individuals remaining as sentinels for possible predators, and three indri *Indri indri*, sunning themselves toward a small opening in the forest canopy. *Lemur catta* still occurs in the immediate vicinity of Ampoza, but the range of *Indri indri* is now 400 km to the east. The small stream in the foreground would have been a tributary to the larger river figured in Plate 7. For a key to the different animals, see black-and-white inset for Plate 8 in color gallery. (Plate by Velizar Simeonovski.)





can tell us about environmental change in this region of Madagascar since the beginning of the Holocene, that is, over a period of less than 12,000 years.

Plate 8 is a depiction of the forest, which would have been on slightly higher ground and above the gallery and aquatic habitats. The forest was probably composed mostly of permanent evergreen trees, although another portion of the trees would have lost their leaves during the dry season (deciduous). The stream in the foreground was a tributary of the larger river illustrated in Plate 7. As we have tried to capture in this illustration, the forest would have hosted a certain number of lianas and vines, as well as epiphytic plants, such as orchids and ferns, growing on trees. Further, structurally it would have been largely closed canopy based on the locomotor habits—observed and inferred—of certain inhabitants, particularly lemurs, which are discussed below.

The site of Ampoza has provided a wealth of subfossil remains from a variety of presumably forest-dwelling vertebrates (see Table 6). The lemur fauna is notably dramatic, and among the extinct species, the following have been identified (121, 133): *Archaeolemur edwardsi*, *Palaeopropithecus ingens*, *Megaladapis edwardsi*, *Megaladapis madagascariensis*, and *Pachylemur insignis*. Variation in size of the bones attributed to both *Archaeolemur* and *Palaeopropithecus* is quite extreme at Ampoza, with some small elements falling into the ranges more typical of *Archaeolemur major*, known from many southwestern subfossil sites, and *Palaeopropithecus kelyus*, recognized only from a few specimens from the northwest (138). This impressive variation may simply be “normal” for a species, especially one sampled over many generations. However, it is also possible that these other, smaller and rarer elements represent lemur species not currently recognized in the expansive Ampoza subfossil lemur community.

Farther inland and about 75 km to the northeast of Ampoza is Tsirave, another paleontological site well known for its abundance of subfossil lemurs. Despite its proximity to Ampoza, its lemur community was rather different: *Hadropithecus stenognathus* and *Mesopropithecus globiceps* were there, along with *Pachylemur insignis*, *Archaeolemur majori*, and *Megaladapis madagascariensis*; but there are no reports of *Archaeolemur edwardsi*, *Megaladapis edwardsi*, or *Palaeopropithecus ingens*. It is not clear whether this disparity is due to the vagaries of chance or some unknown aspect of subfossil depositional (taphonomy) bias, or if it reflects real differences in habitat and overall biotic

community structure between the two sites. It has been proposed that the presence of the rare “monkey-lemur” *Hadropithecus* and the small sloth-lemur species of *Mesopropithecus* might indicate a greater abundance of C<sub>4</sub> or CAM plants near Tsirave (72). *Lemur catta* is also still found today near Tsirave.

The abundance of *Palaeopropithecus* bones at Ampoza implies a forest structure that includes a closed canopy because it is hard to imagine this extinct lemur traveling in a terrestrial fashion. If it did, it probably slithered slowly across the ground in a manner recalling the awkward serpentine movement of New World sloths (270). *Palaeopropithecus* was one of the most specialized suspensory (“hanging”) mammals to evolve anywhere on Earth (122). When its bones were first mentioned in the scientific literature, they were isolated elements attributed by Guillaume Grandidier to an unknown Malagasy sloth dubbed “*Bradytherium*” (177). It took many years to elucidate which limb bones actually belonged to *Palaeopropithecus*, but the distinguished paleontologist and morphologist Charles Lamberton (231) finally clarified the confusion and argued convincingly that the supposed sloth bones belonged instead to a giant extinct lemur—*Palaeopropithecus*. However, Grandidier’s belief that Madagascar was once home to a real sloth is not as far-fetched as it might seem anatomically; some of the limb bones do in fact bear striking similarities to living tree sloths. Although the living orangutan from Southeast Asia might be a better primate analogue for *Palaeopropithecus* (231, 380), we still honor Grandidier’s anatomical observations today by calling all palaeopropithecids “sloth-lemurs.”

In Plate 8, we therefore depict *Palaeopropithecus* as hanging beneath a large branch in a decidedly sloth-like posture. Their upper limbs were much longer than their hindlimbs; their hands and feet were long, hook-like grasping organs, and their shoulder, hip, and ankle joints were loose and extremely mobile. The extinct sloth-lemurs are closely related to living indriids (including their namesake, *Propithecus*), and although the latter are best known as acrobatic “vertical clingers and leapers,” they too often adopt beneath-branch, sloth-like hanging postures while feeding. A forest with a closed canopy and an assortment of connecting lianas and vines would also facilitate arboreal travel by *Palaeopropithecus* and other extinct and living lemurs, including *Pachylemur insignis* and *Megaladapis madagascariensis*. We suspect that *Archaeolemur* often descended to the forest floor and foraged on foot, as does *Lemur catta* today, and pre-

sumably the arboreal-terrestrial “koala-lemur” *Megaladapis madagascariensis* occasionally did likewise.

During a recent excavation at Ampoza, a partially damaged humerus “that probably belonged to an *Indri indri*” was recovered (126), which, if correct, provides important insight into the level of habitat change in this portion of southwestern Madagascar. The current distribution of *Indri* is north of the Mangoro River, more than 400 km to the northeast of Ampoza, and this lemur is known today only from eastern humid forest formations. There is other evidence that the range of this genus has diminished dramatically in the past few millennia, with subfossils having also been found in the Ankarana Caves in the far north (Plate 17) and at Ampasambazimba in the Central Highlands (Plate 12) (210); Ankarana and Ampasambazimba are both considerable distances from currently known sites for this largest living lemur. Its presence in the Ampoza lemur community is further testimony to the presence of humid forest in the past. In Plate 8, three individuals are depicted in forest canopy openings taking a sunbath during the morning hours and on their perches high above the ground. This is often the moment that different groups of eastern *Indri* vocalize a distinct and eerie humpback whale-like song, which can last for several minutes; these haunting calls are unique to *Indri* and produce primordial feelings in some people.

Coming down to the river to drink is a troop of ring-tailed lemurs *Lemur catta*. This lemur occurs in nearby forests today but is a relatively new addition to the faunal list of Ampoza excavations. In the lower-left portion of the image is an adult keeping guard for the safety of the troop against the attacks of raptors and large Carnivora, such as *Cryptoprocta spelea* (see Plate 19). If a *Cryptoprocta* were spotted by the sentinel male, it is likely that after the proper signal, members of the troop on the ground would quickly flee into the trees, and the forest would suddenly be filled with warning “clicks and yaps” rather than the “rasps, shrieks, barks and chirps” reserved for worrisome raptors. *Lemur catta* anti-predator vocalizations are class-specific and distinguish between Carnivora and birds of prey (295).

*Lemur catta* have been included prominently in this plate to emphasize that numerous organisms known from subfossil remains still exist today in the immediate area of the site; they also serve as a reminder that the factors that led to the extinction of certain species did not have the same impact on others. Recent work on the genetics of *Lemur catta*

in southwestern Madagascar has shown that in the recent past they have gone through a genetic bottleneck (292). Whether or not this was associated with climatic shifts or human perturbations is unclear, but regardless *Lemur catta* can be invoked as a model species that was on the slide toward notable population reduction, but was able to bounce back to a seemingly stable population. This ability to rebound back may in part be associated with its size, generalist diet, or other aspects of its natural history.

Remains of two different genera of extinct elephant birds, *Mullerornis* and *Aepyornis*, have been identified from Ampoza (144) (see Table 6). We know little about the ecology of these massive birds (see Plate 1), and whether they occurred in forest or in more open habitats is difficult to surmise. Recent data generated from carbon isotope values from radiocarbon-dated bones provide some insight into the diet of elephant birds (71). It was found that these birds were feeding mostly on C<sub>3</sub> plants and therefore were probably not restricted to open habitats. Regrettably, aspects of their habitat use are inconclusive as extrapolated from other large living non-flying birds (ratites of the superorder Palaeognathae) that probably have shared origins associated with Gondwana: the African Ostrich *Struthio camelus* (order Struthioniformes), the Australian Emu *Dromaius novaehollandiae* (order Struthioniformes), and the American Rhea *Rhea americana* (order Rheiformes) are largely birds of open plains, while the New Guinea Cassowary *Casuaris* spp. (order Struthioniformes) typically lives in tropical forests. In any case, if elephant birds were forest inhabitants, they would have come down to the river habitat, at least on occasion, drinking water and feeding on different plants occurring in this habitat.

Ground-rollers, an endemic Malagasy family (Brachypteraciidae) of forest-dwelling birds, are known from different sites on the island, with the genera *Geobiastes*, *Atelornis*, and *Brachypteracias* occurring in the eastern humid forests, and *Uratelornis* from a small area of spiny bush to the north of Toliara. The former group of genera occurs only in non-degraded humid forest habitat, with the exception of the Pitta-like Ground-roller *Atelornis pittoides* that can be found in some slightly degraded forest formations. Among the subfossil remains collected at Ampoza by Errol White in 1929 was a humerus of a ground-roller that was allocated to the genus *Brachypteracias* based on different osteological characters and before a generic revision of the Malagasy ground-rollers (146, 218). The bone is distinctly longer than any liv-

ing member of *Brachypteracias* and was described as an extinct species new to science, *Brachypteracias langrandi*. The name was chosen to honor Olivier Langrand for his important contributions to conservation and modern Malagasy ornithology. Based on inferences from the habitats of the living members of this genus, *Brachypteracias langrandi* is presumed to have lived in notably more humid forests than occur in the region of Ampoza today, again consistent with conclusions discussed above.

Other extraordinary animals known from bone remains at Ampoza include *Plesiorycteropus mada-gascariensis*, belonging to its own order of mammals (Bibymalagasiasia) (see Plate 14). This genus, known from two extinct species, was thought to be related to armadillos, but it has recently been suggested that this was not the case, and the similarity was a case of convergence (250). More recent analyses of the affinities of Bibymalagasiasia indicate that they were part of a radiation of African animals known as Afrotheria, which includes the armadillos (382).

A number of bone remains of extinct giant tortoises have been recovered from the site, which are referable to *Aldabrachelys abrupta* (36). A single radiocarbon date from this tortoise from Ampoza indicated that it was alive 2,035 years BP (mean calibrated date of 1,920) (69). It is unclear if these tortoises were truly forest-dwelling or occurred in more open forested areas, but in any case, they presumably composed an important herbivore biomass in the local ecosystem (see Plate 4).

Today the giant jumping rat *Hypogeomys antimena* is restricted to a small region in the Central Menabe, north of Morondava, and is considered Endangered. Until a few millennia ago, this species had a much broader distribution in the southern portion of Madagascar, with skeletal remains being identified from Ampoza. A radiocarbon date from the site indicated that it occurred locally 1,350 years BP (mean calibrated date of 1,190) (69, 153). Its decline has been cited as a combination of natural aridification, followed by human modification of the environment, which continues to force this species to the brink of extinction.

Now we return to the question posed at the beginning of the Ampoza I account concerning the observation of Raxworthy and Nussbaum (326) that reptiles and amphibians occurring today on the Isalo and Analavelona Massifs, both zones of transitional dry western deciduous forest, include species found in eastern humid forests. While this issue might seem

esoteric to some, it provides an interesting window into just how dynamic that levels of change can be on our planet, taking place in the equivalent of milliseconds of geological history. The subfossil fauna recovered from the Ampoza deposits contain a wide variety of taxa no longer found in the southwestern portion of Madagascar. Some of these organisms are extinct, and others occur elsewhere on the island. Either based on ecological inference for the extinct taxa or on direct observations in nature for the living species, many of these organisms occurred in permanent aquatic or in moist forest environments—in both cases, these habitats, with one exception, are not found today in southwestern Madagascar. Hence, it is clear that since the time that these bone remains were deposited at Ampoza, a considerable amount of ecological change has taken place. To provide a timescale to the period associated with this change, seven radiocarbon dates are available from subfossils recovered at the site, and all, with the exception of one, fall within the mean calibrated date range of 2,950 to 1,830 years BP (54, 69). So all of these animals were alive within a period covering a single millennium, and as recently as 120 AD, suitable mesic habitat remained at the site to support these now-extinct organisms. The more recent date is for *Hypogeomys antimena*, which still occurred at the site at the end of the sixth century!

Based on current information from the archaeological record, the first human colonization of Madagascar took place roughly 2,500 years BP (see Part 1, “History of Human Colonization of Madagascar”). While the majority of radiocarbon dates from Ampoza are after this critical date, two points are important. As human colonization took place starting from the coast, it seems reasonable and conservative to presume that it took hundreds of years before people had a major ecological impact on the animals and ecosystems in the island’s interior (86), such as the region of Ampoza. Coinciding with this last point, not one bone from Ampoza shows any sign of human intervention, such as butchering marks, unlike bones that have been found elsewhere on the island (see Plate 5). Until other evidence to the contrary emerges, it seems prudent to conclude that the Ampoza bone deposits are natural accumulations.

Now putting all of this together, southwestern Madagascar was distinctly moister during the Holocene. The forests surrounding areas such as Ampoza were probably dense, mostly closed canopy, with some epiphytes, and a floristic mixture of dominant

trees with eastern (humid) and western (deciduous) affinities, relative to the zones of the island where these floras are found today. We presume that a Miombo-like woodland habitat with some areas of open canopy and the ground vegetation dominated by grasses (see Plate 12 for further details) occurred adjacently or interdigitated with the mixed forest. An extensive system of small streams and rivers with permanent water formed an important aquatic habitat for a variety of birds and other animals. The different local types of environments were occupied by a wide variety of organisms that no longer exist in this zone or have vanished from Earth. The climatic regime was not as severe at that time, and the Ampoza area did not experience an extended dry season of six to eight months, which would be typical today.

It is very probable that a continuous humid forest corridor existed as an extension from the east—for example, at the level of the Andringitra Massif, across to Isalo, Zombitse-Vohibasia, to at least Analavelona—that provided the means for forest-dwelling animals to disperse. The last remnant of this habitat today in the region surrounding Ampoza can be found on the Analavelona Massif, specifically in the summital zone, from about 1,000 to 1,320 m (Figure 53). Here the upper portion of the mountain is a sort of cloud or fog forest, catching moisture in passing weather systems and keeping the remaining habitat notably moist. We imagine that the area surrounding Ampoza several millennia ago had a similar vegetational structure, as illustrated in Plate 8. Further, deep in the sandstone canyons of Isalo, permanent water still occurs, and these zones are protected from the harshness of the regional climate. A recently found subfossil site close to the southern limit of the Isalo Massif contains numerous mammalian remains dating to slightly less than 10 millennia ago that attest to more extensive forest and aquatic environments during that period (282). Hence, existing populations of reptiles and amphibians in Analavelona and Isalo with eastern affinities probably represent relict populations from the time when the region was moister and linked to the east. This corridor would also help explain the presence of *Hadropithecus* on the Central Highlands and *Indri* and *Archaeolemur edwardsi* in the southwest. The observations of Raxworthy and Nussbaum that started the text for the Ampoza plates can thus be explained by certain paleoecological inferences that are fully consistent with regard to the fauna that once occurred at Ampoza only a few thousand years ago.



Figure 53. This photo was taken toward the summit of Analavelona, some 75 km southwest of Ampoza. The upper portion of the massif, largely associated with its orographic position and height, is able to catch passing weather systems with moisture, which produces a very distinct cloud or fog forest. The habitat depicted here is proposed to have been similar to that which occurred in the former Ampoza Forest, with a distinct closed canopy, dense understory, lianas, and epiphytes. The surrounding habitat at the base of the massif and surrounding areas is distinctly dry. (Photograph by Harald Schütz.)

## Plate 9: Belo sur Mer—a Window into Different Hypotheses Associated with Environmental Change: Natural versus Human-Induced

A number of subfossil sites are known in the immediate area of Belo sur Mer, about 60 km south of Morondava, and these include Ambararata, Ankevo (or Ankaivo), Antsirasa, and Ankilibehandry. Research for bone-rich localities in the region appears to have commenced with Monsieur Grevé, who col-

lected material for Alfred Grandidier. Soon after the French declared war on the Imerina government in 1894, Grevé was taken prisoner and executed by the Imerina army (11, 93). Subfossils collected by Grevé were sent back to Paris and studied by different scientists, including Henri Filhol, Alfred Grandidier, and

---

On the basis of different organisms identified from subfossil deposits excavated from various sites near coastal Belo sur Mer, here is depicted a panoramic view from a freshwater source eastward toward the forest. Even today, in the nearby coastal dunes, there are freshwater pools formed by the percolation of groundwater to the surface. Presumably, several thousand years ago, when the local climatic conditions were wetter, there was a greater amount of freshwater filtering into these areas. The forest is postulated to have been a relatively dense mixed deciduous formation with some humid forest elements and was probably separated from the estuary by open Miombo-like woodland, with a mixture of open grassland areas and closed-canopy forest. The four depicted “monkey-lemurs” are those that would have been comfortable on the ground, while several other species led an arboreal life in the forest. Here we have shown the forest at the height of the rainy season, wonderfully green, and populated by animals at different stages in their breeding cycle. For a key to the different animals, see black-and-white inset for Plate 9 in color gallery. (Plate by Velizar Simeonovski.)



Alphonse Milne Edwards. In 1895 several new species of subfossil animals were described from these remains in the first published volume of the *Bulletin du Muséum d'Histoire Naturelle*, which included the bird *Coua primavea*, the lemurs *Archaeolemur majori* and *Pachylemur insignis*, and what was to become the still enigmatic bibymalagasias *Plesiorycteropus mada-gascariensis* (102, 250, 273).

The region was subsequently visited by several scientists looking for subfossils, including Guillaume Grandidier in 1900, Lieutenant Bühner in 1910, and Charles Lambertson in 1934 (62). Many decades later, between July and August 1995, David Burney with a team of specialists, including Bill Jungers, opened excavations at Ankilibehandry, 2 km northeast of the village of Belo sur Mer (51) (Figure 54). Burney and colleagues organized a second visit to the site in 2000. Ankilibehandry was a partially dried pond located behind some coastal dunes and in an area with a shallow water table. While these conditions are ex-

cellent for preservation of bone, pollen, and microbes, they made the physical excavation of the site difficult. The water table was reached within a meter of digging, with excavation pits quickly turning into pools of murky water—and this was during the dry season! The team enlisted a technique that Burney had developed and successfully employed elsewhere—excavation below the water table (subphreatic). A gasoline-powered water pump was used to empty the flooded pits, and excavation could then continue for another meter or so. Even with the pump going non-stop, digging much deeper than this was precarious because the risk was very high indeed of having the saturated walls collapse in on anyone working in the pit. Another benefit of using the pump was the ability to drain the water many meters away from the excavation and use it for washing and wet screening the sediments and fossil bones pulled from the pit.

During the meticulous excavations, Burney and colleagues paid strict attention to the order of the

Figure 54. In 1995 and again in 2000, David Burney with a team of specialists conducted excavations at Ankilibehandry, 2 km northeast of the village of Belo sur Mer. Here are shown two expedition members working in an excavation pit and partially shaded from the sun by a tarpaulin. The site was a largely dried pond; the water table was reached within a meter of digging from the surface, and holes in the ground quickly turned into pools of murky water. The team enlisted a technique known as subphreatic excavation, where a water pump was used to empty the flooded pits. (Photograph by William L. Jungers.)



sediments and the bones they contained (stratigraphy) and obtained valuable cores for different types of analyses mentioned below. Subsequently, based on radiocarbon dates, it was determined that the deposits spanned the period from before humans colonized this portion of Madagascar to sometime after this event. David Burney summarizes the importance of Ankilibehandry in the following manner: “If a rich site like Ankilibehandry (Belo sur Mer), which probably contains fossils from the entire period of the ‘extinction window,’ also shows that some of the megafauna sustained hunting pressure and other human impacts for nearly a millennium,” then several competing models proposed to explain these events “have been refuted” (54, p. 39). As the site provided many different sources of information—ranging from subfossil animal bone, details on microscopic carbon in the deposits and a history of local fire regimes (charcoal particles), to fungus spores from the dung of large-bodied animals—different questions can be addressed in what can be characterized as an “integrated approach.”

As mentioned in Part 1, several different hypotheses have been proposed to explain the extinction of a diversity of animals that formerly existed on Madagascar in recent geological time (48):

- (1) Widespread fire introduced by humans, with extensive transformation of the natural landscape and subsequent extinctions (197).
- (2) A period of notable aridification in the southwestern portion of the island and associated desiccation leading to habitat change and extinctions (257).
- (3) The “overkill” hypothesis associated with the rapid disappearance of different naive animals after first contact with hunting humans and their subsequent extinction (262).
- (4) The “hypervirulent disease” hypothesis with pathogens introduced by humans or their domestic animals being lethal to the native fauna (252).
- (5) The “synergy” hypothesis, which includes a variety of human-induced factors playing different roles through time and/or in different geographic areas, as well as natural climatic change, leading eventually to extinctions (48).

Excluding evidence of human-modified hippopotamus bones from coastal southwestern Madagascar dated to 2,020 years BP (mean calibrated date of

2,005) (69) (see Plate 5), the archaeological evidence of people in this general region of the island dates from 1,500 years BP (24). Now if one uses this date as the temporal window when humans started to modify the environment in different manners and the period when numerous animals may have been pushed toward extinction, information unearthed from Ankilibehandry can test the different hypotheses mentioned above, as each implies different timing and duration of critical events.

- (1) *Widespread fire*: Using microscopic charcoal particles found in the stratified sediments at the site and believed to be associated with fire, there was a notable increase in the concentration about 1,800 years BP as compared to presumed natural “background” rates; this has been used as a sign of human arrival in the area (48). Subsequently, notably higher concentrations were maintained from about 1,400 to 900 years BP, and then they dropped rather precipitously. These data imply that rates of fire increased abruptly soon after human arrival in the area, which at least at a local level gives some support to this hypothesis. However, there is no evidence of an extremely rapid, catastrophic wildfire.
- (2) *Aridification*: Unpublished pollen data from the Ankilibehandry site being studied by Toussaint Rakotondrazafy indicate that little change has taken place in the vegetation in the past 2,000 years (48). This would not support a dramatic local change in the climate. However, two points are worth mentioning. These cores document a record of wind-dispersed pollen, which represents only a portion of the local flora. Farther to the south, near Ranobe (see Plate 6), such a desiccation event did take place, which is in agreement with the original hypothesis. Hence, the shift to greater aridity may have been more dramatic to the south of Belo sur Mer. (As a side note, recent modeling exercises associated with Malagasy primates and climate change predicts that with anticipated global temperature shifts in the near future, the distribution of certain lemur parasites will expand up to 60 percent [20]. Hence, if correct, this demonstrates one of several potential factors that could affect local animal health and lead to possible population declines apart from anthropogenic aspects.)

- (3) *Overkill and “blitzkrieg”*: On the basis of radio-carbon dates—which included relatively recent dates of, for example, 1,280 years BP (mean calibrated date of 1,135) for an elephant bird tentatively assigned to the genus *Mullerornis*, and 1,370 years BP (mean calibrated date of 1,230) for remains of the lemur *Archaeolemur majori* (48, 69)—strong evidence emerges that members of the “megafauna” coexisted for several hundred years with people after they colonized this region. As one of the tenets of the overkill hypothesis is *rapid* loss of the fauna, the radiocarbon evidence indicates that this was not the case. There is evidence from the site of people interacting with now-extinct animals, such as a human-modified bones (48), which in turn implicates possible hunting, although not necessarily “butchering” like that proposed for Taolambiby (see Plate 5).
- (4) *Hypervirulent disease*: To date, no laboratory examination has been made to search for pathogens in the bone remains recovered from the site, particularly after human arrival in the area. However, using a more indirect line of evidence, inherent in the hypervirulent disease hypothesis is a *rapid* decline and disappearance of animals after initial contact with humans or their commensal animals. As we have discussed under the overkill hypothesis, several species that subsequently went extinct co-existed with humans for several hundred years, which would not provide support for the hypervirulent disease hypothesis. Moreover, it would have had to be a very unusual disease that targeted animals of different classes of vertebrates (birds, reptiles, and mammals). As mentioned above under the aridification hypothesis, shifts in climate can have important bearing on the health of wild animals and associated population dynamics, but the jury is still out concerning any evidence of the introduction of a virulent pathogen.

In an innovative study of fungus spores recovered from site samples, David Burney and colleagues conducted an analysis from the Ankilibeandry cores (53). The spores in question are of the genus *Sporormiella*, which occur only associated with the dung of large plant-eating (herbivore) animals, such as lemurs and domestic cattle; concentrations of these spores can be used as a proxy for the abundance of such animals (also see 390). They found a

drastic decline in these spores slightly less than 2,000 years BP, which largely coincides with an augmentation of human-induced perturbations (fire). In recent centuries, there was a notable increase in the spores, almost certainly associated with the introduction of domesticated cattle.

Hence, these data have important implications, but in the case of the hypervirulent disease hypothesis, there was not a contemporaneous decline in large lemurs associated with the transplanting of different domestic animals to the island, as would be predicted if the latter introduced a pathogen to the former.

- (5) *Synergy*: Of the four different hypotheses outlined above, all have features that might explain either ecological transformations or the disappearance of certain faunistic elements in the Ankilibeandry area. Many aspects of these different models are difficult to outright refute, and the evidence to support or disprove can be a bit fuzzy at times. Rather than trying to pin a single cause on these changes, it is reasonable to imagine that different factors led to the modifications of the local environment and associated vicissitudes. The multiple causes of the synergy hypothesis seem to have the best flexibility and resolution to explain what actually happened. In short, some natural climatic changes almost certainly took place in the region in the past few millennia; humans colonized the area and modified the environment with fire and presumably some forest clearing; local animals were hunted and domestic animals were introduced; and, together, these aspects led synergistically to the local extinction of numerous animal species.

What further clues does the modern environment provide as to what happened? In the immediate area of Belo sur Mer, considerable forest remains, which includes a 77,000 ha Kirindy Mitea National Park named in 1997. (This is not to be confused with the Kirindy Forest to the north of Morondava and on the road toward Belo Tsiribihina.) In fact, the name *mite* comes from the Malagasy word from the Sakalava dialect for dripping or seeping water. In the coastal area inland from the barrier dunes, in many places not far from Belo sur Mer, there are some areas where water through artesian pressure percolates out of the ground and forms freshwater pools. Human population density in this portion of the island is notably



low, although villages are often associated with these artesian sources.

Portions of the modern forest habitats were selectively logged several decades ago for commercial purposes, such as the western portions of the Kirindy Mitea National Park, which has considerable secondary forest habitat. During a biological inventory to this protected area in November 2002 by Steve Goodman and colleagues, cut and rotten stumps from the exploitation were still apparent, and little regeneration in the immediate vicinity of the felled trees was noted. This underscores the long periods of time such a forest takes to recover after natural or human disturbance. In any case, the surface area of the remaining forest (secondary and relatively intact) since the 1990s has been stable, which has been interpreted optimistically that conservation protection in this area is working (386).

However, the local people of the Sakalava cultural group living in close proximity to the forest still hunt forest animals for bush meat, which include lemurs, carnivorans, birds, and tenrecs (157). This hunting pressure over time has seriously reduced the density of the animals they exploit and has given rise to a strange phenomenon known as the “silent forest”: large tracts of relatively intact natural forest habitat remain, but animals are rarely noted, which is assumed to be a direct result of human hunting pressure. Hence, it is in portions of the Kirindy Mitea forest where one can really appreciate the impact of “traditional” hunting practices on wild animals; even without firearms, animal populations may be pushed by hunting toward low density and local extinction (extirpation). Accordingly, and this is an important take-home message, one cannot simply point the finger at climate change and give human impact a pass when noting the absence of a certain species in a large block of persisting forest.

Another stark regional example of how quickly things can disappear comes from the Antserananomby Forest, which is in the same area, but further inland than the Kirindy Mitea National Park. When Robert Sussman visited this site in the 1970s, a significant and relatively intact forest parcel was present and hosted a diversity of lemur species (216). When Elizabeth Kelley and Kathleen Muldoon returned to the site in 2004, drastic changes had occurred. The village that was in close proximity to the forest during the visit of Sussman was now barren savanna, the better part of the forest was gone, and the density of most lemur species had decreased substantially.

Previously, the late Father Otto Appert noted that this sacred forest was protected by local taboos (13). Subsequently, between an epidemic that killed many local people, migration of other cultural groups who did not follow the same taboos, and the introduction of commercial maize crops exported for animal food, the local conditions rapidly declined and culminated in the current situation. This is another sobering reminder of how quickly things can transform based on the impact of human-induced changes.

Now we return to information from the paleontological sites near Belo sur Mer. The subfossil fauna is notably rich (see Table 7), with seven species of extinct lemurs (121), including three species that were first described from these deposits: *Archaeolemur majori*, *Palaeopropithecus ingens*, and *Pachylemur insignis*. Other extinct species known locally include *Mesopropithecus globiceps*, *Archaeolemur edwardsi*, *Hadropithecus stenognathus*, and *Megaladapis madagascariensis*. If one adds the current eight species of lemurs that are documented from the immediate region (216, 397) to this list, the total comes to fifteen species. No site in the western portion of Madagascar today holds such a high diversity, but these impressive numbers are comparable to the inferred primate fauna at other southwestern subfossil sites such as Ankilitelo (see Plate 6).

Other interesting extinct animals have been identified from the Belo sur Mer sites. A large and terrestrial coua, *Coua primavea*, was named based on some of the subfossils excavated by Grevé (273). Subsequently, this species has been identified from remains in Anjohibe Cave (see Plate 14), more than 600 km to the north. As with many species of extinct lemurs, the disappearance of *Coua primavea* from such an extensive range cannot be tied to local shifts or pressures, but instead must have been the result of broad-scale factors. Another extraordinary animal known from the Belo sur Mer regional subfossil sites is bibymalagasias *Plesiorycteropus madagascariensis* (250), which was aardvark-like and is placed in its own order known as Bibymalagasias (see Plate 14 for further details). In addition, identified from local deposits is *Cryptoprocta spelea*, a Carnivora notably larger than any extant species on the island. The smaller living member of the same genus, *Cryptoprocta ferox*, identified based on morphology and size, is also known from these same deposits based on earlier excavated remains; however, without radiocarbon dates or stratigraphic control, it is impossible to know if these two *Cryptoprocta* lived in the area at the same time (165).

**Table 7**

List of land vertebrates identified from subfossil remains excavated in the Belo sur Mer region (36, 156, 165, 250). Extinct species are indicated with †, and the author(s) and description date are given. For living taxa, the English common names are given. Listing does not include introduced species.

**Order Reptilia**

Family Testudinidae

†*Aldabrachelys abrupta* (A. Grandidier, 1866)

*Astrochelys* cf. *radiata* radiated tortoise

Family Crocodylidae

†*Voay robustus* (A. Grandidier & Vaillant, 1872)

*Crocodylus niloticus* Nile crocodile<sup>1</sup>

**Class Aves****†Order Aepyornithiformes**

†Family Aepyornithidae

†*Aepyornis maximus* I. Geoffroy-Saint-Hilaire, 1851

†*Aepyornis medius*? Milne-Edwards & A. Grandidier, 1866

†*Mullerornis rudis* Milne-Edwards & A. Grandidier, 1894

**Order Ardeiformes**

Family Ardeidae

*Ardea humbloti* Humblot's Heron

**Order Anseriformes**

Family Anatidae

†*Alopochen sirabensis* (Andrews, 1897)

*Dendrocygna* sp. whistling duck

**Order Cuculiformes**

Family Cuculidae

†*Coua primavea* Milne-Edwards & A. Grandidier, 1895

**Class Mammalia****†Order Bibymalagasia**

†*Plesiorycteropus madagascariensis* Filhol, 1895

**Order Primates****Suborder Strepsirrhini****Infraorder Lemuriformes**

†Family Archaeolemuridae

†*Archaeolemur edwardsi* Filhol, 1895

†*Archaeolemur majori* Filhol, 1895

†*Hadropithecus stenognathus* Lorenz von Liburnau, 1899

†Family Palaeopropithecidae

†*Mesopropithecus globiceps* Lamberton, 1936

†*Palaeopropithecus ingens* G. Grandidier, 1899

Family Lemuridae

†*Pachylemur insignis* Filhol, 1895

†Family Megaladapidae

†*Megaladapis madagascariensis* Forsyth-Major, 1894

**Order Carnivora**

Family Eupleridae

†*Cryptoprocta spelea* G. Grandidier, 1902

*Cryptoprocta ferox* fossa

**Order Artiodactyla**

Family Hippopotamidae

†*Hippopotamus guldbergi*? Fovet, Faure & Guérin, 2011

†*Hippopotamus lemerlei* A. Grandidier, 1868

1. Subfossils referred to this taxon from Belo sur Mer need to be reevaluated to verify they are not of *Voay robustus*.

In our reconstruction of the site (Plate 9), we have tried to imagine what the zone would have been like a few millennia ago. The percolating water, emerging at the inland side of the coastal dunes and creating substantial areas of freshwater, probably formed a chain of lakes, connected intermittently to coastal estuaries, which would have provided a haven for certain extinct animals. These would have included a dwarf hippo *Hippopotamus lemerlei*, a crocodile *Voay robustus*, and waterbirds such as the shelduck *Alopochen sirabensis*. Depending on fluctuating water levels, as well as soil types, the neighboring forest may or may not have come down to the water's edge, and it is possible that these two habitats were separated by a zone of open wooded savanna like that pictured here, similar to an open Miombo woodland of southern Africa today (see Figure 25 and Part 1, "Savanna and Grassland Formations"). This could have been an important habitat of the giant tortoise *Aldabrachelys abrupta* and regularly visited by elephant birds such as *Mullerornis rudis* and the aardvark-like animal mentioned earlier, *bibymalagasia Plesiorycteropus madagascariensis*. It can be presumed that there was an important density and diversity of invertebrates in the past as there are today. For example, we depict the landscape as scattered with numerous large termite mounds, a type of insect that *bibymalagasia* presumably fed on. Termites would have also been an important component in the recycling of soil and vegetational nutrients.

Given the presence of certain animals in the Belo sur Mer deposits—such as the highly arboreal "sloth-lemur" *Palaeopropithecus ingens* and other forest-dependent species, including *Pachylemur insignis*, *Megaladapis madagascariensis*, and *Mesopropithecus globiceps*—one can infer that portions of the local forests were structurally dense and provided a continuous pathway aboveground of lianas and branches for

these lemurs to navigate across. In Plate 9, we have depicted the zone as a relatively dense deciduous forest, with some humid forest elements, including some good-size emergent trees and a relatively open understory. The three species of “monkey-lemurs” (*Hadropithecus stenognathus*, *Archaeolemur majori*, and *Archaeolemur edwardsi*) were all comfortable traveling and foraging on the ground in open habitats outside the forest, and they may have interacted near watering sites as we have illustrated here. *Hadropithecus* was feeding in its own specialized way on C<sub>4</sub> or CAM plants (see Plate 3), but precisely how the two species of *Archaeolemur* co-existed and tolerated each other is unknown; territorial tendencies may have created some tension and aggressive displays between them during such close encounters.

In the modern deciduous forests of the region, the presence of trees and vegetation with leaves and animal activity is notably dramatic after the start of the first serious annual rains (see Figure 21). Our rendition of the local scene several millennia ago is during the height of the rainy season, with the forest being a distinctly verdant color and very “alive.” Associated with this season, different animals would be actively breeding and reproducing, such as the pair of mating tortoises or the female hippo nursing her baby. The morning chorus of birds would have commenced well before dawn and still be relatively intense until the heat of the day started, and birds would be actively defending territories and searching for nesting material.

Another fascinating aspect of this area of the island is its other special sources of insight into the window when certain animals may have gone extinct or been extirpated. Among the local people of the Belo sur Mer region, a rich local oral history still remains, which include tales of some seemingly extinct beasts. During their fieldwork to the region in 1995 to excavate subfossil remains, David Burney and Ramilisonina were able to collect important details from local elders on some weird and wonderful animals that were “remembered” as former residents of the area (50).

Among the information they collected were several stories related to hippopotamus-like animals with local vernacular names of *kilopilopitsofy* or *songomby*. For example, one of their interviewees, a Monsieur Pascou, recounted the following history:

*He had also seen the kilopilopitsofy several times, best and most recently in 1976. According to Pascou, this ani-*

*mal is cow sized, but without horns. He had only seen it at night, and, in that poor light, it was very dark-skinned, perhaps black, except it had some pink (mavokely) coloration around the eyes and mouth. Its ears were fairly large and flopped about. When we showed him a color picture of an elephant, on the theory that these stories were perhaps borrowings from the African coast, brought by sailors who navigate the Mozambique Channel for regional trade, he was quite amused. “Oh no,” he chuckled knowingly, “that’s an elephant.” He said that he had seen an elephant years ago, when a French farmer brought one to Mahajanga (Majunga), and that the kilopilopitsofy was not as big, had a larger mouth, no trunk, and escaped by running to the water.*

The narrative continued, “He imitated for us the call of the kilopilopitsofy. He gave a series of deep, drawn-out grunts, very similar to *Hippopotamus amphibius* (and quite different from the bush pig).”

The same gentleman also presented information on another strange beast, this time dubbed the *kidoky*.

*This animal, he said, was something like a sifaka [= Propithecus], but with a face like a man, and about the size of a seven-year-old girl, his great-granddaughter, standing nearby when he related the story. He said he got a particularly good look at one nearby in 1952, and it had a dark coat but a conspicuous white spot on the forehead and another below the mouth. It is a shy animal, he says, and when encountered, flees on the ground rather than climbing trees like a sifaka. It moves by a series of leaps, and perhaps can stand on two legs, he believes.*

In their analysis and interpretation of the *kilopilopitsofy*, Burney and Ramilisonina point out that all of the physical and behavioral characters outlined by their informants match that of a hippo. Across the island, the most recent radiocarbon date of subfossil remains of a *Hippopotamus* is from Itampolo, which yielded a date of 980 years BP (mean calibrated date of 905) (69). The identity of the *kidoky* is less apparent. Several possibilities have been suggested, including either of the extinct lemur genera *Archaeolemur* and *Hadropithecus*, for which the most recent radiocarbon dates are 1,020 years BP (mean calibrated date of 870) and 1,413 years BP (mean calibrated date of 1260), respectively. It is difficult to answer the critical question if these accounts and recollections are based on real animals that once roamed western Madagascar, or if they are some hybrid formulation between fictitious

creations and now-extinct animals that once actually lived in the vicinity. If the former, than how long can oral tradition be maintained after the source has disappeared? Tales of fantastic animals are known from different areas of Madagascar (119), and the possibility cannot be excluded that numerous animals now extinct still roamed the forests of Madagascar into a period later than radiocarbon dates indicate.

## Plate 10: Mananjary—the Former Estuary System of Eastern Lowland Madagascar and Some of Its Faunal Elements

A recently published map of different sites on Madagascar that yielded radiocarbon dates of animal bone or other organic material included twenty-seven paleontological localities (54), of which Mananjary was the only one in the eastern lowlands, a zone that stretches along a north-south axis over a 1,200 km

distance. In contrast, fourteen different dated sites were listed from just the southwestern portion of the island alone. This bias creates several important problems in interpreting Holocene changes in the climate, habitat, and organisms of the vast eastern lowlands. So the question needs to be posed, why are

---

Very little information is available from subfossil sites in the eastern portion of Madagascar, perhaps associated with the lack of sufficient exploration, logistic difficulties, and poor conditions of preservation. The only site known to date is near Mananjary in the coastal area of the central southeast, where a few bones were recovered in the early portion of the twentieth century. Here we depict a marshland area, close to an estuary, where the dominant animal, *Hippopotamus laloumena*, is shown wallowing and feeding on grasses at the water's edge. This extinct species was almost the same size of the living African counterpart, *Hippopotamus amphibius*, and notably bigger than the pygmy hippo common in western and southwestern subfossil deposits of Madagascar. A number of waterbirds are also shown, all of which still occur in eastern Madagascar today, and include the duck *Anas melleri*, one female defending her recently hatched brood; an ibis *Plegadis falcinellus* in the central and left foreground, and an assortment of egrets in the background. For a key to the different animals, see black-and-white inset for Plate 10 in color gallery. (Plate by Velizar Simeonovski.).



so few paleontological or integrated archaeological/paleontological sites (see Part 1, “The Types of Subfossil Sites”) known from this portion of the island? As discussed below, this is associated with several different factors—level of exploration and local geology and climate.

Generations of paleontologists working on late Pleistocene-Holocene bone deposits have concentrated their efforts in the west, where in many cases logistics to get in and out of sites can be easier than for much of the lowland east. This is in part because of the dense vegetation cover of much of the east; this increases the difficulty of exploration and physically finding sites, as compared to notably sparser vegetation in the west and especially the southwest. With a good four-wheel drive vehicle, or at the worst an oxen-cart, a research team can get to most places in the west during the dry season. In contrast, portions of the east are topographically complex, few roads or tracks exist, and vast areas are accessible only by hiking in. These factors create logistical complications, and the only remaining option in some cases is to engage a considerable number of porters to get supplies into the site and specimens out.

Another critical aspect is geology. A large area of almost continuous limestone runs in parallel to much of the island’s west coast, from the extreme south to the northern tip of the island. These water-eroded karst landscapes contain numerous caves, crevasses, and canyons, which are ideal sites for animals to be trapped, left largely undisturbed, and their bone remains preserved for millennia. For example, the limestone Ankarana Massif in the far north contains a large number of caves, with more than 110 km of mapped passages, making it one of the most extensive cave complexes in the African region (58). This massif has a very rich subfossil history (Plates 16–18). Other western or southwestern sites are represented by deep vertical shafts, which provide natural pitfall traps for animals (see Plates 6 and 15). There are other types of sedimentary rock in the central west, namely, sandstone, which can also be eroded by water, providing lots of nooks and crannies for the deposition of animal bone. In contrast, very few deep caves are known from the east, as most of the bedrock is granitic, which does not erode in the same fashion as sedimentary rock (limestone and sandstone). Those that exist tend to be relatively shallow rock shelters, the deepest portions of which are largely exposed to the natural elements, which in turn severely degrade any deposited bone remains.

The smaller streams and rivers of the west provide ideal situations for the deposition of bone, particularly during periods of flooding. The site of Ampoza (see Plate 7) is such a setting. Many of these western watercourses have backwater swamps that can be well suited for bone and organic material deposition. In contrast, many rivers in the east descend abruptly from the Central Highlands and within 50–100 km empty into the sea (see Figure 13, left). In this region, some bottomland marshes occur that, at least in principle, should have bone deposits, so perhaps the lack of prospecting in such areas is the primary reason that there are virtually no examples other than the region of Mananjary, the subject of this plate and discussed below.

Climate is a critical factor that influences the preservation of organic material, such as animal bone. The eastern lowlands with its distinctly greater rainfall and high levels of humidity (see Part 1, “Humid Forest”) produces all kinds of different fungi, mold, and so on that degrades bone. In contrast, the relatively dry west, particularly the southwest, has conditions conducive to relatively little degradation of bone, and in some places remains have been found with pieces of flesh still attached to bones. In active caves with dripping water, a remarkable number of well-preserved animal bones have been found imbedded in calcite formations (speleothems), providing specimens literally “frozen in time” (see Figure 4). Even in certain western sites (see Plate 9), water can be the enemy of paleobiologists; DNA in waterlogged bones and teeth degrade rapidly. For example, ancient DNA could not be extracted from *Archaeolemur* jaws and teeth provided to Anne Yoder, now director of the Duke Lemur Center, from the 1995 subphreatic Belo sur Mer excavations (see Plate 9).

As mentioned above, one of the few paleontological sites known from the east is a few kilometers to the south of Mananjary, which was discovered during dredging of a waterway system known as the Canal des Pangalanes. This is one of the longest canals in the world and was formed by a series of man-made connections of coastal lakes and rivers running from Toamasina at the northern limit to Mananjary at the southern limit, a distance of about 400 km. Between 1896 and 1904, the French constructed the canal, and over time at different points, it has needed rehabilitation. The natural system before the construction of the canal would have been a series of lowland or coastal estuaries, often adjacent to marshes, and composed of lakes, rivers, and streams that eventu-

**Table 8**

List of land vertebrates identified from Mananjary subfossil remains (62, 98, 279). Extinct species are indicated with †, and the authors and description date is given. Listing does not include introduced species.

---

**Class Aves**

**†Order Aepyornithiformes**

†Family Aepyornithidae

†*Aepyornis* sp.

**Class Mammalia**

**Order Artiodactyla**

Family Hippopotamidae

†*Hippopotamus laloumena* Faure & Guérin, 1990

---

ally flowed into the sea. Hence, the zone comprised an extensive freshwater ecosystem, where water remained in permanence.

In a short communication published in 1922, Louis Monnier and Charles Lamberton announced to the Académie Malgache the discovery of a new subfossil deposit at Mananjary (279). Among the material recovered from the site, they listed the following remains in an excellent state of conservation, which contained few native species (see Table 8):

- (1) A portion of a maxillary (“*un demi-maxillaire inférieur*”) of an indeterminate young ruminant, as well as upper jaws of [presumably introduced] bush pigs (*Potamochoerus*),
- (2) Bony skin plates of an undetermined aquatic animal,
- (3) Vertebrae, ribs, forearm, nearly complete pelvis, and lower jaw of a hippopotamus.

These authors compared the hippo remains to those of *Hippopotamus lemerlei*, presumably from the west, and they were struck by the large size of the Mananjary material. On the basis of different dental characters, they concluded that the Mananjary specimens were closest to *Hippopotamus amphibius* of Africa, but different nonetheless, and named them as a new variety or subspecies. In order to pay tribute to Herbert F. Standing, who had collected and studied subfossils on Madagascar, they proposed the name *Hippopotamus amphibius standini*. Monnier and Lamberton also mentioned that about twelve years earlier a molar of what was probably a hippo was found in the lower Mangoro River valley. They concluded that hippos might have existed at one time along the complete east coast of the island. A number of

archaeological excavations have been conducted in the Mananjary area in the past decade, but no further remains of hippos have surfaced (186).

Laurie Godfrey and Bill Jungers attempted to relocate the Mananjary hippo site in 1998. They rented a small boat with a guide and interviewed villagers along the banks of the Pangalanes for recollections of fossil hunters and unusual bones. At one village, they were informed that big unknown bones were once found during dredging, but the people feared sorcery and supposedly threw them back into the water! More poignantly, at another cluster of huts, the local elders made it clear that they did not want to talk about any old bones related to the construction or repair of the canal. Their relatives were forced to do the backbreaking work, and discussion of this period evoked bad memories of the French colonial period.

After the presentation of Monnier and Lamberton to the Académie Malgache, the Mananjary material was deposited at the academy’s museum. It was not until nearly 70 years later that two paleontologists, Martine Faure and Claude Guérin, who had worked on different hippo remains from Madagascar and elsewhere in the world, had the opportunity to examine the Mananjary material (98). They noted that the Mananjary mandible was distinctly larger than the two previously recognized species of Malagasy subfossil hippos, *Hippopotamus lemerlei* and *Hippopotamus madagascariensis* (358; but see below for further comments on their classification), and slightly smaller than the extant African *Hippopotamus amphibius*. They also found a number of toe bones (metapodials) in the same collection, also notably larger than and osteologically different from the two recognized Malagasy subfossil species. Based on these results, they named a new species to science, *Hippopotamus laloumena*, for the remains originally described by Monnier and Lamberton. The word *laloumena* is derived from the Malagasy name used in local folklore, particularly in the eastern portion of the island, for an animal that best fits the description of a hippo.

