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Book Review

Lothagam. The Dawn of Humanity in Eastern Africa. Edited by Meave G. Leakey and John M. Harris. New York: Columbia University Press. 2003. 678 pp. $195 (cloth). ISBN 0-231-11870-8.

Lothagam is an extensive Neogene fossil site in northwestern Kenya, distinctive for its preservation of a rich fossil record (including some of the oldest known hominids) from an interval poorly represented but crucial for the emergence of modern ecosystems in Africa. This edited volume covers in detail the geology, paleontology, biogeography, and palaeoecology of the site, with emphasis on recent collections. Few Mio-Pliocene Afro-Arabian sites are of similar research importance—only a handful temporally overlap significantly with Lothagam, and none preserve as diverse a fauna from the interval of 7–5 Ma. Of these, only the Tugen Hills and Kanapoi, Kenya, and the Middle Awash, Ethiopia have sequences radiometrically dated and that rival Lothagam in the reliability of their chronostratigraphy (Harris and Leakey, 2003; Haile-Selassie *et al*., 2004). With fieldwork at Lothagam completed over a decade ago, and advertisements appearing well in advance of its publication (delayed by production problems), there have been great expectations and much anticipation for this volume.

In the unlikely event that there is any Afro-Arabian specialist who does not appreciate the significance of Lothagam (a concern raised in the Introduction, nevertheless), the observations in this book should indelibly underscore the importance of Lothagam for understanding the complex relationships of processes involved in the transformation of archaic and unfamiliar ecosystems to their present-day conditions in eastern Africa. The Lothagam fossil-bearing sequence documents the emergence of many modern mammalian taxa in Africa, a sampling of which includes hystricid rodents, cercopithecine monkeys, carnivoran genera such as *Viverra* and *Genetta*, elephants, black rhinos, and a wealth of bovids, notably providing the foundation for the endemic African tribes Tragelaphini, Hippotragini, Alcelaphini, and Aepycerotini. It also preserves a window into a period of faunal and ecological upheaval that opened up new niches throughout the Old World tropics, fostering progressive waves of faunal immigrations and complex interconnections within and between Afro-Arabia, Eurasia, and Indo-Pakistan. During this time, the replacement of entire archaic Miocene mammalian assemblages occurred, hastened by continuous and often rapid evolution and diversification of numerous taxa (tetraconodontine suids, for example), some in response to exploitation of novel habitats. Within these dynamic circumstances, hominids made their first appearance, and because it provides—in a broad sense—the most complete picture we have of the context of our own origins, Lothagam, and this volume, deserve special attention.

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The volume and chapters are logically organized, beginning with an Introduction that succinctly delineates the present physical and biological circumstances of the site and recounts the successive geological and paleontological discoveries made there since the 1930s. The most materially impressive of these are from the 1989–1993 expeditions led by Meave Leakey, which added substantially to prior collections (thousands of new fossil specimens and 65 new mammal taxa), and in the