The mandible was on display at the Académie Malgache at Tsimbazaza in Antananarivo, and the metapodials stored in the academy collections at the Queen’s Palace in a building known as Tranovola or Silver Palace (Figure 55). In early November 1995, a fire occurred in the Queen’s Palace complex and largely destroyed the Tranovola, and it is unknown if the hippo bones survive. Three radiocarbon dates have been associated with Mananjary hippo remains

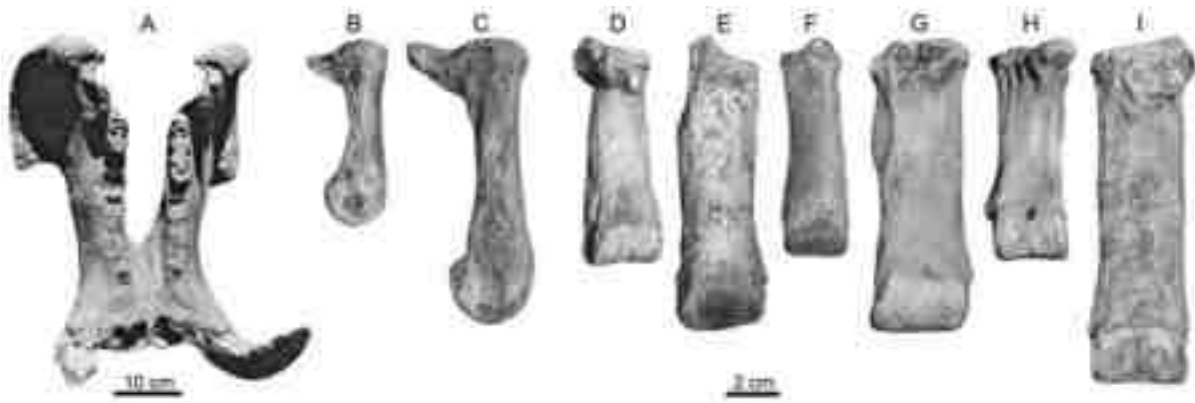


Figure 55. In 1922 Dr. Monnier and Charles Lambertson published a paper in the *Bulletin de l'Académie Malgache* describing some bone remains discovered in sediments along the Canal des Pangalanes near Mananjary. Many years later, the hippo material from this collection was studied by Martine Faure and Claude Guérin, and they described a new species of extinct hippo to science under the name *Hippopotamus laloumena*. (Photograph adapted from 98.)

(54). Two of these are very recent and derive almost certainly from imported material of *Hippopotamus amphibius* from Africa (99). The third date is notably older at 2,327 years BP and is probably from Mananjary.

Subsequently, some other developments have taken place concerning Malagasy hippos, specifically aspects associated with their classification (taxonomy). The first point to mention is that when *Hippopotamus madagascariensis* was described in 1883 (187), the language of the paper was the archaic Norwegian Riksmål. Hence, the specific details of this publication had not been properly discerned until a recent translation into French (107). In fact, the animal discussed by Guldberg is *Hippopotamus lemerlei*, described in 1868 by Alphonse Grandidier (175). Guldberg wanted to provide further anatomical details to augment information presented by Grandidier, and he decided to change the name from *lemerlei* to *madagascariensis*. This goes against the rules of nomenclature, where the first name used for a species sticks with it. Hence, in this case, the name *Hippopotamus madagascariensis*, as used by Guldberg, is a synonym of *Hippopotamus lemerlei*. The next use of the name *Hippopotamus madagascariensis* was some years later by Forsyth Major (259), and the specimens assigned to this species are indeed distinct from *Hippopotamus lemerlei*. As the scientific name *Hippopotamus madagascariensis* would be inappropriate to use for the Major specimens, as it is a synonym of *Hippopotamus lemerlei*, a new name, *Hippopotamus guldbergi*, was proposed (107).

A recent paper was published describing new hippo remains from the central west, specifically

from the Belobaka cave system, a few kilometers east of Mahajanga, that were also noted as being larger than *Hippopotamus lemerlei* and *Hippopotamus madagascariensis* (99). However, as explained above, the name *madagascariensis* is a synonym of *lemerlei*. These authors concluded that the Belobaka remains are simply larger than *lemerlei* and should be allocated to *Hippopotamus laloumena*. However, where *Hippopotamus guldbergi* fits in is uncertain, as the Belobaka remains were published one year before the description of *Hippopotamus guldbergi*. In any case, based on currently published information, it would appear that *Hippopotamus laloumena* had a broad distribution on Madagascar, along the east coast and slightly inland from the west coast. To make things even more complicated, the validity of *Hippopotamus laloumena* has been called into question, and it is considered by some authorities to be a synonym of African *Hippopotamus amphibius* (33). One of the interesting aspects of the Belobaka find is the dating of the deposits at 21,650 to 19,050 years BP, which makes them Upper Pleistocene and the oldest hippo subfossils known from Madagascar.

A few points should be mentioned about the “ruminant” remains reported on by Monnier and Lambertson. Ruminants are members of the order Artiodactyla, and other than hippos, there are no native species certain to have occurred on Madagascar. The bush pig *Potamochoerus larvatus*, also an artiodactyl, was probably introduced to Madagascar from Africa (164). Implicit in the context of the young ruminant material mentioned in the Monnier and Lambertson report, therefore, is that it is presumed to be an introduced animal. Hence, and combining these



two aspects together, this could imply that all of the Mananjary “subfossil” material listed above was from a relatively modern period after certain ruminants were introduced to the island. By further extrapolation, introduced (cattle and bush pigs) and native (hippos) artiodactyls might have mixed naturally. Alternatively, there was accidental mixing between the older layer with the hippo remains and more recent deposits containing the introduced species. Without more detailed information on the site stratigraphy, specifically where these specimens were collected, this issue remains unresolved.

In Plate 10, we have tried to re-create the estuary marsh scene where the *Hippopotamus laloumena* remains were found. It was probably a relatively large expanse of aquatic habitat, similar to the modern Canal des Pangalanes, a series of lake complexes, and presumably attached to one another through water connections or by relatively narrow stretches of land separating the different aquatic ecosystems. Important areas of reeds and terrestrial grasses were found on slightly higher ground, where the hippos fed. On the ridges above would have been dense, tall eastern humid forest with a myriad of different organisms. As we do not have any other identifiable vertebrate remains of native species from the site, we have decided to illustrate only aquatic birds known from the area today, such as the Glossy Ibis *Plegadis falcinellus* and Meller’s Duck *Anas melleri* (in one case a bird is guarding her newly hatched young).

## Plate 11: Antsirabe Region—Ecology of Highland Marsh and Forest Habitats as a Measure of Change through Time

The Central Highlands, between Antsirabe and Betafo, has been very productive for the recovery of subfossil bones at different sites, and the nearby Lake Tritrivakely has provided well-documented pollen deposits. In the latter case, the pollen cores yielded a record dating back nearly 36,000 years, which provides

a clear view of ecological change in this area relatively deep in time and well before human colonization of the island. After people arrived in this region, the pollen records and associated levels of fine charcoal in the sediments provide an important window into the ecological impacts of human-induced (anthropo-

---

On the basis of the different types of animals identified from the subfossil deposits in the Antsirabe region, it appears that several millennia ago the local ecosystem was composed of large marsh systems with neighboring montane forest. An assortment of extinct aquatic birds have been identified from the deposits, including a gallinule-like rail *Hovacrex roberti*, a good-size shelduck *Alopochen sirabensis*, and a massive long-legged waterbird with large spurs on its wing *Centrornis majori*. Remains of two species of elephant birds are known from the area, the notably large *Aepyornis hildebrandti* and the smaller ostrich-size *Mullerornis agilis*. Two of the species of large extinct lemur found at the Antsirabe region deposits include the “koala-lemur” *Megaladapis grandidieri*, here drinking water at the marsh edge and not too far from the forest limit, and a “sloth-lemur” *Palaeopropithecus maximus* dangling from a tree at the forest edge. Another important member of the aquatic ecosystem would have been the hippo *Hippopotamus guldbergi*. For a key to the different animals, see black-and-white inset for Plate 11 in color gallery. (Plate by Velizar Simeonovski.)



genic) perturbations. Several sites in the general Antsirabe region have been excavated, most at the elevation of around 1,500 m above sea level, which include those within close vicinity of Antsirabe (sometimes referred to in the older literature as Sirabe or Sirabé): Betafo, Morarano, and Masinandrana (also referred to as Masinandreina). In order to give a broader view of the former fauna and ecology of this zone, we have combined information from these different but related sites.

The original discovery of the bone-bearing beds in the Antsirabe region is closely linked to a religious missionary, Thorkild Guttormsen Rosaas (Figure 56). He arrived in Madagascar in 1869 as part of the Norwegian Missionary Society, where he first took up residence in the small village of Loharano, not too far from Antsirabe, then at Masinandrana, and subsequently in Antsirabe, where he lived until 1907. During his nearly 40 years in residence, he conducted numerous humanitarian and development projects, among which was the exploitation of the thermal hot springs in the volcanically active region of Antsirabe for the water's therapeutic capacities (329). As a by-product of enlarging these sources, as well as some exploitation of lime, he was responsible for the excavation of several thermal springs, where quantities of subfossils were found. A portion of this bone collection was sent to a museum in Christiania, Norway; this city was later to be renamed Oslo. Among the specimens was a considerable number of hippo bones, which were described by Guldberg under the name *Hippopotamus madagascariensis* and started a long taxonomic controversy about Malagasy hippos that was recently resolved (see Plate 10). Reconstructions of these dwarf hippos remain on display today in the Naturhistorisk Museum in Oslo.

Rosaas is credited with founding the modern plan of the city of Antsirabe—particularly laying out the principal roads, sewage canals, and water supply of the existing town. During his long residence there, different paleontologists passed through the region to make collections, and he provided considerable aid, including collaborations with paleontologists from the Académie Malgache and other institutions (Figure 57, left and right). C. I. Forsyth Major writes, "I left Ambositra for Sirabé, to learn only then, from the Rev. Mr. Rosaas, the discoverer of the fossil bones at Sirabé, who himself been collecting in the marshes for over 20 years. . . . I have to acknowledge with thanks the Rev. Mr. Rosaas's friendly help at this place" (258). Rosaas also donated subfossils to visiting naturalists



Figure 56. Thorkild Guttormsen Rosaas was a Norwegian missionary who lived in the Antsirabe region from 1869 until 1907. During his many years in residence, he initiated different types of development projects, including the exploitation of lime in hot spring deposits, and considerable numbers of subfossils were found. These deposits, excavated by different paleontologists, provide an extraordinary window into some of the previous ecological settings of the region based on the inferred habitats of the species recovered. The statue of Rosaas shown here is located in a small park in the center of Antsirabe and attests to the recognition of his historical activities in the development of the region. (Photograph by Hesham T. Goodman.)

and scientists, such as Johannes Hildebrandt from Germany and Georges Muller from France during their visits to Antsirabe. In both cases, different elephant birds were named after these gentlemen, based on the material they then sent back to their respective institutions, including *Aepyornis hildebrandti*, *Aepyornis mulleri*, and the genus *Mullerornis* (272).

The collections of extinct lemurs from the Antsirabe region (see Table 9) include *Mesopropithecus pithecoides*, *Megaladapis grandidieri*, and *Pachylemur jullyi* from Antsirabe proper; from nearby Morarano-Betafo, *Palaeopropithecus maximus*, *Megaladapis gran-*



Figure 57. Historical photographs from excavations in the Antsirabe region from the Fond Grandidier collection. At certain sites, rather extraordinary quantities of overburden soils had to be removed in order to reach the level of the subfossils. This can be readily seen in the image of an Académie Malgache excavation (*top*). Guillaume Grandidier presumably took this image during his 1899 site visit. In other cases, more shallow excavations were made, as shown here in the middle of a rice field (*left*). Georges Muller probably took this photograph in 1895 during an excavation he made in the Antsirabe region. (Courtesy of the Académie Malgache.)

*didieri*, *Pachylemur jullyi*, and *Archaeolemur edwardsi* were found; and from a few kilometers away at Masinandrana, there are remains of *Archaeolemur edwardsi*, *Megaladapis grandidieri*, and *Pachylemur jullyi* (12, 96, 121, 360). Overall, the subfossil species diversity is slightly reduced as compared to another site in the Central Highlands, Ampasambazimba (see Plate 12), which is several hundred meters lower in elevation and some 120 km to the northwest.

Missing from the deposits near Antsirabe are *Hadropithecus* and *Archaeoindris*. This could represent a problem of sampling, but the number of sites and abundance of fossils from this region argues against

that interpretation. There is considerable overlap in other vertebrates from both Antsirabe and Ampasambazimba, so it is difficult to accept that there were no suitable habitats for the missing lemurs. The presence of *Archaeolemur* at these two subfossil localities implies at least some open habitat, which is probably the environment also favored by *Hadropithecus* and *Archaeoindris*. No obvious reason for the subtle differences in the lemur communities comes to mind, with the exception of possible differences in forest type associated with the elevational differences mentioned above, but it is worth noting that *Hadropithecus* and especially *Archaeoindris* are rare

throughout the island's fossil sites. *Daubentonia robusta*, the extinct giant aye-aye, may have been at Ampasambazimba too (126), but was misidentified as present at Masinandrana by Tore Ekblom in 1953 based on bones now known to be referable to *biby-malagasia* *Plesiorycteropus* (see below). Also known from the Antsirabe region is *Megaladapis grandidieri*, an arboreal, leaf-eating browser closely related to *Megaladapis madagascariensis* in the south and southwest. Given its bulk, it was safe on the ground from most non-human predators, as it is shown in Plate 11 coming to the water's edge to drink. Although the highly suspensory sloth-lemur *Palaeopropithecus* was not common to all the Antsirabe localities, we invoke slight artistic license here and show it hanging from a branch off in the distance.

A considerable number of bird bones have been recovered from the Antsirabe regional sites, comprising sixteen species (see Table 9), of which six, or 38 percent, are extinct, and several extant species no longer occur in this portion of Madagascar (144). There are numerous bird species, including extinct subfossil ones, in common between the Antsirabe region and Ampasambazimba sites. This underscores that this former avifauna probably had a broad distribution in the Central Highlands (and elsewhere on the island for some species).

Remains of two species of elephant birds are known from the Antsirabe region, the large *Aepyornis hildebrandti* and the smaller ostrich-size *Mullerornis agilis*. As we know little about the feeding ecology of these birds, it is difficult to interpret aspects of their diet and habitat use (see Plate 1). In any case, given their presumed biomass relative to other organisms in the ecosystem, their disappearance probably gave rise to important changes, such as the dispersal of different seeds and fruits passing through their digestive systems. This in turn would have had an impact on forest plant regeneration. One radiocarbon date is available from an *Aepyornis* bone from Masinandrana, which yielded a date of 4,496 years BP (mean calibrated date of 5,075) (69).

As discussed for Ampasambazimba (see Plate 12), a number of extant aquatic birds were also recovered from the Antsirabe region subfossil sites. These include the extant Red-billed Teal *Anas erythrorhynchos*, Meller's Duck *Anas melleri*, and Bernier's Teal *Anas bernieri*; the latter two species have notably reduced modern ranges and are considered Endangered by the International Union for Conservation of Nature. There is one waterbird identified from the Antsirabe

region deposits that no longer occurs on Madagascar but perhaps persists elsewhere in the world. Bones of a large cormorant *Phalacrocorax* sp. were identified from subfossil remains, which are larger than the only cormorant known from the island today—the Reed Cormorant *Phalacrocorax africanus*, which was also identified from the deposits. Whether this larger species still occurs in Africa, for example, or is extinct will need further research.

Two extinct waterfowl were excavated from the Antsirabe region deposits, both of which had broad distributions on the Central Highlands and in lowland and coastal areas of the island. The first is *Alopochen sirabensis*, which was described by Charles William Andrews of the then British Museum, London, based on material from the Antsirabe region (8). As determined by Lucien Rakotozafy, remains of this species are abundant in the deposits (313). If the habits and habitats of *Alopochen sirabensis* were like the living member of this genus, the shelduck *Alopochen aegyptiacus*, they would have been gregarious, often feeding on vegetation along the edge of aquatic habitat, particularly on herbaceous plants and seeds, as well as invertebrates and small vertebrates. Two radiocarbon dates from Antsirabe for *Alopochen sirabensis* yielded dates of 19,250 and 17,100 years BP (mean calibrated dates of 22,860 and 20,170) (69).

The second extinct waterbird found in the deposits is *Centrornis majori*, named as a genus and species new to science based on material from Antsirabe (8). The species name is in honor of its discoverer C. I. Forsyth Major, who sent back to the British Museum considerable quantities of subfossil remains from the Central Highlands (203). Certain physical aspects of *Centrornis* are rather special. On the basis of different bone characteristics, it was clearly a waterbird, probably best placed in the shelduck subfamily Tadorninae. It was a distinctly large fowl, greater in size and body mass than *Alopochen sirabensis*, with notably long legs and probably long toes. It would most likely have been more at ease wading, rather than swimming, while searching for food in shallow water. One of the other characteristics of this bird includes spurs on the leading edge of the wings toward the "wrists." With little doubt, these would have been used for aggressive interactions between individuals of the same species (intraspecific) or perhaps for some type of defense against predators. One can almost imagine, during the courtship season, the raucous screams heard from the marsh edges during a sort of sparring match, as males launched at each other armed with

their spurs. A radiocarbon date from bone remains recovered at Antsirabe for this species was 17,370 years BP (mean calibrated date of 20,480) (69); this overlaps with the dates of *Alopochen* and indicates that these two species occurred in the marshes at the same time.

Also based on the collections brought back by Forsyth Major to London, Andrews described another species of bird, a rail *Tribonyx roberti* (8), which was subsequently transferred to the endemic and extinct genus *Hovacrex*. This species, as well as several others, was named in honor of Alphonse Robert, who worked as Forsyth Major's assistant during his 1894–96 mission to Madagascar (203). In Plate 11, we have modeled *Hovacrex roberti* as a sort of gallinule, with which it shows some osteological similarities. Accordingly, one can envision this extinct bird feeding at the edge of reeds and dense vegetation, occasionally running or swimming. Wing bones attributed to this rail have yet to be found, and it is impossible to know if it was capable of sustained flight. Remains of the Purple Gallinule *Porphyrio porphyrio* have also been identified from the Antsirabe region subfossil deposits, and *Hovacrex* and *Porphyrio* probably lived in the same wetlands.

Two other animals that formerly inhabited the aquatic habitats of the Antsirabe region are noteworthy. The first was a large endemic crocodile *Voay robustus*, which reached lengths of up to about 5 m long and would have been a formidable predator. It presumably fed on the different types of aquatic life living in these marshes, as well as terrestrial animals that came to the water's edge to drink. The second was a hippo, now referred to as *Hippopotamus guldbergi*, which was recently described (107) (see Plate 10). Several radiocarbon dates are available for *Hippopotamus guldbergi* from Antsirabe, which include 1,800, 1,260, and 1,215 years BP (mean calibrated dates of 1,665, 1,150, and 1,075) (69). As we will discuss later, these dates are slightly before the first known sign of human presence in this area of the Central Highlands.

While the number of bones of extinct terrestrial species recovered from these sites is notably less than aquatic ones, some other extraordinary beasts have been identified in addition to those mentioned above. Perhaps one of the more fantastic animals recovered from the Antsirabe and Masinandrana deposits is bibymalagasias or *Plesiorycteropus*—a sort of aardvark-like animal that recently was placed in its own order, *Bibymalagasias* (250), whose distributional range also includes the southwest (e.g., Ampoza, Plates 7 and 8)

and the northwest (e.g., Anjohibe, Plates 13 and 14). There is only one specimen from Masinandrana, a partial pelvis, and that was originally misidentified as being from *Daubentonia robusta* (96). Both C. I. Forsyth Major and Charles Lamberton discovered other specimens of *Plesiorycteropus* in the Antsirabe region (230). A radiocarbon date is available from a bibymalagasias specimen obtained at Masinandrana, which yielded a date of 2,154 years BP (mean calibrated date of 2,125) (69). Hence, this enigmatic animal was recently living. Certain portions of the skeleton of the locally occurring species, *Plesiorycteropus madagascariensis*, are not known, and some critical aspects of how it may have moved and if it had any teeth remain unclear. However, it is presumed to have specialized on eating insects or soft-bodied invertebrates; with notable heavy digging claws, it extracted its prey from the ground, rotten wood, or termite mounds. A second species, *Plesiorycteropus germainepetterae*, was described from the Central Highlands, probably Ampasambazimba (see Plate 12), from where *Plesiorycteropus madagascariensis* is also identified. More recent work on the phylogenetic relationships of a mammalian group now known as Afrotheria—a diverse assembly of different animals that are thought to come from a common ancestor and diversified on the African continent—suggests that *Plesiorycteropus* may in fact be the “sister group” (close relative) of aardvarks (382), an animal with which it shares many peculiar anatomical features.

While there are a number of citations to giant tortoise bones being recovered from the Antsirabe region, the specific identity remains uncertain (36). The description of the lengths of some tortoise bones recovered from the “bains de la Reine” in Antsirabe would have been from enormous animals with a carapace length of at least 200 cm. Given that turtles obtain body heat from external sources, specifically the sun, and taking into account the cool temperatures of a high elevation area such as Antsirabe, one can imagine that this region, based on the metabolic requirements of these animals, was toward their upper altitudinal limit.

Both the extinct carnivoran-predator *Cryptoprocta spelea* (see Plate 19) and extant *Cryptoprocta ferox* are known from the Antsirabe region subfossil deposits (165). In light of no clear stratigraphic control by early paleontologists associated with the excavation of the deposits where the bones were recovered, it is not possible to know if these two Carnivora lived in the area during the same period.

The final mammal to mention is *Hypogeomys australis*, which was a terrestrial rodent, probably at least 2 kg in body mass. Its living congeneric species, *Hypogeomys antimena*, is known from subfossil deposits in southern and southwestern Madagascar, and its modern range is in the Central Menabe region north of Morondava (see Plate 2). *Hypogeomys antimena* is a nocturnal species that digs deep burrows into the ground and feeds principally on seeds and tubers. It would be reasonable to imagine that *Hypogeomys australis* had similar adaptations associated with how it made its living.

So with all of this as a window into the terrestrial and aquatic fauna that used to occur in the Central Highlands near Antsirabe, many species of which are now extinct, it is important to try to explain what happened to these organisms and what changes took place in the local ecosystems. We are fortunate that two different research teams have extracted pollen cores from a high mountain lake known as Tritrivakely (or Andraikiba), not too far from Antsirabe. Tritrivakely occurs at about 1,500 m elevation, which is about the same as the subfossil bone deposits of the region.

The upper 13 m of a 40 m deep continuous sediment sample of the first core yielded a record of the past 36,000 years, providing an extraordinary window into the vegetation around this lake and aspects of the aquatic ecosystem (113, 114, 115, 327). Organic materials in different portions of the sediment were radiocarbon dated, which provides a time frame associated with the different shifts in environmental history. About 36,000 years BP, the lake was similar in certain aspects to its current conditions, but with a higher proportion (80 percent) than today of plant pollen characteristic of high mountain areas, specifically heathers of the family Ericaceae, probably representing a period with a colder climate than today. Considerable peat horizons were deposited during this period and until about 14,400 years BP. The next stage, dated between approximately 36,000 and 20,000 years BP, shows some fluctuations, including a volcanic eruption about 35,000 years BP (see below) and notable changes in the aquatic environment of the lake, most likely associated with the era leading up to the Late Glacial Maximum. This is a period when considerable portions of the Earth, including high mountains in Madagascar (373), were glaciated. The pollen in this portion of the deposit is still dominated by plants of the family Ericaceae.

The next notable interval in the record, between

19,000 and 4,000 years BP, coincides with the period after the Late Glacial Maximum, when the Earth started warming up and biological productivity increased. During this period, the volcanic lake was a swamp of sorts, dominated by papyrus. The amount of Ericaceae pollen, as well as that representing other high mountain flora in the deposits, dropped considerably, reflecting adjacent forests with more mesic and temperate conditions and vegetation; several genera of trees typical of lower-elevation formations on the island were common. The pollen core terminates with the period of the Upper Holocene, and the ecological conditions reflect those of a peat marsh similar to about 36,000 years BP and the dominance of the Ericaceae vegetation. The data obtained from this core would seem to represent a complete climatic cycle, from relatively warm to cold and back to warm, over the past 40 millennia and clearly shows how natural climate and ecological conditions varied.

A recently published study presents another time sequence for some of these crucial events (327). A new stratigraphic series analyzed from terrestrial sediments of the Antsirabe region reveals that between about 35,000 to 14,400 years BP, there was alternating deposition of different types of alluvial deposits (sand, silts, and gravel) and thick peat horizons, indicating notable fluctuating meteorological circumstances correlated with shifting Pleistocene conditions. Then sometime around 14,400 years BP, volcanic activity is recorded, which lasted some 6,000 years and deposited up to 20 m of thick fragmented volcanic material. The impact of these eruptions would certainly have been important at a local scale and probably drastically altered weather conditions in at least the central portion of the Central Highlands.

Another core, this one to a depth of 5 m, was taken by David Burney and colleagues from the same lake, and provides a glimpse into about the last 11,000 years of geological history (43). The types of analyses conducted with this second core provides a more focused window into the period before humans colonized the Central Highlands and the events that followed thereafter. As with the previous core, organic samples taken from different sections were submitted for radiocarbon dating and provide the temporal framework for the various phases. One of the first important aspects of the Burney study derives from charcoal particles in the pre-human section of the core, and it is clear from this that fire was a natural aspect of the environment. As we previously discussed, until

**Table 9**

List of land vertebrates identified from different subfossil sites in the Antsirabe region subfossil (29, 36, 39, 107, 144, 165, 250). Extinct species are indicated with †, and the author(s) and description date are given. For living taxa, the English common names are given. Listing does not include introduced species.

**Order Reptilia**

Family Testudinidae

†*Aldabrachelys* sp.<sup>1</sup> (Vaillant, 1885)

Family Crocodylidae

†*Voay robustus* (A. Grandidier & Vaillant, 1872)

**Class Aves****†Order Aepyornithiformes**

†Family Aepyornithidae

†*Aepyornis hildebrandti* Burckhardt, 1893

†*Mullerornis agilis* Milne-Edwards & A. Grandidier, 1894

†*Mullerornis betsilei* Milne-Edwards & A. Grandidier, 1894

**Order Pelecaniformes**

Family Phalacrocoracidae

†? *Phalacrocorax* sp. cormorant (probably undescribed extinct species)

*Phalacrocorax africanus* Reed Cormorant

**Order Ardeiformes**

Family Ardeidae

*Ardea* sp. heron

Family Threskiornithidae

*Platalea alba* African Spoonbill

**Order Anseriformes**

Family Anatidae

†*Centronis majori* Andrews, 1897

†*Alopochen sirabensis* (Andrews, 1897)

*Sarkidiornis melanotos* Knob-billed Duck

*Anas bernieri* Bernier's Teal

*Anas erythrorhyncha* Red-billed Teal

*Anas melleri* Meller's Duck

**Order Falconiformes**

Family Accipitridae

*Accipiter* sp. sparrowhawk

**Order Galliformes**

Family Phasianidae

*Margaroperdix madagarensis* Madagascar Partridge

**Order Gruiformes**

Family Rallidae

†*Hovacrex roberti* (Andrews, 1897)

*Gallinula chloropus* Common Moorhen

*Porphyrio porphyrio* Purple Gallinule

**Order Psittaciformes**

Family Psittacidae

*Coracopsis vasa* Lesser Vasa Parrot

**Class Mammalia****†Order Bibymalagasia**

†*Plesiorycteropus madagascariensis* Filhol, 1895

**Order Afrosoricida**

Family Tenrecidae

*Tenrec ecaudatus* common tenrec

**Order Primates****Suborder Strepsirrhini****Infraorder Lemuriformes**

†Family Archaeolemuridae

†*Archaeolemur edwardsi* Filhol, 1895

†Family Palaeopropithecidae

†*Mesopropithecus pithecoides* Standing 1905

†*Palaeopropithecus maximus* Standing 1903

Family Lemuridae

†*Pachylemur jullyi* G. Grandidier, 1899

†Family Megaladapidae

†*Megaladapis grandidieri* Standing, 1903

**Order Carnivora**

Family Eupleridae

†*Cryptoprocta spelea* G. Grandidier, 1902

*Cryptoprocta ferox* fossa

**Order Artiodactyla**

Family Hippopotamidae

†*Hippopotamus guldbergi* Fovet, Faure & Guérin, 2011

**Order Rodentia**

Family Nesomyidae

†*Hypogeomys australis* G. Grandidier, 1903

1. The species of *Aldabrachelys* that occurred in the Antsirabe region is uncertain.

about 9,000 years BP, ericoid pollen dominated, and then with a warming phase in the climate, different woody trees became more common. Subsequently, at about 2,000–1,500 years BP, charcoal values increase considerably, greater than the natural background levels of the previous millennia, coinciding with a decrease in tree pollen and an increase in grass and species in the family Compositae or Asteraceae.

Now the critical point at this stage is to define when humans first arrived in the Central Highlands and commenced different actions that would have modified the natural vegetation. The first evidence we are aware of from the archaeological record for this portion of the Central Highlands is from the thirteenth century (86), which is about 200–300 years after the notable vegetational changes in Burney's Lake Tritrivakely core. Some of the first plants in-



troduced by humans that are recognized by their distinctive pollen in the core include things like *Cannabis* (marijuana, family Cannabaceae) and *Humulus* (used to make beer, family Cannabaceae). This would indicate that certain aspects of human behavior have been remarkably constant across time and different cultures! If all of the dates are indeed correct, the presence of these pollens in the core suggest human presence for a few centuries before it is picked up in the archaeological record. In any case, during this period and until modern times, a lot of different plants and animals were introduced to Madagascar (224). The soils of this montane volcanic area are very rich, and it is easy to imagine, as today, that early settlers exploited this very agriculturally productive area of the island.

Now we put all of this diverse information together in a more condensed and integrated fashion. The region around Antsirabe experienced the typical cooling and heating periods of the end of the Pleistocene and early Holocene that occurred in other areas of the globe at the same latitude, which is part of natural climate cycling. During this period, a montane ecosystem occurred in the Antsirabe area, with associated extensive marshlands and a rich diversity of animals, including many large body-size ones that are now extinct. There were fluctuations in habitats associated with broad-scale patterns of freshwater being tied up in glaciers (cooler and dry) or their melting (warmer and wet). By the thirteenth century, and perhaps several hundred years earlier, people colonized the region, and notable changes occurred in the vegetation toward more open and seemingly disturbed habitats—in other words, increases in grasses and more frequent fires. The last radiocarbon dates of some of the now-extinct animals, such as hippos, are from roughly 1,000–1,100 years BP or just before the archaeological record signals humans in the area. Hence, based on current information from the Antsirabe region, there is no direct evidence of humans and extinct animals co-occurring during the same period. However, we anticipate when the regional archaeological record is better known, there will be support of some temporal overlap between people and the fauna that no longer occurs in this region. The pollen record points strongly to this likelihood.

The proposed scenario is that natural climatic changes were responsible for notable biological shifts in the region, probably pushing certain organisms with specialized habits or diets toward reduced populations or extinction. Although not supported

by the archaeological record known to date, we hypothesize that subsequent human pressure on the environment, which could have included habitat transformation and hunting, pushed several declining populations to their disappearance. The arrival of domesticated animals like the zebu into the Central Highlands might well have been the final deathblow. Further research and new data will provide insights into this hypothesis.



Plate 1: Cap Sainte Marie—the Ecology of Elephant Birds and Their Interface with Humans (see pages 59–64 for further details)







Plate 2: Andrahomana I—the Ecology of Extreme Southeastern Madagascar and a Barometer of Change (see pages 65–73 for further details)

Species identifications: 1. Madagascar Long-eared Owl *Asio madagascariensis*, 2. \**Microgale macpheeii*, 3. red forest rodent *Nesomys rufus*, 4. \**Megaladapis madagascariensis*, 5. \**Hypogeomys australis*, 6. \**Megaladapis edwardsi*, 7. \**Aldabrachelys abrupta*





Plate 3: Andrahomana II—Evidence of a Holocene Tsunami in the Southern Indian Ocean and Predator-Prey Relations (see pages 74–78 for further details)





Plate 4: Tsimanampetsotsa—Rapid Ecological Shifts in the Face of Natural Climate Change (see pages 79–86 for further details)

Species identifications: 1. Unidentified cormorant *Phalacrocorax* sp. extinct on Madagascar, 2. Bernier's Teal *Anas bernieri*, 3. \**Hippopotamus lemerlei*, 4. \**Aldabrachelys abrupta*, 5. \**Megadapis edwardsi*, 6. \**Archaeolemur majori*, 7. \**Mullerornis agilis*, 8. Madagascar Fish Eagle *Haliaeetus vociferoides*, 9. \**Aepyornis maximus*











Plate 5: Taolambiby—Hypotheses Associated with Animal Extinction and Hunting by Humans: Physical Evidence and Interpretation (see pages 87–93 for further details)







Plate 6: Ankilitelo—a Deep Pit Cave and Inferences about Recent Ecological and Faunal Change (see pages 94–101 for further details)

Species identifications: 1. *Daubentonia robusta*, 2. Grandidier's vontsira *Galidictis grandidieri*, 3. Petter's big-footed mouse *Macrotarsomys petteri*, 4. Madagascar hissing cockroach *Gromphadorhina* sp.









Plate 7: Ampoza I—Reconstruction of the Ecology and Fauna in a Formerly Permanent Riverine Habitat in the Southwest (see pages 102–6 for further details)

Species identifications: 1. *\*Archaeolemur edwardsi*, 2. *\*Voay robustus*, 3. *\*Hippopotamus lemerlei*, 4. *\*Alopochen sirabensis*, 5. *\*Vanellus madagascariensis*, 6. *\*Megaladapis edwardsi*, 7. Humblot's Heron *Ardea humbloti*, 8. African Openbill Stork *Anastomus lamelligerus*











Plate 8: Ampoza II—Ecological Change in a Forest Community and Connecting Humid Forest Corridors to the Eastern Portion of the Island (see pages 107–11 for further details)

Species identifications: 1. *Brachypteracias langrandi*, 2. *Palaeopropithecus ingens*, 3. ring-tailed lemur *Lemur catta*, 4. indri *Indri indri*







Plate 9: Belo sur Mer—a Window into Different Hypotheses Associated with Environmental Change: Natural versus Human-Induced (see pages 112–19 for further details)

Species identifications: 1. \**Voay robustus*, 2. \**Hippopotamus lemerlei*, 3. \**Alopochen sirabensis*, 4. \**Archaeolemur majori*, 5. \**Archaeolemur edwardsi*, 6. \**Hadropithecus stenognathus*, 7. \**Plesiorycteropus madagascariensis*, 8. \**Aldabrachelys abrupta*, 9. \**Mullerornis rudis*









Plate 10: Mananjary—the Former Estuary System of Eastern Lowland Madagascar and Some of Its Faunal Elements (see pages 120–24 for further details)

Species identifications: 1. *Anas melleri*,  
2. *Plegadis falcinellus*, 3. \**Hippopotamus*  
*laloumena*







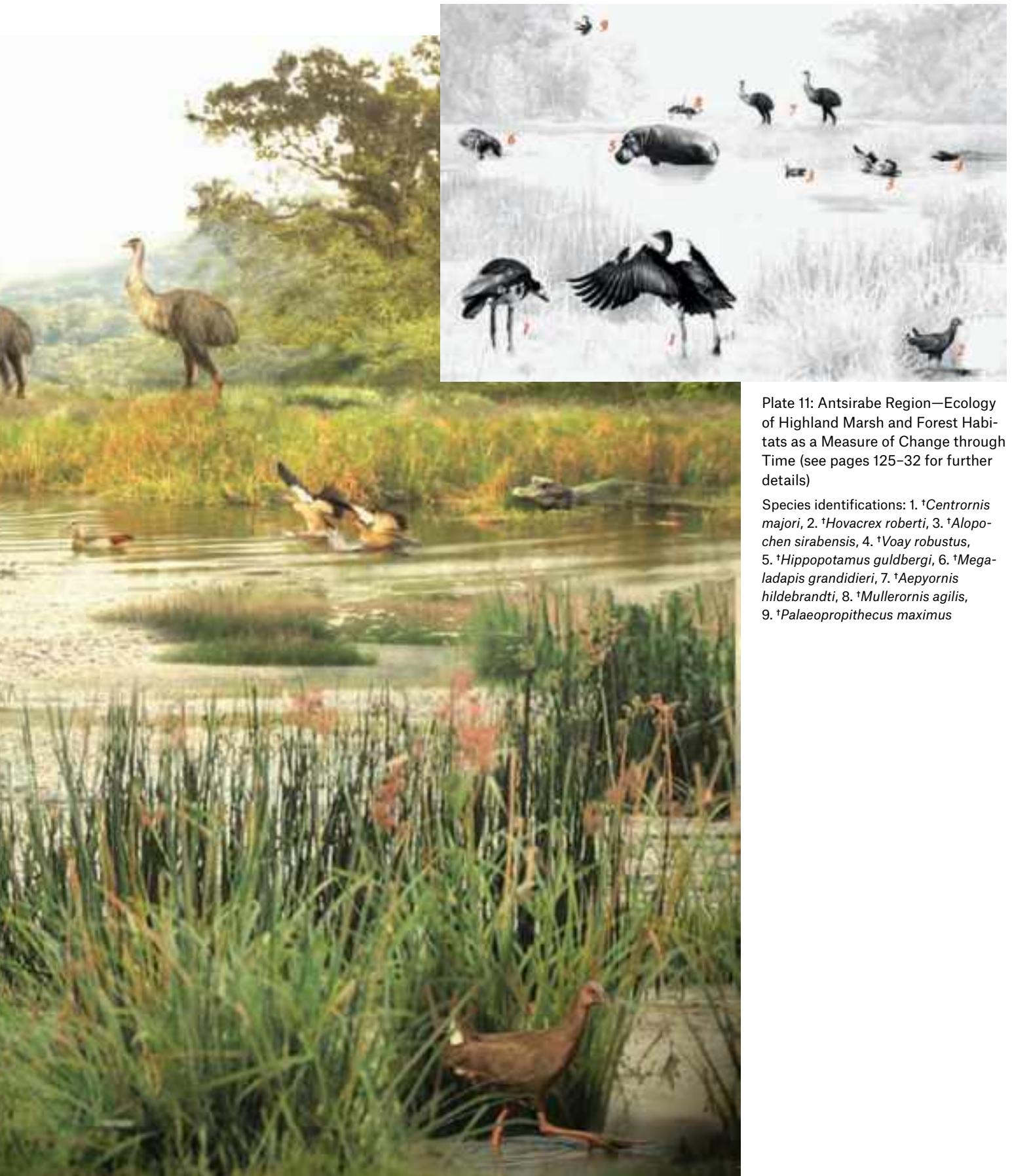


Plate 11: Antsirabe Region—Ecology of Highland Marsh and Forest Habitats as a Measure of Change through Time (see pages 125–32 for further details)

Species identifications: 1. \**Centronis majori*, 2. \**Hovacrex roberti*, 3. \**Alopochen sirabensis*, 4. \**Voay robustus*, 5. \**Hippopotamus guldbergi*, 6. \**Megaladapis grandidieri*, 7. \**Aepyornis hildebrandti*, 8. \**Mullerornis agilis*, 9. \**Palaeopropithecus maximus*





Plate 12: Ampasambazimba—Reconstruction of a Montane Forest and Woodland Habitat that No Longer Occurs on the Island (see pages 133–43 for further details)

Species identifications:  
 1. *Coua berthae*,  
 2. *Archaeoindris fontoynontii*, 3. *Plesiorycteropus germainepetterae*,  
 4. *Aepyornis hildebrandti*,  
 5. *Mesopropithecus pithecooides*, 6. *Stephanomastus mahery*









Plate 13: Anjohibe I—Secrets of the Past Disclosed by Careful Study of Subfossil Bone and Pollen in a Cave (see pages 144–49 for further details)

Species identifications: 1. *Hipposideros besaoka*, 2. *Triaenops goodmani*, 3. *Hippopotamus lemerlei*, 4. *Eidolon dupreanum*





Plate 14: Anjohibe II—Inferences Based on Cave Remains and Aspects of the Organisms Living in the Adjacent Ecosystem (see pages 150–56 for further details)

Species identifications: 1. *\*Nesomys narindaensis*, 2. *\*Coua primavea*, 3. *\*Hapalemur simus*, 4. *\*Palaeopropithecus kelyus*, 5. *\*Archaeolemur edwardsi*, 6. *\*Plesiorycteropus madagascariensis*









Plate 15: Anjavy—a Trapdoor Cave, Ecology of an Extinct Lemur, and Untold Extinct and Extant Biodiversity (see pages 157–61 for further details)





Plate 16: Ankarana I—Ecological Change of a Forest Community, a View from the Ground Up (see pages 162–67 for further details)

Species identifications: 1. *Haplemur simus*, 2. *Haplemur griseus*, 3. *Nesomys* cf. *narindaensis*, 4. *Eulemur coronatus*



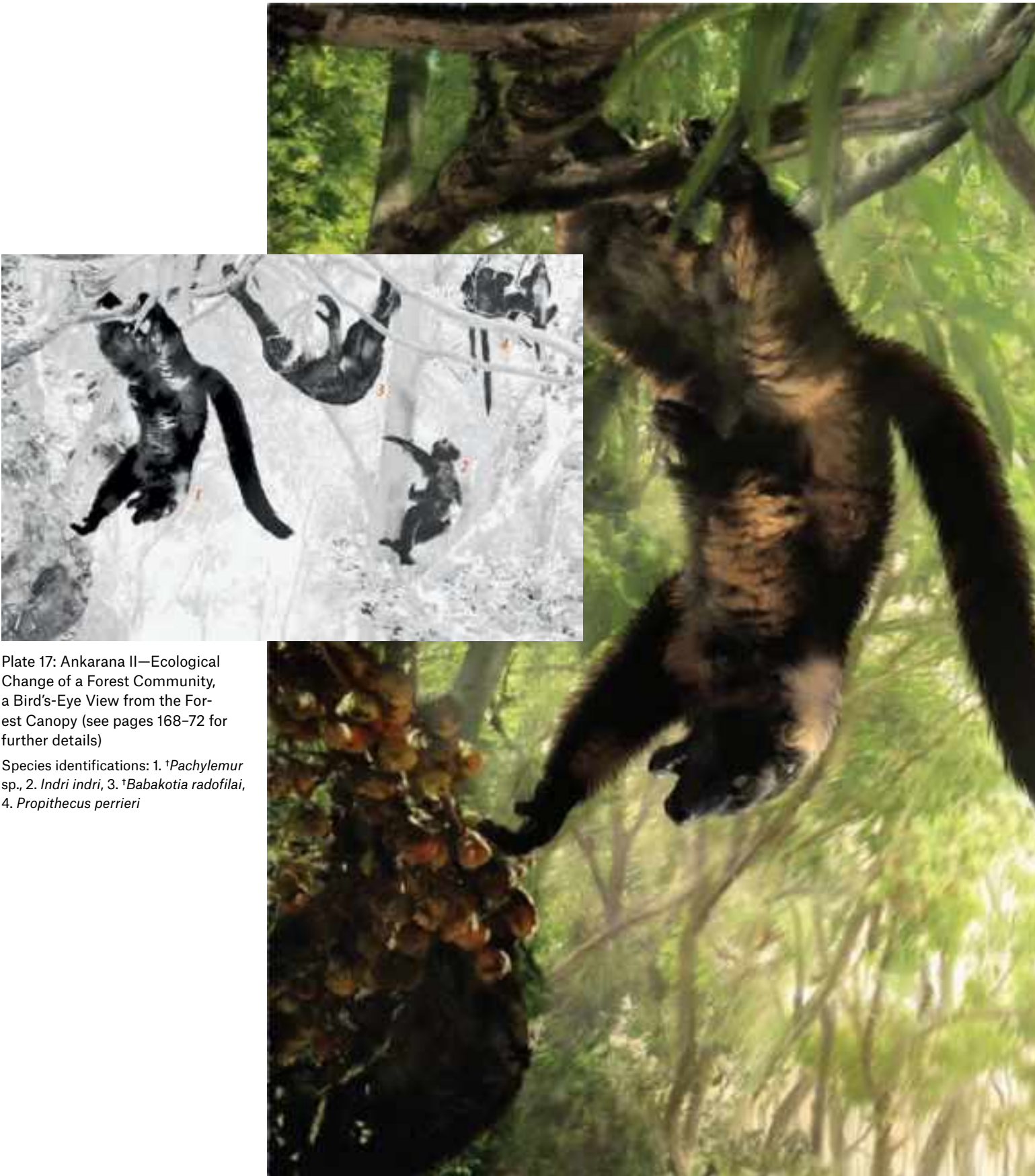


Plate 17: Ankarana II—Ecological  
 Change of a Forest Community,  
 a Bird's-Eye View from the For-  
 est Canopy (see pages 168–72 for  
 further details)  
 Species identifications: 1. *\*Pachylemur*  
 sp., 2. *Indri indri*, 3. *\*Babakotia radofilai*,  
 4. *Propithecus perrieri*











Plate 18: Ankarana III—Tragedy and How the Bone Remains of an Extinct Lemur Can Help Piece Together How It Lived and the Former Local Forest Ecology (see pages 173–76 for further details)

Plate 19: *Cryptoprocta spelea*—an Extinct Mega-Predator and Aspects of How It May Have Lived and Hunted (see pages 177–81 for further details)









Plate 20: *Stephanoaetus mahery*—a Presumed Primate Specialist and Its Role in the Evolution of Behavioral Aspects of Living and Extinct Lemurs (see pages 182–86 for further details)



## Plate 12: Ampasambazimba—Reconstruction of a Montane Forest and Woodland Habitat that No Longer Occurs on the Island

The best-known and most celebrated subfossil locality in the Central Highlands is Ampasambazimba. The name of the site needs some explanation. It literally means in Malagasy “the place of the Vazimba tomb.”

The Vazimba were the Proto-Malagasy in a widely accepted popular version of Madagascar’s history. That is, they are often viewed as the original colonizers of the island, and many ideas about these people, some

---

The paleontological site of Ampasambazimba is the best known from the Central Highlands, with a remarkable assortment of vertebrates identified from the subfossil remains, including eighteen species of lemurs, eight of which are extinct. On the basis of the different types of animals recovered from the site, inferred aspects as to how they may have lived, and data from pollen cores, it is clear that the former habitat of this area is unlike any existing ecosystem in the Central Highlands today. The former forest structure was probably a mixture of closed-canopy humid forest, areas of distinctly more open forested woodland, and zones dominated by grasses in non-shaded areas. One of the extraordinary animals known only from Ampasambazimba and forming the centerpiece of this plate is *Archaeoindris fontoynontii*. Remains of this huge animal are limited to just a handful of specimens, including a nearly complete skull still on display at the Académie Malgache museum in the capital of Antananarivo. Adult body size of this beast has been estimated to be almost 200 kg, and this rivals the largest male gorillas alive in Africa today. Because of its enormous body size, we have portrayed this species foraging on the ground, but its anatomy suggests that it was probably also a capable climber within the forested portion of this ecosystem. For a key to the different animals, see black-and-white inset for Plate 12 in color gallery. (Plate by Velizar Simeonovski.)







Figure 58. Historical photograph of excavations conducted by the Académie Malgache at Ampasambazimba at the turn of the twentieth century. The scene shows a long line of workers in an excavated trench spanning most of the middle portion of the photo. The person standing in the central area is Ramamonjy, who was a member of the technical staff of the academy and often took part in paleontological excavations, and those individuals crouched to the left include Henri Perrier de la Bâthie and Herbert F. Standing. This image is from the Fond Grandidier collection and was presumably taken by Guillaume Grandidier on a site visit to Ampasambazimba. (Courtesy of the Académie Malgache.)

linked with the supernatural, continue today. The locality name was presumably associated with physical remains, probably a tomb, which was attributed to the Vazimba. A cultural group exists today in the central lowland west, specifically the southern portion of the Bemaraha in the region of Bekopaka, who consider themselves descendants of the Vazimba. Other ethnic groups or “tribes” on the island also assert their ancestral affinities to the Vazimba.

Ampasambazimba was visited and excavated by paleontologists on different occasions starting in 1902 to recent years (227, 255, 356, 379) (Figure 58). Bill Jungers was part of yet another excavation here in 1989, but the bulk of the important fossils derive from the earlier efforts of Herbert F. Standing and Charles Lamberton. Subfossils were found in considerable density, and it has been noted by Standing, “In the comparatively small area already explored some 60 skulls of Lemuroids, mostly in an excellent state of preservation . . . have been found. In addition . . . at least 200 skeletons of Hippopotami . . . have been exhumed, besides numerous remains of *Cryptoprocta*, *Centetes* [= *Tenrec*] . . . *Aepyornis*, Chelonians, crocodiles . . .” (356, p. 60).

Numerous studies have been conducted on bones

recovered from this site, and many comparisons have been made to specimens from other subfossil localities. Several earlier mistakes in their taxonomic attribution have been clarified along the way. Meticulous and broad-scale comparative analyses have provided important insight into how some of these animals lived.

Eighteen species of lemurs have been identified from the subfossil remains, of which eight are extinct (126). To put this in perspective, the modern site on the island with the highest known lemur diversity is the Makira Forest, to the west of Maroantsetra, with thirteen species (320). Hence, the species richness of Ampasambazimba in itself is extraordinary, but one of the most unusual lemurs is *Archaeoindris fontoynontii*. It is one of the largest primates ever to evolve on our planet and is known only from this site based on a complete skull and a few other bones (see below). Further, as much of the Central Highlands no longer retains the natural habitats that existed before considerable human-induced degradation of the region over the past millennium or so (see below), the different species recovered from Ampasambazimba provide an important window to the ecosystems of the recent past.

The region surrounding the subfossil site is part of a volcanic complex that is in proximity to the Itasy Massif. The site of Ampasambazimba contained a lake and marsh complex formed after the damming of a river associated with a lava flow (255, 379). The bone-bearing beds are within lake sediment (see Figure 6). Today the zone is largely continuous grasslands and rice paddies. In a few places on crests and hills not too far from Ampasambazimba, monospecific stands of the fire-resistant tree *Uapaca bojeri* (family Phyllanthaceae) occur, also known as *tapia* woodland. Some remnant forested areas can be found in this general portion of the Central Highlands, often in bottomlands or associated with riverine settings (see Figure 26, left). To some extent, these remaining forest parcels seem partially protected from the nearly annual fires set by local people to stimulate grass growth for cattle pastureland. However, we are jumping ahead too quickly here and will return later on to the critical question of the habitat transformation of the Central Highlands.

It is important to establish at the onset that the bone remains excavated at Ampasambazimba were deposited over a relatively long period. The oldest radiocarbon dates available for the site are from a giant “monkey-lemur” *Archaeolemur* dating from about 29,000 years BP and an extinct shelduck *Alopochen sirabensis* from a little less than 23,000 years BP (both of these dates are too old for calibration). Of the more than forty dates available from the site, many occur within the period from 7,000 to 2,000 years BP, with the most recent being from a giant “koala-lemur” *Megaladapis* at 1,035 years BP (mean calibrated date of 875) (69). Hence, based on what we have discussed for sites farther south—for example, Ampoza (Plates 7 and 8)—it is easy to imagine that during the course of 28,000 years of recent geological history (which includes the Last Glacial Maximum 20,000 years ago), a lot of natural ecological change has taken place at Ampasambazimba. This is an important point that needs to be kept in mind when trying to understand the local transformations and extinction events.

In 1983 and 1984, Ross MacPhee and colleagues revisited Ampasambazimba and opened a series of excavation trenches to obtain a stratigraphic record of the deposits. One of the principal objectives was to provide insight into the former vegetational cover of this area. Radiocarbon analyses of wood found in these deposits yielded mean calibrated dates of 9,080 to 5,380 years BP. Pollen associated with the deposits contained a preponderance of the genus *Eugenia*

(family Myrtaceae) (255), which they interpreted as evidence of a savanna-woodland in the area. Subsequent taxonomic studies of the Malagasy flora has resulted in a considerable number of *Eugenia* species being described as new to science (351), many of which are found in closed-canopy humid forest. Hence, the occurrence of *Eugenia* in these deposits does not necessarily translate into the presence of a continuous savanna-woodland. The next most common type of pollen was grass (family Poaceae). Significantly and regardless of current discussion about *Uapaca* being a naturally dominant member of the original climax forest of the Central Highlands or not (222), pollen of this genus, which is in part transported by the wind, was largely absent from the samples analyzed by MacPhee and colleagues. This is the same case for another pollen core at the nearby Lake Kavitaha, spanning the period of the past 1,500 years, where *Uapaca* pollen never form a prominent proportion in the core, which presumably reflects its relative rarity in the local environment (44).

Now we turn to evidence from the subfossil fauna recovered from Ampasambazimba (see Table 10) to provide further extrapolations on the habitat that occurred in the area; first, we will examine lemurs. On the basis of the ten species of lemurs identified from the subfossil deposits that are still with us today, all are forest-dwelling. Certain species are able to tolerate some level of habitat degradation and can traverse several hundred meters between forest parcels across open savanna, such as members of the genera *Eulemur* and *Propithecus*. *Propithecus diadema*, *Indri indri*, *Varecia variegata*, and *Hapalemur simus* are distinctly humid forest species, while the balance occurs in dry deciduous forest or transitional dry-humid forests. Hence, if the habitat requirements of these taxa remain today, as they were several thousand years ago, at least a portion of the Ampasambazimba vegetational formation can be inferred to have been moist forest with largely closed canopy.

If we focus on the extinct lemur species, some mixed signals exist with regard to the local former habitat. A very diverse lemur community occurred near Ampasambazimba in the Holocene (and earlier), and the subfossil component included species more comfortable on the ground, such as the *Archaeolemuridae*, but also species hard to imagine anywhere but in the trees. The latter includes the “sloth-lemur” *Palaeopropithecus maximus* of the family *Palaeopropithecidae*, one of the most suspensory primates ever to evolve on Earth (122, 211). Recalling

both orangutans from southeastern Asia and tree sloths of South America in its skeletal anatomy, this highly arboreal beast was a large-bodied (perhaps as much as 50 kg), slow-moving, and deliberate animal that used its long forelimbs and short hindlimbs to move suspended upside-down in the forest upper strata. It would have been awkward at best when on the ground. Hence, this implies that in order for this species to negotiate the forest, at least a portion of the local habitat must have had a close cover, which included an important network of middle to upper canopy branches and lianas.

Just as fascinating side points, in Standing's remarks about the material recovered from the site, he noted the presence of crocodile teeth marks in the bones of *Palaeopropithecus*. Hence, some of the bones deposited at the site were proposed as croc prey remains, almost certainly *Voay robustus*, and, if this inference is correct, these lethal encounters obviously took place on the ground. This aspect is discussed in more detail in the narrative under Plate 20. As insightful and successful as Standing was in most respects, he also made a series of mistakes, sometimes repeating the errors of earlier workers, but others may simply reflect the intellectual milieu of the early twentieth century. For example, he suggested that most of the features separating the larger subfossil lemur species from their living kin were "degenerate," having somehow reversed or re-evolved certain features that he considered more primitive than those seen in any living lemur. Following Guillaume Grandidier before him, he misattributed the arm and forearm bones of *Palaeopropithecus* to the koala-lemur *Megaladapis*, and vice versa. To be fair, the bones collected from sites like Ampasambazimba were isolated elements and disassociated from more diagnostic teeth and skulls from the same deposits. Bizarre and fanciful hybrid reconstructions that confuse the various bones of these two genera appear in plates published by Henri Perrier de la Bâthie (297). Based on these faulty associations, Standing reconstructed *Palaeopropithecus* as a swimmer, and this aquatic theme was more fully developed later on by the rather eccentric Italian paleontologist Guiseppe Sera (342). For example, Sera envisioned an adaptation for vertical climbing of tree trunks, and then diving into the water from an arboreal perch.

*Palaeopropithecus* and some of the still extant lemurs recovered from Ampasambazimba imply that at least portions of the forest were likely with closed canopy. On the opposite extreme, we can cite two or

three extinct lemurs that were more comfortable on the ground than in the canopy—*Archaeolemur*, *Hadropithecus*, and *Archaeoindris* (see below). Hence, based on the lemur evidence, MacPhee and his colleagues' idea of a forest habitat mosaic seems correct.

After the numerous excavations that have been conducted on Madagascar in search of subfossil lemurs—for example, in the Central Highlands—the general results indicate that most taxa were broadly distributed, at least at the genus level. The principal exception is *Archaeoindris fontoynontii* for which remains are only known from Ampasambazimba. This is the centerpiece of Plate 12. Bones of this animal are still limited to one nearly complete skull (Figure 59), a few other skull pieces from a second individual, a complete thighbone (a femur originally attributed to "*Lemuridotherium*"—see 375), and a few other skeletal elements, including an immature specimen—all excavated long ago. Based on the size of the teeth and the dimensions of the femur of *Archaeoindris*, its body size has been estimated to be almost 200 kg (212); this rivals the largest male gorillas alive in Africa today and suggests that *Archaeoindris* was one of the largest primates ever to exist on our planet. Because of its enormous body size, we have reconstructed this species foraging on the ground, but its anatomy suggests that it was probably also a capable climber when necessary.

*Archaeoindris* is a member of the extinct sloth-lemur group (also including *Palaeopropithecus*, *Babakotia*, and *Mesopropithecus*), and an analogy to extinct giant ground sloths from the New World is sometimes invoked to help visualize this huge and remarkable animal. Analysis of its teeth indicates that its preferred diet was leaves, supplemented by fruits and seeds (128). Similar to other members of its family, the Palaeopropithecidae, it possessed a relatively small brain. It had forsaken the lower "toothcomb" so characteristic of living lemurs and re-evolved stout teeth for cropping vegetation. Like its fellow sloth-lemur *Palaeopropithecus*, it had unusually prominent rings of bone around its eye sockets and very oddly projecting bones at the base of its nose, the significance of which remains obscure. Its eyes were relatively small, an indication it was almost certainly active primarily during the day (diurnal). Why it appears to have been restricted to the Central Highlands and when it became extinct both remain mysteries.

We have already characterized the highly specialized anatomy and suspensory locomotion of *Palaeopropithecus maximus* (see Plate 11). This impression is



Figure 59. Shown here are the skull and mandible of *Archaeoindris fontoynontii* excavated by Charles Lamberton. This animal is known from only a few bones, all from Ampasambazimba, including this skull and mandible. *Archaeoindris fontoynontii* is estimated to have reached almost 200 kg, which is close to the weight of large male African gorilla. (Photograph adapted from 227.)

reinforced by long and curved, almost hook-like hand and feet. Its teeth recall those of *Archaeoindris*, and it probably fed primarily on leaves and fruit while in trees. Unlike its close living relatives and namesake, the sifakas (*Propithecus*), it lacked a toothcomb, and we have no evidence of a “toilet claw” either (211); one can only wonder about its self-grooming habits! It was relatively small-brained and almost certainly diurnal.

Like living Indriidae and its fellow sloth-lemurs elsewhere on the island, *Palaeopropithecus maximus* developed cheek teeth at an embryonic stage (122). This pattern of tooth eruption suggests that infants were probably weaned early in their development, with relatively complete teeth, and able to consume vegetation, mostly leaves, as in adults. Other aspects of sloth-lemur social behavior must remain matters of speculation based on extrapolations from their

morphology. One thing seems certain—*Palaeopropithecus* was forest-adapted and survived through the climatic swings and associated vegetational changes in the Late Pleistocene and Holocene.

Another type of sloth-lemur was discovered and named by Standing in 1905 from Ampasambazimba (355). Based on four skulls, he described a new genus and species, *Mesopropithecus pithecoides*. Similarities to living sifakas were noted, including a toothcomb, and some later authorities believed they were very closely related (362). The limb bones of *Mesopropithecus pithecoides* tell a very different story, however (122). They are large and robust; the forelimbs and hindlimbs are nearly equal in length and very different from the very long, clinger-leaping hindlimbs of *Propithecus*. *Mesopropithecus* is now recognized as the most generalized member of the sloth-lemurs. As reconstructed in Plate 12, *Mesopropithecus* was a

cautious arboreal quadruped, which sacrificed leaping ability and developed a capacity for hanging and below-branch activities (which *Palaeopropithecus* took to the extreme). A mixed diet of fruits, leaves, and seeds is suggested by dental anatomy and tooth wear (128). Small orbits reflect reduced eyes and a diurnal activity cycle. We regard this as another primarily forest-adapted and forest-limited lemur species at Ampasambazimba.

Standing also discovered the first bones of *Megaladapis grandidieri*, which he diagnosed and named from subfossils found at Ampasambazimba. Three members of the genus *Megaladapis*, known colloquially as koala-lemurs, are currently recognized. The scientific name is based on perceived similarities to the primitive Eocene primate from Europe called *Adapis*; hence, a “huge *Adapis*.” The skull and teeth of *Megaladapis grandidieri* exhibit a surprising combination or mosaic of features, with some characters like the larger *Megaladapis edwardsi* and some like the smaller *Megaladapis madagascariensis*. Overall, it appears to have been more closely related to the latter species than to the former. Its skull was long, but the teeth were small. The limb bones were intermediate in size, but it was still a very large lemur (estimated to weigh in as much as 60 kg) (212). Like the other members of this genus, *Megaladapis grandidieri* lacked upper front teeth (incisors) and probably sported instead a tough pad at the end of its snout that would be suitable for plucking leaves with its lower toothcomb. Based on this peculiar anatomy and the pattern of tooth wear, it was an arboreal, browsing folivore. Both forelimbs and hindlimbs are relatively short for the size of the animal and exceedingly robust, but the forelimbs are much longer than the hindlimbs—adapted for life in the trees. It no doubt, when necessary, came to the ground to travel on all four limbs (quadruped) between trees or perhaps even forest patches—and when it did, the adults, based on their size, probably had few concerns about predators. The different species of *Megaladapis* have an unusually flaring and flat (front to back) upper hipbone (ilium). This feature stimulated the vivid imagination of Guiseppe Sera again, who believed it was designed for underwater concealment—a huge and flat, almost two-dimensional aquatic lemur! Other aspects of koala-lemur biology are discussed in the Plate 2 narrative.

The enigmatic and large-bodied (more than 25 kg) monkey-lemur *Hadropithecus* is also part of the faunal list at Ampasambazimba, but is better known from Andrahomana in the extreme southeast (Plate 3) and

Tsirave in the southwest. If we accept it as the same species at all of these localities, then it is one of the rarest but most widespread forms of subfossil lemur. We discuss its adaptations in detail under Plate 3, such as its apparently unique diet and unusual skull and dental anatomy, but certain of these details are important to the theme of mosaic habitats we have developed here for Ampasambazimba. Along with *Archaeolemur*, the other genus of monkey-lemur, *Hadropithecus* was one of the most terrestrial lemurs to evolve on Madagascar. Analogies to the African gelada baboon *Theropithecus gelada* are common in the scientific literature, but similarities are actually quite limited. Nevertheless, its presence in the subfossil record is testimony to open woodland habitats in the not-too-distant past and, more precisely, its presence at Ampasambazimba bears witness to this vegetational type found among those supporting the exceedingly diverse local community of primates.

*Archaeolemur edwardsi* is well represented at Ampasambazimba, thanks again in large part to Standing's extensive material. The larger of the two recognized species of the genus (probably tipping the scales over 25 kg) (212), *Archaeolemur edwardsi* was actually first recovered at another site in the Central Highlands, in the marsh deposits of Antsirabe (see Plate 11). The *Archaeolemur* specimens of the north (Ankarana; see Plates 16–18) and northwest (Anjo-hibe; see Plates 13 and 14) are best included as part of this species; the genus *Archaeolemur* is found almost everywhere on the island where there are subfossil deposits. It was clearly a very adaptable group, but it is also a good signal—like *Hadropithecus*—of relatively open landscapes. This monkey-lemur was a short-limbed and stocky animal with some anatomical convergences on African monkeys (e.g., baboons) and clear adaptations for overland travel (211). The stubby hands and feet would have made climbing and movement in the trees challenging but still possible. It was no doubt an eclectic feeder with a broad range of items in its diet, including perhaps even small animals; it has thick cheek teeth that would permit feeding on very hard items like seeds and nuts (129). It also had lost the typical lemur toothcomb and re-evolved a formidable series of front teeth for chomping and cutting. In retrospect, it is not hard to understand why this genus, diagnosed from incomplete specimens, was initially thought to be a “higher primate” (anthropoid monkey).

*Pachylemur* is yet another extinct cousin of the living lemurs, and in many ways it is the most similar

to the extant species among the extinct forms, with especially close connections to the smaller *Varecia*—a genus in which some scientists prefer to place it. However, it was much larger at 10 kg or so (212), and its limb proportions were different too—relative short limbs for the size of the animal and more nearly equal forelimbs and hindlimb lengths (211). The first member of this genus to be named was *Pachylemur insignis* from Belo sur Mer in the west (see Plate 9). The discovery of *Pachylemur* bones in the Central Highlands followed soon afterward at Antsirabe (see Plate 11). These new bones were given a new species designation, *Pachylemur jullyi*, due to their slightly larger body size and other minor details. Standing's efforts at Ampasambazimba vastly improved the sample size of *Pachylemur jullyi*. From its anatomy, we can confidently reconstruct it as a large-bodied arboreal quadruped, perhaps leaping less and moving more cautiously than *Varecia*, and as a predominately fruit-eating specialist (frugivore). Like other lemurs in seasonal environments, its diet no doubt varied throughout the year and occasional consumption of tougher, more fibrous foods, such as leaves and bark, seems plausible. One can imagine it moving carefully on the ground through open habitats to get to the next stand of trees, but it was most definitely dependent upon closed habitats and forest.

The bird remains from the site provide some interesting insights into the former community (144). Of the fourteen forms identified, seven were endemic to Madagascar and are now extinct. Among the four different raptors identified from the site, two eagles (*Stephanoaetus mahery* and *Aquila* sp.) were notably large and capable of taking hefty prey (see Plate 20 for further details). Hence, by extrapolation, there must have been an important local prey base for these raptors.

Two different genera of elephant birds have been identified, including *Aepyornis* and *Mullerornis*. The taxonomy of elephant birds is in need of revision, but as it currently stands, remains of *Aepyornis medius*, *Aepyornis hildebrandti*, and *Mullerornis agilis* have been identified from Ampasambazimba (226, 227). On the basis of ancient DNA analysis of extinct moas from New Zealand, an apparent ecological parallel to elephant birds, up to four species occurred in the same immediate area (5); accordingly, why not three elephant bird species at Ampasambazimba? While we know little about the ecology of these massive extinct birds (see Plate 1), it is presumed that they represented a considerable biomass relative to most

other local land vertebrates and would have been an ecologically important grazer and seed disperser. Whether they were strictly forest-dwelling is a matter of conjecture at this point, but their disappearance would almost certainly have had an important impact on the local ecosystems.

Another large ground-dwelling bird known from the Ampasambazimba subfossil remains is *Coua berthae* of the subfamily Couinae (158). This species was named in honor of the late Madame Berthe Rakotosamimanana, who for many years was in charge of the Paleontology Department at the University of Antananarivo and helped advance studies on the subfossil fauna of the island. A number of *Coua* spp. still occur on the island, the largest being the Giant Coua *Coua gigas*, which reaches a body mass of slightly more than 400 g. Based on extrapolation of different bone measurements and body mass of the living species, *Coua berthae* would have weighed nearly 750 g, so nearly twice the size of *Coua gigas*.

The final point to be made about the bird fauna is the considerable number of waterbirds represented in the deposits, including living species such as the Common Moorhen *Gallinula chloropus*, the Knob-billed Duck *Sarkidiornis melanotos*, Bernier's Teal *Anas bernieri*, and Meller's Duck *Anas melleri*—all of these occur in areas with open slow-moving water or marshlands. *Anas bernieri* today is known only from western Madagascar and is considered Endangered by the International Union for Conservation of Nature. However, during the Holocene it had a distinctly broader distribution across the island (144) (see Plates 4 and 11). Two rather remarkable extinct waterbirds have been identified from the subfossil remains: *Alopochen sirabensis* closely related to the shelduck *Alopochen aegyptiacus*, and *Centronis majori*, perhaps also closely related to shelducks. As illustrated in Plate 11, this latter bird was morphologically rather particular with distinctly long legs and spurs on the wings, showing notable convergence toward South American screamers (family Anhimidae). After the research of Lucien Rakotozafy, bones of *Alopochen sirabensis* were common in the Ampasambazimba subfossil deposits, while those of *Centronis* are somewhat rare (313).

Other notable animals recovered from the deposits included extinct hippos (*Hippopotamus guldbergi*) and crocs (*Voay robustus*), further attesting to the extensive river and marsh system that pass through the area. Among the terrestrial animals were giant tortoises *Aldabrachelys abrupta* (36), the bizarre biby-



malagasias *Plesiorycteropus germainepetterae* (250) (see under Plate 11 for details on bibymalagasias), an extant Carnivora *Cryptoprocta ferox* (165), and a large extant rodent *Hypogeomys antimena* that today is restricted to the region north of Morondava (see Plate 2). A second species of bibymalagasias is also recognized from the site, *Plesiorycteropus madagascariensis*. On the basis of this diversity and different life habits of the vertebrates recovered from the site, it can easily be surmised that several different terrestrial and aquatic habitats occurred in the immediate vicinity. Once again, it needs to be emphasized that the bone remains recovered from Ampasambazimba encompass at least 28,000 years of history, and it is almost certain that some natural shifts in the local habitats occurred during this period.

Based on extrapolation of habitats used today by certain extant lemurs identified from the deposits, there is ample evidence that an important component of the habitat at Ampasambazimba was similar to modern eastern humid forest. For example, the bone remains of *Indri indri*, a denizen of this vegetational formation, have been identified from the site. Two radiocarbon dates are available from 3,815 years BP and 2,425 years BP (mean calibrated dates of 4,115 and 2,505) (69). Another example is *Haplemur simus*, which feeds almost exclusively on a large bamboo that occurs today only in eastern humid forests. Three radiocarbon dates are available for this bamboo lemur from Ampasambazimba, and these span the range from 8,160 to 2,835 years BP (mean calibrated dates of 9,090 and 2,875). The distribution of these two lemur species was much more extensive a few thousand years ago, and a broad pattern of habitat transformation can best explain their reduced geographical ranges (see under Plates 14 and 16). We can now add Ampasambazimba as part of this general pattern, where about 2,500 years ago the ecological conditions changed sufficiently to push these two species to local extirpation. On the basis of current evidence, it seems unnecessary to implicate humans in this limited extirpation event.

Ross MacPhee and colleagues reconstructed the landscape of Ampasambazimba of some 8,000–7,000 years BP as being “a mosaic of woodlands, bushlands, and savanna.” This is compared to earlier inferences of the area being continuous closed-canopy montane humid forest. We have formulated the ancient habitat of Ampasambazimba presented in Plate 12 based on the different aspects of animals recovered from

the subfossil deposits, specifically direct information for living taxa or extrapolation for extinct taxa. Putting this all together in a succinct manner, we propose that the ecosystem was in part closed-canopy forest, with an aspect resembling modern montane humid forest—relatively short canopy, notable understory vine and liana systems, and some epiphytic plants. In turn, perhaps associated with soil structure or adaphic aspects, sections of the forest had fewer trees and was distinctly more open, and grasses would have formed an important portion of the ground cover. A parallel can be found in undisturbed Miombo woodlands in portions of southern Africa (see Part 1, “Savanna and Grassland Formations,” Figure 25). Finally, freshwater marshland and riverine habitats passed through or were close to the mixed forested zone. This type of varied habitat, which is not known at any site on the island today, would help explain the wide variety of organisms recovered from the bone deposits of Ampasambazimba and, in particular, the diversity in natural history traits represented in the primate community.

So what happened to the natural landscape of the region, and did humans play a role in these changes? Several studies on pollen cores obtained in the Central Highlands—specifically at Lake Tritrivakely, not too far from Antsirabe—have provided ecological signal records going back 36,000 years (43, 113). The results of this work are discussed in detail under Plate 11, but, in short, during the Late Pleistocene and Holocene, important natural climatic shifts took place. On the basis of pollen profiles, the ancient forested habitat of Ampasambazimba area has been likened to Lake Mahery, a modern forested area in the far north of the island at the foot of Montagne d'Ambre (45). However, this site has lowland and distinctly dry deciduous forest, which might show some parallels in dominant pollen types to Ampasambazimba, but we suspect would have been structurally different. Most important for the current discussion, about 4,000 years BP, a period of warmer and drier climatic conditions prevailed, which would have had an important impact on the Central Highlands forest structure. On the basis of radiocarbon dates of extinct animals from Ampasambazimba (69), many species—such as *Archaeoindris fontoynontii*, *Archaeolemur edwardsi*, *Megaladapis grandidieri*, *Pachylemur jullyi*, and *Palaeopropithecus maximus*—survived the initial stages of these climatic changes. Further, at least *Megaladapis*, *Pachylemur*, and *Mesopropithecus*

were still present in the Ampasambazimba area after people colonized the Central Highlands about 1,400 years BP (see below). Hence, the disappearance of these animals cannot simply be associated with late Quaternary climate change, nor was there almost immediate extinction after initial contact with humans as would have been predicted from the overkill hypothesis (see Part 1, “Hypotheses on What Caused the Extinctions during the Holocene”; and Plate 2).

Another important clue into the role of humans in the demise of the local fauna would be signs of human intervention in the deposition of the animal bones at Ampasambazimba, as extrapolated at Taolambiby (Plate 5) with butchering marks. During the early excavations at Ampasambazimba, which is a mixed site with both paleontological and archaeological remains, signs were found to potentially implicate humans in the deposition of some of the extinct animal material, including a modified elephant bird leg bone, a wood tool, and a ceramic pot (105). Based on subsequent interpretations of this evidence and more controlled excavations, it was determined that these inferences are insufficient to definitively implicate humans in the deposition of some of the animal material (21, 255).

On the basis of pollen core samples from Lake Kavitaha, not far from Ampasambazimba, the first evidence of large-scale transformation of the area by people dates from about 1,400 years BP (44). This included a reduction in woody tree pollen and a proportional increase in grass pollen, as well as a very notable increase in charcoal remains. These measured ecological shifts largely coincide with archaeological evidence from the same period, which demonstrates development of village clusters in several zones of the region (86). By the fourteenth century, there is good archaeological evidence of rice cultivation and cattle herding. By the sixteenth century, settlements were distinctly denser, some holding up to 1,000 individuals, and, presumably, there was ever-increasing human pressure on the environment and natural resources, such as conversion of marshlands to irrigated rice paddies.

Now what happened thereafter is a point of considerable discussion (see 219). With reference to the Central Highlands, it has been proposed that large-scale human destruction of the remaining large forest blocks was associated with population growth, slash-and-burn agriculture, exploitation of wood products, fire, the increase need for cattle pasture, and military

actions to reduce areas “where the enemies could hide.” In short, one side of the debate would state that the destruction of the regional forests was at the hand of humans (109).

Based on different lines of evidence, the other side of this debate proposes that an important portion of the island’s modern grasslands is a natural formation (see Part 1, “Savanna and Grassland Formations”) (35). One very important point not supporting this proposition, at least for the Central Highlands and on current evidence, is that under stable conditions montane forest takes over grasslands, rather than vice versa (190, 291)—providing strong evidence that the forest is the climax vegetation. While it is not our purpose here to evaluate these different views on the natural vegetation of the Central Highlands and whether people were capable of clearing such a vast area, some further observations are useful.

Ample physical evidence exists that portions of the Central Highlands that are now grasslands were forested within the past few hundred years ago, and that humans played an important role in this degradation (see Figure 26, left) (235). More important for the point at hand, the type of habitat we propose that existed several thousand years ago in the Ampasambazimba area would have been forest by definition, with certain portions closed canopy and other areas open forest with patches of natural grasslands (see Part 1, “Savanna and Grassland Formations”). Such a configuration might explain the observation of a certain number of endemic grasses and open-country birds occurring in the Central Highlands. Now we turn to what subfossil sites from this portion of the island can tell us about the distribution of plants and animals (biogeography) in this region today.

As formalized in different studies on the geographic distribution of plants and associated ecosystems (phytogeography) on Madagascar (299), two main zones have been cited, the dry forests of the west and the humid forests of the east. To a large extent, the affinities of the Central Highlands—defined here as the area in the central portion of Madagascar occurring above 900 m—was left somewhat ambiguous. This was probably because there was little remaining forest cover when botanists such as Henri Perrier de la Bâthie did their field exploration, based on which they formulated their phytogeographic models.

With greater exploration of the species of plants and animals occurring in the remnant forests of

**Table 10**

List of land vertebrates identified from Ampasambazimba subfossil remains (36, 107, 121, 126, 144, 165, 250, 255, 356). Extinct species are indicated with †, and the author(s) and description date are given. For living taxa, the English common names are given.

**Order Reptilia**

Family Testudinidae

†*Aldabrachelys abrupta* (A. Grandidier, 1866)

Family Crocodylidae

†*Voay robustus* (A. Grandidier & Vaillant, 1872)

**Class Aves****†Order Aepyornithiformes**

†Family Aepyornithidae

†*Aepyornis hildebrandti* Burckhardt, 1893

†*Aepyornis medius* Milne-Edwards & A. Grandidier, 1866

†*Mullerornis agilis* Milne-Edwards & A. Grandidier, 1894

**Order Anseriformes**

Family Anatidae

†*Centronis majori* Andrews, 1897

†*Alopochen sirabensis* (Andrews, 1897)

*Sarkidiornis melanotos* Knob-billed Duck

*Anas bernieri* Bernier's Teal

*Anas melleri* Meller's Duck

**Order Falconiformes**

Family Accipitridae

†*Stephanaetus mahery* Goodman, 1994

†? *Aquila* sp. a (specific designation uncertain)

†? *Aquila* sp. b (specific designation uncertain)

*Buteo brachypterus* Madagascar Buzzard

**Order Gruiformes**

Family Rallidae

*Gallinula chloropus* Common Moorhen

**Order Cuculiformes**

Family Cuculidae

†*Coua berthae* Goodman & Ravoavy, 1993

**Class Mammalia****†Order Bibymalagasia**

†*Plesiorycteropus germainepetterae* MacPhee, 1994

†*Plesiorycteropus madagascariensis* Filhol, 1895

**Order Afrosoricida**

Family Tenrecidae

*Tenrec ecaudatus* common tenrec

**Order Primates****Suborder Strepsirrhini****Infraorder Lemuriformes**

†Family Archaeolemuridae

†*Archaeolemur edwardsi* Filhol, 1895

†*Archaeolemur majori*? Filhol, 1895

†*Hadropithecus stenognathus* Lorenz von Liburnau, 1899

†Family Palaeopropithecidae

†*Archaeoindris fontoynontii* Standing, 1909

†*Mesopropithecus pithecoides* Standing, 1905

†*Palaeopropithecus maximus* Standing, 1903

Family Indriidae

*Avahi laniger* eastern woolly lemur

*Indri indri* indri

*Propithecus diadema* diademed sifaka

*Propithecus verreauxi*? Verreaux's sifaka<sup>1</sup>

Family Lemuridae

†*Pachylemur jullyi* G. Grandidier, 1899

*Eulemur fulvus* brown lemur

*Eulemur mongoz* mongoose lemur

*Hapalemur simus* greater bamboo lemur

*Varecia variegata* ruffed lemur

†Family Megaladapidae

†*Megaladapis grandidieri* Standing, 1903

Family Daubentoniidae

†*Daubentonia robusta*? Lamberton, 1934

Family Cheirogaleidae

*Microcebus* sp. mouse lemur

*Cheirogaleus major* greater dwarf lemur

Family Lepilemuridae

*Lepilemur* spp. sportive lemur

**Order Carnivora**

Family Eupleridae

*Cryptoprocta ferox* fossa

*Galidictis* sp. vontsira

**Order Artiodactyla**

Family Hippopotamidae

†*Hippopotamus guldbergi* Fovet, Faure & Guérin, 2011

**Order Rodentia**

Family Nesomyidae

*Hypogeomys antimena* Malagasy giant jumping rat

1. We treat here *Propithecus coquereli* as a subspecies of *Propithecus verreauxi*.

the Central Highlands, a new understanding has emerged. It is now clear that the separation of the east and west in the formalized classifications of the island's ecosystems was artificial and that these two zones represent extremes of a continuum. For example, the western portion of the Central Highlands has close affinities to the western dry forests, and as one moves toward the east, there is a transition toward more humid forests. With the destruction of considerable areas of natural forested habitats on the Central Highlands, its role as a transitional area between the wet and dry extremes was obscured. As Ampasambazimba is found dead center in the Central Highlands,

the subfossils identified from the site might provide a good barometer of ecological changes along this proposed east-west gradient.

Two interesting examples can be gleaned from the lemur subfossils identified from Ampasambazimba. The first includes *Eulemur fulvus*, which has a broad distribution in humid and deciduous forests across the island and still exists in the Central Highlands, and *Eulemur mongoz*, which is today a strictly dry deciduous forest species in the lowland formations to the west and within the Mahajanga Province. The presence of *Eulemur mongoz* remains in the Ampasambazimba deposits indicates that this species formerly occurred farther east and higher in elevation; this implies that during a recent period in geological history, the Central Highlands was more of an ecological transition zone. Perhaps an even better example is between two *Propithecus* lemurs identified from Ampasambazimba. Today *Propithecus diademata* is strictly eastern humid forest-dwelling, and *Propithecus verreauxi* is restricted to western dry forest. However, based on the presence of bones of these two species among the Ampasambazimba subfossils, they both occurred in the Central Highlands. As far as we know, this is the first case of two species of this genus co-existing in the same forest, and it would be fascinating to know how they divided available resources. These examples provide evidence from what is known about the habitat preferences of living species that the strict east or west distributions of some of these animals today may be associated with aspects of climate change overlaid on human habitat transformation of the Central Highlands.

In summary, Ampasambazimba provides an extraordinary window into habitats that formerly occurred in the Central Highlands. There is good evidence that the climatic shifts associated with broad-scale patterns at the end of the Pleistocene resulted in important vegetational shifts, which impacted certain organisms. Then some time about 1,400 years BP, at least based on current archaeological evidence, people started to transform this zone; and in more recent periods, the level of deforestation was accelerated. Widespread habitat destruction resulted from human modification, including the loss of large areas of Miombo-like woodland, as well as fragmentation and isolation. The ecotone between forest and savanna in remaining fragmented natural forest zones can remain stable over several decades, which is probably associated with continued or long-lasting human-induced impacts.

## Plate 13: Anjohibe I—Secrets of the Past Disclosed by Careful Study of Subfossil Bone and Pollen in a Cave

Caves, and specifically the pollen and bone subfossils deposits they hold, have provided an extraordinary window into different aspects of environmental vicissitudes on Madagascar in recent geological time. This type of information has been particularly insightful into the role of natural change, linked most frequently to climatic shifts, as compared to human

ecological interventions and anthropogenic degradation of the environment. In many cases, caves have functioned as natural traps for animals that accidentally wandered into them and expired; some predators bring their prey back into caves for consumption, resulting in bone accumulations. Prey remains are also often deposited in the cave as con-

---

An ancient moment of desperation and mayhem deep in Anjohibe Cave. A group of extinct dwarf hippos *Hippopotamus lemerlei* probably got washed into the cave by heavy rains and a flash flood of sorts, and were lost in the near obscurity. The group included at least five adults, three immatures, and one apparent newborn. In the chaos that ensued, they thrashed around, knocking over stalagmites, and one can imagine the rumble punctuated by their urgent cries; colonies of bats were disturbed from their day-roost sites and took flight. On the basis of recent work on the bat subfossil fauna from Anjohibe, two extinct species have been discovered, *Hipposideros besaoka* and *Triaenops goodmani*, as well as *Eidolon dupreanum*, which is still extant but probably exterminated from the cave by recent human hunting pressure. For a key to the different animals, see black-and-white inset for Plate 13 in color gallery. (Plate by Velizar Simeonovski.)





Figure 60. During several decades, different paleontologists and archaeologists have excavated various deposits in the extensive Anjohibe Cave to uncover some of its hidden secrets. One such group directed by Dominique Gommery is a French-Malagasy team. They have made several important discoveries. Here the paleontologist Pierre Mein is shown searching for small animal subfossils between some calcite speleothems. (Photograph courtesy of Mission Archéologique et Paléontologique dans la Province de Mahajanga—Centre National de la Recherche Scientifique.)

centrations of predator scats or as undigested bone and hair regurgitated by raptors (hawks and owls) as pellets (see Figure 5, right). In some cases, specifically in areas of limestone, calcite crystals formed by water passing through the bedrock can cement together such concentrations. These sorts of deposits often retain the order that they were laid down, hence providing a stratigraphic record and preserving a sequential time line of change. In the case of such accumulations excavated from caves on Madagascar, they have provided an enormous amount of information on shifts in biotic communities over the past 30,000 years.

A number of different cave sites have been excavated in the past few decades by paleontologists paying close attention to the stratigraphy of the deposits (see Plates 2 and 3, for example). With this type of detailed information, it has been possible to test different hypotheses about what transpired on the island with regards to the biotic communities before and after human colonization of Madagascar, which based on the current record was approximately 2,500 years ago (see Part 1, “History of Human Colonization of Madagascar”). Perhaps no cave has been more

important in this regards as that of Anjohibe, to the northeast of Mahajanga. Anjohibe, which means “big cave” in Malagasy, has about 5.3 km of underground passages and numerous entrances (81). It is part of a series of caves referred to in the older literature as the “Grottes d’Andranoboka,” translated from the Malagasy as the “caves where water exits.” The bedrock of Anjohibe is limestone that has been eaten away by eons of water erosion, typical of a karst landscape. It has been excavated by several generations of paleontologists and archaeologists (Figure 60) (e.g., 52, 78, 139, 254).

When David Burney and colleagues worked Anjohibe in 1996, they deployed several different techniques to piece together aspects of environmental change through time and to discern the potential role of humans in at least a portion of that process. The team excavated a large quantity of animal bone from the site. For example, at least in part based on the careful analysis of Helen James, over thirty-five different bird species have been identified from the remains recovered in the cave (see Table 11), including two species of extinct giant coua (subfamily Couinae) and an apparently unnamed extinct mesite (family



Mesitornithidae), both groups endemic to the island. A wide variety of mammals were recovered, including a bizarre aardvark-like beast placed in its own order (Bibymalagasia) and an extinct “sloth-like” lemur *Babakotia radofilai* that was previously known only at Ankarana (see Plate 17) in the far north. Associated with Plate 13, we discuss the different types of animal remains recovered from the cave and try to reconstruct the local pre-human ecosystem. The calcite deposits are very rich in microfauna, from which, for example, a relatively small block containing a skull of *Archaeolemur* yielded five different orders of mammals after a painstaking extraction process (see Figure 4) (334).

In Anjohibe George Brook and colleagues cored several large speleothems, which are cave formations resulting from the evaporation of water and the deposition of small crystals. These cores were then used in uranium dating and pollen analysis (41, 52). As speleothems form, the surface has a fine layer of airborne pollen, which is subsequently covered with a thin coating of calcite and, hence, through time builds a striated record of the local plant communities; when properly analyzed, it can be used as a barometer of change. In fact, annual cycles of growth were visible in the layers of calcite coating. The oldest of the formations was about 40,000 years old, and information from the pollen remains indicates environmental shifts. In the most ancient deposits, ranging from about 40,000 to about 6,500 years BP, woody tree plants and different fern spores dominated, giving the impression of a distinctly cooler and moister environment than today. Throughout this period, grass pollen was also present, and the local habitat, as could be measured by this technique, was probably a relatively dense wooded savanna with an important concentration of palms, perhaps approaching the Miombo-like woodland described in detail in Part 1 (see “Savanna and Grassland Formations”) and in the narrative of Plate 12. The outer section of the core, starting about 6,500 years BP, was interpreted as showing a shift toward an open palm savanna with considerable grasslands, which is seemingly typical of the current ecological setting. As the types of pollen represented in this sample are restricted to those transported by the wind and along with the fact that the speleothem was deep within a cave, it is easy to imagine that the pollen record was not proportionately representative of the external vegetational community. Hence, the proposed seemingly stable palm

savanna in the area since 6,500 years BP will need substantiation from other sources of evidence.

What is important about this record, based on current archaeological information, is that these shifts to more modern conditions took place before human colonization of the island. Hence, the onset of these changes was a natural process. Remains of charcoal are present throughout the 40,000-year core history, indicating infrequent natural fires passing through the zone. However, toward the outer section of the speleothem cores, there was a notable increase in the quantity of charcoal with amplified quantities of grass-derived charcoal; this strongly suggests human influence and modification of the immediate environment (52).

An assortment of cultural artifacts was found in the cave, many of which were of a ritualistic nature and in some cases encrusted in calcite deposits. In addition, bone concentrations of introduced domestic animals and different ceramic wares were also excavated. At least some of these items were associated with human burials in the cave. On the basis of current cultural evidence, human utilization of the cave only goes back a few centuries.

During the relatively recent French colonial period, the cave was commercialized, with lights, walkways, and ramps installed into parts of the cave to facilitate the passage of visitors. Remnants of this infrastructure can still be seen today. During that period, the 65 km road leading from the main highway (east of Mahajanga) to the cave was in much better shape; rather than taking the current three to four hours, the trip could be made in less than one hour. Remnants of at least one restaurant can be found in the nearby local village, which during its heyday served fine French meals and cold drinks to weekend visitors. Even today with a largely collapsed infrastructure, the cave remains a tourist destination for both Malagasy and foreign visitors.

After several decades of research in the cave, many different facets of the former fauna can be reconstructed. Here we discuss aspects of the cave fauna and certain special finds, but in Plate 14, we present information on the biota that occurred outside the cave in the local environment. Today Anjohibe Cave and the immediate surroundings are known to have at least eighteen species of bats (148, 166). In the subfossil remains studied by Karen Samonds from deposits of cemented bone concentrations excavated by the research team in 1996, two extinct bat species were

**Table 11**

List of land vertebrates identified from Anjohibe subfossil remains (36, 52, 99, 121, 250, 333, 334). Extinct species are indicated with †, and the author(s) and description date are given. For living taxa, the English common names are given. Listing does not include introduced species.

**Order Reptilia**

Family Testudinidae

†*Aldabrachelys abrupta*? (A. Grandidier, 1866)

Family Crocodylidae

†*Voay robustus* (A. Grandidier & Vaillant, 1872)

*Crocodylus niloticus* Nile crocodile<sup>1</sup>

**Class Aves****†Order Aepyornithiformes**

†Family Aepyornithidae

†*Mullerornis* sp.

**Order Ardeiformes**

Family Ardeidae

*Bubulcus ibis* Cattle Egret

Family Ciconiidae

*Anastomus lamelligerus* African Openbill Stork

Family Threskiornithidae

*Lophotibis cristata* Madagascar Crested Ibis

Family Phoenicopteridae

*Phoeniconaias minor* Lesser Flamingo

**Order Falconiformes**

Family Accipitridae

*Milvus aegyptius* Yellow-billed Kite

*Buteo brachypterus* Madagascar Buzzard

Family Falconidae

*Falco newtoni* Madagascar Kestrel

**Order Galliformes**

Family Phasianidae

*Coturnix* sp. quail

**Order Gruiformes**

Family Mesitornithidae

†? *Monias* sp. (probably undescribed species)

Family Turnicidae

*Turnix nigricollis* Madagascar Buttonquail

**Order Columbiformes**

Family Columbidae

*Streptopelia picturata* Madagascar Turtle Dove

**Order Psittaciformes**

Family Psittacidae

*Coracopsis vasa* Lesser Vasa Parrot

*Agapornis cana* Gray-headed Lovebird

**Order Cuculiformes**

Family Cuculidae

†*Coua berthae* Goodman & Ravoavy, 1993

†*Coua primavea* Milne-Edwards & A. Grandidier, 1895

*Coua gigas* Giant Coua

*Coua* sp. coua

*Cuculus rochii* Madagascar Lesser Cuckoo

*Centropus toulou* Madagascar Coucal

**Order Strigiformes**

Family Tytonidae

*Tyto alba* Barn Owl

Family Strigidae

*Otus rutilus* Madagascar Scops Owl

*Ninox supercilialis* White-browed Owl

*Asio madagascariensis* Madagascar Long-eared Owl

**Order Apodiformes**

Family Apodidae

*Apus barbatus* African Black Swift

**Order Coraciiformes**

Family Alcedinidae

*Alcedo vintsioides* Madagascar Malachite Kingfisher

Family Meropidae

*Merops superciliosus* Madagascar Bee-eater

Family Leptosomatidae

*Leptosomus discolor* Madagascar Cuckoo-roller

**Order Passeriformes**

Family Alaudidae

*Mirafr hova* Madagascar Bush Lark

Family Hirundinidae

*Phedina borbonica* Mascarene Martin

Family Pycnonotidae

*Hypsipetes madagascariensis* Madagascar Bulbul

Family Vangidae

*Newtonia brunneicauda* Common Newtonia

Family Ploceidae

*Foudia madagascariensis* Madagascar Fody

**Class Mammalia****†Order Bibymalagasia**

†*Plesiorycteropus madagascariensis* Filhol, 1895

**Order Afrosoricida**

Family Tenrecidae

*Tenrec ecaudatus* common tenrec

*Microgale* sp. shrew-tenrec

**Order Primates****Suborder Strepsirrhini****Infraorder Lemuriformes**

†Family Archaeolemuridae

†*Archaeolemur edwardsi* Filhol, 1895

†Family Palaeopropithecidae

†*Babakotia radofilai* Godfrey, Simons, Chatrath & Rakotosamimanana, 1990

†*Palaeopropithecus kelyus* Gommery, Ramanivosoa, Tombomadiana-Raveloson, Randrianantenaina & Kerloc'h, 2009

Family Lepilemuridae

*Lepilemur* sp. sportive lemur

**Table 11** (continued)

Family Cheirogaleidae
<i>Microcebus</i> sp. mouse lemur
<i>Cheirogaleus medius</i> fat-tailed dwarf lemur
Family Lemuridae
<i>Eulemur fulvus</i> brown lemur
<i>Eulemur mongoz</i> mongoose lemur
<i>Hapalemur simus</i> greater bamboo lemur
†Family Megaladapidae
† <i>Megaladapis grandidieri/madagascariensis</i> <sup>2</sup>
Family Indridae
<i>Propithecus verreauxi</i> Verreaux's sifaka
<b>Order Chiroptera</b>
Family Pteropodidae
<i>Eidolon dupreanum</i> Madagascar straw-colored fruit bat
<i>Rousettus madagascariensis</i> Madagascar rousette
Family Hipposideridae
† <i>Hipposideros besaoka</i> Samonds, 2007
<i>Hipposideros commersoni</i> Commerson's leaf-nosed bat
† <i>Triaenops goodmani</i> Samonds, 2007
<i>Triaenops</i> cf. <i>furculus</i> Trouessart's trident bat
Family Vespertilionidae
<i>Myotis goudoti</i> Malagasy mouse-eared bat
<b>Order Carnivora</b>
Family Eupleridae
† <i>Cryptoprocta spelea</i> G. Grandidier, 1902
<i>Cryptoprocta ferox</i> fossa
cf. <i>Fossa fossana</i> spotted fanaloka
<b>Order Artiodactyla</b>
Family Hippopotamidae
† <i>Hippopotamus lemerlei</i> <sup>3</sup> A. Grandidier, 1868
<b>Order Rodentia</b>
Family Nesomyidae
<i>Eliurus</i> sp. tuft-tailed rat
<i>Eliurus myoxinus</i> western tuft-tailed rat
† <i>Nesomys narindaensis</i> Mein, S��n��gas, Gommery, Ramanivosoa, Randrianantenaina & Kerloc'h, 2010

1. Reported subfossil remains of crocodiles in the cave need to be reevaluated to determine if they are referable to the extinct genus *Voay* or the extant genus *Crocodylus*. Radiocarbon remains assigned to *Crocodylus* yielded a date from the modern era (71).

2. The long bones of animals from Anjohibe are intermediate in size between *Megaladapis madagascariensis* and *Megaladapis grandidieri*, and anatomically very similar to both. The Anjohibe subfossil *Megaladapis* have particularly small teeth.

3. Hippo remains from the nearby Belobaka Caves have recently been identified as *Hippopotamus laloumena*. The species identification of remains from Anjohibe needs further study.

identified, as well as several that still occur in the cave (333). The extinct species have been named *Triaenops goodmani* and *Hipposideros besaoka*, both illustrated in Plate 13; the term *besaoka* is from the Malagasy and means "big chin." Bone remains of a third species, *Eidolon dupreanum*—a large fruit-eating bat—are notably common on the cave floor. While this species still occurs throughout much of western Madagascar, it has been extirpated from Anjohibe Cave. Based on discussions with older members of a local village, they remember from their childhoods the presence of *Eidolon* in the cave. Through over-exploitation by humans as bush meat, *Eidolon* has disappeared from the Anjohibe system within the last 50 years. Bone material of this species collected from the cave floor was submitted for radiocarbon analysis and yielded a modern-era date (54, 71), which supports the local oral history with respect to the fate of this species.

On the basis of radiocarbon dating, the oldest Quaternary paleontological sites on Madagascar date to no more than 30,000 years BP, hence falling within the periods of the Late Pleistocene and Holocene (54, 69). The search for older deposits has been important in the quest to provide a deeper window into change through time. On the basis of uranium dating techniques, Karen Samonds was able to establish that a portion of the bone concentrations she studied in her bat project dated to about 80,000 years BP and represent the oldest known subfossils from the island.

When excavating a low alcove in a part of the cave known as the "Salle R. de Joly," which is a few hundred meters from an underground river known as the Ruisseau Decary, David Burney and colleagues found two skulls of an extinct pygmy hippopotamus, *Hippopotamus lemerlei*, partially exposed in the sediments. Adults of this hippo are estimated to have weighed about 275 to 400 kg (383), and they fed on C<sub>3</sub> plants (71). The presence of these bones on the surface was a good sign that the immediate site might contain more extensive deposits. An area of 2 m<sup>2</sup> was excavated and produced the remains of at least eight individual hippos, which included five adults, three immatures, and one apparent newborn or fetus. Many of the skeletons were in a small area, still partially articulated, and nestled together. Given the position of the different bones and the observation that they were in the same deposit, it seems reasonable to infer that the hippos died at the same time and were deposited together (52). As no evidence of human intervention in their demise was found—such as broken bones, signs

of damage from weapons and knives, and so on—the death of these animals is assumed to have been a natural catastrophic event. Further evidence that people were not involved is that a radiocarbon date of the hippo bone remains yielded a date of 3,730 years BP (mean calibrated date of 4,035), at least 1,200 years before the current estimate of first human colonization of the island. So what happened?

Here is our imagined scenario, which is depicted in Plate 13. A pod of hippos somehow found their way into the cave, perhaps dabbling in the water at an opening forming the underground passage of the Ruisseau Decary. The group may have been composed of a bull with a group of females and young, all of whom were suddenly washed down the river system within the cave, where they then found themselves stranded. Another possibility is that they fell through one of the skylight holes in the cave ceiling, but this seems unlikely, as certain animals would have sustained injury, for which no sign was found among the bone remains. In any case, once in the cave, the group probably tried to stay together in the near darkness with perhaps only some distant dim light from a ceiling skylight, their panic-stricken grunts and belching calls echoing in the chamber as they shuffled around within the complex looking for a means to escape. The ruckus caused day-roosting bats in the immediate vicinity to take flight.

Toward the end, there was a moment of complete panic, with certain animals in the group wildly thrashing about, resulting in the breakage of limestone formations. Indeed, among the excavated hippo bones were a number of broken stalagmites, further testament to the frenzied pandemonium. It is easy to imagine that the immatures were still nursing, and with bleating sounds attempted to call their mothers closer. It is conceivable in the moment of intense stress, one of the females aborted her fetus or gave birth prematurely—accounting for the neonatal or fetal hippo specimen found within the remains. No matter the manner of their entrance, the group did not find an exit from the cave and succumbed to some mixture of panic, thirst, and starvation, only for their story of “natural” death to be uncovered by paleontologists nearly four millennia later.

## Plate 14: Anjohibe II—Inferences Based on Cave Remains and Aspects of the Organisms Living in the Adjacent Ecosystem

As discussed under Plate 13, recent excavations in the Anjohibe Cave by David Burney and colleagues have provided an extraordinary window into the diverse fauna that lived in the area surrounding the cave in recent geological history (see Table 11). On the basis

of the different bone and pollen remains that they identified (52), and with some historical perspective, we can partially reconstruct aspects of the local ecosystem and many of the animal species in the formerly rich community.

---

Over the past 8,000 years, the forested habitat in the region of the Anjohibe Cave has become distinctly drier, and many of the organisms that require wetter, more mesic environments have disappeared. Here we depict portions of the forested habitat that existed in this area, with one of the cave entrances in the central background. Some of the presumed subtleties of the area include a bamboo patch in which is seen feeding a greater bamboo lemur *Hapalemur simus*, an extant species that is now found only in limited areas of the eastern humid forest. An extinct coua *Coua primavea*, notably larger than any living member of this genus, is shown having a slight spat with an extinct rodent *Nesomys narindaensis*, which is feeding on the fruits of a *Canarium* (family Burseraceae) tree. Other extinct animals depicted include the partially terrestrial “monkey-lemur” *Archaeolemur edwardsi* and the very specialized, arboreal “sloth-lemur” *Palaeopropithecus kelyus*. One of the most bizarre mammals recovered from the cave—or anywhere else in Madagascar—is the aardvark-like bibymalagasia *Plesiorycteropus madagascariensis*, placed in its own order Bibymalagasia, which is about to feed on termites. For a key to the different animals, see black-and-white inset for Plate 14 in color gallery. (Plate by Velizar Simeonovski.)





Figure 61. The natural vegetation of the region surrounding Anjohibe Cave has been modified over the past few millennia. First, this was associated with natural climatic change and shifts from relatively moist to drier conditions. The second wave of modification was related to human modifications of the natural environment. Here we show the principal south entrance of the cave in 2012 with some remnant vegetation; this is the same entrance illustrated in Plate 14. (Photograph by Corrie Schoeman.)

The current habitat around Anjohibe Cave is a mixed savanna with some palm trees of the genus *Medemia* (family Arecaceae) and scattered remnant patches of degraded to heavily degraded dry deciduous forest. For example, only remnant vegetation occurs near the entrance of the cave illustrated in Plate 14 (Figure 61). Clear signs of large-scale human perturbation are evident, including limited agricultural areas in the bottomlands, nearly annual burning of the savanna habitat to stimulate fresh pasture for cattle, and cutting of forest trees for firewood and building supplies. However, based on the types of animals identified from the bone remains and some associated radiocarbon dates, it is clear that the zone also experienced considerable natural ecological change over the past 8,000 years, which is notably before original human colonization of the island. See the previous narrative for precise details on these changes.

On the basis of both pollen and bone subfossils recovered from the cave, the local Holocene ecosystem was a mosaic of habitats. Perhaps a good place to start is noting that today most of the river systems within close proximity to the cave are dry or with little water throughout most of the year, except during and immediately after the rainy season. However, extrapo-

lating from the types of animals recovered from the cave deposits, it is clear that aquatic habitat occurred in the immediate region and that water was present throughout the year. The remains of Lesser Flamingos *Phoeniconaias minor*, African Openbill Stork *Anastomus lamelligerus*, as well as dwarf hippos *Hippopotamus lemerlei* (see Plate 13), all attest to the presence of permanent water. Radiocarbon dates from nine different hippo specimens yielded dates spanning the range from 6,310 to 2,636 years BP (mean calibrated dates of 7,150 to 2,635) (52, 69, 334). The most recent of these dates can be used as the benchmark when conditions were still sufficiently humid to support populations of hippos. Presumably, the presence of the flamingos and storks in the bone remains represent birds killed by predators and dismantled or consumed in the cave.

Among the terrestrial fauna, there were a number of extraordinary finds. Elephant birds (family Aepyornithidae) were identified from remains in local caves, specifically a member of the small genus *Mullerornis*. This would have been a terrestrial bird, about the size or slightly smaller than a living ostrich *Struthio camelus*, that presumably fed mostly on vegetation. Madagascar had two genera and several species of elephant birds (see Plate 1), and they cer-



tainly played an important role in ecosystem functioning, for example, as herbivores/frugivores that dispersed the seeds of different food plants. The term “small” concerning *Mullerornis* is relative, as another elephant bird genus, *Aepyornis*, not known from Anjohibe was distinctly larger. Eggshell remains tentatively identified to *Mullerornis* from the nearby cave of Lavakasaka produced a radiocarbon date of 2,380 years BP (mean calibrated date of 2,425) (52).

Among some of the other terrestrial bird bones, a species of mesite of the genus *Monias* was identified; this bird belongs to an endemic family, Mesitornithidae, which represents an ancient lineage. On the basis of the original comparisons made by Helen James, who was responsible for the identification of most bird bones recovered from the cave, the represented species is probably extinct and remains undescribed. The only existing species of *Monias* is the Subdesert Mesite *Monias benschi*, which is currently restricted to a small area of spiny bush in the extreme southwestern portion of the island.

Several different species of couas, birds of the endemic subfamily Couinae, were identified from the bone remains. These included three large species, all presumed to be terrestrial, two of which are extinct. The first of the extinct species, *Coua berthae* (named in honor of the late Malagasy primatologist and paleontologist Madame Berthe Rakotosamimanana) was the size of a small wild turkey and originally described from Anjohibe and Ampasambazimba (see Plate 12) (158). The other extinct coua, *Coua primavea*, is illustrated in Plate 14 and was named long ago from deposits near Belo sur Mer (273), some 600 km farther south (see Plate 9). The third identified member of this genus, giant coua *Coua gigas*, is extant and still has a broad distribution across the dry forests of Madagascar. In addition to these three forms, two other couas were identified in the deposits—a medium-size animal and a smaller one. Hence, the forests of the Anjohibe region supported at least five co-occurring (sympatric) species of coua during the Holocene, including three large taxa, which are presumed to have existed locally during the same period. Today no forest on the island has such a diversity of couas, and extinction appears to have concentrated on the larger forms—a common theme in the story of extinctions on the island. How these different species divided up their world with respect to food resources is most curious and will probably never be resolved.

Two other terrestrial mammals are of note, both of which have gone extinct. The first is a large spe-

cies of forest rodent of the genus *Nesomys*, belonging to the endemic subfamily Nesomyinae. In the cave report published by Burney and his colleagues, this rodent was noted as probably extinct and undescribed (52). Subsequently, an extinct species of this genus, *Nesomys narindaensis*, was named from Holocene remains obtained north of Mahajanga (268) (see Plate 15) and is almost certainly the same species that occurred at Anjohibe. In general, *Nesomys* are granivorous, often predating seeds such as those of *Canarium* (family Burseraceae), as illustrated in Plate 14. In other areas of the range of this rodent genus, they cache the fruits of this plant some distance from the mother tree and may play a role in seed dispersal (161).

Another extraordinary beast identified from Anjohibe, previously referred to as the “Madagascar aardvark” *Plesiorycteropus madagascariensis*, is known from scattered bone remains from different sites on the island (250). Material recovered from Anjohibe helped greatly to resolve certain aspects of the peculiar skull morphology of this animal and its obscure phylogenetic relationships to other mammals. In Ross MacPhee’s detailed analysis of the higher-level relationships of *Plesiorycteropus*, he concluded that it was not related to aardvarks (order Tubulidentata), to which it had previously thought to be allied, and showed no close affinity to any described group of mammals. Hence, he created a new order of mammals, Bibymalagasia, for the genus *Plesiorycteropus*. He further suggested that the name “Madagascar aardvark” was a misnomer and recommended instead the common name bibymalagasia, which we use throughout this book. More recent phylogenetic analyses have resurrected possible affinities with aardvarks, but it still seems prudent to place the order as *incertae sedis*, or “of uncertain placement,” within the higher-level classification of mammals (382). As no mandibles assignable to this genus have yet to be identified, it is unknown if bibymalagasia had teeth or was toothless. In any case, it is assumed that this animal fed on soft-body invertebrates, such as termites, whose mounds still abound in this region. In Plate 14, we have depicted it about to break into such a mound and feed on these invertebrates.

One of the fantastic aspects of the mammal bones recovered from Anjohibe Cave is the diversity of lemurs. In total, eleven taxa have been identified, including *Haplemur simus*, which no longer occurs in the region, and four species that are extinct: *Babakotia radofilai*, *Archaeolemur edwardsi*, *Palaeopropithecus*

*kelyus*, and a member of the genus *Megaladapis*. In comparison, the nearby large forest block of Ankarafantsika, which is a well-studied protected area, contains only seven species of lemurs (340). The only genus known from Ankarafantsika not recovered at Anjohibe is the nocturnal woolly lemur *Avahi*; otherwise, the Ankarafantsika fauna is a subset of the Holocene fauna of Anjohibe. Radiocarbon dates for *Propithecus verreauxi* and *Lepilemur edwardsi* bones from the cave are quite recent, only 195 to 360 years BP (mean calibrated dates of 145 and 385) (69).

*Hapalemur simus* is a species in modern times only occurring in the eastern humid forests and considered very rare (394). It is a bamboo specialist, specifically giant bamboo (*Cathariostachys* spp., family Poaceae), which has the property of containing considerable quantities of cyanide (17, 117) that this lemur is able to metabolize without detrimental effects. In Ranomafana, where the lemur has been studied in detail, about 95 percent of this species' diet is giant bamboo (359). Hence, as depicted in Plate 14, given the presence of abundant bones of this bamboo lemur in Anjohibe, it is assumed that *Cathariostachys* or a similar bamboo grew at the site. Inherent in this assumption is that the climate near Anjohibe in the recent geological past was distinctly more mesic than today, and that aridification resulted in the disappearance of the giant bamboo and, concordantly, the greater bamboo lemur. Extinctions of this species are also documented in the Central Highlands at Ampasambazimba (see Plate 12), in the extreme north at Ankarana (see Plate 16), and farther to the south in the Bemaraha region.

*Babakotia radofilai* is a relatively new addition to the impressive roster of extinct lemurs on Madagascar and is much better known from the caves of the Ankarana Massif farther to the north (122). We discuss this species in greater detail elsewhere (see Plate 17), but a thumbnail sketch includes the following attributes: long-faced like the living *Indri indri*, much larger than any living lemur (~20 kg), forelimbs longer than hindlimbs, long and curved finger and toe bones, vestigial tail, and cheek teeth designed to shear foliage and chew seeds (211). It retained the typical indriid-like toothcomb, and its lower jaws were not fused together. Details of its limb bones, hands, and feet indicate it was quite suspensory, frequently hanging and moving upside down to feed and travel in an arboreal fashion through the forest canopy. It was no doubt an accomplished, slow-moving climber that was most at home in the trees.

In comparison to other extinct lemurs, this species is not well represented at Anjohibe, but its presence is important because it signals a nearly 400 km range extension farther south beyond the Ankarana Massif. It also reinforces the reconstruction of a wetter climate than seen today, with at least a portion of the local forested habitat being closed canopy.

*Archaeolemur* fossils are common at Anjohibe, and for now it seems reasonable to attribute these bone remains to the larger species known from the Central Highlands (and probably from Ankarana and Ampoza), *Archaeolemur edwardsi*. Radiocarbon dates for this species at Anjohibe span an appreciable amount of time, from 7,790 to 1,700 years BP (mean calibrated dates of 8,530 and 1555). A fecal pellet attributed to *Archaeolemur* from the nearby cave of Anjohikely ("small cave") is more recent still at 830 years BP (mean calibrated date of 1000) (69, 334). Hence, based on these dates, *Archaeolemur* was apparently still roaming the Anjohibe countryside centuries after humans initially colonized the island (see Part 1, "History of Human Colonization of Madagascar"). With monkey-like front and back teeth, thickly enameled and structurally reinforced cheek teeth, and armed with forceful chewing muscles, this species was almost certainly an eclectic omnivore that could feed on just about anything, including both hard and tough food items (95). Based on carbon isotope values from radiocarbon-dated bones of this lemur, its diet was based on  $C_3$  plants (71). We have provided additional details of this genus's adaptive profile elsewhere (see Plates 8, 11, and 12), but the popular name of monkey-lemur hints at important differences between *Archaeolemur* and most other living and extinct lemurs. It does converge on the anatomy of Old World monkeys (baboons, mandrills, and relatives) in the globular shape of its cranium, in the geometry of its cheek teeth, in its elbow and hip morphology, and in its shortened fingers and toes. It was very stocky and powerfully built, with relatively short and robust limbs. Like many Old World monkeys but few lemurs, it was designed to travel on the ground, and its presence at Anjohibe attests to open habitats, such as woodlands, in the vicinity. However, these monkey-like osteological similarities are imprinted over an underlying, fundamentally lemur-like skeleton, and ancient DNA points to a special relationship with living family Indriidae (286), which are notably arboreal. We portray it as a social species in this plate, but this is pure conjecture. We suspect it entered Anjohibe to drink water, but we doubt it

used caves for refuge or sleeping sites. On occasion, this beast almost certainly misplaced its steps and fell through the numerous ground-surface skylights openings into the cave or became lost in its quest for water, only to be entombed in the ground forever—or at least until paleontologists arrived on the scene.

The most sloth-like of the extinct sloth-lemurs is *Palaeopropithecus*. This very specialized genus, which has figured prominently in other narratives (Plates 8 and 12), was widespread across Madagascar in the recent past (122). Initially mistaken as a Malagasy sloth (“*Bradytherium*”), its lemur affinities are now obvious, and a close connection to living indriids (including sifakas of the genus *Propithecus*) has been confirmed by both anatomy and ancient DNA (214). Only two species were recognized until very recently, *Palaeopropithecus maximus* and *Palaeopropithecus ingens*, and their taxonomic separation is based mostly on average size differences and geographic distributions. A third species, *Palaeopropithecus kelyus* (*kely* means “small” in Malagasy) was named a few years ago by Dominique Gommery and colleagues (138) based on remains from the northwestern sites of Belobaka and Ambongonambakoa, both not far from the city of Mahajanga and Anjohibe Cave. As the name suggests, its specific difference from the other two named species is based mostly on its smaller size. The type specimen of this distinct species is most of a right upper jaw from Belobaka.

There is a certain historical quirk of fate to the naming of *Palaeopropithecus kelyus*. Small specimens of *Palaeopropithecus* have been known for a long time from this region, including from Anjohibe Cave and the nearby marsh site of Amparihingidro. Raymond Decary discovered a complete ulna from Anjohibe in the late 1930s, and Joel Mahé recovered a partial skull in the 1960s (122); both clearly belong to what would be named many decades later as *Palaeopropithecus kelyus*. Ross MacPhee and colleagues excavated at Anjohibe in the early 1980s and discovered a remarkably complete specimen that also clearly pertains to this new species (254). A reconstruction from plastic casts of this marvelous specimen is on display at the Duke Lemur Center in Durham, North Carolina (Figure 62), in its sloth-like pose. Like *Babakotia*, the presence of *Palaeopropithecus kelyus* at Anjohibe strongly implies the former presence of relatively dense closed-canopy forest.

A species of *Megaladapis* is also known from Anjohibe and other localities on the Mahamavo (Mahajanga) Peninsula (e.g., the marsh site of Am-

parihingido). This animal is clearly not the giant *Megaladapis edwardsi*, known from all over the south and southwest of Madagascar. Its closer affinities are with *Megaladapis grandidieri* (from the Central Highlands) and *Megaladapis madagascariensis*, the smaller species sympatric with *Megaladapis edwardsi* throughout much of the south. We have hedged our bets a bit here and assign the “koala-lemur” from Anjohibe to *Megaladapis grandidieri/madagascariensis*, a conservative taxonomic approach that we also employed for the poorly known species from the north at Ankarana. Regardless of its precise species designation, this was an arboreal-terrestrial species that was forest-dependent.

Using different types of inference on the habitats employed by extinct animals recovered from Anjohibe Cave, as well as direct observations on living species, some clear notions can be offered on the local habitat types before their transformation to the present palm savanna. We propose the local forest would have been a sort of mosaic, ranging from dense closed-canopy, largely humid forest with patches of large bamboo, to more open forest with grassy areas growing outside tree shadows. Hence, in a similar manner discussed for the habitat of Ampasambazimba (see Plate 12), the local habitats would have been home to different animals spanning the range from purely arboreal to terrestrial, with closed-canopy humid forest interdigitated with a formation in parallel to African Miombo woodland (see Part 1, “Savanna and Grassland Formations”).

A study was conducted to assess the dietary preferences of extinct and introduced animals recovered in the bone remains of Anjohibe Cave (71). Based on carbon isotope values from radiocarbon-dated bones—largely of lemurs, one of which is extinct, and some other animals, including hippos—certain inferences can be made. Of the species that are now extinct, all before the date of 1,500 years BP, little preference was found for the consumption of  $C_4$  plants. Subsequently thereafter, particularly for introduced species, there is a distinct shift toward the ingestion of  $C_4$  plants. This is a crucial point, which we interpret to mean that  $C_4$  plants, probably mostly grasses, were not an important part of the natural environment until habitat changes associated with human disturbances.

Based on different lines of evidence, it is clear that major changes have taken place in the forests in the Mahajanga area and in the types of animals occupying these areas over the past eight millennia. The

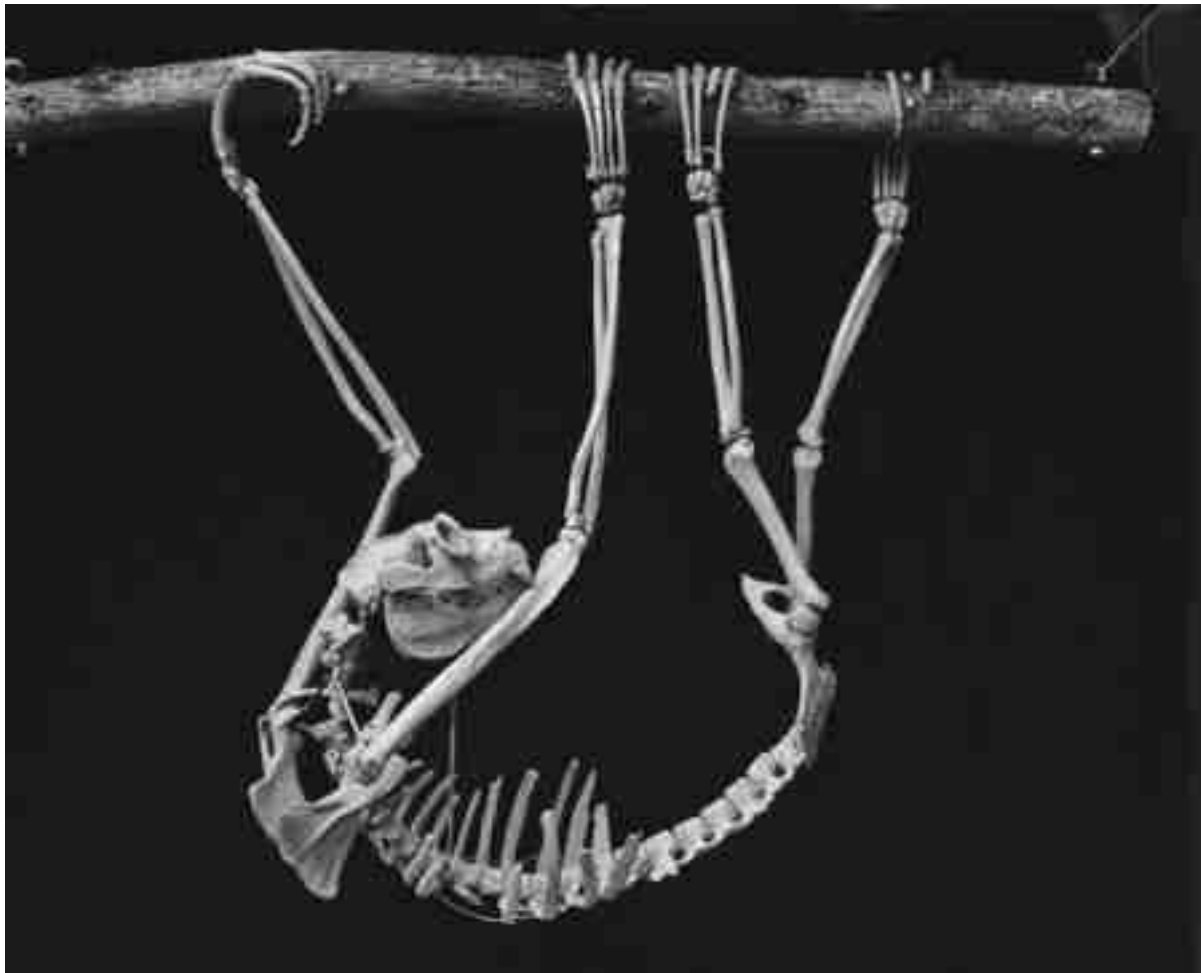


Figure 62. In the early 1980s, Ross MacPhee and colleagues discovered a remarkably complete specimen of a small *Palaeopropithecus* in Anjohibe. Casts of this specimen were made and reconstructed in its sloth-like position of locomotion. This model is now on display at the Duke Lemur Center. This species was to be named several years later by Dominique Gommery and colleagues as new to science, *Palaeopropithecus kelyus*, based on less complete material from elsewhere in the Mahajanga Province (see Plate 15). The occurrence of this species in the Anjohibe subfossil deposits strongly implies the former presence of relatively dense forest with closed canopy. (Duke Lemur Center Division of Fossil Primates/ David Haring.)

shifts have been from relatively mesic habitats, as well as the presence of some permanent wetlands, to distinctly drier habitats with a pronounced season without rain. The vast majority of these transformations took place well before humans colonized the northwestern portion of Madagascar, and more intensive human presence is estimated to have been about 500 years ago (54). Further, based on radiocarbon dates of now-extinct animals and inferences from the archaeological record, there was a period several hundred years when certain animals coexisted with humans. So at least the human impact associated with the disappearance of these animals was gradual, rather than quick as in other major extinction events—for

example, certain portions of the megafauna of New Zealand and Australia (194, 328).

For the specific case of the region of Anjohibe, the current evidence tips toward natural climatic change, specifically desiccation, that led to considerable habitat change, and then an important human impact associated with degradation of natural forest habitat. It is important to point out that these processes persist today. Based on observations within Anjohibe Cave, aridification apparently continues with a marked reduction in groundwater. During visits to this site over the past 20 years, it is clear that many of the massive calcite formations, which need at least some humidity, if not dripping water, are now dry and “dying.”

This transformation may be related to recent shifts in seasonal water tables associated with a reduction in subterranean aquifers, which in turn may be related to deforestation and/or with broad patterns of human-induced climate change. Concerning deforestation, the remaining dry deciduous forests of the island have been hit hard, and between the 1950s and about 2000, over 40 percent of the surface area of this formation has been lost (191). Finally, human exploitation of different animals as bush meat has shifted to animals of decreasing body size. As mentioned in Plate 13, the fruit bat *Eidolon dupreanum*, with an average body mass of about 350 g, has disappeared from Anjohibe Cave in the past few decades, almost certainly associated with human exploitation. Between 2010 and 2012, the zone has experienced drought, and rice crop production has been drastically reduced. During this period, local people entered caves and exploited as a protein resource different small insect-eating bats, including some weighing less than 10 g. On the basis of observations made by Steve Goodman in late 2012, certain bat populations have abandoned these caves probably because of these perturbations. Hence, while factors that led to the first wave of Holocene extinctions in the region of Anjohibe Cave have changed, continued transformations, in this case largely human-induced, have pushed or are pushing a variety of local organisms and habitats to another wave of extirpation.

## Plate 15: Anjajavy—a Trapdoor Cave, Ecology of an Extinct Lemur, and Untold Extinct and Extant Biodiversity

Not far from the city of Mahajanga in northwestern Madagascar are a series of subfossil localities that provide unique insights into this region's past biotic communities. Most are limestone cave sites, as this area is rich in karst landscapes, but paleontolo-



gists also know important marsh sites (e.g., Amparihingidro). We have already discussed one of the most famous cave sites—Anjohibe—in considerable detail (Plates 13 and 14). Although Walter Kaudern discovered bones of *Pachylemur* in an unknown cave during an expedition between 1911 and 1912 (140, 215) somewhere outside of the city of Mahajanga in the Boeny Region, until very recently the Anjohibe Cave complex dominated our understanding of the extinct animals and former ecosystems of this part of Madagascar (52). However, the novel efforts of Dominique Gommery (Figure 63), Beby Ramanivosoa, and their Franco-Malagasy colleagues have greatly expanded the scope of research in this region and augmented our understanding of its ancient natural history (134). Their productive excavations have centered on the Mahamavo (Mahajanga) Peninsula and the adjacent Narinda Peninsula (which includes Anjajavy). The site of Bungo Tsimanindroa received their first attention, and they recovered numerous specimens of *Archaeolemur edwardsi* from this cave (135). They subsequently discovered new localities (e.g., Antsin-giavo, see below) that yielded extinct lemurs in association with microfauna (rodents, bats, small lemurs) that still live today in the local forests (136).

They also visited caves reserved for visitors by the Anjajavy Hotel, and one known as Raulin Zohy is the resting place of several individuals of the sloth-lemur

---

Small trapdoor caves in western Madagascar have provided very important information on the former fauna of the region. Here in a sinkhole (the “Raulin Zohy site”) at Anjajavy on the Narinda Peninsula of northwestern Madagascar, a “sloth-lemur” *Palaeopropithecus* has fallen about 10 m and has sustained serious injuries. Being unable to exit the cave, it will succumb in a short period and join other deceased members of its species cemented by calcite into the wet cave floor. This cave is now a tourist attraction on the grounds of an exclusive resort. (Plate by Velizar Simeonovski.).





Figure 63. Recent advances have been made in documenting a variety of subfossils in northwestern Madagascar, and the importance of this material in understanding environmental change in the recent geological past is now emerging. One such research group working on this theme is a French-Malagasy team organized by Dominique Gommery and Beby Ramanivosoa. Here Dominique Gommery is shown in the Anjohibe Cave mapping the position of some pygmy hippo remains. (Photograph courtesy of Mission Archéologique et Paléontologique dans la Province de Mahajanga—Centre National de la Recherche Scientifique.)

*Palaeopropithecus*, but more on that site and its fossils below. Gommery and Ramanivosoa returned to the Mahamavo Peninsula with similar successes, finding rich new localities, one of which—Belobaka—is just a few kilometers outside of Mahajanga and the type site for the newest subfossil lemur to science, *Palaeopropithecus kelyus* (also discussed in Plate 14), described just a few years ago (138). These fossils are now curated in the museum Mozea Akiba of the University of Mahajanga.

As mentioned in the Plate 2 narrative, recent paleontological and archaeological excavations have employed much finer techniques than in the old days, including wet and dry sieving of sediments with fine screens and water floatation in order to obtain different types of bone and botanical samples. Although the quest for megafauna remains are the primary goal of many paleontologists, remains of smaller animals are being recovered from cave deposits that also represent important new finds. For example, at sites in the lowland central west, not too far from Anjajavy, Pierre Mein and his colleagues (268) have uncovered several extinct microfauna species (see Figure 60)

that provide exceptional windows into the biogeography of two mammal genera and important information on past climates and vegetational formations of the region.

The first new rodent species that this team described is *Brachytarsomys mahajambaensis* (endemic subfamily Nesomyinae), based on a series of cheek teeth (molars) that are notably small, but with the distinct “lamina” structure of living members of this genus. Among the extant small mammal fauna, two species of *Brachytarsomys* are recognized: *Brachytarsomys albicauda*, an inhabitant of lowland and montane humid forest running most of the eastern length of the island, and *Brachytarsomys villosa*, known from montane formations in the central north and northwest (353). These two species are nocturnal, arboreal, and largely frugivorous, with adults weighing between 250 and 350 g.

The second species described by Mein and colleagues is also a member of the same subfamily and given the name *Nesomys narindaensis*, coming from the aforementioned site of Antsingiavo, which is very close to Anjajavy. In contrast to the subfossil

*Brachytarsomys*, the new *Nesomys* is distinctly larger than any extant member of this genus, which include three recognized taxa: *Nesomys lambertoni*, restricted to the *tsingy* forests of the limestone Bemaraha Plateau in the central west and notably to the south of Anjajavy; *Nesomys rufus*, common in lowland and montane humid forests in the eastern and northwestern portions of the island; and *Nesomys audeberti*, with a patchwork distribution overlapping largely with *Nesomys rufus* but tending to occur at lower elevations (353). Members of this genus are active at dawn and dusk (crepuscular), terrestrial, and have a mixed diet of seeds and nuts (granivorous). Material recovered of a large *Nesomys* at Ankarana (see Plate 16) is presumed to be of this species or another closely related extinct taxa.

No precise dates are available for the rodent material described by Mein and his collaborators, but based on context all have been assigned to the Late Pleistocene and Holocene. What is important about these finds is that they provide an important range extension for *Brachytarsomys*. Further, based on the extrapolation of the way these two genera live today, particularly *Brachytarsomys*, it can be stated that western central lowland Madagascar in the recent geological past contained dense closed canopy, with important concentrations of lianas, and almost certainly more humid conditions. These different aspects would have also been ideal for animals such as sloth-lemurs of the genus *Palaeopropithecus*. Also noteworthy, given that *Brachytarsomys* is considered frugivorous and that the current dry deciduous forests of the lowland central west go through a pronounced dry season when fruits are notably rare, it can be assumed that during the period when *Brachytarsomys mahajambaensis* roamed the regional forests, rainfall was more constant and different types of forest fruits were available on a regular basis. These data support other information showing that this area of Madagascar was distinctly wetter or more mesic several millennia ago. Finally, among the rodent teeth recovered from the subfossil deposits, material of the genera *Brachyuromys* and *Voalavo* were identified but have not yet been identified to species. Both of these genera are strict inhabitants of eastern lowland and montane forest formations (353), further supporting the habitat reconstructions presented above.

Range extensions of extinct animals found in paleontological contexts provide extremely valuable information about former habitats and biotic communities, but the lowland west central region

of Madagascar has also surprised scientists by the unanticipated presence of previously unknown living terrestrial vertebrates. This alone clearly signals just how poorly explored the zone is, even today. For example, in the central western deciduous forests, new species of terrestrial bird and small mammals have been discovered and described as new to science in the past few years, such as the conspicuous, terrestrial, and diurnal Tsingy Wood Rail *Mentocrex beankaensis* (173) and nocturnal small mammals ranging from forest rodents such as *Eliurus antsingy* (subfamily Nesomyinae) to small shrew-tenrecs such as *Microgale grandidieri* (endemic family Tenrecidae) (60, 284).

Until a few years back, the bat fauna of Madagascar was very poorly known, and nearly 40 percent of the species recognized on the island today have been found or described over the past decade (148). One group of bats that was inadequately represented in museum collections from Madagascar is the genus *Scotophilus*, which is widespread across much of the tropical portions of the Old World. Given the rarity of specimens of this genus from Madagascar, an odd aspect is that members of this genus often make their day roosts in human-built structures (synanthropic), giving rise to the common name “house bat.” In 2003, Fanja Ratrimomanarivo captured a small *Scotophilus* to the south of Anjajavy, within the Bemaraha region, which based on its color and size was unknown to science. This led to a review of all known museum specimens of this genus from Madagascar, as well as comparisons with named African and Asian taxa. In mid-August 2004, a paper was submitted to describe the new species obtained by Fanja Ratrimomanarivo, subsequently named *Scotophilus tandrefana* (167); the species name is derived from the Malagasy and means “from the west.” At the point of finishing their review, these researchers were under the impression that the taxonomy of Malagasy *Scotophilus* was worked out.

Less than four months after this manuscript was sent off for possible publication, Steve Goodman and Fanja Ratrimomanarivo traveled to the Narinda Peninsula, where Anjajavy is located, on the quest to located roosting sites of synanthropic and cave-dwelling bats. During the rainy season, it is a long haul to reach this area of Madagascar by road, and not to waste too much time associated with Fanja’s thesis research, they decided to travel in a private plane piloted by Jacques Cauvin. While based out of Anjajavy, they interviewed a fellow by the name of Abel Nirina,



Figure 64. The skull and some long bones of a sloth-lemur of the genus *Palaeopropithecus* partly encrusted in calcite in the bottom of the trapdoor cave known as Raulin Zohy. This animal and several others at some point in the recent past fell through the opening of this sinkhole cave to their doom. On the basis of current information, it is not possible to identify this material to species, but it is too large for the recently described *Palaeopropithecus kelyus*. (Photograph by Olivier Langrand.)

who was visiting Anjajavy and resided about 20 km to the north in the village Marovaza. He mentioned that a number of bats lived in the thatched roof of his house. However, because of a brewing major storm, logistics, and time, it was not possible to visit his village. Abel mentioned that he could try to capture the bat and send it alive to us at Anjajavy with someone traveling by boat. We gave him several cloth bags, wished him the best of luck, and departed. During the next days, we explored several caves in the Anjajavy area, including the Raulin Zohy, and documented different species of bats, including one that would be named a few years later as new to science, *Paremballonura tiavato* (168); this name is also derived from the Malagasy and means “rock-loving,” as the bats like to roost on vertical rock faces. Unfortunately, the weather turned for the worse, and within two days, the area was hit with a minor cyclone; our rendez-

vous with Jacques Cauvin to return to Mahajanga by plane was postponed.

During the morning of the third day after the commencement of the storm, the weather calm down, and Jacques buzzed the Anjajavy Hotel in his plane. This was a clear sign for us to head to the landing strip to meet him and then head back to Mahajanga. As we were loading the gear into the plane, a gentleman came running toward the air strip with one of our cloth bags given to Abel Nirina on which was written (our translation): “For Mr. Batman at the Anjajavy Hotel.” Jacques was in a hurry before the wind picked up again, and off we went back toward Mahajanga. In mid-route the bat was remembered, and upon opening the sack, it was immediately clear, based on its distinct coloration and size, that the animal represented yet another undescribed species of *Scotophilus*! Steve Goodman was subsequently able

to visit Marovaza, work with Abel Nirina, and obtain some more animals, which were named *Scotophilus marovaza* (169).

Turning back to our wounded sloth-lemur in the pit of the Raulin Zohy site featured in Plate 15, we should note that there are several individuals of *Palaeopropithecus* interred in the calcite floor. The tourist-worthy, spectacular skulls coated in calcite are the most obvious specimens in the cave (Figure 64), but Bill Jungers was able to inspect the cave and its fossils several years ago, and he noticed various limb bones and other parts of the postcranial skeleton in association with the skulls. One skull was eventually extracted and is now displayed to guests of the Anjajavy Hotel in a lovely red velvet-lined box. The nose of this cranium is damaged, and rumor has it that this injury occurred when the specimen was stolen from the cave one night and ended up briefly in Mahajanga before being returned to the hotel. The only specimen to our knowledge that was ever excavated from this cave floor and properly prepared for scientific study is a mandible, which has been figured in a scientific paper (137). This is a very important specimen because it reveals that it does not belong to the small new species found relatively nearby, which was dubbed *Palaeopropithecus kelyus* (see Plate 14). The teeth in this lower jaw are simply too big and fall in the range of the much larger *Palaeopropithecus maximus* (see Plates 11 and 12) and *Palaeopropithecus ingens* (see Plate 8). As we also noted earlier, the biogeography and systematics of the genus *Palaeopropithecus* is complex, especially for northern forms, and major revisions may be necessary down the road. Radiocarbon dates from the Raulin Zohy, which to date are lacking, might assist in this task, but for now the possibility exists that two closely related species were once sympatric just north of Mahajanga. As desirable as it might seem from a scientific perspective to fully excavate the tourist cave of Anjajavy, one can also argue that there is real value in preserving a fossil site or two relatively intact for posterity and Malagasy heritage.

## Plate 16: Ankarana I—Ecological Change of a Forest Community, a View from the Ground Up

The Ankarana Massif in the north of Madagascar is a very special place, with its extraordinary landscapes and many closely guarded secrets concerning its plants and animals, past and present. Over the last few decades, based on intensive exploration of the zone by biologists studying living forest-dwelling organisms and paleontologists working on the subfossils

preserved in caves, a new perspective has emerged on the level of complexity of this area and how rapidly things can change in a few millennia. Given the amount of information available on Ankarana and its subfossil and modern fauna, we have devoted three different plates to this site, which are separated in a vertical sense: Plate 16 (here)—some of the ground-

---

A scene in the lower and middle understory of the Ankarana forest several thousand years ago, in an area with large bamboo and mixed humid and dry deciduous closed-canopy forest. The moment captured is at dusk, with considerable activity of three different lemurs, which include *Hapalemur simus* feeding on the shoot pith of bamboo, *Hapalemur griseus* calmly resting and digesting a quantity of bamboo leaves it has just consumed, and a troop of *Eulemur coronatus* settling in for the evening. The rodent in the lower right clambering over an old lava flow that inundated the limestone Ankarana Massif is of the genus *Nesomys*. For a key to the different animals, see black-and-white inset for Plate 16 in color gallery. (Plate by Velizar Simeonovski.)



dwelling and mid-story animals; Plate 17—a bird's-eye view of some of the canopy-dwelling lemurs; and Plate 18—the intricate history of a giant lemur lost in the cave and what its remains can tell us about how it lived. The Ankarana, including the massif with its extensive cave systems, is now a protected area and hosts many ecotourists every year.

The Ankarana Massif is composed of a block of limestone that formed at the bottom of the ocean during the Jurassic Period, roughly 150–160 million years ago (see Figure 3). This is the period that Indo-Madagascar was starting to pull away from other masses of Gondwana (see Figure 9), and when dinosaurs ruled the Earth. If one takes a close look at the limestone at the site today, fossils of different marine organisms can still be seen, many of which were associated with coral reefs and responsible for the creation of the rock. Then the incredible forces of the inner Earth, known as tectonic action, pushed the block upward and to the surface, forming the massif we call today Ankarana.

During the period of uplift, the massif was subjected to variable forces that tilted the block, resulting in the western side being higher than the eastern. Further, this forceful action created several major cross fractures and joints leading from the upper surface deep into the massive limestone block. Ankarana is a typical karst geological formation, as found in other areas of the world, formed by dissolving the limestone bedrock through the action of mildly acidic water that penetrates into surface openings and continues to eat away the rock. This weak acidic water is formed when rain combines with carbon dioxide in the atmosphere and the decomposition of organic material in the soil. Through time, there is an increase in the size of the openings until underground drainage systems form—or, in other words, cave systems.

In well-developed karst areas, many caves can occur. Ankarana is such an example, with 114 km of passages mapped in over seventy-six caves (57, 307). From the west side, facing the exposed cliff, one is impressed that the structure is like a natural sponge, with hundreds of holes, nooks, and crannies. It is one of the most extensive cave systems in the Africa region. The largest of these networks is the Andrafiabe Cave, which has more than 8 km of mapped passages and harbors chambers deep in the Earth the size of football fields. Through time, based on continued erosion and tectonic activity, portions of cave ceilings can collapse, forming open cavities, known as sinkholes; many such formations can be found across the

Ankarana landscape. In such openings in the interior of the massif, some of which are large, as well as in deep crevices, dense “hidden forests” can develop. Such sites are in the shade most of the day and provide notably mesic conditions for plants to grow and different animals to live.

A special feature of several limestone areas on Madagascar—namely, Ankarana, Montagne des Français, Namoroka, and Bemaraha (see Figure 16, left)—is that the upper surface of the limestone has been eroded in a fashion to form sharp and pointed pinnacles, which in Malagasy is referred to as *tsingy* (Figure 65). The translation of this word has been presented in several different manners, but with a little poetic license, it means “the place you cannot walk without shoes.” The typical physical aspect of *tsingy* develops due to notably intensive rainfall, particularly in rock that is pure, not very porous, and with many small fracture points. The rainwater dissolves the rock and infiltrates along different cracks and openings, which widen over time and form the distinct sword and needle-like formations (330). It was once proposed that these formations develop under the soil, which is then eroded and washed away, but this has recently been shown not to be the case (369).

As evidence of the ancient nature of Ankarana's underground drainage systems, there are many organisms found deep in these caves and nowhere else in the world. These include several largely colorless and blind animals, known as troglobites, such as springtails and scorpions (244, 288), whose extreme adaptations attest to their long evolutionary history in underground isolation. Further, these caves have a variety of aquatic animals, such as endemic blind cavefish (18). An extensive cave toward the southern portion of the massif, known as the Crocodile Cave, heralds another reptilian denizen, the Nile crocodile *Crocodylus niloticus*, which takes advantage of perennial water sources deep inside this system (387).

Montagne d'Ambre, to the north of Ankarana, is volcanic in origin. Eruptions as recent as 8,000 years BP (22) resulted in major lava streams radiating out a substantial distance from the massif. These include flows that reached Ankarana and entered into some of the limestone canyons. Today, in different places around the massif, the layered effects of dark lava, often broken up, over the clear light gray limestone are striking. Explorations of the remaining forests within some of the deep-cut canyons of the Ankarana and in surrounding zones have revealed a remarkable assortment of previously unrecognized and endemic





Figure 65. In certain limestone areas of Madagascar, the exposed rock has been eroded by the long-term action of draining water into sharp and pointed pinnacles. This type of formation is known in Malagasy as *tsingy*, which can be translated with a bit of artistic license as “the place you cannot walk without shoes.” The *tsingy* block shown here is in the Ankarana National Park. (Photograph by Olivier Langrand.)

---

species. These include several lemurs, *Microcebus varatra* and *Lepilemur ankarensis* (343, 319), as well as an assortment of plants, small mammals, frogs, reptiles, and so on (e.g., 118, 172, 317). The flora of the massif is very rich, with new species being described on a regular basis (e.g., 56, 77). The massif and some surrounding areas, in total about 18,000 ha, were named as a protected area in 1956 as the Ankarana Special Reserve and in recent years reclassified as the Ankarana National Park.

Work conducted by Jörg Ganzhorn in 1987 on the lemurs of Ankarana found ten species, all living in relatively intact forest, and a few also occurring in degraded habitats (192). He and his colleagues conducted a number of transects in different sections of the forest, as well as in the nearby savanna, and were able to derive estimates of relative population density. For the three common lemurs at the site, two of which are cathemeral—that is, active during the day and night—(*Eulemur coronatus* and *Eulemur fulvus sanfordi*) and one nocturnal species (now referred to as *Lepilemur ankarensis*), he recorded relatively high densities ranging from 1.4 to 3.3 kg per km<sup>2</sup>. The largest species occurring in Ankarana today is *Eulemur fulvus sanfordi*, weighing in at less than 2.5 kg. However, as we will discuss associated with this and the next two plates, the local primate community has changed dramatically over the past few thousand years, with the extinction of primates as large as 50 kg or more.

Starting in the late 1980s, a group of Malagasy, French, and American paleontologists—including Laurie Godfrey, Bill Jungers, the late Berthe Rakotosamimanana, Martine Vuillaume-Randriamanantena, and Elwyn Simons—commenced excavating subfossils in the caves of Ankarana, with their primary focus being lemurs. Simply remarkable things were found, including one genus and several species previously unknown to science (see Table 12). While it is indeed exceptional to find new extinct lemurs, perhaps the most extraordinary aspect was the body forms of these new animals. These included *Babakotia radoilai* and *Mesopropithecus dolichobrachion* (124, 348), both referred to now as “sloth-lemurs” (122), with forelimbs notably longer than hindlimbs; as their nickname might suggest, these amazing beasts probably moved through the upper portion of the forest suspended upside down like a New World sloth. In total, six lemur species were recovered that are now extinct, with the specific identification of a couple

yet to be worked out (see Plates 17 and 18 for further discussion).

Three extant lemur species were identified from the Ankarana cave deposits that no longer occur in the area: *Hapalemur simus*, *Indri indri*, and *Propithecus tattersalli* (126). Remains of *Hapalemur simus* (or *Prolemur simus* to taxonomic “splitters”) were common in the subfossil deposits, with material being recovered in eleven of the thirteen caves excavated; this primate is depicted in Plate 16. The density of this species in some of the caves was exceptional, so much so that it was difficult to walk without stepping on specimens; many bones, including several hundred jaws, were collected and now reside in specimen drawers of the Duke Lemur Center and University of Antananarivo. This species, which can reach body masses of up to 2.5 kg, is enigmatic with regards to its distribution. It was originally described from a locality not precisely defined, but which is perhaps in the northeast in the region of the Bay of Antongil. There are very few modern records of it until the period from the 1970s to 1980s, when it was observed in the region of Ifanadiana, specifically near Ranomafana and Kianjavato (267, 303). Subsequently, it has been found in several places in the central eastern portion of the island, including some lowland sights near Farafangana (394). However, on the basis of subfossils, it had a distinctly broader distribution until a few millennia ago, with remains known from Ampasambazimba (see Plate 12), Bemaraha, Anjohibe (see Plate 14), and Ankarana, approximately 175 km west, 400 km west, 400 km northwest, and 600 km north, respectively, of the known current range of this species (123, 127). To place this in a greater context, radiocarbon dates are available from a subfossil obtained at Ankarana that yielded a date of about 4,560 years BP (mean calibrated date of 5,155) and another from Bemaraha at 2,410 years BP (mean calibrated date of 2,055) (54, 69). These dates give a concrete time frame to help understand the rapid and massive range contraction of this primate, which is considered one of the most endangered in the world (275).

Human-induced habitat degradation has been cited for the modern decline of *Hapalemur simus* (394), but important tracts of forest remain today in the Bemaraha and Ankarana areas, so this aspect alone cannot explain their local disappearance from these sites. Another important aspect could be human hunting pressure, which can locally reduce lemur populations. Perhaps, the most critical factor is that

this species feeds almost exclusively on a bamboo of the endemic genus *Cathariostachys* (family Poaceae) and more specifically on *Cathariostachys madagascanensis*. Currently, two species of this genus are recognized from Madagascar, both restricted to the eastern humid forest in areas, including disturbed habitats, with more than 2 m of annual rainfall (94); all known areas where these bamboos occur are without pronounced dry seasons. As discussed under the narrative concerning Anjohibe (Plate 14), close to 95 percent of the diet of *Hapalemur simus* at Ranomafana is composed of the shoots, young and mature leaves, and pith of this bamboo (359). While the current rainfall profile for Ankarana is about 2 m per year, this site and all of the other western sites with subfossils of this species have pronounced dry seasons. Hence, the disappearance of *Hapalemur simus* from different portions of its former northern and western range can be explained in the most parsimoniously manner by natural climate shifts, toward drier conditions, and the disappearance of the critical *Cathariostachys* bamboo (see Plate 14 for further discussion).

Another species of bamboo lemur, *Hapalemur griseus*, is known from both the modern and the subfossil faunas of Ankarana and depicted in Plate 16. While this species also feeds on bamboo, it has a distinctly broader range of food plants as compared to *Hapalemur simus* (184), and in modern Ankarana, where there are non-*Cathariostachys* bamboos, the local *Hapalemur griseus* population probably has a varied diet. This species weighs up to 800 g, about one-quarter the body mass of *Hapalemur simus*, and these two bamboo lemurs have different aspects of their natural history that allow them to divide resources and co-exist in the same forest (sympatry).

A dispersed troop of *Eulemur coronatus* is also shown in Plate 16. This species has been identified in the local cave subfossil remains and is one of the more common primates in the Ankarana today. Tourists arriving in the Ankarana campgrounds will often hear the muffled grunts of this species, and then after scanning the trees around them have their first look at this notably handsome animal. Paleontologists searching for the bones of subfossil lemurs within the caves also have the pleasure and inspiration of passing through forests around the massif that are occupied by the living relatives of the extinct ones.

Other animals depicted in Plate 16 include a large crepuscular rodent belonging to the genus *Nesomys*. This genus is currently known from eastern humid

**Table 12**

List of land vertebrates identified from Ankarana subfossil remains (121, 126, 165). Extinct species are indicated with †, and the author(s) and description date are also given. For living taxa, the English common names are given. Listing does not include introduced species. To date, only the primate remains from the site have been studied, “but Aves (including giant extinct ratites), Reptilia, Insectivora, Chiroptera, Rodentia, Artiodactyla, Carnivora . . . have also been found there” (62, 346).

## Order Reptilia

Family Testudinidae

†*Aldabrachelys* sp.

## Class Aves

### †Order Aepyornithiformes

†Family Aepyornithidae

†*Aepyornis* sp.

## Class Mammalia

### Order Primates

#### Suborder Strepsirrhini

#### Infraorder Lemuriformes

†Family Archaeolemuridae

†*Archaeolemur edwardsi*

†Family Palaeopropithecidae

†*Babakotia radofilai* Godfrey, Simons, Chatrath & Rakotosamimanana, 1990

†*Mesopropithecus dolichobrachion* Simons, Godfrey, Jungers, Chatrath & Ravaoarisoa, 1995

†*Palaeopropithecus* sp.

Family Lepilemuridae

*Lepilemur* sp. sportive lemur

Family Daubentoniidae

*Daubentonia madagascariensis* aye-aye

Family Cheirogaleidae

*Microcebus* sp. mouse lemur

Family Lemuridae

†*Pachylemur* sp.

*Eulemur coronatus* crowned lemur

*Eulemur fulvus* brown lemur

*Hapalemur griseus* lesser bamboo lemur

*Hapalemur simus* greater bamboo lemur

†Family Megaladapidae

†*Megaladapis grandidieri*/madagascariensis

Family Indriidae

*Avahi* sp. woolly lemur

*Indri indri* indri

*Propithecus perrieri* Perrier's sifaka

*Propithecus tattersalli* golden-crowned sifaka

## Order Carnivora

Family Eupleridae

†*Cryptoprocta spelea* G. Grandidier, 1902

*Cryptoprocta ferox* fossa

## Order Rodentia

Family Nesomyidae

†*Nesomys* cf. *narindaensis* Mein, S  n  gas, Gommery,  
Ramanivosoa, Randrianantenaina & Kerloc'h,  
2010

---

forest sites, where two smaller species (*Nesomys rufus* and *Nesomys audeberti*) occur, and from western dry deciduous forests, where a larger species in the Bemaraha *tsingy* formation occurs (*Nesomys lambertoni*). Recently, an extinct subfossil species, *Nesomys narindaensis*, has been described from Holocene remains from the Mahajanga area (see Plate 14), which is even bigger than *Nesomys lambertoni* (268). We suspect that the material from Ankarana referred to this genus may be closely related to *Nesomys narindaensis*. The disappearance of this rodent from its former range in Ankarana is presumed to be associated not with human modification of the environment but rather with natural climatic change, and as such bolsters our inferences about the disappearance of *Hapalemur simus* from the same region.

As discussed in the next two plates, based on radiocarbon dates of lemur bones recovered from the cave deposits at Ankarana, it is clear that very significant changes have taken place to the local environment, which in turn led to the extinction or local disappearance of certain primates. Using different anatomical and natural history traits of animals identified from the subfossil deposits, we reconstruct that a few thousand years ago portions of the local forests were a mixture of closed-canopy deciduous and humid formations. What is critical is that the disappearance of these animals was before any extensive and notable human population pressures in the region, at least based on the currently published archaeological record.

On the basis of the detailed work of Robert Dewar and colleagues, the first evidence of humans in the northern portion of Madagascar is distinctly more recent than the radiocarbon dates from extinct animal bones (see Plate 17 for more details). Excavated rock shelters not too far from Ankarana, within the Montagne des Fran  ais, were short-term human occupation sites, which, based on published information, were not inhabited before about 1,100 years ago. Giant tortoises and large extinct lemurs have been identified in the bone remains found in a cultural context in one of these rock shelters, which is firm evidence that people lived contemporaneously with and proba-

bly hunted these animals (84). However, at this stage, no evidence exists of extensive local human pressure that might have pushed certain of these animals into extinction. The first human settlements—as opposed to temporary encampments—were distinctly later (86). Hence, putting these different points together, the working hypothesis is that based on natural climatic shifts, specifically desiccation and a more pronounced dry season, a number of organisms in northern Madagascar were declining or already gone before human colonization of the region. In some cases, certain of these taxa were able to hang on, and perhaps their final *coup de gr  ce* may have been associated with human modifications of the environment or hunting. In any case, the climatic changes had a very rapid impact on the local natural environments, and this took place just over a few thousand years, the equivalent of milliseconds in geological time.

## Plate 17: Ankarana II—Ecological Change of a Forest Community, a Bird’s-Eye View from the Forest Canopy

In modern lemur communities, there tends to be vertical stratification in the habitats used by different species, particularly in the portion of the forest where they search for food. For example, different bamboo lemurs tend to occur in the lower and middle portions of the understory, and some of the smaller nocturnal species, such as mouse lemurs (*Microcebus*), can be found relatively close to the ground. A variety

of larger genera—such as indri (*Indri*), ruffed lemurs (*Varecia*), and sifakas (*Propithecus*)—tend to use the upper half of the forest, where they pluck young tender leaves, consume fruits, or find appropriate open places for their morning sunbaths.

In many cases, based on different osteological (bone) designs and different bodily proportions—for example, hand and foot structure, length of fore-

---

Here we have depicted different lemur species that would have been found just a few thousand years ago in the upper portion of the Ankarana forest canopy. Among the extinct forms are *Babakotia radofilai*, a “sloth-lemur” that used a suspensory means of locomotion, and *Pachylemur*, a large arboreal quadruped that was also capable of suspending itself by its hind feet in a fashion similar to the living ruffed lemur of the genus *Varecia*. We have shown *Pachylemur* feeding in this position on a group of figs, and this technique would have substantially enlarged its reaching distance while foraging. Also included is a troop of Perrier’s sifaka *Propithecus perrieri*, a species that seems to have disappeared from Ankarana in the past few decades, and indri *Indri indri*, today restricted to the eastern humid forest. For a key to the different animals, see black-and-white inset for Plate 17 in color gallery. (Plate by Velizar Simeonovski.)



limbs as compared to the hindlimbs, geometry of joints, and so on—it is possible to infer how different lemur species physically move and, even more specifically, whether on or off the ground. Within the order Primates, there are numerous modes of posture and locomotion (“positional behavior” in the general sense), such as vertical clingers and leapers, arboreal quadrupeds and climbers, terrestrial knuckle-walkers, and those that move from tree to tree suspended from their limbs—sometimes using only the forelimbs (brachiators) or more commonly forelimbs and hindlimbs together (quadrumanous clamberers). Based on direct observations in nature of locomotion and posture practiced by living primates, it is possible to verify the relationship between different aspects of bony morphology and bodily proportions and how different animals move and rest. This type of controlled comparison, sometimes referred to as ecomorphology, has guided our reconstructions throughout this book of the modes of locomotion of extinct lemurs.

Among the seventeen different types of lemurs identified from bone remains recovered in Ankarana caves, six are extinct (126) (see Table 12). For the extinct subfossil species, using analogies and aspects of their anatomy extrapolated from living primates, it is possible to have a window into the manner they might have moved around and in which vertical portions of the forest they might have lived. As described in Plate 16 and below, the forests that ring and traverse the Ankarana Massif were once full of lemurs engaged in various types of locomotion and using different feeding or resting postures. Very few sites known to harbor the remains of subfossils exhibit as much total lemur ecomorphological diversity as this region once did (but see Ampasambazimba, Plate 12). The massif and some surrounding areas, in total about 18,000 ha, were named as a protected area in 1956 as the Ankarana Special Reserve, and in recent years it has been reclassified as the Ankarana National Park.

The six different extinct species identified from the Ankarana remains include *Mesopropithecus dolichobrachion*, *Babakotia radofilai*, *Archaeolemur edwardsi*, *Pachylemur* sp., *Palaeopropithecus* sp., and *Megaladapis grandidieri/madagascariensis*. A few points need to be mentioned about why some of the species identifications of extinct lemurs are not very precise; the two biggest question marks are indicated with a “sp.” The bone remains of these taxa demonstrate similarities with species better known from other sites on the

island, and the differences are insufficient to name a new species. Both *Palaeopropithecus* and *Pachylemur* are part of the extinct lemur assemblage at Ankarana, but they are quite rare in the subfossil samples, and this complicates any effort to identify them to species with complete confidence. Others have suggested that these two species are best referred to their counterparts known from the Central Highlands (133), but we take a more conservative view here. The ecogeographic variation and systematics of *Palaeopropithecus* in particular are complex and in flux; we discuss some of these issues in the narratives for Plates 15 and 19.

The ambiguous designation of *Megaladapis grandidieri/madagascariensis* is a slightly different story because these two species are very closely related and in many respects simply hard to distinguish (376). This same taxonomic problem applies to some other subfossil sites with *Megaladapis* such as Anjohibe (see Plate 14) and Amparihingidro in northwest Madagascar, and we return to this issue in the next narrative (Plate 18). On the other hand, the “monkey-lemur” *Archaeolemur* from Ankarana is similar in size and shape as *Archaeolemur edwardsi* bones recovered from sites in the Central Highlands, and our species designation reflects this greater confidence (but see some complications detailed by 321). If our assignment is correct, the Ankarana material also represents a significant range extension for this widespread species. *Babakotia radofilai* and *Mesopropithecus dolichobrachion* are relatively new to science and unambiguously linked to the Ankarana, from where they were named. More work on the systematics and taxonomy of the northern subfossils clearly remains to be done, but these lingering questions do not influence our ability to reconstruct the lifestyles and habitat preferences of the locally occurring extinct lemurs.

Perhaps a good place to start with the reconstruction of aspects of the extinct lemur fauna of Ankarana is to frame it in the period when certain of these animals were still alive based on radiocarbon dates (54, 69). Two dates are available for *Megaladapis grandidieri/madagascariensis*: 26,150 years BP (too old for calibration) and 12,760 years BP (mean calibrated date of 14,970), the former date is one of the oldest known for a lemur and approaches the upper technical limit for radiocarbon dating. Other dates available from Ankarana lemur subfossils include *Haplolemur simus* at 4,560 years BP (mean calibrated date of 5,155), *Babakotia radofilai* at 4,400 years BP (mean calibrated date of 5,045), and *Archaeolemur edwardsi*



at 1,020 years BP (mean calibrated date of 870). This latter estimate is the most recent known for this species. Hence, these dates span about 25,000 years, with the earliest from the Late Pleistocene and the most recent after humans first colonized Madagascar (see Part 1, “History of Human Colonization of Madagascar”). This is a substantial period, during which many changes took place to the local forest environment.

In Plate 17 we have illustrated four different types of lemurs that would have occurred in the upper portion of the Ankarana forest, from the middle to upper canopy. We have depicted this forest with a closed canopy, which is largely continuous vegetational cover that blocks much of the sun reaching the forest floor. Further, it probably contained a mixture of deciduous and humid forest plants; here it is shown as distinctly green, which would have coincided with the rainy season. Four different types of lemurs are depicted, *Babakotia radofilai* and *Pachylemur* sp., which are extinct; indri *Indri indri*, which is still extant but now limited to the eastern humid forests; and Perrier’s sifaka *Propithecus perrieri*. This sifaka still occurs in the north and was recorded in Ankarana as recently as 1987, but apparently has since disappeared from the park (19).

*Babakotia radofilai* was described a few years back based on an upper jawbone with unique teeth recovered from Antsiroandoha Cave in the Ankarana (124); this was the first new genus of extinct lemur described in many decades. Subsequent work on new finds of *Babakotia radofilai*, including specimens from Anjohibe (see Plate 14), provided many additional insights into aspects of this species’ anatomy (122, 209, 347). This animal is estimated to have weighed up to 20 kg or so (212). A relatively complete skeleton was recovered in mid-July 1991 in the Ankarana by a team led by Elwyn Simons, then at Duke University (see Figure 62). Bill Jungers participated in this expedition; the team ventured into a muddy cave known locally—in translation from the Malagasy—as the “Lone Barefoot Stranger Cave,” a name based supposedly on finding a single pair of footprints that led into the cave but never exited (*Fitsangantsanganan’ ilay olona tokana*)! A bone of the forearm was seen sticking up from within a pool of water, and closer inspection revealed a complete skull and many other bones. Everything that could be detected was removed from the muddy pool and packed back to camp; the team was delighted in discovering one of the most complete subfossil lemur skeletons ever found (Figure 66). A party ensued that evening.



Figure 66. *Babakotia radofilai* was described in 1990 based on subfossil bones recovered from Ankarana in 1988; this was the first new genus of extinct lemur described in many decades. Subsequently, in 1991 a nearly complete skeleton, figured here, was recovered, which provided important insight into the ecomorphology of this remarkable animal, particularly its limbs, hands, and feet. This “sloth-lemur” is estimated to have weighed approximately 20 kg, was adapted to climbing and hanging in the trees, rarely came to ground, and fed on leaves, fruits, and seeds. (Photograph by William L. Jungers.)

On the basis of its distinctly long forelimbs, which were about 20 percent longer than the hindlimbs, as well as other anatomical adaptations, including long and curved finger and toe bones, *Babakotia radofilai* traveled through the trees with a suspensory means of locomotion, including upside-down quadrupedalism, quadrumanous clambering, and possibly even occasional brachiation. It was probably not capable of any significant leaping behavior. With its short hindlimbs and grasping feet, it would have been very inept when walking on the ground, and we suspect it did so rarely; in other words, it was primarily arboreal. Inherent in this lifestyle and this means of getting around, it would have lived in closed-canopy

or nearly closed-canopy forest, probably with extensive branch and liana connections between the taller portions of the vegetation. As we have depicted in Plate 17, suspension probably involved the use of all four limbs in various combinations, sometimes alternating (when moving) and sometimes simultaneous (when hanging). Based on its dental anatomy and tooth wear, it was a mixed feeder, eating leaves (folivorous), fruits (frugivorous), seeds (granivorous), and was capable of chewing hard objects (128, 211).

Soon after the discovery and diagnosis of *Babakotia radofilai*, yet another new species of sloth-lemur was discovered and described as *Mesopropithecus dolichobrachion*, the “long-armed” species of this widespread genus (348). Its teeth are similar to the *Mesopropithecus* species from the Central Highlands and southwest, but its limb proportions are unique for the genus (relatively longer forelimbs as its specific name suggests). It was another large-bodied, quadrumanous, highly arboreal forest-dwelling browser.

The other extinct species depicted in Plate 17 is *Pachylemur*, a genus closely allied to the living ruffed lemurs *Varecia*, but notably bigger, weighing somewhat over 10 kg (212), as compared to 3.0–4.5 kg in *Varecia*. Of all of the genera of subfossil lemurs, *Pachylemur*, with two recognized species, is one of the most widely distributed (122), rivaled perhaps only by *Archaeolemur*. *Pachylemur jullyi* is known from different sites in the Central Highlands and *Pachylemur insignis* from localities in the west and southwest. The specific identity of the Ankarana specimens still needs to be worked out because we have only a few fragmentary specimens from this site. Like *Varecia*, the dentition of *Pachylemur* was that of a frugivore and not a seed predator (128); it probably passed seeds intact through its digestive system and contributed thereby to forest plant dispersal and regeneration. The forelimbs and hindlimbs of *Pachylemur* were nearly the same length, contrary to *Varecia*, which is more hindlimb dominated; accordingly, *Pachylemur* was likely to have been a slower and more deliberate climber. It was also probably strictly arboreal and used both hands and feet (quadrupedalism) to negotiate the canopy. As illustrated in Plate 17, we infer that *Pachylemur*—like its close cousin *Varecia*—was capable of suspending itself by its hind feet to reach food resources, in this case figs. This versatility in feeding postures increases what one might call the “feeding sphere” from one location; an animal can reach both above and below the support it occupies.

In Plate 17, tucked a bit behind and in an arboreal

position, is depicted a group of Perrier’s sifaka *Propithecus perrieri*. This all-black species of sifaka is the typical *Propithecus* today of the limestone areas of extreme northern Madagascar. A number of subfossil remains from the Ankarana were allocated initially to *Propithecus diadema* (126). Formerly, *perrieri* was considered a subspecies of *Propithecus diadema*, and it can be presumed that the *Propithecus* remains from Ankarana are indeed of *Propithecus perrieri*. The only exception is material from a single cave, which has been tentatively identified as the golden-crowned sifaka *Propithecus tattersalli*; this species is known from the Daraina region, less than 100 km to the south of Ankarana. *Propithecus perrieri* feeds largely on leaves, flowers, and fruits (238).

According to some of the older local guides at Ankarana, during their younger days they actually saw or their elders mentioned that black sifakas were common in the protected area. In 1987 during an intensive biological survey of the Ankarana forests, a few observations of this species were made by Jörg Ganzhorn and his colleagues (192); subsequently it seems to have disappeared, although it is still known from nearby forest blocks (19). Why this species no longer occurs in the park is open to speculation. However, this information, combined with similar observations that the lesser bamboo lemur *Haplemur griseus* is also locally becoming rare, leads to the impression that changes in the local habitat and the associated distribution of lemurs continues to the present. This is reinforced by the observation that the most common subfossil lemur bones found in the caves of the Ankarana are those of the greater bamboo lemur *Haplemur simus*. In some caves, the floor was literally blanketed with the remains of this species, which is now known only from pockets in the central eastern humid forests (see Plate 16 for further discussion).

The last species depicted in Plate 17 is the indri *Indri indri*, which today has a broad distribution in the eastern humid forest from near Andapa south to the Mangoro River. This species is rare in the subfossil collections from the Ankarana (210), and these remains have not been dated with radiocarbon techniques. As shown in the illustration, *Indri* today in the northern portion of its modern range tends to be darker than those farther to the south. The remaining populations of this species do not occur at any site with dry deciduous or transitional forest. As explained in Plate 8, this lemur once had a notably broader distribution on the island, even extending down into the

southwest. The initial decline of these former populations is most plausibly tied to shifts in forest type directly linked with natural climate change. Given what we know about the habitat requirements of this living lemur, these changes are best explained by shifts from humid to drier forest formations. The only radiocarbon dates of subfossil *Indri* bone that we are aware of come from Ampasambazimba (see Plate 12) on the Central Highlands and yielded measurements of about 3,800 and 2,400 years BP (mean calibrated dates of 4,115 and 2,505) (69).

The subfossil remains recovered in caves in the Ankarana provide an extraordinary window into a very rich and diverse lemur community that existed in this zone during the recent past. Extrapolations based on radiocarbon dates of extinct and living lemurs, as well as the habitat requirements of species that still occur on Madagascar today, indicate that local changes in forest structure, almost certainly associated with shifting meteorological conditions, can happen very quickly on a geological time scale. While we have no physical evidence among the subfossil remains that lemurs were formerly hunted, today in the Ankarana there is evidence of wild animal exploitation as bush meat (59). Of critical importance is that over the past few centuries, particularly the past few decades, the forests surrounding the massif have been heavily degraded and fragmented by humans. This was associated with both legal and illegal exploitation of hardwoods, as well as a massive infiltration of the protected area by people searching for sapphire deposits. Little forest habitat remains today in and around Ankarana. A formerly important forested ecosystem, perhaps showing some ecological similarities to Miombo-like woodland (see Plate 12 for further discussion of this proposed habitat), immediately adjacent to the western face of the massif has been transformed into grassland with some occasional trees. We propose that several factors have been responsible for the reduction in the extraordinary diversity of lemurs at the site, presented in sequential order: natural climatic change transforming local forested habitats into drier formations, and then modification by people of the forested ecosystems into fragments incapable of supporting the larger taxa—and possibly punctuated by hunting pressure as human populations grew.

## Plate 18: Ankarana III—Tragedy and How the Bone Remains of an Extinct Lemur Can Help Piece Together How It Lived and the Former Local Forest Ecology

Fossil and subfossil material studied by vertebrate paleontologists is the direct result of some natural or possibly unpleasant ending of an animal. Death is inherent in the process, with portions of the carcass or bones being recovered sometime in the future by field collectors. In the context of the different types of bone material from Madagascar discussed in this book, all are subfossils—that is, they remain as bone, and the process of being replaced by minerals, known as permineralization, and subsequent transforma-

tion into fossil “bone” have yet to commence. One of the advantages of subfossil bones is that they contain organic and inorganic material, which can be used to study different aspects of when the animal was living (radiocarbon dating; 54, 69), aspects of its diet (stable isotope analysis; 73), and even in certain cases genetic aspects (DNA analysis; 214). When these different techniques are applied to subfossil material, this breathes new life into their skeletons and opens windows into their former natural history. The study of

---

A scene from the Ankarana of a subadult “koala-lemur” *Megaladapis grandidieri/madagascariensis* lost in a cave passage known as the “Galerie des Gours sec.” To enhance the sense of being in total darkness, we have used a sort of infrared “night-scope” imagery. This animal would soon succumb to the lack of water, food, and the horror of being lost. Paleontologists recovered its partially articulated skeleton several thousand years later, providing new insights into the morphology of these giant lemurs and aspects of how they lived and moved. (Plate by Velizar Simeonovski.).



“functional anatomy” also adds flesh to the bones in a complementary fashion, and can tell us much about how the animal moved and what they ate.

In many cases, particularly in relatively dry cave settings, after the death of an animal, the body decomposes, and the remaining bone material does not become too disassembled unless disturbed by scavengers or by floodwaters. By finding portions of the skeleton more or less together, including the small and complex bones of the feet and hands, this fortuitous association provides important information for paleontologists and functional anatomists attempting to reconstruct, for example, how the animal walked or how they manipulated objects with their hands and feet. Here we give a case study of how the remains of some giant lemurs found in caves provide important and interesting insight into aspects of their anatomy and, by extrapolation, contributed to a fuller appreciation of their natural history.

The focal species in Plate 18 is a subadult individual of the “koala-lemur” *Megaladapis*. This is one of six extinct lemurs that have been recovered from caves in Ankarana (see Plates 16 and 17; and Table 12). We refer to this lemur here somewhat ambiguously as *Megaladapis grandidieri*/*madagascariensis* because these two species are closely related and overlap in size and morphology (376). *Megaladapis madagascariensis* is the smallest member of this genus found at subfossil localities all over the southern and southwestern portions of the island, whereas *Megaladapis grandidieri* is known from sites in the Central Highlands. The remains of *Megaladapis* from the northwest and extreme north of Madagascar, including the Ankarana Massif, recall aspects of both of these species, but precise allocation to one or the other—or to a new species—awaits further study. This particular individual, which is remarkably complete, was discovered in a chamber of Andrafiabe Cave called the “Galerie des Gours sec” (*gours* is a type of speleothem or cave formation that typically creates a stone dam, also known as rimstone).

*Megaladapis* was the first subfossil lemur genus to be diagnosed and described scientifically (106); this was “a strange gigantic Lemuroid skull” from the southwestern site of Ambolisatra (see Figure 39), which was named *Megaladapis madagascariensis*. In this landmark publication, Forsyth-Major drew attention to similarities with the Australian koala bear, *Phascolarctos*, and this analogy has taken hold—hence, today we refer to them as koala-lemurs. A complex history of discoveries, attributions, misat-

tributions, and synonymies ensued, and three species were eventually agreed upon (121): *madagascariensis*, *grandidieri*, and *edwardsi*.

Attempts to reconstruct the lifestyle of the koala-lemurs were plagued by the paucity of specimens with associated skulls and skeletons, although proper attention to the seminal publication of Lorenz von Liburnau (242) by his contemporaries might have spared some of the confusion. Several different reconstructions have been presented over the last century, some bordering on fanciful (Figure 67). Regardless, associated discoveries by Charles Lamberton of *Megaladapis* at Beavoha (288) helped to remedy this taxonomic mess. Along the way, *Megaladapis* was analogized to everything from gorillas to cave bears, and was even attributed an aquatic habitus by the eccentric Italian paleontologist Giuseppe Sera. As Robert Martin remarked in a review article: “*Megaladapis* remains an enigma. It has been suggested that this genus was arboreal, terrestrial or even aquatic; though a systematic search of the literature has failed to reveal any suggestion that *Megaladapis* was adapted for flying” (263, p. 338). The associated remains from the chamber Galerie des Gours sec and from other caves of the Ankarana Massif have revealed important new details that help greatly to refine our understanding of its biology (see below).

One conclusion that is shared by virtually everyone who has studied *Megaladapis* is that it was a browsing leaf-eater (folivore) with a bizarre cranial anatomy. Its cheek teeth are similar in shape to the much smaller and living sportive lemur (*Lepilemur*), also feeding almost exclusively on leaf matter. In addition to this dental similarity, *Megaladapis* and *Lepilemur* share an unusual geometry of the jaw joint where the mandible articulates with the cranium (362). These shared anatomical details convinced many scientists that these two genera, although vastly different in size and in how they moved (locomotor adaptations), belonged in the same taxonomic family. Ancient DNA was extracted from the bones of *Megaladapis* relatively recently (214), however, and it appears likely that *Megaladapis* is actually more closely related to the living Lemuridae of the genera *Eulemur*, *Lemur*, *Varecia*, and *Haplemur*. This means that the observed similarities between *Megaladapis* and *Lepilemur* are actually the result of evolutionary convergence.

The analysis of tooth wear based on magnified images, including mostly patches of parallel scratches, and the prominent shearing crests on the cheek teeth indicate that *Megaladapis* fed predominantly

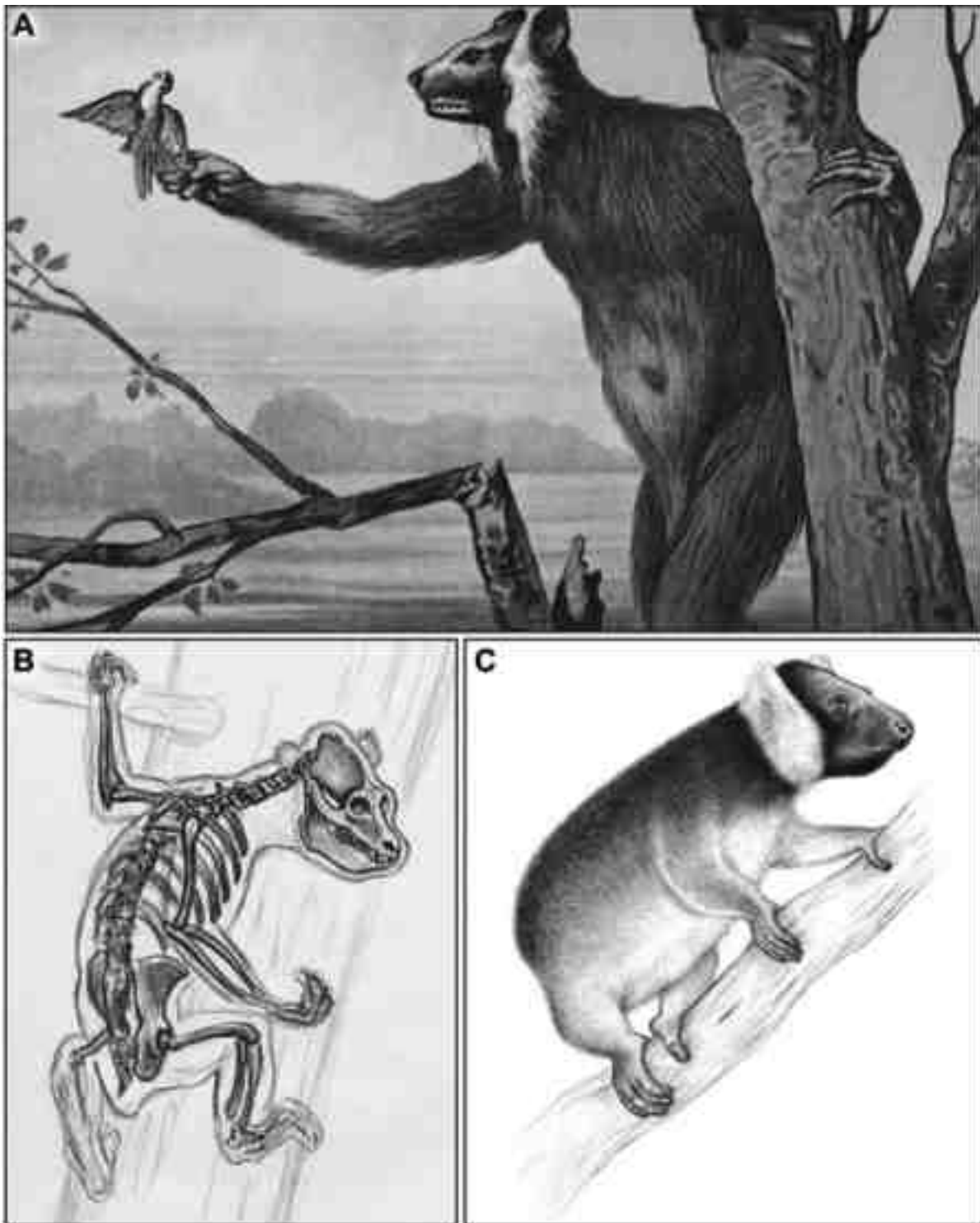


Figure 67. As new associated material of subfossil lemur skulls and skeletons has become available and taken into account by functional anatomists and paleoartists, better insights into their natural history and reconstructions that are more accurate are now possible of how they moved. A perfect example is the genus *Megaladapis*. Figure A: an early twentieth-century fanciful reconstruction of this beast based on little detailed anatomical information and presenting it as a sort of gorilla-like (32), as compared to Figures B and C: much finer-detailed reconstructions based on precise anatomical information. (Drawings by Stephen Nash.)



on leaves (128, 341). Its skull is unique among primates: it is very elongated, the front end is angled upward, it lacks permanent upper incisors, it has a large space (diastema) between front and back teeth, and its nasal bones are long and droop down over the nasal opening. The postcranial skeleton that includes the limbs, bony girdles, and vertebral column—or in other words, everything behind the skull—of *Megaladapis* is also quite unusual. The upper limbs are longer than the lower ones, and this difference increases from the small *Megaladapis madagascariensis* to the huge *Megaladapis edwardsi* (208). However, relative to estimated body mass all of the limb bones are short and exceptionally robust. Koala bear analogies have been offered for its locomotor adaptations too, and most anatomists agree that *Megaladapis* was a large-bodied, primarily arboreal folivore (211, 380). It climbed powerfully and cautiously, was capable of suspended postures, and was presumably agile enough to come to the ground when necessary to find water or move between stands of forest. Given their size, when moving on land, adults at least probably had few predators to worry about (see Plate 19).

Despite all the work on this remarkable primate over the years, it was only in the Ankarana that fossils of *Megaladapis* were found with associated hands and feet, and the subadult subject of Plate 18 was a major contributor to some fascinating new insights. For example, the feet were huge grasping organs, longer than the rest of the hindlimb, composed of the shin (tibia) and thigh (femur) bones, to which they were attached (395). Foot length as a percentage of total hindlimb length was greater than 40 percent, a world record among all known living and extinct primates. The big toe was huge and helped form a pincer-like mechanism that would have served the animal well in climbing and clinging to tree trunks and thick branches of almost any orientation.

Returning to Plate 18, we know that the unfortunate animal was a subadult because its limb bones had not quite finished growing. Perhaps it was following the scent of water into the recesses of the Galerie des Gours sec, where it lost its orientation and perished alone and distraught from inevitable thirst and hunger and perhaps unbearable anxiety. There is no evidence of trauma to suggest otherwise. It probably eventually curled up and died on the jumble of karstic blocks, where it was found many hundreds, if not thousands, of years later, with its different skeleton elements still partially associated.

Bill Jungers can relate personally to the ease of being turned around and lost in the pitch-dark caves of the Ankarana. One morning in the early 1990s, he ventured with one other researcher deeper and deeper into a massive cave called Antsiroandoha in search of more subfossils. As lunchtime approached, they attempted to backtrack to join the rest of the team. After returning to the same distinctive speleothem several times, it was clear they were walking in a circle and were hopelessly lost. Although it was clear that the other team members would search for them when they failed to make it back for lunch, the period spent in total silence and in complete darkness was incredibly unnerving and disorienting. This story has a much happier conclusion than the one for our subadult *Megaladapis* because they were found in short order by team member Jeannette Ravaoari-soa after the missed appointment. Bill remarks to this day that his brain size was much larger than that of *Megaladapis*, so this could happen to any primate venturing deep into the Ankarana caves, with or without flashlights!

# Species Plates

## Plate 19: *Cryptoprocta spelea*—an Extinct Mega-Predator and Aspects of How It May Have Lived and Hunted

The current native Carnivora fauna of Madagascar is composed of ten species (149), the largest being *Cryptoprocta ferox*, which is now well-known to the general public thanks to the *Madagascar* film series produced by DreamWorks. This species closely resembles a puma *Puma concolor* in its external morphology and size, with cat-like facial features, a sleek muscular body and long torso, and tail length nearly equal to the head-plus-body length. It is a member of a Car-

nivora family unique to Madagascar, the Eupleridae. *Cryptoprocta ferox* demonstrates sexual dimorphism, with males being larger than females. Although populations of the living species have declined over the past decades, it is broadly distributed in the remaining forested zones of Madagascar, including the eastern humid lowland forest, montane forest, dry deciduous forest, and spiny bush.

*Cryptoprocta ferox* is the principal predator of a

---

The extinct *Cryptoprocta spelea* would have been a formidable predator and, based simply on size, no doubt capable of taking prey larger than the living *Cryptoprocta ferox*. One extinct lemur within the appropriate size range (~10+ kg) of prey would have been *Pachylemur insignis*, which is known from several of the same subfossil sites as *Cryptoprocta spelea*. Here we depict the successful result of a communal hunt between two adult males. Living *Cryptoprocta ferox* hunt in this same fashion. (Plate by Velizar Simeonovski.)



wide assortment of living lemurs, specifically large diurnal species and to a lesser extent the smaller nocturnal species. In some portions of its range, more than 50 percent of its diet is composed of primates (90, 318). This magnificent carnivore is a formidable hunter. In terrestrial mode, it can easily chase down prey on the ground, and in arboreal mode, it can scale nearly vertical tree trunks, gallop across horizontal limbs, and leap between trees. Its semi-retractable claws help it to grip woody substrates off the ground and act as powerful weapons when bringing down and subduing prey.

*Cryptoprocta ferox* has been documented to take animals nearly their own body mass, such as 6 kg sifakas (*Propithecus*). Further, bone fragments of notably larger introduced animals such as zebu and bush pigs (*Potamochoerus*) have been recovered in their scats; whether these food items were hunted or scavenged is impossible to discern. In any case, today it is the top predator of Madagascar, forming the pinnacle of the food chain, in the same manner as lions do in portions of Africa. However, in the recent past, another species of *Cryptoprocta* occurred on the island that was larger and an even more formidable predator (Figure 68).

Bones referable to the genus *Cryptoprocta* were recovered from a wide variety of paleontological sites dating from the Holocene of Madagascar, as well as more recent archaeological sites, particularly in the west and extreme south (165). All of these remains are subfossil just like the other vertebrates in the same assemblages; in other words, we have yet to recover an ancient, mineralized fossil version of this animal (or its predecessors)—although the molecular evidence suggest its founding ancestor arrived on Madagascar millions of years ago (396). Huge gaps in the paleontological record of Madagascar are the frustrating norm, with essentially no evidence of terrestrial fossils between the Late Cretaceous and the Late Pleistocene, a period of nearly 60 million years (221)! Hence, until Pliocene, Pleistocene, or earlier Neogene deposits are discovered on the island holding terrestrial fossil vertebrates, important questions will remain about the evolutionary history of different Malagasy animals.

Guillaume Grandidier, the son of Alfred Grandidier, studied *Cryptoprocta* bones recovered from the paleontological sites of Ambolisatra (see Figure 39), to the north of Toliara, and Andrahomana Cave (see Plate 3), to the west of Tolagnaro. In both cases, his paleontological studies at these sites set the founda-



Figure 68. Lateral views of the cranium of a recently collected *Cryptoprocta ferox* (above) and a subfossil *Cryptoprocta spelea* (below). The specimen of *Cryptoprocta ferox* was collected at Manakara in 1931, and it is among the largest known modern individuals of this species. (Photograph from 165.)

tion for a rich history of exploration that has continued for more than a century (Figure 69). He concluded that the Carnivora material recovered from these sites represented a new form larger than extant *Cryptoprocta ferox* and proposed the name "*Cryptoprocta ferox* var. *spelea*" (178, 180).

To a large extent, the taxonomic status of the big *Cryptoprocta* remained unresolved, until a comparative study of modern and subfossil bones was conducted about a decade ago. This study concluded that rather than considering *spelea* as a form of *Cryptoprocta ferox*, it was best to recognize it as a full species, albeit a now-extinct one (165, 302). Bone remains referable to *Cryptoprocta spelea* have been identified from a number of sites on the island: Lakaton'ny Akanga and Ankarana (see Plates 16–18) in the far north, those in the central lowland west, numerous localities in the extreme south and southwest, and a few localities in the Central Highlands. Hence, not too long ago, this species had a very broad distribution on the island (165, 225). At Ankarana, Antsirabe (see Plate 11), Beavoha, Beloha, Belo sur Mer (see Plate 9),



Figure 69. Guillaume Grandidier took this historical photograph at the turn of the twentieth century looking out of the seaside entrance of Andrahomana Cave. This image is in the collection of the Fond Grandidier at the Académie Malgache in Antananarivo. (Photograph courtesy of the Académie Malgache.)

and Manombo (Toliara), bones of both *Cryptoprocta ferox* and *Cryptoprocta spelea* are represented among the excavated subfossils. However, because most of this material dates from a period of paleontology excavations when there was no stratigraphic control of deposits, it is difficult to discern if these two species lived in these different regions during the same period. Further, as discussed below, available radiocarbon dates from *Cryptoprocta* subfossil remains are uninformative about this point.

Based on a mandible collected at Tsiandroina that had a distinctly different morphology, Charles Lamberton described another species of subfossil in this genus, *Cryptoprocta antamba* (225). The name an-

tamba is from the Malagasy and derived from a legendary animal living in southern Madagascar. In 1658 the *antamba* was described by Etienne de Flacourt, "This is a large beast, like a big dog, with a round head and based on information from local people, it resembles a leopard, and it devours both humans and calves. It is rare and lives only in less-frequented places in the mountains" (104, p. 221; our translation). Local folklore and Lamberton notwithstanding, the Tsiandroina specimen probably represents a malformed or somewhat pathological individual of *Cryptoprocta spelea*.

Several radiocarbon dates have recently been published of *Cryptoprocta* subfossils, all allocated

to *Cryptoprocta spelea* (69): Ampasambazimba (see Plate 12)—2,835 years BP (mean calibrated date of 2,870); Andolononby—three dates of 1,905, 1,610, and 1,520 years BP (mean calibrated dates of 1,790, 1,450, and 1,355); Ankazoabo Cave (Itampolo)—1,865 years BP (mean calibrated date of 1,740); Taolambiby (see Plate 5)—two dates of 3,115 and 2,005 years BP (mean calibrated dates of 3,270 and 1,905); and Tsirave—two dates of 2,560 and 2,425 years BP (mean calibrated dates of 2,555 and 2,500). As noted above, at several of these sites, subfossil material included bones of both members of this genus based on size and morphological characters. Unfortunately, it is not possible to verify the identifications of the specimens used to derive the above radiocarbon dates, which would help to establish in a finer sense when *Cryptoprocta spelea* went extinct. The only date that is unquestionably referable to the extinct species is from Ankazoabo-Sud at 1,865 years BP. In either case, most of the dates are recent, and several postdate inferred human colonization of the island—that is, within the past 2,500 years BP.

So why did *Cryptoprocta spelea* go extinct? It is difficult to respond unequivocally to the question, but some ideas can be proposed. If this species was indeed a specialist on large lemur species—that is, animals larger in body weight than living species—the extinction of its principal prey base, no matter what the cause, would have been devastating. The extinct species was up to 30 percent larger than the extant species (165), and the former probably had a body weight approaching 10–15 kg. In this case, because of body-size limitations, *Cryptoprocta spelea* may not have been as deft of an arboreal hunter as *Cryptoprocta ferox* is today. By extrapolation, one can imagine it being more of a predator on larger and often terrestrial lemurs, all of which are now extinct (see below).

A few of the *Cryptoprocta* radiocarbon dates mentioned above overlap with the period after human colonization of the island, and potentially there is a causal relationship. If the two species of *Cryptoprocta* lived together sympatrically and synchronically (in other words, at the same time and in the same forest habitats), one can imagine the larger *spelea* feeding extensively on big prey, which have disappeared, and the smaller *ferox* preying on smaller prey, which are still extant. Further, *Cryptoprocta ferox* seems at some level to be a generalist and takes an extraordinary wide variety of animal prey depending on the forest type and available prey (149). For example, in the high mountains of Andringitra, above the forest line, it

feeds extensively on animals weighing less than 10 g (162). With this flexible means to adjust its diet, it was able to deal with the changing ecological conditions and shifting vegetation of the past few millennia. In contrast, perhaps *Cryptoprocta spelea* was too big and too much of a specialist to be able to cope.

Bones of *Cryptoprocta ferox* have been recovered from a number of archaeological sites. These remains represent animals that were either killed taking domestic animals, such as cattle or fowl, or perhaps consumed as bush meat and then disposed of in a garbage pit, or individuals hunted specifically for the stew pot. The site of Rezoky, north of Ankazoabo-Sud, was an ancient village dating from roughly 1,200–1,400 years BP (86, 370), and numerous bone remains of *Cryptoprocta ferox* have been identified from the site (314). The occupants of this village were pastoralists with considerable cowherds; it seems highly likely that *Cryptoprocta* took domestic animals on occasion. Hence, it is not surprising that humans hunted *Cryptoprocta* in order to decrease their deprivations, and such persecution has no doubt existed on the island for centuries and continues until today. In portions of western central Madagascar, the principal source of *Cryptoprocta ferox* population declines is probably related to these carnivorans being killed by villagers in the act of taking domestic animals.

As mentioned earlier, the largest living predator on Madagascar is *Cryptoprocta ferox*, which is capable of taking prey up to the size of the genus *Propithecus* (roughly 3–6+ kg). *Cryptoprocta spelea* was up to one-third larger than living *Cryptoprocta ferox*. Based on this extrapolation, *Cryptoprocta spelea* was probably capable of hunting animals approaching 10 kg, which would have included a wide assortment of lemur species that are now extinct. Of course, immature individuals of even larger extinct lemur species might also have been at risk. One candidate prey species of *Cryptoprocta spelea* would have been *Pachylemur insignis*, estimated to have weighed around 10 kg as adults (212); this predator-prey relationship is illustrated in Plate 19. Both of these species have been identified from several of the same subfossil sites and lived during the same period. Because *Cryptoprocta ferox* is known to feed on *Varecia* today, it is no stretch of the imagination to depict *Cryptoprocta spelea* consuming the carcass of *Pachylemur* after a successful hunt.

*Cryptoprocta ferox* often forages solitarily, but it has been observed hunting communally in groups of two to three individuals. In the case of communal hunting of arboreal lemurs, one *Cryptoprocta* will chase

the prey, scaling trunks and leaping from tree to tree, and force the lemur to the ground, where the hunting partner can easily subdue it. In a well-documented observation of communal hunting, three males were observed chasing a Verreaux's sifaka (*Propithecus verreauxi*), switching positions between them with regards to the animals on the ground and while moving between trees, often breaking branches and crashing down to the ground. The hunt terminated after about a 45-minute hot pursuit with the primate being dispatched by a mortal bite to the neck (246). It has been shown that males that hunt communally are larger in body size than solitarily hunting males and have a higher mating success (247).

We have used this theme in Plate 19, which shows two adult male *Cryptoprocta spelea* having taken a *Pachylemur* after a bout of social hunting. Another intriguing explanation for this communal hunting behavior in living *Cryptoprocta ferox*, other than sexual selection and access to females, is that it might represent relic or residual behavior from the recent geological past designed originally to allow them to take larger prey, specifically large-bodied lemurs that are now extinct (246). This may indeed be correct, but as mentioned above, if the extinct and extant *Cryptoprocta* occupied the same forests and divided the lemur prey base by size, the living species would rarely taken larger prey. Alternatively, perhaps the communal hunting in this species was a strategy needed to out-compete *Cryptoprocta spelea* for larger prey. In Plate 19, the scenario we propose is that one *Cryptoprocta spelea* was able to attack the *Pachylemur*, perhaps from a sturdy arboreal perch, while this lemur was traveling, feeding, or resting in the trees. *Pachylemur* was fundamentally arboreal in its habits. However, even *Varecia* descends to the ground occasionally, and we suspect that *Pachylemur* did too, if only infrequently and perhaps in desperation by being threatened by the stalking predator. Depending on the strategy of the communal hunt, perhaps one *Cryptoprocta spelea* chased its prey into the waiting claws and teeth of another individual nearby in the canopy, but it is more likely that a panicked *Pachylemur* was forced to the ground, where it was more vulnerable, and there it met its sudden and violent end.



## Plate 20: *Stephanoaetus mahery*—a Presumed Primate Specialist and Its Role in the Evolution of Behavioral Aspects of Living and Extinct Lemurs

The modern raptor community of Madagascar includes sixteen species ranging in size from small falcons feeding mostly on invertebrates to relatively large eagles and goshawks predating on different vertebrates, including some of considerable size. A few species of living Malagasy diurnal birds of prey have been documented taking lemurs, but such acts seem

to be relatively rare (147). In spite of this, several species of living lemur have instinctive responses when they have visual or vocal contact with different avian predators and give distinct “alarm calls” (101). Considerable debate has appeared in the literature over whether or not predation has an important impact on the evolution of social behavior in primates, specifi-

---

This scene captures the moment that an extinct large predatory eagle, *Stephanoaetus mahery*, attacks a subadult extinct “sloth-lemur,” *Palaeopropithecus ingens*, just before the raptor pierces the shoulder blades with its powerful and sharp claws. Thereafter, given the substantial weight of the prey, it is not clear if the eagle would have been capable to carry it off for consumption. Alternatively, the eagle may have knocked the lemur down off its tree perch and subsequently dismantled it on the ground. (Plate by Velizar Simeonovski.)



cally diurnal species (66, 202, 338). For Madagascar in particular, there has been discussion if modern levels of predation on lemurs are sufficient to have been responsible for the current innate responses of diurnal lemurs, or if these are a remnant behavioral responses associated with recently extinct raptors (74, 142, 174). At some level, this question is difficult to resolve in a definitive manner, but it is certain that current levels of predation would be adequate to reinforce any hard-wired lemur response associated with extinct birds of prey. In any case, information from the subfossil record provides important insight into predator-prey relations between raptors and lemurs during recent geological periods.

On the basis of isolated subfossil bird bones excavated many years ago by paleontologists such as Alfred Grandidier, Charles Lamberton, and Errol White, at different sites across the island, it has been possible to document the extinction of three raptor species, of which two were distinctly large in body size. In 1995 a published paper identified two different species of eagle from subfossil remains belonging to the genus *Aquila* (155), a genus that is not represented in the modern avifauna of Madagascar. In both cases, because of considerable osteological similarity between living members of the genus *Aquila* and the fact that males and females of the same species show size sexual dimorphism, it remains unclear if the two Malagasy eagles represent endemic species that have gone extinct. Another possibility is that the bones are of living species with populations elsewhere in the world, such as Africa, with the Malagasy population having been extirpated. One of these subfossil species was a relatively small *Aquila* that would have certainly been an important predator of medium-size mammals, perhaps with a maximum body weight of a few kilograms. The other eagle was notably large and similar in size to the living Golden Eagle *Aquila chrysaetos* or Tawny Eagle *Aquila rapax*, which have been documented carrying off prey up to 4 kg in body mass and killing animals weighing up to 40 kg (42).

An even more impressive extinct bird of prey was described from subfossil remains in 1994 (141); based on different bones, including portions of the legs and claws, this raptor would have been a truly formidable predator. As these diagnostic elements show osteological similarity to the African Crowned Eagle *Stephanoaetus coronatus*, the new subfossil was placed in the same genus, and the species name assigned to it was *mahery*, which means “strong” or “powerful” in Malagasy. While it is true that all we have of



Figure 70. As evidence of their capacity to subdue prey, members of the genus *Stephanoaetus* possess proportionately very large claws relative to their size. These talons are extremely proficient in piercing the bone and flesh of prey. Here we illustrate the claws of the living African Crowned Eagle *Stephanoaetus coronatus* (above) and the extinct Madagascar species *Stephanoaetus mahery* (below). (Adapted from 141.)

*Stephanoaetus mahery* is a few bones, a considerable literature exists on aspects of the natural history and diet of the African *Stephanoaetus coronatus*, which provides important insight into aspects of how the extinct *Stephanoaetus mahery* may have lived.

*Stephanoaetus coronatus* is a massive and powerful raptor, weighing over 4 kg, and capable of strong and direct flight. Bearing large curved, sharp claws, proficient at piercing bone and flesh (Figure 70), and a massive strong bill able to dismantle prey in a skillful manner, it is a hunting machine, subduing prey weighing up to 20 kg (42). This species appears to be equally at home in forest or wooded savanna ecosystems. No radiocarbon dates are currently available for *Stephanoaetus mahery* or for that matter the two subfossil *Aquila* eagles known from different sites on the island. However, based on some associated contexts, tentative dates can be proposed that are very recent (see below).

A number of studies conducted on prey remains found in and around the nests of *Stephanoaetus coronatus* indicate that it clearly specializes on mammal prey, feeding on an assortment of primates, duikers, Carnivora, hyrax, and so on. In certain forested areas, more than 50 percent of its diet is composed of primates (344). This eagle has several hunting techniques, and the late Leslie Brown, one of the foremost specialists on African raptors, noted that it is “re-

puted to attract monkeys to their doom by uttering a soft whistle, and then seizing the nearest and bearing it to the ground" (42, p. 708). They are able to grab and subdue relatively large prey on the wing, often surprising the animal while flying through the forest. A frequently employed hunting technique is "sit and wait," where the raptor observes from a prominent tree perch animals passing through the landscape, and when in the proper position, drops down on them. This eagle is capable of capturing diurnal primates of considerable size moving through the tree canopy, such as arboreal colobus monkeys (*Ptilo-colobus*) weighing over 8 kg. In this case, they will often subdue prey from behind, planting their massively powerful claws into the shoulders, piercing the scapula bones, and then carrying off the struggling or dead animal to a perch or the ground to be taken apart and devoured.

These acts of predation have considerable bearing on the population dynamics of primates. In the Kibale Forest of Uganda, it is estimated that 2 percent of the diurnal primate community, including 1 percent of the red-tail monkeys *Cercopithecus ascanius*, succumb each year to predation by *Stephanoaetus coronatus* (274). Of equal importance, recent work on the food habitats of this eagle in the Taï Forest, Ivory Coast, indicate that about 50 percent by number of individuals or biomass of the prey consumed are primates (204, 344). Furthermore, this raptor has a higher estimated density in the Taï Forest than leopards *Panthera pardus* and, hence, is one of the most important mammal predators.

Several studies have been conducted on *Stephanoaetus coronatus* to document how they subdue prey, particularly primates, and the types of marks they leave in the associated bone remains (357). In an analysis of prey material from the Kibale Forest, this species has been cited as being "fastidious eaters" that do not cause much damage to bone as compared to, for example, certain Carnivora, such as cats or hyenas. In fact, nearly intact skulls, leg and arm bones, and scapula from preyed-upon animals, all stripped of meat, can be recovered below nest sites. Most importantly, different bone elements show signs of eagle predation, such as puncture marks of the claws forming "can opener"-like perforations, particularly in the shoulder blades (scapulae) or nicks from the powerful bill in different bones (336). The distinct marks left behind by this species in prey remains have a distinct "signature" that distinguishes them from other types of predators, such as Carnivora, owls, and humans

(365). In fact, these marks are sufficiently distinct that this eagle genus has been implicated in the deposit of different fossil bone accumulations, such as Pliocene remains in South Africa, and among its prey remains is the skull of a young hominid, *Australopithecus africanus* (27). If this is correct, human-like primates were the subject of predation by *Stephanoaetus* eagles millions of years ago.

Now extrapolating these different details on *Stephanoaetus coronatus* back to the subfossil *Stephanoaetus mahery*, the two of which were approximately the same size (141), it is reasonable to imagine that the extinct Madagascar species would have been a formidable mammal predator that targeted lemurs. Given the capacity of the African species to take prey weighing up to 20 kg, we assume that the Malagasy eagle would have been similar. This would mean that it was capable of preying upon all of the living diurnal lemurs, the largest of which weighs about 6.5 kg, as well as an assortment of extinct lemurs of appreciably larger body size.

In the subfossil bone collections of the Department of Paleontology at the University of Antananarivo, there are a number of *Palaeopropithecus* shoulder blades that have distinct piercing and shatter marks, reminiscent of those that have been illustrated for African primates taken by *Stephanoaetus coronatus* (266, 336). It is in part based on this inference that we illustrate *Stephanoaetus mahery* taking a subadult *Palaeopropithecus ingens* (Plate 20), at the split second the lemur realizes that it is about to be attacked by the eagle, who will instantaneously plant its massive talons into the shoulders of the unlucky primate. The open-mouth threat is no avail.

Herbert F. Standing, one of the paleontologists who excavated subfossils at Ampasambazimba (see Plate 12), where material of the extinct eagle was also found, noted that *Palaeopropithecus maximus* bones from the site had what he thought might be crocodile teeth marks (356). Because crocodiles are known to digest bones of consumed animals, this suggestion seems unlikely. Perhaps these marks were instead from acts of predation by the extinct crowned eagle. In any case, given its proclivity for climbing and traveling through the forest canopy, only rarely descending to ground, it is easy to imagine, as shown here, *Palaeopropithecus* resting or climbing a tree trunk, thereby exposing itself to a hunting *Stephanoaetus mahery*.

Three species of *Palaeopropithecus* have been described from Madagascar's subfossil record (122, 138).

They are estimated to have ranged in adult body mass from about 20 kg in the smaller *Palaeopropithecus kelyus* to more than 40 kg in both *Palaeopropithecus ingens* and *Palaeopropithecus maximus* (212). As this upper range of body mass surpasses the known hunting capacity of *Stephanoaetus coronatus*, we assume that *Stephanoaetus mahery* probably fed on subadults of *Palaeopropithecus maximus* and *Palaeopropithecus ingens* but dined on both subadults and adults of *Palaeopropithecus kelyus*. There is considerable variation in the size of adult *Palaeopropithecus ingens* in the southwest, especially at Ampoza (Plate 8), and some individuals converge on the small size of *Palaeopropithecus kelyus*. The unfortunate animal we depict here could therefore represent one of these small adults or—more likely—a solitary subadult that ventured out alone and paid the ultimate price.

Subfossils of *Stephanoaetus mahery* are known from the Central Highlands (Ampasambazimba; see Plate 12) and sites in the southwest (Ankilitelo, Lamboharana). Hence, this species probably had a broad distribution across the island. This range overlaps with the three extinct species of *Palaeopropithecus*, known from the top to the bottom of the western and central portions of the island and from all three of the sites mentioned above with *Stephanoaetus mahery* bones (122). Three radiocarbon dates, including one of *Palaeopropithecus ingens*, are available from lemur bones excavated at Ankilitelo (see Plate 6). These are very recent and date from between 630 and 510 years BP (mean calibrated dates of 585 and 475) (69). Hence, by extrapolation, this eagle was probably still living in recent times. For certain extinct lemurs, which presumably started breeding in the second or third year after birth, this time span represents only a few hundred generations.

What impact did the extinction of this presumed lemur-hunting eagle have on the modern fauna? This has been a subject of considerable discussion in the literature on lemurs with respect to adaptations for species having different lifestyles and activity patterns—ranging from being active during the day (diurnal), the night (nocturnal), or with the capacity to switch between these periods (cathemeral) (92). A good point of comparison for these aspects is the observation that living sifakas *Propithecus* have a mixture of adaptations to being both nocturnal and diurnal (339). One proposed hypothesis is that with the disappearance of the diurnal-hunting *Stephanoaetus mahery* as a driving evolutionary force for lemurs to adapt against predation, certain nocturnal

species moved toward being diurnal or cathemeral. If true, this might explain some of the mixed anatomical and behavioral characters in members of the genus *Propithecus*. Other scholars, like Ian Colquhoun (66), agree that cathemerality in lemurs is linked to predation pressures, but argue instead that threats from cathemeral *Cryptoprocta* have selected for some species matching their activity with this formidable predator (Plate 19). It is worth noting that all extinct lemurs, with the exception of the giant aye-aye *Daubentonia robusta*, have been reconstructed as having diurnal activity cycles (131). Could the demise of this eagle have opened diurnal niches for living lemurs that made it through the extinction window?

It has been pointed out that with current levels of predation on diurnal lemurs by living raptors, there is no reason to invoke the role of extinct predators in the evolution of certain behavioral adaptations (74, 337). However, as we have tried to show here, based on the parallels between the feeding ecology of the modern African *Stephanoaetus coronatus* and the extinct Malagasy *Stephanoaetus mahery*, the latter species was almost certainly an important predator of lemurs and probably absent from the modern ecosystem of Madagascar for only a few hundred years. It, as well as the large *Aquila* eagle mentioned earlier, can be assumed to have been a *tour de force* associated with evolutionary pressure on lemurs, specifically with respect to adaptations of living and extinct species to reduce predation pressure.

We have one other interesting tidbit to add to the history of *Stephanoaetus mahery*. Numerous Middle

---

Figure 71. Numerous illustrations have appeared of the *rokh*, and the one shown here is taken from an early version of Edward William Lane's translation of *A Thousand and One Nights*. Based on accounts from Marco Polo, a very large bird of prey lived on the island of Madagascar, capable of preying upon elephants. While certainly fanciful, this indicates the power of this raptor. The tale may have been based on the extinct large eagle *Stephanoaetus mahery*. (Adapted from 233.)



Age travelers brought home stories of a legendary bird, often referred to as the *rokh*. Perhaps the most famous of these tales comes from *The Voyage of Sinbad* and *A Thousand and One Nights*, where in certain accounts Madagascar can be construed as the origin of the *rokh*. Here is an account from Edward William Lane's translation from the Arabic of *A Thousand and One Nights*:

*Of this bird, Marco Polo heard during his travels. He says, "The people of the island [of Madagascar] report that at a certain season of the year, an extraordinary kind of bird, which they call a 'rukḥ,' makes its appearance from the southern region. In form it is said to resemble the eagle; but it is incomparably greater in size; being so large and strong as to seize an elephant with its talons, and to lift it into the air; from whence it lets it fall to the ground, in order that, when dead, it may prey upon the carcass. Persons that have seen the bird assert that when the wings are spread they measure sixteen paces in extent, from point to point; and that the feathers are eight paces in length, and thick in proportion" (234).*

Certain naturalists have interpreted this celebrated creature to be the elephant bird of the family Aepyornithidae (see Plate 1), while others have equated it with other life-forms, including a raptor (6, 80, 236). Some of the illustrated manuscripts dating from this era show a large bird of prey, with massive claws, carrying off elephants (Figure 71). As elephants do not occur on Madagascar, and if the illustration has its origins from that island, there is certainly a fantastic aspect to it. On the other hand, if the source of the *rokh* legend is indeed Madagascar, the possibility is that it stems from observations of *Stephanoaetus mahery* cannot be excluded.

# References

1. Abbott, D. H., Bryant, E. F., Gusiakov, V., Masse, W. B. & Breger, D. 2008. Comment: Impacts, mega-tsunami, and other extraordinary claims. *GSA Today*, 18: 12. doi: 10.1130/GSATG9C.1
2. Ali, J. R. & Aitchison, J. C. 2008. Gondwana to Asia: Plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through latest Eocene (166–35 Ma). *Earth-Science Reviews*, 88: 145–166.
3. Ali, J. R. & Huber, M. 2010. Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature*, 463: 653–656.
4. Ali, J. R. & Krause, D. W. 2011. Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: Refutation of the Gunnerus Ridge causeway hypothesis. *Journal of Biogeography*, 38: 1855–1872.
5. Allentoft, M. E., Bunce, M., Scofield, R. P., Hale, M. L. & Holdaway, R. N. 2010. Highly skewed sex ratios and biased fossil deposition of moa: Ancient DNA provides new insight on New Zealand's extinct megafauna. *Quaternary Science Reviews*, 29: 753–762.
6. Allibert, C. 1992. Le monde austronésien et la civilisation du bambou: Une plume qui pèse lourd: l'oiseau Rokh des auteurs arabes. *Taloha*, 11: 167–181.
7. Amadon, D. 1947. An estimated weight of the largest known bird. *Condor*, 49: 159–164.
8. Andrews, C. W. 1897. On some fossil remains of carinate birds from central Madagascar. *Ibis*, seventh series, 3: 343–359.
9. Andrianarimisa, A., Andrianjakarivelo, V., Rakotomalala, Z. & Anjeriniaina, M. 2009. Vertébrés terrestres des fragments forestiers de la Montagne d'Ambatotsirongorongo, site dans le Système des Aires Protégées de Madagascar de la Région Anosy, Tolagnaro. *Malagasy Nature*, 2: 30–51.
10. Andriatsimietry, R., Goodman, S. M., Razafimahatratra, E., Jeglinski, J. W. E., Marquard, M. & Ganzhorn, J. U. 2009. Seasonal variation in the diet of *Galidictis grandieri* Wozencraft, 1986 (Carnivora: Eupleridae) in a sub-arid zone of extreme southwestern Madagascar. *Journal of Zoology*, London, 279: 410–415.
11. Anonymous. 1895. Une dépêche de Majunga du 25 avril dit que les Hovas ont fusillé un Français nommé Grevé et martyrisé un créole du nom de Joseph. *Le Petit Parisien* (Paris), 27 April 1995.
12. Anonymous. 1921 (for 1919). Procès-verbaux. Séance du 27 février 1919. *Bulletin de l'Académie Malgache*, nouvelle série, 4: 48–49.
13. Appert, O. 1966. La distribution géographique des lémurins diurnes de la région du Mangoky au sud-ouest de Madagascar. *Bulletin de l'Académie Malgache*, 44: 43–45.
14. Arnold, E. N. 1979. Indian Ocean giant tortoises: Their systematics and island adaptations. *Philosophical Transactions of the Royal Society of London B*, 286: 127–145.
15. Austin, J. J., Arnold, E. N. & Bour, R. 2003. Was there a second adaptive radiation of giant tortoises in the Indian Ocean? Using mitochondrial DNA to investigate speciation and biogeography of *Aldabrachelys* (Reptilia, Testudinidae). *Molecular Ecology*, 12: 1415–1424.
16. Balanoff, A. M. & Rowe, T. 2007. Osteological description of an embryonic skeleton of the extinct elephant bird, *Aepyornis* (Palaeognathae: Ratitae). *Journal of Vertebrate Paleontology*, Memoir 9, 27 (supplement to number 4): 1–53.
17. Ballhorn, D. J., Kautz, S. & Rakotoarivelo, F. P. 2009. Quantitative variability of cyanogenesis in *Cathariostachys madagascariensis*—the main food plant of bamboo lemurs in southeastern Madagascar. *American Journal of Primatology*, 71: 305–315.
18. Banister, K. E. 1994. *Glossogobius ankaranensis*, a new species of blind cave goby from Madagascar. *Journal of Ichthyology & Aquatic Biology*, 1 (3): 25–28.
19. Banks, M. A., Ellis, E. R., Antonio & Wright, P. C. 2007. Global population size of a critically endangered lemur, Perrier's sifaka. *Animal Conservation*, 10: 254–262.
20. Barrett, M. A., Brown, J. L., Junge, R. E. & Yoder, A. D. 2013. Climate change, predictive modeling and lemur health: Assessing impacts of changing climate on health and conservation in Madagascar. *Biological Conservation*, 157: 409–422.
21. Barthère, F.-M. 1915. Observations sur une Hache en os, provenant des fouilles exécutées par l'Académie Malgache, à Ampasambazimba en 1908 (Madagascar). *Bulletin de la Société Préhistorique Française*, 12: 358–361.
22. Battistini, R. 1965. Problèmes géomorphologiques de l'Extrême Nord de Madagascar. *Madagascar, Revue de Géographie*, 7: 1–61.
23. Battistini, R. & Verin, P. 1967. Ecologic changes in protohistoric Madagascar. In *Pleistocene extinctions: The search for a cause*, eds. P. S. Martin & H. E. Wright Jr., pp. 407–424. Yale University Press, New Haven.
24. Battistini, R. & Verin, P. 1971. Témoignages archéologiques sur la côte vezo de l'embouchure de l'Onilahy à la baie des Assassins. *Taloha*, 4: 51–63.



25. Battistini, R., Vérin, P. & Rason, R. 1963. Le site archéologique de Talaky. *Annales Malgaches*, 1: 111–153.
26. Beaujard, P. 2011. The first migrants to Madagascar and their introduction of plants: Linguistic and ethnological evidence. *Azania*, 46: 169–189.
27. Berger, L. R. & Clarke, R. J. 1995. Eagle involvement in accumulation of the Taung child fauna. *Journal of Human Evolution*, 29: 275–299.
28. Bertram, B. C. R. 1992. *The ostrich communal nesting system*. Princeton University Press, Princeton, New Jersey.
29. Bickelmann, C. & Klein, N. 2009. The late Pleistocene horned crocodile *Voay robustus* (Grandidier & Vaillant, 1872) from Madagascar in the Museum für Naturkunde Berlin. *Fossil Record*, 12: 13–21.
30. Blake, S., Wikelski, M., Cabrera, F., Guezou, A., Silva, M., Sadeghayobi, E., Yackulic, C. B. & Jaramillo, P. 2012. Seed dispersal by Galápagos tortoises. *Journal of Biogeography*, 39: 1961–1972.
31. Blench, R. 2010. New evidence for the Austronesian impact on the East African coast. In *The global origins and development of seafaring*, eds. C. Anderson, J. Barrett & K. Boyle, pp. 239–248. McDonald Institute for Archaeological Research, Cambridge.
32. Bölsche, W. 1900. *Tiere der Urwelt*. Verlag der Kakao-Compagnie, Hamburg.
33. Boisserie, J.-R. 2005. The phylogeny and taxonomy of Hippopotamidae (Mammalia: Artiodactyla): A review based on morphology and cladistic analysis. *Zoological Journal of the Linnean Society*, 143: 1–26.
34. Bond, W. J. & Silander, J. A. 2007. Springs and wire plants: Anachronistic defences against Madagascar's extinct elephant birds. *Proceedings of the Royal Society B*, 274: 1985–1992.
35. Bond, W. J., Silander, J. A., Ranaivonasy, J. & Ratsirarson, J. 2008. The antiquity of Madagascar's grasslands and the rise of C<sub>4</sub> grassy biomes. *Journal of Biogeography*, 35: 1743–1758.
36. Bour, R. 1994. *Recherches sur des animaux doublement disparus: Les tortues géantes subfossiles de Madagascar*. Ecole Pratique des Hautes Etudes, Montpellier.
37. Bourgeois, J. & Weiss, R. 2009. "Chevrons" are not mega-tsunami deposits—a sedimentologic assessment. *Geology*, 37: 403–406.
38. Bradbury, W. C. 1919. Some notes on the egg of *Aepyornis maximus*. *The Condor*, 21: 97–101.
39. Brochu, C. A. 2007. Morphology, relationships, and biogeographical significance of an extinct horned crocodile (Crocodylia, Crocodylidae) from the Quaternary of Madagascar. *Zoological Journal of the Linnean Society*, 150: 835–863.
40. Brodkorb, P. 1963. Catalogue of fossil birds. Part 1 (Archaeopterygiformes through Ardeiformes). *Bulletin of the Florida State Museum*, 7: 179–293.
41. Brook, G. A., Rafter, M. A., Railsback, L. B., Sheen, S.-W. & Lundberg, J. 1999. A high-resolution proxy record of rainfall and ENSO since AD 1550 from layering in stalagmites from Anjohibe Cave, Madagascar. *The Holocene*, 9: 695–705.
42. Brown, L. H., Urban, E. K. & Newman, K. 1982. *The birds of Africa*, volume 1. Academic Press, New York.
43. Burney, D. A. 1987. Pre-settlement vegetation changes at Lake Tritrivakely, Madagascar. *Palaeoecology of Africa and the Surrounding Islands*, 18: 357–381.
44. Burney, D. A. 1987. Late Holocene vegetational change in central Madagascar. *Quaternary Research*, 28: 130–143.
45. Burney, D. A. 1988. Modern pollen spectra from Madagascar. *Paleogeography, Paleoclimatology, Paleocology*, 66: 63–75.
46. Burney, D. A. 1993. Late Holocene environmental change in arid southwestern Madagascar. *Quaternary Research*, 40: 98–106.
47. Burney, D. A. 1997. Theories and facts regarding Holocene environmental change before and after human colonization. In *Natural change and human impact in Madagascar*, eds. S. M. Goodman & B. D. Patterson, pp. 75–89. Smithsonian Institution Press, Washington, D. C.
48. Burney, D. A. 1999. Rates, patterns, and processes of landscape transformation and extinction in Madagascar. In *Extinction in near time*, ed. R. D. E. MacPhee, pp. 145–164. Kluwer/Plenum, New York.
49. Burney, D. A. & Flannery, T. F. 2005. Fifty millennia of catastrophic extinctions after human contact. *Trends in Ecology and Evolution*, 20: 395–401.
50. Burney, D. A. & Ramilisonina. 1998. The *kilopilopitsofy*, *kidoky*, and *bokyboky*: Accounts of strange animals from Belo-sur-Mer, Madagascar, and the megafaunal "extinction window." *American Anthropologist*, 100: 957–966.
51. Burney, D. A., Burney, L. P., Griffin, W., Wright, H. T., James, H. F., Jungers, W. L., MacPhee, R. D. E., Rafamantanantsoa, J.-G., Rakotondrazafy, T., Ramilisonina, Warren, D. & Yoder, A. D. 1996. Belo-sur-Mer and other integrated sites from Holocene Madagascar. In *Abstracts of papers, 9–12 June 1996. Six North American Paleontological Convention Abstracts of Papers*, p. 56. Washington, D. C.
52. Burney, D. A., James, H. F., Grady, F. V., Rafamantanantsoa, J.-G., Ramilisonina, Wright, H. T. & Cowart, J. B. 1997. Environment change, extinction and human activity: Evidence from caves in NW Madagascar. *Journal of Biogeography*, 24: 755–767.
53. Burney, D. A., Robinson, G. S. & Burney, L. P. 2003. *Sporormiella* and the late Holocene extinctions in Madagascar. *Proceedings of the National Academy of Sciences, USA*, 100: 10800–10805.
54. Burney, D. A., Burney, L. P., Godfrey, L. R., Jungers, W. L., Goodman, S. M., Wright, H. T. & Jull, A. J. T. 2004. A chronology for late Prehistoric Madagascar. *Journal of Human Evolution*, 47: 25–63.
55. Burney, D. A., Vasey, N., Godfrey, L. R., Ramilisonina, Jungers, W. L., Ramarolahy, M. & Raharivony, L. 2008. New findings at Andrahomana Cave, southeastern Madagascar. *Journal of Cave and Karst Studies*, 70: 13–24.
56. Callmander, M. W., Laivao, M. O. & Randrianaivo, R. 2010. A new species of Pandanaceae from northern Madagascar, *Pandanus ankaranensis*. *Novon*, 20: 243–247.
57. Cardiff, S. G. 2006. *Bat cave selection and conservation in Ankarana, northern Madagascar*. Master's thesis, Columbia University, New York.
58. Cardiff, S. & Befourouack, J. 2003. The Réserve Spéciale d'Ankarana. In *The natural history of Madagascar*

- car, eds. S. M. Goodman & J. P. Benstead, pp. 1501–1507. University of Chicago Press, Chicago.
- 59.** Cardiff, S. G., Ratrimomanarivo, F. H., Rembert, G. & Goodman, S. M. 2009. Hunting, roost disturbance and roost site persistence of bats in caves at Ankarana, northern Madagascar. *African Journal of Ecology*, 47: 640–649.
- 60.** Carleton, M. D., Goodman, S. M. & Rakotondravony, D. 2001. A new species of tufted-tailed rat, genus *Eliurus* (Muridae: Nesomyinae), from western Madagascar, with notes on the distribution of *E. myoxinus*. *Proceedings of the Biological Society of Washington*, 114: 972–987.
- 61.** Caudey, H. 1931. Etude sur l'*Aepyornis*. *L'Oiseau et la Revue française d'Ornithologie*, 1: 624–644.
- 62.** Chanudet, C. 1975. *Conditions géographiques et archéologiques de la disparition des subfossiles malgaches*. Mémoire de maîtrise, Université de Bretagne Occidentale, Brest.
- 63.** Clarke, J. A., Tambussi, C. P., Noriega, J. I., Erickson, G. M. & Ketchum, R. A. 2005. Definitive fossil evidence for the extant avian radiation in the Cretaceous. *Nature*, 433: 305–308.
- 64.** Clarke, S. J., Miller, G. H., Fogel, M. L., Chivas, A. R. & Murray-Wallace, C. V. 2006. The amino acid and stable isotope biogeochemistry of elephant bird (*Aepyornis*) eggshells from southern Madagascar. *Quaternary Science Reviews*, 25: 2343–2356.
- 65.** Coe, M. J., Bourn, D. & Swingland, I. R. 1979. The biomass, production and carrying capacity of giant tortoises on Aldabra. *Philosophical Transactions of the Royal Society B*, 286: 163–176.
- 66.** Colquhoun, I. C. 2006. Predation and cathemerality. Comparing the impact of predators on the activity patterns of lemurs and ceboids. *Folia Primatologica*, 77: 143–165.
- 67.** Cooper, A., Lalueza-Fox, C., Anderson, S., Rambaut, A., Austin, J. & Ward, R. 2001. Complete mitochondrial genome sequences of two extinct moas clarify ratite evolution. *Nature*, 409: 704–707.
- 68.** Cox, M. P., Nelson, M. G., Tumonggor, M. K., Ricaut, F. X. & Sudoyo, H. 2012. A small cohort of island southeast Asian women founded Madagascar. *Proceedings of the Royal Society B*, 279: 2761–2768.
- 69.** Crowley, B. E. 2010. A refined chronology of prehistoric Madagascar and the demise of the megafauna. *Quaternary Science Reviews*, 29: 2591–2603.
- 70.** Crowley, B. E. & Godfrey, L. R. 2013. Why all those spines? Anachronistic defences in the Didieroidea against now extinct lemurs. *South African Journal of Science*, 109: 1–7.
- 71.** Crowley, B. E. & Samonds, K. E. 2013. Stable carbon isotope values confirm a recent increase in grasslands in northwestern Madagascar. *The Holocene*, 23: 1066–1073.
- 72.** Crowley, B. E., Godfrey, L. R. & Irwin, M. T. 2011. A glance to the past: Subfossils, stable isotopes, seed dispersal, and lemur species loss in southern Madagascar. *American Journal of Primatology*, 73: 25–37.
- 73.** Crowley, B. E., Godfrey, L. R., Guilderson, T. P., Zermeno, P., Koch, P. L. & Dominy, N. J. 2012. Extinction and ecological retreat in a community of primates. *Proceedings of the Royal Society B*, 279: 3597–3605.
- 74.** Csermely, D. 1996. Antipredator behavior in lemurs: Evidence of an extinct eagle on Madagascar or something else? *International Journal of Primatology*, 17: 349–354.
- 75.** Dahl, O. 1951. *Malgache et Maanyan*. Egede Instituttet, Oslo.
- 76.** Davies, S. J. J. F. 1978. The food of emus. *Austral Ecology*, 3: 411–422.
- 77.** Davis, A. P. & Rakotonasolo, F. 2001. Two new species of *Coffea* L. (Rubiaceae) from northern Madagascar. *Adansonia*, 23: 337–345.
- 78.** Decary, R. 1927. Une mission scientifique dans le Sud-est de Madagascar. *Bulletin de l'Académie Malgache*, nouvelle série, 9: 79–86.
- 79.** Decary, R. 1934. Les grottes d'Anjohibe. *La Revue de Madagascar*, 8: 81–85.
- 80.** Decary, R. 1937. La légende du Rokh et l'*Aepyornis*. *Bulletin de l'Académie Malgache*, nouvelle série, 20: 107–113.
- 81.** De Saint-Ours, J. & Paulian, R. 1953. *Les grottes d'Andranoboka*. L'Institut de Recherche Scientifique, Antananarivo.
- 82.** Dewar, R. E. 1984. Extinctions in Madagascar: The loss of the subfossil fauna. In *Pleistocene extinctions: The search for a cause*, eds. P. S. Martin & R. G. Klein, pp. 574–593. Yale University Press, New Haven.
- 83.** Dewar, R. E. 1997. Were people responsible for the extinction of Madagascar's subfossils, and how will we ever know? In *Natural change and human impact in Madagascar*, eds. S. M. Goodman & B. P. Patterson, pp. 364–377. Smithsonian Institution Press, Washington, D. C.
- 84.** Dewar, R. E. & Rakotovololona, S. 1992. La chasse aux subfossiles: Les preuves de XI<sup>ème</sup> siècle au XIII<sup>ème</sup> siècle. *Taloha*, 11: 4–15.
- 85.** Dewar, R. E. & Richard, A. F. 2012. Madagascar: A history of arrivals, what happened, and will happen next. *Annual Reviews of Anthropology*, 41: 495–517.
- 86.** Dewar, R. E. & Wright, H. E. 1993. The culture history of Madagascar. *Journal of World Prehistory*, 7: 417–466.
- 87.** Dewar, R. E., Radimilahy, C., Wright, H. T., Jacobs, Z., Berna, F. & Kelly, G. 2013. Stone tools and foraging in northern Madagascar challenge Holocene extinction models. *Proceedings of the National Academy of Sciences, USA*, 110: 12583–12588.
- 88.** de Wit, M. 2003. Madagascar: Heads it's a continent, tail it's an island. *Annual Review of Earth Planetary Science*, 31: 213–248.
- 89.** Diallo, B. O., Joly, H. I., McKey, D., Hossaert-McKey, M. & Chevallier, M. H. 2007. Genetic diversity of *Tamarindus indica* populations: Any clues on the origin from its current distribution? *African Journal of Biotechnology*, 6: 853–860.
- 90.** Dollar, L. J., Ganzhorn, J. U. & Goodman, S. M. 2006. Primates and other prey in the seasonally variable diet of *Cryptoprocta ferox* in the dry deciduous forest of western Madagascar. In *Primate anti-predator strategies*, eds. S. L. Gursky & K. A. I. Nekaris, pp. 63–76. Springer Press, New York.
- 91.** Domergue, C. 1974. Considérations sur la minéralisation des eaux de l'extrême sud. *Bulletin de l'Académie Malgache*, 52: 119–125.
- 92.** Donati, G. & Borgognini-Tarli, S. M. 2006. From dark-

ness to daylight: Cathemeral activity in primates. *Journal of Anthropological Sciences*, 84: 1–11.

93. Dorr, L. J. 1997. *Plant collectors in Madagascar and the Comoro islands*. Royal Botanic Gardens, Kew.
94. Dransfield, S. 2003. Poaceae, Bambuseae, bamboos. In *The natural history of Madagascar*, eds. S. M. Goodman & J. P. Benstead, pp. 467–471. University of Chicago Press, Chicago.
95. Dumont, E. R., Ryan, T. M. & Godfrey, L. R. 2011. The *Hadropithecus* conundrum reconsidered, with implications for interpreting diet in fossil hominins. *Proceedings of the Royal Society B*, 278: 3654–3661.
96. Ekblom, T. 1953. Studien über subfossile Lemuren von Madagaskar. *Bulletin of the Geological Institute of Uppsala*, 34: 123–190.
97. Eagles, G. & Konig, M. 2008. A model of plate kinematics in Gondwana breakup. *Geophysical Journal International*, 173: 703–717.
98. Faure, M. & Guérin, C. 1990. *Hippopotamus laloumena* nov. sp., la troisième espèce d'hippopotame holocène de Madagascar. *Comptes Rendus de l'Académie des Sciences*, série 11, 310: 1299–1305.
99. Faure, M., Guérin, C., Genty, D., Gommery, D. & Ramanisova, B. 2010. Le plus ancien hippopotame fossile (*Hippopotamus laloumena*) de Madagascar (Belobaka, Province de Mahajanga). *Comptes Rendus Palévol*, 9: 155–162.
100. Feakins, S. J., Levin, N. E., Liddy, H. M., Sieracki, A., Eglinton, T. I. & Bonnefille, R. 2013. Northeast African vegetation change over 12 m.y. *Geology*, doi: 10.1130/G33845.1
101. Fichtel, C. & Kappeler, P. M. 2002. Anti-predator behavior of group-living Malagasy primates: Mixed evidence for a referential alarm call system. *Behavioral Ecology and Sociobiology*, 51: 262–275.
102. Filhol, H. 1895. Observations concernant les mammifères contemporains des *Aepyornis* à Madagascar. *Bulletin du Muséum National d'Histoire Naturelle*, Paris, 1: 12–14.
103. Fisher, D. 2011. The world's worst economies. *Forbes Magazine*, 5 July 2011.
104. Flacourt, E. de. 1658 [reprinted in 1995]. *Histoire de la Grande Isle Madagascar*. Edition présentée et annotée par Claude Allibert. INALCO-Karthala, Paris.
105. Fontoynt, M. 1909. Les gisements fossilifères d'Ampasambazimba. *Bulletin de l'Académie Malgache*, 6: 3–8.
106. Forsyth-Major, C. I. 1894. On *Megaladapis madagascariensis*, an extinct gigantic lemuroid from Madagascar, with remarks on the associated fauna, and on its geologic age. *Philosophical Transactions of the Royal Society of London B*, 185:15–38.
107. Fovet, W., Faure, M. & Guérin, C. 2011. *Hippopotamus guldbergi* n. sp: Révision du statut d'*Hippopotamus madagascariensis* Guldborg, 1883, après plus d'un siècle de malentendus et de confusions taxonomiques. *Zoosystema*, 33: 61–82.
108. Fritz, U., Branch, W. R., Gehring, P.-S., Harvey, J., Kindler, C., Meyer, L., Du Preez, L., Široký, P., Vieites, D. R. & Vences, M. 2012. Weak divergence among African,

Malagasy and Seychellois hinged terrapins (*Pelusios castanoides*, *P. subniger*) and evidence for human-mediated oversea dispersal. *Organisms, Diversity and Evolution*, doi: 10.1007/s13127-012-0113-3.

109. Gade, D. W. 1996. Deforestation and its effects in highland Madagascar. *Mountain Research and Development*, 16: 101–116.
110. Ganzhorn, J. U. 1994. Les lémuriens. Dans *Inventaire biologique Forêt de Zombitse*, eds. S. M. Goodman & O. Langrand. *Recherches pour le Développement, Série Sciences Biologiques*, No. Spécial: 70–72.
111. Ganzhorn, J. U. & Randriamanalina, M. H. 2003. Les lémuriens de la forêt de Mikea. Dans *Inventaire floristique et faunistique de la forêt de Mikea: Paysage écologique et diversité biologique d'une préoccupation majeure pour la conservation*, eds. A. P. Raselimanana & S. M. Goodman. *Recherches pour le Développement, Série Sciences Biologiques*, 21: 87–93.
112. Gardner, C. J., Fanning, E., Thomas, H. & Kidney, D. 2009. The lemur diversity of the Fiherenana–Manombo complex, southwest Madagascar. *Madagascar Conservation & Development*, 4: 38–43.
113. Gasse, F. & Van Campo, E. 1998. A 40,000 year pollen and diatom records from Lake Tritrivakely, Madagascar, in southern tropics. *Quaternary Research*, 49: 299–311.
114. Gasse, F. & Van Campo, E. 2001. Late Quaternary environmental changes from a pollen and diatom record in the southern tropics (Lake Tritrivakely, Madagascar). *Palaeogeography, Palaeoclimatology & Palaeoecology*, 167: 287–308.
115. Gasse, F., Cortijo, E., Disnar, J. R., Ferry, L., Gibert, E., Kissel, C., Laggoun-Defarge, F., Lallier-Vergès, E., Miskovsky, J. C., Ratsimbazafy, B., Ranaivo, F., Robison, L., Tucholka, P., Saos, J.-L., Sifeddine, A., Taieb, M., Van Campo, E. & Williamson, D. 1994. A 36 ka environmental record in the southern tropics: Lake Tritrivakely (Madagascar). *Comptes Rendus de l'Académie des Sciences*, Paris, série II, 318: 1513–1519.
116. Gautier, L. & Goodman, S. M. 2003. Introduction to the flora of Madagascar. In *The natural history of Madagascar*, eds. S. M. Goodman & J. P. Benstead, pp. 229–250. University of Chicago Press, Chicago.
117. Glander, K. E., Wright, P. C., Seigler, D. S., Randrianasolo, V. & Randrianasolo, B. 1989. Consumption of cyanogenic bamboo by a newly discovered species of bamboo lemur. *American Journal of Primatology*, 19: 119–124.
118. Glaw, F., Gehring, P.-S., Köhler, J., Franzen, M. & Vences, M. 2010. A new dwarf species of day gecko, genus *Phelsuma*, from the Ankarana pinnacle karst in northern Madagascar. *Salamandra*, 46 (2): 83–92.
119. Godfrey, L. R. 1986. The tale of the tsy-aomby-aomby. *The Sciences*, 1986: 49–51.
120. Godfrey, L. R. & Irwin, M. T. 2007. The evolution of extinction risk: Past and present anthropogenic impacts on the primate communities of Madagascar. *Folia Primatologica*, 78: 405–419.
121. Godfrey, L. R. & Jungers, W. L. 2002. Quaternary fossil lemurs. In *The primate fossil record*, ed. W. Hartwig, pp. 97–121. Cambridge University Press, New York.

122. Godfrey, L. R. & Jungers, W. L. 2003. The extinct sloth lemurs of Madagascar. *Evolutionary Anthropology*, 12: 252–263.
123. Godfrey, L. R. & Vuillaume-Randriamanantena, M. 1986. *Hapalemur simus*: Endangered lemur once widespread. *Primate Conservation*, 7: 92–96.
124. Godfrey, L. R., Simons, E. L., Chatrath, P. S. & Rakotosamimanana, B. 1990. A new fossil lemur (*Babakotia*, Primates) from northern Madagascar. *Comptes Rendus de l'Académie des Sciences*, Paris, série 2, 310: 81–87.
125. Godfrey, L. R., Jungers, W. L., Wunderlich, R. E. & Richmond, B. G. 1997. Reappraisal of the postcranium of *Hadropithecus* (Primates, Indroidea). *American Journal of Physical Anthropology*, 103: 529–556.
126. Godfrey, L. R., Jungers, W. L., Simons, E. L., Chatrath, P. S. & Rakotosamimanana, B. 1999. Past and present distributions of lemurs in Madagascar. In *New directions in lemur studies*, eds. B. Rakotosamimanana, H. Rasamimanana, J. U. Ganzhorn & S. M. Goodman, pp. 19–53. Kluwer Academic/Plenum Publishers, New York.
127. Godfrey, L. R., Simons, E. L., Jungers, W. L., DeBlieux, D. D. & Chatrath, P. S. 2004. New discovery of subfossil *Hapalemur simus*, the greater bamboo lemur in western Madagascar. *Lemur News*, 9: 9–11.
128. Godfrey, L. R., Semperebon, G. M., Jungers, W. L., Sutherland, M. R., Simons, E. L. & Solounias, N. 2004. Dental use wear in extinct lemurs: Evidence of diet and niche differentiation. *Journal of Human Evolution*, 47: 145–169.
129. Godfrey, L. R., Semperebon, G. M., Schwartz, G. T., Burney, D. A., Jungers, W. L., Flanagan, E. K., Cuozzo, F. P. & King, S. J. 2005. New insights into old lemurs: The trophic adaptations of the Archaeolemuridae. *International Journal of Primatology*, 26: 825–854.
130. Godfrey, L. R., Jungers, W. L., Burney, D. A., Ramilisonina, Wheeler, W., Lemelin, P., Shapiro, L. J., Schwartz, G. T., King, S. J., Ramarolahy, M. F., Raharivony, L. L. & Randria, G. F. N. 2006. New discoveries of skeletal elements of *Hadropithecus stenognathus* from Andrahomana Cave, southeastern Madagascar. *Journal of Human Evolution*, 51: 395–410.
131. Godfrey, L. R., Jungers, W. L. & Schwartz, G. T. 2006. Ecology and extinction of Madagascar's subfossil lemurs. In *Lemurs: Ecology and adaptation*, eds. L. Gould & M. L. Sauther, pp. 41–63. Springer, New York.
132. Godfrey, L. R., Jungers, W. L., Schwartz, G. T. & Irwin, M. T. 2008. Ghosts and orphans: Madagascar's vanishing ecosystems. In *Elwyn Simons: A search for origins*, eds. J. G. Fleagle & C. C. Gilbert, pp. 361–395. Springer, New York.
133. Godfrey, L. R., Jungers, W. L. & Burney, D. A. 2010. Subfossil lemurs of Madagascar. In *Cenozoic mammals of Africa*, eds. L. Werdelin & W. J. Sanders, pp. 351–367. University of California Press, Berkeley.
134. Gommery, D. & Ramanivosoa, B. 2011. Les lémuriens subfossiles dans le Nord-Ouest de Madagascar, du terrain à la diffusion des connaissances ou 15 ans de recherches franco-malgache. *Revue de Primatologie*, 3: 1–15.
135. Gommery, D., Ziegler, P., Ramanivosoa, B. & Cauvin, J. 1998. Découverte d'un nouveau site à lémuriens sub-fossiles dans les karsts malgaches. *Comptes Rendus de l'Académie des Sciences*, séries IIA, 326: 823–826.
136. Gommery, D., Senegas, F., Mein, P., Tombomiadana, S., Ramanivosoa, B., Cauvin, J. & Cauvin, C. 2003. Résultats préliminaires des sites subfossiles d'Antsingiavo (Madagascar). *Comptes Rendus Palevol*, 2: 639–648.
137. Gommery, D., Tombomiadana, S., Valentin, F., Ramanivosoa, B. & Bezoma, R. 2004. Nouvelle découverte dans le Nord-Ouest de Madagascar et répartition géographique des espèces du genre *Palaeopropithecus*. *Annales de Paléontologie*, 90: 279–286.
138. Gommery, D., Ramanivosoa, B., Tombomiadana-Raveloson, S., Randrianantenaina, H. & Kerloc'h, P. 2009. Une nouvelle espèce de lémurien géant subfossile du Nord-Ouest de Madagascar (*Palaeopropithecus kelyus*, Primates). *Comptes Rendus Palevol*, 8: 471–480.
139. Gommery, D., Ramanivosoa, B., Faure, M., Guerin, C., Kerloc'h, P., Ségas, F. & Randrianantenaina, H. 2011. Les plus anciennes traces d'activités anthropiques de Madagascar sur des ossements d'hippopotames subfossiles d'Anjohibe. *Comptes Rendus Palevol*, 10: 271–278.
140. Gommery, D., Senegas, F., Valentin, F., Ramanivosoa, B., Randriamantaina, H. & Kerloc'h, P. 2011. Madagascar. Premiers habitants et biodiversité passée. *Archéologie*, 494 (décembre): 40–49.
141. Goodman, S. M. 1994. Description of a new species of subfossil eagle from Madagascar: *Stephanoaetus* (Aves: Falconiformes) from the deposits of Ampasambazimba. *Proceedings of the Biological Society of Washington*, 107: 421–428.
142. Goodman, S. M. 1994. The enigma of antipredator behavior in lemurs: Evidence of a large extinct eagle on Madagascar. *International Journal of Primatology*, 15: 129–134.
143. Goodman, S. M. 1996. Description of a new species of subfossil lapwing (Aves, Charadriiformes, Charadriidae, Vanellinae) from Madagascar. *Bulletin du Muséum National d'Histoire Naturelle*, Paris, série 4, section C, 18: 607–614.
144. Goodman, S. M. 1999. Holocene bird subfossils from the sites of Ampasambazimba, Antsirabe and Ampoza, Madagascar: Changes in the avifauna of south central Madagascar over the past few millennia. In *Proceedings of the 22nd International Ornithological Congress*, Durban, eds. N. J. Adams & R. H. Slotow, pp. 3071–3083. BirdLife South Africa, Johannesburg.
145. Goodman, S. M. 1999. Description of the Réserve Naturelle Intégrale d'Andohahela, Madagascar, and the 1995 biological inventory of the reserve. In A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar, ed. S. M. Goodman. *Fieldiana: Zoology*, new series, 94: 1–9.
146. Goodman, S. M. 2000. A description of a new species of *Brachypteracias* (Family Brachypteraciidae) from the Holocene of Madagascar. *Ostrich*, 71: 318–322.
147. Goodman, S. M. 2003. Predation on lemurs. In *The natural history of Madagascar*, eds. S. M. Goodman & J. P. Benstead, pp. 1221–1228. University of Chicago Press, Chicago.

148. Goodman, S. M. 2011. *Les chauves-souris de Madagascar*. Association Vahatra, Antananarivo.
149. Goodman, S. M. 2012. *Les Carnivora de Madagascar*. Association Vahatra, Antananarivo.
150. Goodman, S. M. & Ganzhorn, J. U. 2004. Biogeography of lemurs in the humid forests of Madagascar: The role of elevational distribution and rivers. *Journal of Biogeography*, 31: 47–55.
151. Goodman, S. M. & Hawkins, A. F. A. 2008. Les oiseaux. Dans *Paysages naturels et biodiversité de Madagascar*, ed. S. M. Goodman, pp. 383–434. Muséum National d'Histoire Naturelle, Paris.
152. Goodman, S. M. & Rakotoarisoa, J.-A. 1998. Un regard sur l'utilisation historique et sur la régénération des habitats naturels à Madagascar. *Akon'ny Ala*, 24: 3–4.
153. Goodman, S. M. & Rakotondravony, D. 1996. The Holocene distribution of *Hypogeomys* (Rodentia: Muridae: Nesomyinae) on Madagascar. In *Biogéographie de Madagascar*, ed. W. R. Lourenço, pp. 283–293. Editions ORSTOM, Paris.
154. Goodman, S. M. & Rakotondravony, D. 2000. The effects of forest fragmentation and isolation on insectivorous small mammals (Lipotyphla) on the Central High Plateau of Madagascar. *Journal of Zoology*, London, 250: 193–200.
155. Goodman, S. M. & Rakotozafy, L. M. A. 1995. Evidence for the existence of two species of *Aquila* on Madagascar during the Quaternary. *Geobios*, 28: 241–246.
156. Goodman, S. M. & Rakotozafy, L. M. A. 1997. Subfossil birds from coastal sites in western and southwestern Madagascar: A paleoenvironmental reconstruction. In: *Natural change and human impact in Madagascar*, eds. S. M. Goodman & B. D. Patterson, pp. 257–279. Smithsonian Institution Press, Washington, D. C.
157. Goodman, S. M. & Raselimanana, A. 2003. Hunting of wild animals by Sakalava of the Menabe region: A field report from Kirindy-Mite. *Lemur News*, 8: 4–5.
158. Goodman, S. M. & Ravoavy, F. 1993. Identification of bird subfossils from cave surface deposits at Anjohibe, Madagascar, with a description of a new giant *Coua* (Cuculidae: Couinae). *Proceedings of the Biological Society of Washington*, 106: 24–33.
159. Goodman, S. M. & Soarimalala, V. 2004. A new species of *Microgale* (Lipotyphla: Tenrecidae: Oryzorictinae) from the Forêt des Mikea of southwestern Madagascar. *Proceedings of the Biological Society of Washington*, 117: 251–265.
160. Goodman, S. M. & Soarimalala, V. 2005. A new species of *Macrotarsomys* (Rodentia: Muridae: Nesomyinae) from the Forêt des Mikea of southwestern Madagascar. *Proceedings of the Biological Society of Washington*, 118: 450–464.
161. Goodman, S. M. & Sterling, E. J. 1996. The utilization of *Canarium* (Burseraceae) seeds by vertebrates in the Réserve Naturelle Intégrale d'Andringitra, Madagascar. In *A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation*, ed. S. M. Goodman. *Fieldiana: Zoology*, new series, 85: 83–89.
162. Goodman, S. M., Langrand, O. & Rasolonandrasana, B. P. N. 1997. The food habits of *Cryptoprocta ferox* in the high mountain zone of the Andringitra Massif, Madagascar (Carnivore, Viverridae). *Mammalia*, 61: 185–192.
163. Goodman, S. M., Raherilalao, M. J., Rakotomalala, D., Rakotondravony, D., Raselimanana, A. P., Razakarivony, H. V. & Soarimalala, V. 2002. Inventaire des vertébrés du Parc national de Tsimanampetsotsa (Toliara). *Akon'ny Ala*, 28: 1–36.
164. Goodman, S. M., Ganzhorn, J. U. & Rakotondravony, D. 2003. Introduction to the mammals. In *The natural history of Madagascar*, eds. S. M. Goodman & J. P. Benstead, pp. 1159–1186. University of Chicago Press, Chicago.
165. Goodman, S. M., Rasoloarison, R. M. & Ganzhorn, J. U. 2004. On the specific identification of subfossil *Cryptoprocta* (Mammalia, Carnivora) from Madagascar. *Zoosystema*, 26: 129–143.
166. Goodman, S. M., Andriafidison, D., Andrianaivoarivelo, R., Cardiff, S. G., Ifticene, E., Jenkins, R. K. B., Kofoky, A., Mbohoahy, T., Rakotondravony, D., Ranivo, J., Ratrimomanarivo, F., Razafimanahaka, J. & Racey, P. A. 2005. The distribution and conservation of bats in the dry regions of Madagascar. *Animal Conservation*, 8: 153–165.
167. Goodman, S. M., Jenkins, R. K. B. & Ratrimomanarivo, F. H. 2005. A review of the genus *Scotophilus* (Chiroptera: Vespertilionidae) on Madagascar, with the description of a new species. *Zoosystema*, 27: 867–882.
168. Goodman, S. M., Cardiff, S. G., Ranivo, J., Russell, A. L. & Yoder, A. D. 2006. A new species of *Emballonura* (Chiroptera: Emballonuridae) from the dry regions of Madagascar. *American Museum Novitates*, 3538: 1–24.
169. Goodman, S. M., Ratrimomanarivo, F. H. & Randrianandrianina, F. H. 2006. A new species of *Scotophilus* (Chiroptera: Vespertilionidae) from western Madagascar. *Acta Chiropterologica*, 8: 21–37.
170. Goodman, S. M., Vasey, N. & Burney, D. A. 2006. The subfossil occurrence and paleoecological implications of *Macrotarsomys petteri* (Rodentia: Nesomyidae) in extreme southeastern Madagascar. *Comptes Rendus Palevol*, 5: 953–962.
171. Goodman, S. M., Vasey, N. & Burney, D. A. 2007. Description of a new species of subfossil shrew-tenrec (Afrosoricida: Tenrecidae: *Microgale*) from cave deposits in extreme southeastern Madagascar. *Proceedings of the Biological Society of Washington*, 120: 367–376.
172. Goodman, S. M., Raheriarisena, M. & Jansa, S. A. 2009. A new species of *Eliurus* Milne Edwards, 1885 (Rodentia: Nesomyinae) from the Réserve Spéciale d'Ankarana, northern Madagascar. *Bonner zoologische Beiträge*, 56: 133–149.
173. Goodman, S. M., Raherilalao, M. J. & Block, N. L. 2011. Patterns of morphological and genetic variation in the *Mentocrex kiolooides* complex (Aves: Gruiformes: Rallidae) from Madagascar, with the description of a new species. *Zootaxa*, 2776: 49–60.
174. Gould, L. & Sauther, M. L. 2007. Anti-predator strategies in a diurnal prosimian, the ring-tailed lemur (*Lemur catta*), at the Beza Mahafaly Special Reserve, Madagascar. In *Primate anti-predator strategies*, eds. S. L. Gursky & K. A. I. Nekaris, pp. 275–288. Springer Press, New York.
175. Grandidier, A. 1868. Sur les découvertes zoologiques

faites récemment à Madagascar. *Annales des Sciences Naturelles*, 10: 375–378.

- 176.** Grandidier, G. 1900. Note sur des ossements d'animaux disparus, provenant d'Ambolisatra, sur la côte sud-est de Madagascar. *Bulletin du Muséum d'Histoire Naturelle*, 16: 214–218.
- 177.** Grandidier, G. 1901. Une nouvel édente subfossile de Madagascar. *Bulletin du Muséum d'Histoire Naturelle*, 7: 54–56.
- 178.** Grandidier, G. 1902. Observations sur les lémuriens disparus de Madagascar: Collections Alluaud, Gaubert, Grandidier. *Bulletin du Muséum d'Histoire Naturelle*, 8: 497–505, 587–592.
- 179.** Grandidier, G. 1903. Description de l'*Hypogeomys australis*, une nouvelle espèce de rongeur subfossile de Madagascar. *Bulletin du Muséum d'Histoire Naturelle*, 9: 13–15.
- 180.** Grandidier, G. 1905. Les animaux disparus de Madagascar. Gisements, époques et causes de leur disparition. *Revue de Madagascar*, 7: 111–128.
- 181.** Grandidier, G. 1905. Recherches sur les lémuriens disparus et en particulier sur ceux qui vivaient à Madagascar. *Nouvelles Archives du Muséum*, Paris, série 4, 7: 1–142.
- 182.** Grandidier, G. 1928. Description de deux nouveaux mammifères insectivores de Madagascar. *Bulletin du Muséum National d'Histoire Naturelle*, Paris, 34: 63–70.
- 183.** Grandidier, G. 1928. Une variété du *Cheiomys mada-gascariensis* actuel et un nouveau *Cheiomys* subfossile. *Bulletin de l'Académie Malgache*, 11: 101–107.
- 184.** Grassi, C. 2006. Variability in habitat, diet, and social structure of *Haplemur griseus* in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*, 131: 50–63.
- 185.** Green, G. M. & Sussman, R. W. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science*, 248: 212–215.
- 186.** Griffin, W. D. 2009. *The Matitanana archaeological project: Culture history and social complexity in the seven rivers region of southeastern Madagascar*. Ph.D. thesis, Anthropology, University of Michigan, Ann Arbor.
- 187.** Guldberg, G. A. 1883. Undersøgelser over en subfossil flodhest fra Madagascar. *Christiania Videnskabselskab forhandling* 6: 1–24 (in Riksmål).
- 188.** Gusiakov, V. Abbott, D. H., Bryant, E. A., Masse, W. B. & Breger, D. 2010. Mega tsunami of the world oceans: Chevron dune formation, micro-ejecta, and rapid climate change as the evidence of recent oceanic bolide impacts. In *Geophysical hazards*, ed. T. Beer, pp. 197–227. Springer, Berlin.
- 189.** Hamrick, M. W., Simons, E. L. & Jungers, W. L. 2000. New wrist bones of the Malagasy giant subfossil lemurs. *Journal of Human Evolution*, 38: 635–650.
- 190.** Hanssen, S. 2002. *The Ambohitantely Special Reserve in central high land Madagascar—Forest change and forest occurrence*. Masters thesis. Norwegian University of Science and Technology, Trondheim, Norway.
- 191.** Harper, G. J., Steininger, M. K., Tucker, C. J., Juhn, D. & Hawkins, F. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation*, 34: 325–333.

- 192.** Hawkins, A. F. A., Chapman, P., Ganzhorn, J. U., Bloxam, Q. C. M., Barlow, S. C. & Tonge, S. J. 1990. Vertebrate conservation in Ankarana Special Reserve, northern Madagascar. *Biological Conservation*, 54: 83–110.
- 193.** Heuvelmans, D. 1958. *On the track of unknown animals*. Rupert Hart-Davis, London.
- 194.** Holdaway, R. N. & Jacomb, C. 2000. Rapid extinction of the moas (Aves: Dinornithiformes): Model, test, and implications. *Science*, 287: 2250–2254.
- 195.** Holthuis, L. B. 1958. The troglobic Atyidae of Madagascar (*Crustacea Decapoda Natantia*). *Mémoires de l'Institut Scientifique de Madagascar*, série A, 11: 97–111.
- 196.** Houde, P., Cooper, A., Leslie, E., Strand, A. E. & Montañó, G. A. 1997. Phylogeny and evolution of 12S rDNA in Gruiformes (Aves). In *Avian molecular evolution and systematics*, ed. D. P. Mindell, pp. 121–158. Academic Press, San Diego.
- 197.** Humbert, H. 1927. Destruction d'une flore insulaire par le feu. *Mémoires de l'Académie Malgache*, 5: 1–80.
- 198.** Humbert, H. 1955. Les territoires phytogéographiques de Madagascar. In *Colloques internationaux du Centre National de la Recherche Scientifique*, LIX: Les divisions écologiques du monde, moyen d'expression, nomenclature, cartographie, Paris, 1954. *Année Biologique*, série 3, 31: 439–448.
- 199.** Hume, J. P. & Walters, M. 2012. *Extinct birds*. Poyser, London.
- 200.** Hurles, M. E., Sykes, B. C., Jobling, M. A. & Forster, P. 2005. The dual origin of the Malagasy in island south-east Asia and east Africa: Evidence from maternal and paternal lineages. *American Journal of Human Genetics*, 76: 894–901.
- 201.** Huynen, L., Gill, B. J., Millar, C. D. & Lambert, D. M. 2010. Ancient DNA reveals extreme egg morphology and nesting behavior in New Zealand's extinct moa. *Proceedings of the National Academy of Sciences, USA*, 107: 16201–16206.
- 202.** Janson, C. 1998. Testing the predation hypothesis for vertebrate sociality: Prospects and pitfalls. *Behaviour*, 135: 389–410.
- 203.** Jenkins, P. D. & Carleton, M. D. 2005. Charles Immanuel Forsyth Major's expedition to Madagascar, 1894 to 1896: Beginnings of modern systematic study of the island's mammalian fauna. *Journal of Natural History*, 39: 1779–1818.
- 204.** Jenny, D. 1996. Spatial organisation of leopards *Panthera pardus* in Taï National Park, Ivory Coast: Is rainforest habitat a 'tropical haven'? *Journal of Zoology*, London, 240: 427–440.
- 205.** Jernvall, J., Wright, P. C., Ravoavy, F. L. & Simons, E. L. 2003. Report on findings of subfossils at Ampoza and Ampanihy in southwestern Madagascar. *Lemur News*, 8: 21–23.
- 206.** Johnson, B. C. & Melosh, H. J. 2012. Impact spherules as a record of an ancient heavy bombardment of Earth. *Nature*, 484: 75–77.
- 207.** Jolly, C. J. 1970. *Hadropithecus*, a lemuroid small-object feeder. *Man*, new series, 5: 525–529.
- 208.** Jungers, W. L. 1978. The functional significance of skeletal allometry in *Megaladapis* in comparison to living



prosimians. *American Journal of Physical Anthropology*, 49: 303–314.

**209.** Jungers, W. L., Godfrey, L. R., Simons, E. L., Chatrath, P. S. & Rakotosamimanana, B. 1991. Phylogenetic and functional affinities of *Babakotia radofilai*, a new fossil lemur from Madagascar. *Proceedings of the National Academy of Sciences, USA*, 88: 9082–9086.

**210.** Jungers, W. L., Godfrey, L. R., Simons, E. L. & Chatrath, P. S. 1995. Subfossil *Indri indri* from the Ankarana Massif of northern Madagascar. *American Journal of Physical Anthropology*, 97: 357–366.

**211.** Jungers, W. L., Godfrey, L. R., Simons, E. L., Wunderlich, R. E., Richmond, B. G. & Chatrath, P. S. 2002. Ecomorphology and behavior of giant extinct lemurs from Madagascar. In *Reconstructing behavior in the primate fossil record*, eds. J. M. Plavcan, R. F. Kay, W. L. Jungers & C. P. van Schaik, pp. 371–411. Kluwer Academic/Plenum Publishers, New York.

**212.** Jungers, W. L., Demes, B. & Godfrey, L. R. 2008. How big were the “giant” extinct lemurs of Madagascar? In *Elwyn Simons: A search for origins*, eds. J. G. Fleagle & C. C. Gilbert, pp. 343–360. Springer, New York.

**213.** Kappeler, P. M. 2000. Lemur origins: Rafting by groups of hibernators? *Folia Primatologica*, 71: 422–425.

**214.** Karanth, K. P., Delefosse, T., Rakotosamimanana, B., Parsons, T. J. & Yoder, A. D. 2005. Ancient DNA from giant extinct lemurs confirms single origin of Malagasy primates. *Proceedings of the National Academy of Sciences, USA*, 102: 5090–5095.

**215.** Kaudern, W. 1918. Quartäre Fossilien aus Madagaskar. *Zoologisches Jahrbuch*, 41: 521–533.

**216.** Kelley, E. A., Sussman, R. W. & Muldoon, K. M. 2007. The status of lemur species at Antserananomby: An update. *Primate Conservation*, 22: 71–77.

**217.** Kellum-Ottino, M. 1972. Discovery of a Neolithic adze in Madagascar. *Asian Perspectives*, 15: 83–86.

**218.** Kirchman, J. J., Hackett, S. J., Goodman, S. M. & Bates, J. M. 2001. Phylogeny and systematics of the ground rollers (Brachypteraciidae) of Madagascar. *Auk*, 118: 849–863.

**219.** Klein, J. 2002. Deforestation in the Madagascar highlands—established ‘truth’ and scientific uncertainty. *Geojournal*, 56: 191–199.

**220.** Koechlin, J. 1968. Sur la signification des formations graminéennes à Madagascar et dans le monde tropical. *Annales de l'Université de Madagascar, série Sciences de la Nature et Mathématiques*, 6: 211–234.

**221.** Krause, D. W., Hartman, J. H. & Wells, N. A. 1997. Late Cretaceous vertebrates from Madagascar: Implications for biotic change in deep time. In: *Natural change and human impact in Madagascar*, eds. S. M. Goodman & B. D. Patterson, pp. 3–43. Smithsonian Institution Press, Washington, D. C.

**222.** Kull, C. A. 2002. The ‘degraded’ tapia woodlands of highland Madagascar: Rural economy, fire ecology, and forest conservation. *Journal of Cultural Geography*, 19: 95–128.

**223.** Kull, C. A. 2012. Air photo evidence of historical land cover change in the highlands: Wetlands and grasslands give way to crops and woodlots. *Madagascar Conservation and Development*, 7: 144–152.

**224.** Kull, C. A., Tassin, J., Moreau, S., Rakoto Ramiarantsoa, H., Blanc-Pamard, C. & Carrière, S. M. 2012. The introduced flora of Madagascar. *Biological Invasions*, 14: 875–888.

**225.** Lamberton, C. 1930. Contribution à la connaissance de la faune subfossile de Madagascar. Notes IV–VII. Lémuriens et Cryptoproctes. *Mémoires de l'Académie Malgache*, 27: 1–203.

**226.** Lamberton, C. 1931. Contribution à l'étude anatomique des *Aepyornis*. *Bulletin de l'Académie Malgache*, 13: 151–174.

**227.** Lamberton, C. 1934. Contribution à la connaissance de la Faune subfossile de Madagascar. Lémuriens et Ratites. *Mémoires de l'Académie Malgache*, 17: 1–168.

**228.** Lamberton, C. 1937. Fouilles paléontologiques faites en 1936. *Bulletin de l'Académie Malgache*, nouvelle série, 19: 1–19.

**229.** Lamberton, C. 1937 (1938). Contribution à la connaissance de la faune subfossile de Madagascar. Note III. Les Hadropithèques. *Bulletin de l'Académie Malgache*, nouvelle série, 27: 75–139.

**230.** Lamberton, C. 1946. Contribution à la connaissance de la faune subfossile de Madagascar. Note XV. *Plesiorcyteropus madagascariensis* Filhol. *Bulletin de l'Académie Malgache*, nouvelle série, 25: 25–53.

**231.** Lamberton, C. 1947. Contribution à la connaissance de la faune subfossile de Madagascar. Note XVI. *Bradytherium* ou *Palaeopropithecus*? *Bulletin de l'Académie Malgache*, nouvelle série, 26: 89–140.

**232.** Lamberton, C. 1957. Examen de quelques hypothèses de Sera concernant les lémuriens fossiles et actuels. *Bulletin de l'Académie Malgache*, nouvelle série, 34: 51–65.

**233.** Lane, E. W. (translator). 1841. *The thousand and one nights*, volume III. C. Knight & Co., London.

**234.** Lane, E. W. (translator). 1865. *The thousand and one nights*, volume III. Routledge, Warne, and Routledge, New York.

**235.** Langrand, O. & Wilmé, L. 1997. Effects of forest fragmentation on extinction patterns of the endemic avifauna on the Central High Plateau of Madagascar. In *Natural change and human impact in Madagascar*, eds. S. M. Goodman & B. D. Patterson, pp. 280–305. Smithsonian Institution Press, Washington, D. C.

**236.** Lavauden, L. 1931. Animaux disparus et légendaires de Madagascar. *Revue Scientifique, Paris*, 69: 297–308.

**237.** Lawler, R. R. 2008. Testing for a historical population bottleneck in wild Verreaux's sifaka (*Propithecus verreauxi*) using microsatellite data. *American Journal of Primatology*, 70: 1–5.

**238.** Lehman, S. M. & Mayor, M. 2004. Dietary patterns in Perrier's sifakas (*Propithecus diadema perrieri*): A preliminary study. *American Journal of Primatology*, 62: 115–122.

**239.** Lemelin, P., Hamrick, M. W., Richond, B. G., Godfrey, L. R., Jungers, W. L. & Burney, D. A. 2008. New hand bones of *Hadropithecus stenognathus*: Implications for the paleobiology of the Archaeolemuridae. *Journal of Human Evolution*, 54: 405–413.

**240.** Lorenz von Liburnau, L. R. 1899. Einen fossilen Anthropoiden von Madagaskar. *Anzeiger der Kaiserlichen Akademie der Wissenschaften Wien*, 19: 255–257.

- 241.** Lorenz von Liburnau, L. R. 1902. Ueber *Hadropithecus stenognathus* Lz. Nebst bemerkungen zu einigen anderen ausgestorbenen Primaten von Madagascar. *Denkschrift der Kaiserlichen Akademie der Wissenschaften Wien*, 72: 243–254.
- 242.** Lorenz von Liburnau, L. R. 1905. *Megaladapis edwardsi* G. Grandidier. *Denkschriften der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften zu Wien*, 77: 451–490.
- 243.** Louis Jr., E. E., Engberg, S. E., Lei, R., Geng, H., Sommer, J. A., Randriamampionona, R., Randriamanana, J. C., Zaonarivelo, J. R., Andriantompohavana, R., Randria, G., Prosper, Ramaromilanto, B., Rakotoarisoa, G., Rooney, A. & Brennenman, R. A. 2006. Molecular and morphological analyses of the sportive lemurs (Family Megaladapidae: Genus *Lepilemur*) reveals 11 previously unrecognized species. *Texas Tech University Special Publications*, 49: 1–49.
- 244.** Lourenço, W. R. & Goodman, S. M. 2008. Scorpions of the Réserve spéciale d'Ankarana, Madagascar, with particular reference to cave-dwelling animals and the description of two new species (Arachnida, Scorpiones). *Zoosystema*, 30: 665–679.
- 245.** Lowry II, P. P., Schatz, G. E. & Phillipson, P. B. 1997. The classification of natural and anthropogenic vegetation in Madagascar. In *Natural change and human impact in Madagascar*, eds. S. M. Goodman & B. D. Patterson, pp. 93–123. Smithsonian Institution Press, Washington, D. C.
- 246.** Lührs, M.-L. & Dammhahn, M. 2010. An unusual case of cooperative hunting in a solitary carnivore. *Journal of Ethology*, 28: 379–383.
- 247.** Lührs, M.-L., Dammhahn, M. & Kappeler, P. M. 2013. Strength in numbers: Males in a carnivore grow bigger when they associate and hunt cooperatively. *Behavioral Ecology*, 24: 21–28.
- 248.** Mack, A. L. 1995. *Seed dispersal by the Dwarf Casowary, Casuarium bennetti*, in Papua New Guinea. Ph.D. thesis, University of Miami, Coral Gables.
- 249.** MacPhee, R. D. E. 1986. The shrew tenrecs of Madagascar: Systematic revision and Holocene distribution of *Microgale* (Tenrecidae, Insectivora). *American Museum Novitates*, 2889: 1–45.
- 250.** MacPhee, R. D. E. 1994. Morphology, adaptations, and relationships of *Plesiorycteropus*, and a diagnosis of a new order of eutherian mammals. *Bulletin of the American Museum of Natural History*, 220: 1–214.
- 251.** MacPhee, R. D. E. & Burney, D. A. 1991. Dating of modified femora of extinct dwarf *Hippopotamus* from southern Madagascar: Implications for constraining human colonization and vertebrate extinction events. *Journal of Archaeological Science*, 18: 695–706.
- 252.** MacPhee, R. D. E. & Marx, P. A. 1997. The 40,000-year plague: Humans, hypervirulent diseases, and first-contact extinctions. In *Natural change and human impacts in Madagascar*, eds. S. M. Goodman & B. D. Patterson, pp. 169–217. Smithsonian Institution Press, Washington, D. C.
- 253.** MacPhee, R. D. E. & Raholimavo, E. M. 1988. Modified subfossil aye-aye incisors from southwestern Madagascar: Species allocation and paleoecological significance. *Folia Primatologica*, 51: 126–142.
- 254.** MacPhee, R. D. E., Simons, E. L., Wells, N. A. & Vuillaume-Randriamanantena, M. 1984. Team finds giant lemur skeleton. *Geotimes*, 29: 10–11.
- 255.** MacPhee, R. D. E., Burney, D. A. & Wells, N. A. 1985. Early Holocene chronology and environment of Ampasambazimba, a Malagasy subfossil lemur site. *International Journal of Primatology*, 6: 463–489.
- 256.** Mahé, J. 1965. *Les subfossiles Malgaches*. Imprimerie Nationales, Antananarivo.
- 257.** Mahé, J. & Sourdat, M. 1972. Sur l'extinction des vertébrés subfossiles et l'aridification du climat dans le Sud-ouest de Madagascar. *Bulletin de la Société Géologique de France*, 14: 295–309.
- 258.** Major, C. I. F. 1897. On the general results of a zoological expedition to Madagascar in 1894–96. *Proceedings of the Zoological Society of London*, 1896: 971–981.
- 259.** Major, C. I. F. 1902. Some account of a nearly complete skeleton of *Hippopotamus madagascariensis* Guld., from Sirabé, Madagascar, obtained in 1895. *Geological Magazine*, IX, 455: 193–199.
- 260.** Martin, P. S. 1966. Africa and Pleistocene overkill. *Nature*, 212: 339–342.
- 261.** Martin, P. S. 1967. Prehistoric overkill. In *Pleistocene extinctions: The search for a cause*, eds. P. S. Martin & H. E. Wright Jr., pp. 75–120. Yale University Press, New Haven.
- 262.** Martin, P. S. 1984. Prehistoric overkill: The global model. In *Quaternary extinctions: A prehistoric revolution*, eds. P. S. Martin & R. G. Klein, pp. 354–403. University of Arizona Press, Tucson.
- 263.** Martin, R. D. 1972. Adaptive radiation and behavior of the Malagasy lemurs. *Philosophical Transactions of the Royal Society B*, 264: 295–352.
- 264.** Masse, W. B. 2007. The archaeology and anthropology of Quaternary period cosmic impact. In *Comets/asteroid impacts and human society*, eds. P. T. Bobrowsky & H. Rickman, pp. 25–70. Springer Verlag, Berlin.
- 265.** Masse, W. B., Weaver, R. B., Abbott, D. H., Gusiakov, V. K. & Bryant, E. A. No date. Missing in action? Evaluating the putative absence of impacts by large asteroids and comets during the Quaternary period. <http://www.amostech.com/TechnicalPapers/2007/Poster/Masse.pdf>, last downloaded 26 June 2012.
- 266.** McGraw, W. S., Cooke, C. & Shultz, S. 2006. Primate remains from African Crowned Eagle (*Stephanoaetus coronatus*) nests in Ivory Coast's Tai Forest: Implications for primate predation and early hominid taphonomy in South Africa. *American Journal of Physical Anthropology*, 131: 151–165.
- 267.** Meier, B. & Rumpler, Y. 1987. A preliminary survey of *Hapalemur simus* and a new species of *Hapalemur* in eastern Betsileo, Madagascar. *Primate Conservation*, 8: 40–43.
- 268.** Mein, P., Sénégal, F., Gommery, D., Ramanivosoa, B., Randrianantenaina, H. & Kerloc'h, P. 2010. Nouvelles espèces subfossiles de rongeurs du Nord-Ouest de Madagascar. *Comptes Rendus Palevol*, 9: 101–112.
- 269.** Melluso, L., Sheth, H.C., Mahoney, J.J., Morra, V., Petrone, C.M. & Storey, M. 2009. Correlations between silicic volcanic rocks of the St Mary's Islands (southwestern India) and eastern Madagascar: Implications for Late Cretaceous India-Madagascar reconstructions. *Journal of the Geological Society*, 166: 283–294.

- 270.** Mendel, F. C. 1985. Use of hands and feet of three-toed sloth (*Bradypus variegatus*) during climbing and terrestrial locomotion. *Journal of Mammalogy*, 66: 359–366.
- 271.** Midgley, J. J. & Illing, N. 2009. Were Malagasy *Uncarina* fruits dispersed by the extinct elephant bird? *South African Journal of Science*, 105: 467–469.
- 272.** Milne Edwards, A. & Grandidier, A. 1894. Observations sur les *Æpyornis* de Madagascar. *Compte Rendus de l'Académie des Sciences*, Paris, 118: 122–127.
- 273.** Milne Edwards, A. & Grandidier, A. 1895. Sur des ossements d'oiseaux provenant des terrains récents de Madagascar. *Bulletin du Muséum d'Histoire Naturelle*, Paris, 1: 9–11.
- 274.** Mitani, J. C., Sanders, W. J., Lwanga, J. S. & Windfelder, T. L. 2001. Predatory behavior of crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, 49: 187–195.
- 275.** Mittermeier, R. A., Valladares-Pádua, C., Rylands, A. B., Eudey, A. A., Butynski, T. M., Ganzhorn, J. U., Kormos, R., Aguiar, J. M. & Walker, S. 2006. Primates in peril: The world's 25 most endangered primates, 2004–2006. *Primate Conservation*, 20: 1–28.
- 276.** Mlikovsky, J. 2006. Subfossil birds of Andrahomana, southeastern Madagascar. *Annalen des Naturhistorischen Museums in Wien*, 107A: 87–92.
- 277.** Moat, J. & Smith, P. 2007. *Atlas of the vegetation of Madagascar*. Royal Botanic Gardens, Kew.
- 278.** Monnier, L. 1913. Paléontologie de Madagascar. VII. Les *Aepyornis*. *Annales de Paléontologie*, 8: 125–172.
- 279.** Monnier, Dr. & Lambertson, C. 1922. Note sur des ossements subfossiles de la région de Mananjary. *Bulletin de l'Académie Malgache*, nouvelle série, 3 [for 1916–1917]: 211–212.
- 280.** Muldoon, K. M. 2010. Paleoenvironment of Ankilite Cave (late Holocene, southwestern Madagascar): Implications for the extinction of giant lemurs. *Journal of Human Evolution*, 58: 338–352.
- 281.** Muldoon, K. M., DeBlieux, D. D., Simons, E. L. & Chattrath, P. S. 2009. The subfossil occurrence and paleoecological significance of small mammals at Ankilite Cave, southwestern Madagascar. *Journal of Mammalogy*, 90: 1111–1131.
- 282.** Muldoon, K. M., Crowley, B. E., Godfrey, L. R., Ra-soamiaramanana, A., Aronson, A., Jernvall, J., Wright, P. C. & Simons, E. L. 2012. Early Holocene fauna from a new subfossil site: A first assessment from Christmas River, south central Madagascar. *Madagascar Conservation and Development*, 7: 23–29.
- 283.** Nussbaum, R. A. & Raxworthy, C. J. 1998. Revision of the genus *Ebenavia* Boettger (Reptilia: Squamata: Gekkonidae). *Herpetologica*, 54: 18–34.
- 284.** Olson, L. E., Rakotomalala, Z., Hildebrandt, K. B. P., Lanier, H. C., Raxworthy, C. J. & Goodman, S. M. 2009. Phylogeography of *Microgale brevicaudata* (Tenrecidae) and description of a new species from western Madagascar. *Journal of Mammalogy*, 90: 1095–1110.
- 285.** Omar, H., Adamson, E. A. S., Bhassu, S., Goodman, S. M., Soarimalala, V., Hashim, R. & Ruedi, M. 2011. Phylogenetic relationships of Malayan and Malagasy pygmy shrews of the genus *Suncus* (Soricomorpha: Soricidae) inferred from mitochondrial cytochrome *b* gene sequences. *Raffles Bulletin of Zoology*, 59: 237–243.
- 286.** Orlando, L., Calvignac, S., Schaub, C., Douadt, C. J., Godfrey, L. R. & Hanni, C. 2008. DNA from extinct giant lemurs links archaeolemurids to extant indriids. *BMC Evolutionary Biology*, 8: 121.
- 287.** Oskam, C. L., Haile, J., McLay, E., Rigby, P., Allentoft, M. E., Olsem, M. E., Bengtsson, C., Walter, R., Baynes, A., Dortch, J., Parker-Pearson, M., Gilbert, M. T. P., Holdaway, R. N., Willerslev, E. & Bunce, M. 2010. Fossil avian eggshell preserves ancient DNA. *Proceedings of the Royal Society B*, 277: 1991–2000.
- 288.** Palacios-Vargas, J. G. & Wilson, J. 1990. *Troglobius coprophagus*, a new genus and species of cave Collembola from Madagascar, with notes on its ecology. *International Journal of Speleology*, 18: 67–73.
- 289.** Palkovacs, E. P., Gerlach, J. & Caccone, A. 2002. The evolutionary origin of Indian Ocean tortoises (*Dipsochelys*). *Molecular Phylogenetics and Evolution*, 24: 216–227.
- 290.** Palkovacs, E. P., Marschner, M., Ciofi, C., Gerlach, J. & Caccone, A. 2003. Are the native giant tortoises from the Seychelles really extinct? A genetic perspective based on mtDNA and microsatellite data. *Molecular Ecology*, 12: 1403–1413.
- 291.** Pareliussen, I., Olsson, G. A. & Armbruster, W. S. 2006. Factors limiting the survival of native tree seedlings used in conservation efforts at the edges of forest fragments in upland Madagascar. *Restoration Ecology*, 14: 196–203.
- 292.** Parga, J. A., Sauter, M. L., Cuoizzo, F. P., Yousouf Jacky, I. A. & Lawler, R. R. 2012. Evaluating ring-tailed lemurs (*Lemur catta*) from southwestern Madagascar for a genetic population bottleneck. *American Journal of Physical Anthropology*, 147: 21–29.
- 293.** Parker Pearson, M., Godden, K., Ramilisonina, Retsihasetse, Schwenninger, J.-L., Huertebize, G., Radimilahy, C. & Smith, H. 2010. *Pastoralists, warriors and colonists: The archaeology of southern Madagascar*. Archaeopress, Oxford.
- 294.** Pedrono, M., Griffiths, O. L., Clausen, A., Smith, L. L., Griffiths, C. J., Wilmé, L. & Burney, D. A. 2013. Using a surviving lineage of Madagascar's vanished megafauna for ecological restoration. *Biological Conservation*, 159: 501–506.
- 295.** Pereira, M. E. & Macedonia, J. M. 1991. Ringtailed lemur anti-predator calls denote predator class, not response urgency. *Animal Behavior*, 41: 543–544.
- 296.** Perez, V. R., Godfrey, L. R., Nowak-Kemp, M., Burney, D. A., Ratsimbazafy, J. & Vasey, N. 2005. Evidence of early butchery of giant lemurs in Madagascar. *Journal of Human Evolution*, 49: 722–742.
- 297.** Perrier de la Bâthie, H. 1921. La végétation Malgache. *Annales du Musée Colonial de Marseille*, 9: 1–246.
- 298.** Perrier de la Bâthie, H. 1934. Au sujet de l'âge de la faune à *Æpyornis* et hippopotames. *Mémoire de l'Académie Malgache*, 17: 162–168.
- 299.** Perrier de la Bâthie, H. 1936. *Biogéographie des plantes à Madagascar*. Société d'Éditions Géographiques, Maritimes et Coloniales, Paris.

- 300.** Petit, G. 1933. Un poisson aveugle des eaux douces de Madagascar: *Typhleotris madagascariensis*. *Compte Rendus de l'Académie des Science*, Paris, 197: 347–348.
- 301.** Petit, G. 1935. Contribution à l'étude faunistique de la Réserve Naturelle du Manampetsa (Madagascar). *Annales des Sciences Naturelles, Zoologie*, série 10, 18: 421–481.
- 302.** Petit, G. 1935. Description d'un crâne de *Cryptoprocta* subfossile, suivie de remarques sur les affinités de genre *Cryptoprocta*. *Archives Muséum National d'Histoire Naturelle, Paris*, 12: 621–636.
- 303.** Petter, J.-J., Albignac, R. & Rimpler, Y. 1977. *Faune de Madagascar 44: Mammifères Lémuriens (Primates Prosimiens)*. ORSTOM/CNRS, Paris.
- 304.** Phillipson, P. B. 1996. Endemism and non endemism in the flora of south-west Madagascar. In *Biogéographie de Madagascar*, ed. W. R. Lourenço, pp. 125–136. Editions Orstom, Paris.
- 305.** Pinter, N. & Ishman, S. E. 2008. Impacts, megatsunami, and other extraordinary claims. *GSA Today*, 18: 37–38.
- 306.** Quéméré, E., Amelot, X., Pierson, J., Crouau-Roy, B. & Chikhi, L. 2012. Genetic data suggest a natural prehuman origin of open habitats in northern Madagascar and question the deforestation narrative in this region. *Proceedings of the National Academy of Sciences, USA*, 109: 13028–13033.
- 307.** Radofilao, J. 1977. Bilan des explorations spéléologiques de l'Ankarana. *Annales de l'Université de Madagascar, série Sciences de la Nature et Mathématiques*, 14: 195–204.
- 308.** Raison, J.-P. & Verin, P. 1968. Le Site de subfossiles de Taolambiby (Sud-ouest de Madagascar) doit-il être attribué à une intervention humaine ? : Observations à la suite d'une reconnaissance. *Annales de l'Université de Madagascar—Lettres*, 7: 133–142.
- 309.** Rakotoarisoa, J.-A. 1997. Evolution and interpretation of the archeological evidence. In *Natural change and human impact in Madagascar*, eds. S. M. Goodman & B. D. Patterson, pp. 331–341. Smithsonian Institution Press, Washington, D. C.
- 310.** Rakotoarisoa, J.-A. 2000. Souvenirs d'un étudiant devenu collègue. In *L'extraordinaire et le quotidien: Variations anthropologiques. Hommage du Professeur Pierre Verin*, eds. C. Allibert & N. Rajaonarimanana, pp. 595–602. Editions Karthala, Paris.
- 311.** Rakotoarisoa, J.-A. 2002. Madagascar. Background notes. In: *Objects as envoys: Cloth, imagery, and diplomacy in Madagascar*, eds. C. M. Kreamer & S. Fee, pp. 25–30. Smithsonian Institution, Washington, D. C.
- 312.** Rakotomalaza, P. J. & McKnight, M. 2006. Etude de la variation de la structure et de la composition floristique de la forêt des Mikeas du sud-ouest de Madagascar. *Phelsuma*, 14: 13–36.
- 313.** Rakotozafy, L. M. A. 1993. *Etude sur des Anotidae subfossiles et leur paléoenvironnement dans les Hauts-Plateaux Malgaches*. Mémoire Diplôme d'Etudes Approfondies, Faculté des Sciences, Université d'Antananarivo, Antananarivo.
- 314.** Rakotozafy, L. M. A. & Goodman, S. M. 2005. Contribution à l'étude zooarchéologique de la région du Sud-ouest et extrême Sud de Madagascar sur la base des collections de l'ICMAA de l'Université d'Antananarivo. *Taloha*, 14–15: <http://www.taloha.info/document.php?id=137>.
- 315.** Randrianarijaona, P. 1983. The erosion of Madagascar. *Ambio*, 12: 308–311.
- 316.** Rasamimanana, N., Ratsirarson, J. & Richard, A. F. 2012. Influence de la variabilité climatique sur la phénologie de la forêt de la Réserve Spéciale de Bezà Mahafaly. *Malagasy Nature*, 6: 67–82.
- 317.** Raselimanana, A. P., Raxworthy, C. J. & Nussbaum, R. A. 2000. A revision of the dwarf *Zonosaurus* Boulenger (Reptilia: Squamata: Cordylidae) from Madagascar, including descriptions of three new species. *Scientific Papers Natural History Museum University of Kansas*, 18: 1–16.
- 318.** Rasoloarison, R. M., Rasolonandrasana, B. P. N., Ganzhorn, J. U. & Goodman, S. M. 1995. Predation on vertebrates in the Kirindy Forest, western Madagascar. *Ecotropica*, 1: 59–65.
- 319.** Rasoloarison, R. M., Goodman, S. M. & Ganzhorn, J. U. 2000. Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. *International Journal of Primatology*, 21: 963–1019.
- 320.** Rasolofoson, D., Rakotondratsimba, G., Rakotonirainy, O., Rasolofoharivelo, T., Rakotozafy, L., Ratsimbazafy, J., Ratelolahy, F., Andriamaholy, V. & Saroy, A. 2007. Le bloc forestier de Makira charnière de lémuriens. *Lemur News*, 12: 49–53.
- 321.** Rasoloharijaona, S. 1999. Contribution à l'étude du genre *Archaeolemur* sp. (Archaeolemuridae): Un lémurien subfossile provenant de la région de l'Ankarana. Essai de reconstitution du paléoenvironnement de la région de l'Ankarana. *Lemur News*, 4: 7–10.
- 322.** Rasolohery, A. 2007. Western humid forest. In *Atlas of the vegetation of Madagascar*, eds. J. Moat & P. Smith, pp. 39–40. Royal Botanic Gardens, Kew.
- 323.** Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. A., Archibald, S., Lehmann, C. E. R., Anderson, M. T., Higgins, S. I. & Sankaran, M. 2011. When is a 'forest' a savanna, and why does it matter? *Global Ecology and Biogeography*, 20: 653–660.
- 324.** Ratvonamana, R. Y., Rajeriarison, C., Roger, E. & Ganzhorn, J. U. 2011. Phenology of different vegetation types in Tsimanampetsotsa National Park, southwestern Madagascar. *Malagasy Nature*, 5: 14–38.
- 325.** Ravenstein, E. G. 1898. The journal of the first voyage of Vasco da Gama, 1497–1499. Hakluyt Society, London.
- 326.** Raxworthy, C. J. & Nussbaum, R. A. 1997. Biogeographic patterns of reptiles in eastern Madagascar. In *Natural change and human impact in Madagascar*, eds. S. M. Goodman & B. D. Patterson, pp. 124–141. Smithsonian Institution Press, Washington, D. C.
- 327.** Razafimahefa Rasoanimanana, R., Nicoud, G., Mietton, N. & Paillet, A. 2012. Réinterprétation des Formations superficielles Pléistocènes du Bassin d'Antsirabe (Hautes Terres Centrales de Madagascar). *Quaternaire*, 23: 339–353.
- 328.** Roberts, R. G., Flannery, T. F., Ayliffe, L. K., Yoshida, H., Olley, J. M., Prideaux, G. J., Laslett, G. M., Baynes, A., Smith, M. A., Jones, R. & Smith, B. L. 2001. New ages for the last Australian megafauna: Continent-

wide extinction about 46,000 years ago. *Science*, 292: 1888–1892.

**329.** Rosaas, T. G. 1893. Recent discoveries of fossils at Antsirabe. *Antananarivo Annual*, 7: 111–114.

**330.** Rossi, G. 1974. Morphologie et évolution d'un karst en milieu tropical. L'Ankarana. *Mémoires et Documents Centre National de la Recherche Scientifique*, 15: 279–298.

**331.** Ryan, T. M., Burney, D. A., Godfrey, L. R., Gohlich, U. B., Jungers, W. L., Vasey, N., Ramilisonina, Walker, A. & Weber, G. W. 2008. A reconstruction of the Vienna skull of *Hadropithecus stenognathus*. *Proceedings of the National Academy of Sciences, USA*, 105: 10698–10701.

**332.** Sabatier, M. & Legendre, S. 1985. Une faune à rongeurs et chiroptères Plio-Pléistocènes de Madagascar. Actes du 110ème Congrès national des Sociétés savantes, Montpellier, Section des Sciences, 6: 21–28.

**333.** Samonds, K. E. 2007. Late Pleistocene bat fossils from Anjohibe Cave, northwestern Madagascar. *Acta Chiropterologica*, 9: 39–65.

**334.** Samonds, K. E., Parent, S. N., Muldoon, K. M., Crowley, B. E. & Godfrey, L. R. 2010. Rock matrix surrounding subfossil lemur skull yields diverse collection of mammalian subfossils: Implications for reconstructing Madagascar's paleoenvironments. *Malagasy Nature*, 4: 1–16.

**335.** Samonds, K. E., Godfrey, L. R., Ali, J. R., Goodman, S. M., Vences, M., Sutherland, M. R., Irwin, M. T. & Krause, D. W. 2013. Imperfect isolation: Factors and filters shaping Madagascar's modern vertebrate fauna. *PLOS One*, 8(4): e62086. doi:10.1371/journal.pone.0062086.

**336.** Sanders, W. J., Trapani, J. & Mitani, J. C. 2003. Taxonomic aspects of Crowned Hawk-eagle predation on monkeys. *Journal of Human Evolution*, 44: 87–105.

**337.** Sauther, M. L. 1989. Antipredator behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology*, 10: 595–606.

**338.** Schaik, C. P. van. 1983. Why are diurnal primates living in groups? *Behaviour*, 87: 120–144.

**339.** Schaik, C. P. van & Kappeler, P. M. 1996. The social systems of gregarious lemurs: Lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology*, 102: 915–941.

**340.** Schmid, J. & Rasoloarison, R. M. 2002. Lemurs of the Réserve Naturelle Intégrale d'Ankarafantsika, Madagascar. Dans Une évaluation biologique de la Réserve Naturelle Intégrale d'Ankarafantsika, Madagascar, eds. L. E. Alonso, T. S. Schulenberg, S. Radilofe & O. Missa. *Bulletin RAP d'Evaluation Rapide*, 23: 73–82.

**341.** Scott, J. R., Ungar, P. S., Jungers, W. L., Godfrey, L. R., Scott, R. S., Simons, E. L., Teaford, M. F. & Walker, A. 2009. Dental microwear texture analysis of two genera of subfossil lemurs from Madagascar. *Journal of Human Evolution*, 56: 405–416.

**342.** Sera, G. L. 1935. I caratteri morfologici di "*Paleopropithecus*" e l'adattamento acquatico primitivo dei Mammiferi e dei Primati in particolare. Contributo alla morfologia, all'filogenesi e alla paleobiologia dei Mammiferi. *Archivio Italiano di Anatomia e di Embriologia*, 35: 229–370.

**343.** Sera, G. L. 1950. Ulteriori osservazioni sui lemuri fos-

sili ed attuali Significato di alcuni caratteri in rapporto con l'evoluzione dei Primati. *Palaeontographia Italica*, nuova serie 17, 47: 1–97.

**344.** Shultz, S. 2002. Population density, breeding chronology and diet of Crowned Eagles *Stephanoaetus coronatus* in Tai National Park, Ivory Coast. *Ibis*, 144: 135–138.

**345.** Simons, E. L. 1997. Lemurs: Old and new. In *Natural change and human impact in Madagascar*, eds. S. M. Goodman & B. D. Patterson, pp. 142–166. Smithsonian Institution Press, Washington, D. C.

**346.** Simons, E. L., Godfrey, L. R., Vuillaume-Randriamanantena, M., Chatrath, P. S. & Gagnon, M. 1990. Discovery of new giant subfossil lemurs in the Ankarana Mountains of northern Madagascar. *Journal of Human Evolution*, 19: 311–319.

**347.** Simons, E. L., Godfrey, L. R., Jungers, W. L., Chatrath, P. S. & Rakotosamimanana, B. 1992. A new giant subfossil lemur *Babakotia* and the evolution of the sloth lemurs. *Folia Primatologica*, 58: 190–196.

**348.** Simons, E. L., Godfrey, L. R., Jungers, W. L., Chatrath, P. S. & Ravaoarisoa, J. 1995. A new species of *Mesopropithecus* (Primates, Palaeopropithecidae) from northern Madagascar. *International Journal of Primatology*, 16: 653–682.

**349.** Simons, E. L., Simons, V. F. H., Chatrath, P. S., Muldoon, K. M., Oliphant, M., Pistole, N. & Savvas, C. 2004. Research on subfossils in southwestern Madagascar and Ankilite Cave. *Lemur News*, 9: 12–16.

**350.** Simpson, G. G. 1952. Probabilities of dispersal in geologic time. *Bulletin of the American Museum of Natural History*, 99: 163–76.

**351.** Snow, N. W., Rabenantoandro, J., Randriatafika, F., Rabehevitra, D., Razafimamonjy & Cable, S. 2012. Studies of Malagasy *Eugenia* (Myrtaceae)—III: Seven new species of high conservation concern from the eastern littoral forests. *Phytotaxa*, 48: 39–60.

**352.** Soarimalala, V. & Goodman, S. M. 2008. New distributional records of the recently described and endangered shrew tenrec *Microgale nasoloi* (Tenrecidae: Afrosoricida) from central western Madagascar. *Mammalian Biology*, 73: 468–471.

**353.** Soarimalala, V. & Goodman, S. M. 2011. *Les petits mammifères de Madagascar*. Association Vahatra, Antananarivo.

**354.** Souvenir Zafindrajaona, P. & Lauvergne, J. J. 1993. Comparaison de populations de zébu malgache à l'aide des distances génétiques. *Genetics, Selection, and Evolution*, Paris, 25: 373–395.

**355.** Standing, H. F. 1905. Rapport sur des ossements sub-fossiles provenant d'Ampasambazimba. *Bulletin de l'Académie Malgache*, 4: 95–100.

**356.** Standing, H. F. 1908. On recently discovered subfossil primates from Madagascar. *Transactions of the Zoological Society of London*, 18: 59–162.

**357.** Struhsaker, T. & Leakey, M. 1990. Prey selectivity by crowned hawk-eagles on monkeys in the Kibale Forest, Uganda. *Behavioral Ecology and Sociobiology*, 26: 435–444.

**358.** Stuenkel, S. 1989. Taxonomy, habits, and relationships of the subfossil Madagascan hippopotami *Hippopotamus*

- lemerlei and *H. madagascariensis*. *Journal of Vertebrate Paleontology*, 9: 241–268.
- 359.** Tan, C. L. 1999. Group composition, home range size, and diet of three sympatric bamboo lemur species (genus *Haplemur*) in Ranomafana National Park, Madagascar. *International Journal of Primatology*, 20: 547–566.
- 360.** Tattersall, I. 1973. Cranial anatomy of the Archaeolemurinae (Lemuroidea, Primates). *Anthropological Papers of the American Museum of Natural History*, 52: 1–110.
- 361.** Tattersall, I. 2007. Madagascar's lemurs: Cryptic diversity or taxonomic inflation? *Evolutionary Anthropology*, 16: 12–23.
- 362.** Tattersall, I. & Schwartz, J. H. 1974. Craniodental morphology and the systematics of the Malagasy lemurs (Primates, Prosimii). *Anthropological Papers of the American Museum of Natural History*, 52: 139–192.
- 363.** Tofaneli, S. & Bertoini, S. 2010. Origin and evolutionary history of the Malagasy. In *Encyclopedia of life sciences*. John Wiley & Sons, Chichester. doi: 10.1002/9780470015902.a0022885
- 364.** Tovondrafale, T. 1994. *Contribution à la connaissance des Aepyornithidae: Etude de leurs œufs dans deux gisements de l'extrême Sud de Madagascar et discussion comparatives sur leur éco-éthologie et les causes de leur disparition*. Mémoire de Diplôme d'Etudes Approfondies, Université d'Antananarivo, Antananarivo.
- 365.** Trapani, J., Sanders, W., Mitani, J. C. & Heard, A. 2006. Precision and consistency of the taphonomic signature of predation by crowned hawk eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Palaio*, 21: 114–131.
- 366.** U. S. Geological Survey Geologic Names Committee. 2010. Divisions of geologic time—major chronostratigraphic and geochronologic units: U.S. Geological Survey fact sheet 2010–3059, downloaded 5 August 2012 from <http://pubs.usgs.gov/fs/2010/3059/>.
- 367.** Vallan, D. 2000. Influence of forest fragmentation on amphibian diversity in the nature reserve of Ambohitantely, highland Madagascar. *Biological Conservation*, 96: 31–43.
- 368.** Vasey, N. & Burney, D. A. 2007. Subfossil rodent species assemblages from Andrahomana Cave, south-eastern Madagascar: Evidence of introduced species and faunal turnover. Poster presentation made at a conference entitled “Rats, humans, and their impacts on islands”, held at the University of Hawai'i, Honolulu, 27–31 March 2007.
- 369.** Veress, M., Tóth, G., Zentai, Z. & Schläffer, R. 2009. The Ankarana tsingy and its development. *Carpathian Journal of Earth and Environmental Sciences*, 4: 95–108.
- 370.** Vérin, P. 1971. Les anciens habitats de Rezoky et d'Asambalahy. *Taloha*, 4: 29–49.
- 371.** Vérin, P. 1990. *Madagascar*. Karthala, Paris.
- 372.** Vérin, P. & Wright, H. T. 1999. Madagascar and Indonesia: New evidence from archaeology and linguistics. *Indo-Pacific Prehistory Association Bulletin*, 18: 35–42.
- 373.** Vidal Romani, J. R., Mosquera, D. F. & Campos, M. L. 2002. A 12,000 yr BP record from Andringitra Massif (southern Madagascar): Post-glacial environmental evolution from geomorphological and sedimentary evidence. *Quaternary International*, 93: 45–51.
- 374.** Virah-Sawmy, M., Willis, K. J. & Gillson, L. 2009. Threshold response of Madagascar's littoral forest to sea-level rise. *Global Ecology and Biogeography*, 18: 98–110.
- 375.** Vuillaume-Randriamanantena, M. 1988. The taxonomic attributions of giant subfossil lemur bones from Ampasambazimba: *Archaeoindris* and *Lemuridotherium*. *Journal of Human Evolution*, 17: 379–391.
- 376.** Vuillaume-Randriamanantena, M., Godfrey L. R., Jungers, W. L. & Simons, E. L. 1992. Morphology, taxonomy and distribution of *Megaladapis*: Giant subfossil lemur from Madagascar. *Comptes Rendus de l'Académie des Sciences, Paris, série II*, 315: 1835–1842.
- 377.** Yoder, A. D. & Nowak, M. D. 2006. Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annual Review of Ecology, Evolution, and Systematics*, 37: 405–431.
- 378.** Walker, A. C. 1967. Patterns of extinction among the subfossil Madagascan lemuroids. In *Pleistocene extinctions: The search for a cause*, eds. P. S. Martin & H. E. Wright Jr., pp. 425–432. Yale University Press, New Haven.
- 379.** Walker, A. C. 1967. *Locomotor adaptation in recent and subfossil Madagascan lemurs*. Ph.D. thesis, University of London, London.
- 380.** Walker, A. C. 1974. Locomotor adaptations in past and present prosimian primates. In *Primate locomotion*, ed. F. A. Jenkins Jr., pp. 349–381. Academic Press, New York.
- 381.** Walker, A. C. 2002. Looking for lemurs on the Great Red Island. In *Backcountry pilot: Flying adventures of Ike Russell*, ed. T. Bowen, pp. 99–104. University of Arizona Press, Tucson.
- 382.** Werdelin, L. 2010. Bibymalagasias (Mammalia *Incertae Sedis*). In *Cenozoic mammals of Africa*, eds. L. Werdelin & W. J. Sanders, pp. 113–114. University of California Press, Berkeley.
- 383.** Weston, E. M. & Lister, A. M. 2009. Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*. *Nature*, 459: 85–88.
- 384.** White, E. I. 1930. Fossil hunting in Madagascar. *Natural History Magazine*, 2 (15): 209–235.
- 385.** White, F. 1983. *The vegetation of Africa: A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa*. UNESCO, Paris.
- 386.** Whitehurst, A. S., Sexton, J. O. & Dollar, L. 2009. Land cover change in western Madagascar's dry deciduous forests: A comparison of forest changes in and around Kirindy Mite National Park. *Oryx*, 43: 275–283.
- 387.** Wilson, J. M. 1987. The crocodile caves of the Ankarana, Madagascar. *Oryx*, 21: 43–47.
- 388.** Wiman, C. 1935. Über Aepyornithes. *Nova Acta Regiae Societatis Scientiarum Upsaliensis*, series 4, 9, no. 12.
- 389.** Wood, J. R., Rawlence, N. J., Rogers, G. M., Austin, J. J., Worthy, T. H. & Cooper, A. 2008. Coprolite deposits reveal the diet and ecology of the extinct New Zealand megaherbivore moa (Aves, Dinornithiformes). *Quaternary Science Reviews*, 27: 2593–2602.
- 390.** Wood, J. R., Wilmshurst, J. M., Worthy, T. H. & Cooper, A. 2011. *Sporormiella* as a proxy for non-mammalian herbivores in island ecosystems. *Quaternary Science Reviews*, 30: 915–920.



- 391.** Worthy, T. H. & Holdaway, R. N. 2002. *The lost world of the moa*. Indiana University Press, Bloomington.
- 392.** Wozencraft, W. C. 1986. A new species of striped mongoose from Madagascar. *Journal of Mammalogy*, 67: 561–571.
- 393.** Wright, H. T. (ed.) 2007. Early state formation in Central Madagascar: An archeological survey of western Avaradrano. *Memoirs of the University of Michigan Museum of Anthropology*, 53: 1–311.
- 394.** Wright, P. C., Johnson, S. E., Irwin, M. T., Jacobs, R., Schlichting, P., Lehman, S., Louis Jr., E. E., Arrigo-Nelson, S. J., Raharison, J.-L., Rafalirarison, R. R., Razafindratsita, V., Ratsimbazafy, J., Ratelolahy, F. J., Dolch, R. & Tan, C. 2008. The crisis of the critically endangered Greater Bamboo Lemur (*Prolemur simus*). *Primate Conservation*, 23: 5–17.
- 395.** Wunderlich, R. E., Simons, E. L. & Jungers, W. L. 1996. New pedal remains of *Megaladapis* and their functional significance. *American Journal of Physical Anthropology*, 100: 115–138.
- 396.** Yoder, A. D., Burns, M. M., Zehr, S., Delefosse, T., Veron, G., Goodman, S. M. & Flynn, J. J. 2003. Single origin of Malagasy Carnivora from an African ancestor. *Nature*, 421: 734–737.
- 397.** Zinner, D., Ostner, J., Dill, A., Razafimanantsoa, L. & Rasoloarison, R. 2001. Results of a reconnaissance expedition in the western dry forests between Morondava and Morombe. *Lemur News*, 6: 16–18.

# Index to Malagasy Place-Names

*Note: Sections concerning thematic locality plates are in italics.*

- Alaotra, Lake, 36  
 Aldabra (atoll), 33, 34, 85  
 Ambalavao, 23, 41  
 Ambararata, 112  
 Ambariotelo (island), 39  
 Ambatotsirongorongo, 70  
 Ambohiposa, 43  
 Ambohitantely, 32, 54  
 Ambolisatra, 48, 50, 82, 89, 174, 178  
 Ambongonambakoa, 154  
 Ambositra, 126  
 Amparihingidro, 154, 169  
 Ampasambazimba, 13, 14, 15, 22, 31, 34, 35, 47, 48, 61, 105, 109, 127, 128, 129, 133–43, 152, 153, 154, 165, 169, 180, 184, 185  
 Ampoza, 14, 15, 67, 70, 93, 99, 102–11, 121, 129, 135, 153, 185  
 Analavelona (massif), 99, 100, 102, 103, 110, 111  
 Andapa, 171  
 Andasibe, 54  
 Andohahela (national park), 23, 66  
 Andonomby, 45, 180  
 Andrafiabe (cave), 163, 174  
 Andrahomana (cave), 13, 14, 15, 48, 65–78, 98, 138, 178  
 Andraikiba, 130  
 Andringitra (massif, national park), 22, 26, 27, 36, 54, 111, 180  
 Anjajavy, 13, 15, 157–61  
 Anjohibe (cave), 9, 13, 15, 36, 50, 70, 116, 129, 138, 144–56, 157, 158, 165, 166, 169  
 Anjohikely, 153  
 Ankaivo, 112  
 Ankarafantsika (national park), 28, 153  
 Ankarana (massif, national park), 13, 15, 27, 109, 121, 138, 146, 153, 154, 159, 162–76, 178  
 Ankazoabo (cave), 81, 82, 83, 180  
 Ankazoabo-Sud, 88, 103, 180  
 Ankevo, 112  
 Ankilibeandry, 15, 64, 112, 113, 114, 115  
 Ankilitelo, 13, 15, 92, 94–101, 185  
 Anosyenne (mountains), 27, 66, 67, 71, 72  
 Antananarivo, 39, 49, 122, 133  
 Antongil (bay), 44, 165  
 Antserananomby, 116  
 Antsingiavo, 157, 158  
 Antsirabe, 13, 15, 22, 61, 70, 104, 125–32, 138, 139, 140, 178  
 Antsiranana, 44  
 Antsirasira, 112  
 Antsiroandoha (cave), 176  
 Asambalahy, 100  
 Beanka, 28  
 Beavoha, 82, 174, 178  
 Bekopaka, 134  
 Belo sur Mer, 14, 15, 34, 45, 64, 112–19, 139, 152, 178  
 Belo Tsiribihina, 115  
 Belobaka (cave), 40, 123, 148, 154  
 Beloha, 178  
 Bemafandry, 82  
 Bemaraha (massif, national park, plateau), 23, 27, 55, 97, 99, 134, 153, 159, 163, 165, 167  
 Beroroha, 89  
 Betafo, 125, 126  
 Betsiboka (river), 19  
 Beza Mahafaly, 28, 89, 90  
 Bungo Tsimanindroa, 157  
 Burckle Crater, 75  
 Canal des Pangalanes, 121, 122, 123, 124  
 Cap Sainte Marie, 14, 15, 59–64, 75  
 Central Menabe, 110, 130  
 Col d'Ambatomanihina, 66  
 Crocodile Cave, 163  
 Daraina, 32, 171  
 Enijo, 44  
 Erombo, Lake, 67  
 Farafangana, 165  
 Faux Cap, 75  
 Fenambosy, 75  
 Fort Dauphin, 61  
 Grotte d'Andranoboka, 145  
 Horombe (plateau), 30  
 Ifanadiana, 165  
 Ihazoara, 28  
 Irodo, 44  
 Isalo (massif, national park), 93, 99, 102, 103, 110  
 Itampolo, 14, 45, 47, 64, 81, 82, 180  
 Itampolove, 83  
 Itasy (lake, massif), 88, 135  
 Kavitaha, Lake, 141  
 Kianjavato, 165  
 Kirindy (forest), 115  
 Kirindy Mitea (national park), 115, 116  
 Lakaton'i Anja, 43, 44  
 Lakaton'ny Akanga, 178  
 Lamboharana, 14, 48, 82, 89, 185  
 Lavakasaka, 152  
 Lelia, 83  
 Loharano, 126  
 Loky-Manambato (region), 32  
 Mahafaly Plateau, 79, 80, 81, 82, 84, 85, 86, 97  
 Mahajanga, 28, 36, 40, 118, 123, 143, 145, 146, 152, 154, 155, 157, 158, 160, 161  
 Mahamavo Peninsula, 154, 157, 158  
 Mahery, Lake, 140  
 Mahilaka, 45  
 Maintirano, 28  
 Makira (forest), 54, 134  
 Manakara, 178  
 Manamby, 95  
 Mananjary, 13, 120–24

Mandrare (river), 62	Namoroka, 163	Toamasina, 121
Mangoky (river), 19, 21, 27	Namorona (river), 21	Tolagnaro, 23, 27, 61, 178
Mangoro (river), 109, 122	Narinda (peninsula), 157, 159	Toliara, 29, 45, 48, 70, 86, 95, 99, 100, 109, 178
Manombo (Toliara), 179	Nosy Be, 41	Tritrivakely, Lake, 36, 125, 130, 131, 140
Manongarivo (massif), 25	Nosy Mangabe, 44	Tsaratana, 19
Maroantsetra, 54, 134		Tsiandroina, 82, 179
Marodoka, 41	Onilahy (river), 19, 21, 80, 97	Tsihombe, 63
Marovato, 60		Tsimanampetsotsa (lake, national park), 15, 22, 34, 79–86, 92, 97, 98, 101
Marovaza, 160, 161	Ranobe, 29, 86, 99, 100, 114	Tsimanampetsotsa, Lake, 79, 81, 84, 85, 86
Masinandraina, 126, 127, 128, 129	Ranohira, 30	Tsimbazaza, 122, 138
Masinandreina, 126	Ranomafana, 21, 153, 165, 166	Tsirave, 78, 89, 90, 108, 138, 180
Masoala, 22, 25	Raulin Zohy, 157, 160, 161	Tsiribihina (river), 19
Menarandra (river), 44	Rezoky, 100, 180	
Mikea (forest), 70, 98, 99, 101		Vohémar, 43
Mikoboka Plateau, 95, 99	Sakamena (river), 90, 93	
Mitoho Cave, 81, 82, 84	Sakaraha, 70	Zombitse-Vohibasia (national park), 96, 98, 111
Mitsinjo, Lake, 37	Sarodrano, 44, 100	
Montagne d'Ambre (massif, national park), 36, 140, 163	Sirabé, 126	
Montagne de Français, 43, 44, 163, 167	Talaky, 64	
Morarano, 126	Tambozo, 42	
Morondava, 41, 42, 70, 81, 98, 99, 110, 112, 130	Taolambiby, 15, 45, 47, 48, 51, 87–93, 115, 141, 180	

# Index to Scientific Names

- Accipiter*, 131  
*francesii*, 11, 68  
 Accipitridae, 11, 68, 82, 131, 142, 147  
*Adansonia*, 62  
*Adapis*, 138  
*Aepyornis*, 17, 47, 60, 61, 62, 63, 64, 67, 68, 81, 85, 91, 104, 109, 122, 128, 134, 139, 152, 166  
*cursor*, 10, 61  
*gracilis*, 10  
*grandidieri*, 10, 61  
*hildebrandti*, 10, 125, 126, 128, 131, 139, 142  
*ingens*, 10  
*lentus*, 10  
*maximus*, 10, 59, 60, 61, 63, 82, 117  
*medius*, 10, 117, 139, 142  
*modestus*, 10  
*mulleri*, 10, 126  
*titan*, 10  
 Aepyornithidae, 10, 16, 60, 68, 82, 89, 91, 104, 117, 122, 131, 142, 147, 151, 166  
 Aepyornithiformes, 10, 68, 82, 91, 104, 117, 122, 131, 142, 147, 166  
 Afrosoricida, 12, 68, 83, 91, 97, 110, 131, 142, 147  
*Agapornis*  
*cana*, 11, 147  
 Alaudidae, 12, 68, 147  
 Alcedinidae, 12, 147  
*Alcedo*  
*vintsioides*, 12, 147  
*Aldabrachelys*, 72, 84, 85, 91, 93, 166  
*abrupta*, 5, 10, 65, 68, 72, 81, 82, 84, 85, 91, 104, 111, 117, 131, 139, 142, 147  
*gigantea*, 5, 33, 34, 85  
*grandidieri*, 5, 10, 47, 83, 84, 85, 91  
*Alluaudia*, 78  
*Alopochen*, 105, 129  
*aegyptiacus*, 104, 128, 139  
*sirabensis*, 11, 82, 102, 104, 117, 125, 128, 131, 135, 139, 142  
*Anas*  
*bernieri*, 11, 82, 85, 104, 128, 131, 139, 142  
*erythrorhyncha*, 11, 82, 128, 131  
*melleri*, 11, 82, 120, 124, 128, 131, 139, 142  
*Anastomus*  
*lamelligerus*, 11, 82, 104, 147, 151  
 Anatidae, 11, 68, 82, 104, 117, 131, 142  
 Anhimidae, 69, 139  
 Anseriformes, 11, 68, 82, 104, 117, 131, 142  
 Apocynaceae, 29  
 Apodidae, 11, 68, 147  
 Apodiformes, 11, 68, 147  
*Apus*, 68  
*barbatus*, 11, 147  
*Aquila*, 11, 81, 83, 139, 142, 183, 185  
*chrysaetos*, 183  
*rapax*, 183  
*Archaeoindris*, 89, 127, 136, 137  
*fontoynontii*, 12, 133, 134, 136, 137, 140, 142  
*Archaeolemur*, 9, 48, 62, 71, 76, 77, 85, 105, 106, 108, 118, 127, 135, 136, 138, 146, 153, 168, 171  
*edwardsi*, 12, 68, 71, 102, 105, 106, 108, 111, 116, 117, 118, 127, 131, 138, 140, 142, 147, 148, 152, 153, 157, 166, 168  
*majori*, 12, 66, 68, 71, 81, 83, 90, 91, 92, 93, 97, 105, 108, 113, 115, 116, 117, 118, 142  
 Archaeolemuridae, 12, 68, 83, 91, 97, 105, 117, 131, 135, 142, 147, 166  
*Ardea*, 131  
*cinerea*, 11, 104  
*humbloti*, 11, 82, 104, 117  
*purpurea*, 11, 82, 104  
 Ardeidae, 11, 82, 104, 117, 131, 147  
 Ardeiformes, 11, 82, 104, 117, 131, 147  
 Arecaceae, 100, 151  
 Artiodactyla, 13, 69, 83, 91, 97, 105, 117, 122, 131, 142, 148  
*Asio*  
*madagascariensis*, 11, 65, 147  
 Asteraceae, 131  
 Asteropeiaceae, 35  
*Astrochelys*  
*radiata*, 10, 68, 72, 82, 91, 117  
*Atelornis*, 109  
*pittoides*, 109  
*Australopithecus*  
*africanus*, 184  
*Avahi*, 13, 153, 166  
*laniger*, 13, 69, 71, 142  
 Aves, 10, 68, 82, 91, 104, 117, 122, 131, 142, 147, 166  
*Babakotia*, 154  
*radofilai*, 12, 136, 146, 147, 152, 153, 165, 166, 168, 169, 170, 171  
 Bernieridae, 12, 68  
 Bibymalagasias, 12, 16, 83, 89, 91, 105, 110, 116, 117, 131, 142, 146, 147, 150, 152  
 Brachypteracias, 109, 110  
*langrandi*, 12, 104, 107, 110  
 Brachypteraciidae, 12, 104, 109  
 Brachystegia, 30, 31  
*Brachytarsomys*, 82, 83, 158, 159  
*albicauda*, 158  
*mahajambaensis*, 13, 158, 159  
*villosa*, 158  
*Brachyuromys*, 159  
*Bradytherium*, 108, 154  
*Bubulcus*  
*ibis*, 11, 147  
 Burseraceae, 150, 152  
*Buteo*  
*brachypterus*, 11, 83, 142, 147  
*Canarium*, 150, 152  
*Canis*  
*lupus*, 98  
 Cannabaceae, 45, 132  
*Cannabis*, 45, 132  
 Carnivora, 13, 69, 76, 81, 83, 91, 94, 97, 98, 99, 101, 109, 116, 117, 131, 142, 148, 166, 177, 184  
 Casuariidae, 69  
*Casuarina*, 81  
 Casuarinaceae, 81  
*Casuaris*, 60, 109  
*bennetti*, 69  
*Cathariostachys*, 153, 166  
*madagascariensis*, 166

- Centetes*, 134  
*Centropus*  
*toulou*, 11, 147  
*Centronis*, 67, 69, 128, 139  
*majori*, 11, 68, 82, 125, 128, 131, 139, 142  
*Cercopithecus*  
*ascanius*, 184  
Charadriidae, 11, 83, 104  
Charadriiformes, 11, 83, 104  
Cheirogaleidae, 12, 68, 83, 91, 97, 142, 148, 166  
*Cheirogaleus*, 9, 12, 83, 91  
*major*, 12, 142  
*medius*, 12, 19, 68, 71, 97, 148  
*Chenalopec*  
*sirabensis*, 11  
Chiroptera, 13, 69, 83, 97, 148  
Ciconiidae, 11, 82, 104, 147  
Columbidae, 11, 68, 83, 147  
Columbiformes, 11, 68, 83, 104, 147  
Compositae, 131  
Coraciidae, 12, 83  
Coraciiformes, 12, 68, 83, 104, 147  
*Coracopsis*  
*vasa*, 11, 68, 83, 131, 147  
Corvidae, 12, 68  
*Corvus*  
*albus*, 12, 68  
*Coturnix*, 11, 147  
*Coua*, 139, 147  
*berthae*, 11, 139, 142, 147, 152  
*cristata*, 11, 68  
*cursor*, 11, 68  
*gigas*, 11, 68, 139, 147, 152  
*primavea*, 11, 83, 113, 116, 117, 147, 150, 152  
Couinae, 139, 145, 152  
Crocodylidae, 10, 68, 82, 91, 104, 117, 131, 142, 147  
*Crocodylus*, 72, 82, 91, 105, 148  
*niloticus*, 10, 13, 68, 72, 91, 104, 105, 117, 147, 163  
*Cryptogale*  
*australis*, 12, 66  
*Cryptoprocta*, 74, 100, 109, 116, 134, 178, 179, 180, 181, 185  
*antamba*, 13, 179  
*ferox*, 13, 76, 83, 96, 97, 116, 117, 129, 131, 140, 142, 148, 166, 177, 178, 179, 180, 181  
var. *spelea*, 76, 178  
*spelea*, 13, 69, 74, 81, 82, 83, 91, 92, 109, 116, 117, 129, 131, 148, 166, 177, 178, 179, 180, 181  
Cuculidae, 11, 68, 83, 117, 142, 147  
Cuculiformes, 11, 68, 83, 117, 142, 147  
*Cuculus*  
*rochii*, 11, 147  
*Cyanolanius*  
*madagascarinus*, 12, 68  
*Daubentonia*  
*madagascariensis*, 12, 94, 100, 166  
*robusta*, 12, 47, 48, 90, 94, 97, 128, 129, 142, 185  
Daubentoniidae, 12, 97, 142, 166  
*Dendrocygna*, 11, 82, 104, 117  
*Didierea*, 100  
Didiereaceae, 29, 66, 78, 86, 100  
Dinornithiformes, 61  
*Dipsochelys*, 5  
Dromaiidae, 69  
*Dromaius*  
*novaehollandiae*, 69, 109  
*Dryolimnas*  
*cuvieri*, 11, 83  
*Echinops*  
*telfairi*, 12, 68, 97  
*Egretta*, 11, 82  
*Eidolon*, 148  
*dupreanum*, 13, 69, 144, 148, 156  
*Eliurus*, 13, 69, 97, 98, 99, 148  
*antsingy*, 159  
*myoxinus*, 9, 13, 69, 71, 97, 98, 148  
*Emballonura*  
*atrata*, 83  
Emballonuridae, 13, 83  
*Erica*, 26, 27  
Ericaceae, 25, 26, 27, 31, 36, 130  
*Eugenia*, 135  
*Eulemur*, 12, 135, 174  
*coronatus*, 12, 162, 165, 166  
*fulvus*, 12, 22, 97, 142, 143, 148, 166  
*sanfordi*, 165  
*mongoz*, 12, 142, 143, 148  
Euphorbiaceae, 29  
Eupleridae, 13, 16, 69, 83, 91, 97, 117, 131, 142, 148, 166  
*Eurystomus*  
*glaucurus*, 12, 83  
Fabaceae, 29, 30, 31, 95  
*Falco*  
*newtoni*, 11, 68, 147  
Falconidae, 68, 147  
Falconiformes, 11, 68, 82, 131, 142, 147  
*Felis*  
*sylvestris*, 98  
*Flacourtia*  
*rudis*, 11  
*Fossa*  
*fossana*, 13, 69, 148  
*Foudia*  
*madagascariensis*, 12, 68, 147  
*Fulica*  
*cristata*, 11, 68, 83, 104  
*Galidia*  
*elegans*, 9, 13, 97, 99  
*Galidictis*, 142  
*grandidieri*, 13, 94, 97, 98, 99, 101  
Galliformes, 11, 131, 147  
*Gallinula*  
*chloropus*, 11, 68, 83, 131, 139, 142  
*Geobiastes*, 109  
*Geochelone*, 5  
*abrupta*, 5  
*grandidieri*, 5, 72  
*Geogale*  
*aurita*, 12, 68, 83, 97  
Gramineae, 36  
Gruiformes, 11, 68, 83, 104, 131, 142, 147  
*Hadropithecus*, 62, 71, 77, 78, 108, 111, 118, 127, 136, 138  
*stenognathus*, 12, 68, 71, 74, 76, 77, 90, 108, 116, 117, 118, 142  
*Haliaeetus*  
*vociferoides*, 11, 83, 85  
*Hapalemur*, 174  
*griseus*, 12, 162, 166, 171  
*simus*, 12, 135, 140, 142, 148, 150, 152, 153, 162, 165, 166, 167, 171  
*Himantopus*  
*himantopus*, 11, 83  
Hippopotamidae, 13, 69, 83, 91, 97, 105, 117, 122, 131, 142, 148  
*Hippopotamus*, 16, 97, 118  
*amphibius*, 118, 120, 122, 123  
*standini*, 122  
*guldbergi*, 13, 49, 89, 105, 117, 123, 125, 129, 131, 139, 142  
*laloumena*, 13, 120, 122, 123, 124, 148  
*lemerlei*, 9, 13, 45, 48, 69, 72, 81, 83, 85, 89, 91, 93, 102, 103, 105, 117, 122, 123, 144, 148, 151  
*madagascariensis*, 122, 123, 126  
Hipposideridae, 13, 69, 83, 148  
*Hipposideros*, 9  
*besaoka*, 13, 144, 148  
*commersoni*, 13, 69, 83, 148  
Hirundinidae, 12, 147  
*Homo*, 7  
*Hovacrex*, 129  
*roberti*, 11, 83, 125, 129, 131  
*Humulus*, 45, 132  
*Hypogeomys*, 66, 98  
*antimena*, 13, 70, 81, 83, 97, 98, 99, 105, 110, 130, 131, 140, 142  
*australis*, 13, 65, 67, 69, 70, 71, 130  
*Hypsipetes*  
*madagascariensis*, 12, 147  
*Indri*, 109, 168, 171, 172  
*indri*, 13, 105, 107, 109, 135, 140, 142, 153, 165, 166, 168, 170, 171

- Indriidae, 13, 69, 83, 91, 97, 105, 142, 148, 153, 166
- Laridae, 11, 83, 104
- Larus*, 104
- cirrocephalus*, 11, 83
- dominicanus*, 11, 83
- Lemur*, 90, 174
- catta*, 12, 29, 48, 67, 68, 71, 76, 83, 90, 91, 97, 105, 107, 108, 109
- Lemuridae, 12, 68, 83, 91, 97, 105, 117, 131, 142, 148, 166, 174
- Lemuriformes, 12, 68, 83, 91, 97, 105, 117, 131, 142, 147, 166
- Lepilemur*, 12, 142, 147, 166, 174
- ankararensis*, 165
- dorsalis*, 12
- edwardsi*, 12, 153
- leucopus*, 12, 90, 91, 97
- mustelinus*, 12
- ruficaudatus*, 12
- septrionalis*, 12
- Lepilemuridae, 12, 91, 97, 142, 147, 166
- Leptopterus*
- viridis*, 12, 68
- Leptosomatidae, 12, 147
- Leptosomus*
- discolor*, 12, 147
- Lophotibis*
- cristata*, 11, 82, 104, 147
- Macrotarsomys*, 70, 98
- bastardi*, 13, 69, 71, 83, 97, 98
- petteri*, 13, 69, 70, 71, 72, 83, 94, 97, 98, 99, 101
- Malvaceae, 29, 62
- Mammalia, 12, 68, 83, 91, 97, 105, 117, 122, 131, 142, 147, 166
- Margaroperdix*
- madagarensis*, 11, 131
- Medemia*, 36, 100, 151
- Megaladapidae, 12, 69, 83, 91, 105, 117, 131, 142, 148, 166
- Megaladapis*, 5, 48, 65, 72, 90, 91, 97, 106, 135, 136, 138, 140, 148, 152, 169, 174, 175, 176
- edwardsi*, 12, 65, 66, 67, 69, 71, 72, 81, 83, 85, 90, 91, 93, 102, 105, 106, 108, 138, 154, 176
- grandidieri*, 12, 125, 126, 127, 128, 131, 138, 140, 142, 148, 154, 174
- grandidieri/madagascariensis*, 148, 154, 166, 169, 173, 174
- madagascariensis*, 12, 48, 65, 69, 71, 72, 83, 90, 91, 93, 95, 96, 97, 105, 108, 109, 116, 117, 128, 138, 148, 154, 174, 176
- Mentocrex*
- beankaensis*, 159
- Meropidae, 12, 147
- Merops*
- superciliosus*, 12, 147
- Mesitornithidae, 11, 60, 146, 147, 152
- Mesopropithecus*, 108, 136, 137, 140, 171
- dolichobrachion*, 12, 165, 166, 169, 171
- globiceps*, 12, 81, 82, 83, 90, 91, 108, 116, 117
- pithecoides*, 12, 126, 131, 137, 142
- Microcebus*, 9, 12, 71, 83, 142, 148, 166, 168
- griseorufus*, 12, 68, 71, 80, 97
- murinus*, 12, 97
- tavaratra*, 165
- Microgale*, 9, 70, 147
- brevicaudata*, 12, 69, 97
- decaryi*, 12
- grandidieri*, 159
- jenkinsae*, 83
- longicaudata*, 12, 68
- macpheeii*, 12, 65, 67, 68, 69, 70
- majori*, 12, 97
- nasoloi*, 12, 68, 70, 72, 97
- principula*, 12, 68, 70, 72
- pusilla*, 12, 68, 70, 72, 83
- Milvus*
- aegyptius*, 11, 83, 147
- Miniopteridae, 13, 69, 97
- Miniopterus*
- gleni*, 13, 69, 97
- Mirafra*
- hova*, 12, 68, 147
- Mirza*, 98
- coquereli*, 98
- Molossidae, 13, 69, 83, 97
- Monarchidae, 12, 68
- Monias*, 11, 147, 152
- benschi*, 152
- Mops*
- leucostigma*, 13, 69
- Mormopterus*
- jugularis*, 13, 69, 83, 97
- Mullerornis*, 17, 47, 60, 61, 62, 64, 67, 68, 69, 81, 85, 104, 109, 115, 126, 139, 147, 151, 152
- agilis*, 10, 82, 125, 128, 131, 139, 142
- betsilei*, 10, 131
- grandis*, 10
- rudis*, 11, 117
- Mungotictis*
- decemlineata*, 13, 97
- Muridae, 71
- Mus*
- musculus*, 71, 98
- Mycteria*
- ibis*, 11, 82
- Myotis*
- goudoti*, 13, 148
- Myrtaceae, 135
- Nesillas*
- lantzii*, 12, 68
- Nesomyidae, 13, 69, 83, 97, 105, 131, 142, 148, 167
- Nesomyinae, 16, 98, 152, 158, 159
- Nesomys*, 152, 159, 162, 166
- audeberti*, 159, 167
- lambertoni*, 159, 167
- narindaensis*, 13, 148, 150, 152, 158, 167
- rufus*, 13, 65, 69, 70, 159, 167
- Newtonia*
- brunneicauda*, 12, 147
- Ninox*
- superciliaris*, 11, 147
- Numenius*
- phaeopus*, 11, 83
- Otomops*
- madagascariensis*, 13, 97
- Otus*
- rutilus*, 11, 68, 147
- Pachylemur*, 71, 90, 138, 139, 140, 157, 166, 168, 169, 170, 171, 181
- insignis*, 12, 48, 68, 71, 72, 83, 87, 90, 91, 97, 105, 108, 113, 116, 117, 139, 171, 177, 180
- jullyi*, 12, 71, 126, 127, 131, 139, 140, 142, 171
- Pachypodium*, 29
- Palaeognathae, 61, 109
- Palaeopropithecidae, 12, 83, 91, 97, 105, 117, 131, 135, 136, 142, 147, 166
- Palaeopropithecus*, 90, 91, 96, 108, 128, 136, 137, 138, 154, 155, 157, 158, 159, 160, 161, 166, 169, 184, 185
- ingens*, 12, 45, 81, 82, 83, 87, 90, 91, 95, 96, 97, 105, 107, 108, 116, 117, 154, 161, 182, 184, 185
- kelyus*, 12, 108, 147, 150, 153, 154, 155, 158, 160, 161, 185
- maximus*, 12, 48, 105, 125, 126, 131, 135, 136, 137, 140, 142, 154, 161, 184, 185
- Panthera*
- pardus*, 184
- Papio*, 77
- Paramicrogale*
- decaryi*, 12, 66
- Paremballonura*
- atrata*, 13, 83
- tiavato*, 13, 83, 160
- Passeriformes, 12, 68, 147
- Pedaliaceae, 62
- Pelecaniformes, 11, 82, 131
- Pelomedusa*
- subrufa*, 72



- Phalacrocoracidae, 11, 82, 131  
*Phalacrocorax*, 11, 82, 85, 128, 131  
*africanus*, 11, 82, 128, 131  
*Phaner*, 98  
*furcifer*, 98  
*Phascolarctos*, 174  
*Phasianidae*, 11, 131, 147  
*Phedina*  
*borbonica*, 12, 147  
*Phoeniconaias*  
*minor*, 11, 82, 147, 151  
*Phoenicopteridae*, 11, 82, 104, 147  
*Phoenicopterus*  
*ruber*, 11, 82, 104  
*Phyllanthaceae*, 35, 135  
*Platalea*  
*alba*, 11, 82, 104, 131  
*Plegadis*  
*falcinellus*, 120, 124  
*Plesiorycteropus*, 83, 89, 128, 129, 152  
*germainepettrae*, 12, 129, 140, 142  
*madagascariensis*, 12, 91, 105, 110, 113, 116, 117, 129, 131, 140, 142, 147, 150, 152  
*Ploceidae*, 12, 68  
*Ploceus*  
*sakalava*, 12, 68  
*Poaceae*, 33, 135, 153, 166  
*Polyboroides*  
*radiatus*, 11, 83  
*Porphyrio*, 129  
*porphyrio*, 11, 83, 104, 129, 131  
*Potamochoerus*, 122, 178  
*larvatus*, 123  
*Primates*, 12, 68, 83, 91, 97, 105, 117, 131, 142, 147, 166, 169  
*Procellariidae*, 11, 68  
*Procellariiformes*, 11, 68  
*Prolemur*  
*simus*, 165  
*Propithecus*, 13, 90, 108, 118, 135, 137, 143, 154, 168, 178, 180, 185  
*coquereli*, 142  
*diadema*, 13, 135, 142, 143, 171  
*perrieri*, 166, 168, 170, 171  
*tattersalli*, 13, 165, 166, 171  
*verreauxi*, 13, 48, 69, 71, 83, 87, 90, 91, 97, 105, 142, 143, 148, 153, 181  
*Psittacidae*, 11, 68, 83, 131, 147  
*Psittaciformes*, 11, 68, 83, 131, 147  
*Pterocles*  
*personatus*, 11, 83, 104  
*Pteroclididae*, 11, 83, 104  
*Pteropodidae*, 13, 69, 148  
*Pteropus*  
*rufus*, 13, 69  
*Puffinus*, 11, 68  
*Puma*  
*concolor*, 177  
*Pycnonotidae*, 12, 147  
*Rallidae*, 11, 83, 104, 131, 142  
*Rallus*  
*madagascariensis*, 11, 83  
*Rattus*, 71  
*rattus*, 98  
*Recurvirostridae*, 83  
*Reptilia*, 10, 68, 82, 91, 104, 117, 131, 142, 147, 166  
*Rhea*  
*americana*, 109  
*Rheiformes*, 62, 109  
*Rodentia*, 13, 69, 83, 97, 105, 131, 142, 148, 167  
*Rousettus*  
*madagascariensis*, 13, 69, 148  
*Salicornia*, 81  
*Salicorniaceae*, 81  
*Salvadora*, 80, 81  
*Salvadoraceae*, 80, 81  
*Sarcolaenaceae*, 35  
*Sarkidiornis*  
*melanotos*, 11, 131, 139, 142  
*Scolapaciidae*, 11, 83  
*Scotophilus*, 159, 160  
*marovaza*, 161  
*tandrefana*, 159  
*Setifer*  
*setosus*, 12, 68, 83, 97  
*Soricidae*, 71  
*Sporomiella*, 45, 115  
*Stephanoaetus*, 184  
*coronatus*, 183, 184, 185  
*mahery*, 12, 82, 139, 142, 182, 183, 184, 185, 186  
*Strepsirrhini*, 12, 68, 83, 91, 97, 105, 117, 131, 142, 147, 166  
*Streptopelia*  
*picturata*, 11, 68, 83, 147  
*Strigidae*, 11, 68, 147  
*Strigiformes*, 11, 68, 147  
*Struthio*  
*camelus*, 17, 60, 109, 151  
*Struthioniformes*, 60, 109  
*Suncus*  
*etruscus*, 71  
*madagascariensis*, 71  
*Sylviidae*, 12, 68  
*Tadorinae*, 104  
*Tamarindus*  
*indica*, 29, 95  
*Tenrec*, 134  
*ecaudatus*, 12, 68, 80, 83, 91, 97, 131, 142, 147  
*Tenrecidae*, 12, 16, 67, 68, 72, 83, 91, 97, 131, 142, 147, 159  
*Terpsiphone*  
*mutata*, 12, 68  
*Testudinidae*, 10, 82, 91, 104, 117, 131, 142, 147, 166  
*Testudo*  
*grandidieri*, 84  
*Thalassornis*  
*leuconotus*, 11, 82  
*Thamnornis*  
*chloropetoides*, 12, 68  
*Theropithecus*, 77  
*gelada*, 138  
*Threskiornis*  
*bernieri*, 11, 82, 104  
*Threskiornithidae*, 11, 82, 104, 131, 147  
*Triaenops*, 9  
*furculus*, 13, 69, 83, 148  
*goodmani*, 13, 144, 148  
*Tribonyx*  
*roberti*, 11, 129  
*Tubulidentata*, 152  
*Turnicidae*, 11, 68, 147  
*Turnix*  
*nigricollis*, 11, 68, 147  
*Tyto*  
*alba*, 11, 14, 68, 147  
*Tytonidae*, 11, 68, 147  
*Uapaca*, 135  
*bojeri*, 35, 135  
*Uncarina*, 62  
*Upupa*  
*marginata*, 12, 68  
*Upupidae*, 12, 68  
*Uratelornis*, 109  
*Vaccinium*, 27  
*Vanellinae*, 104  
*Vanellus*  
*madagascariensis*, 11, 83, 102, 104  
*Vanga*  
*curvirostris*, 12, 68  
*Vangidae*, 12, 68, 147  
*Varecia*, 71, 72, 139, 168, 171, 174, 180, 181  
*variegata*, 12, 135, 142  
*Vespertilionidae*, 13, 148  
*Voalavo*, 159  
*Voay*, 105  
*robustus*, 10, 13, 68, 72, 83, 91, 102, 104, 105, 117, 131, 139, 142, 147  
*Xanthorrhoeaceae*, 100  
*Zonosaurus*  
*quadrilineatus*, 21  
*Zosteropidae*, 12, 68  
*Zosterops*  
*maderaspatana*, 12, 68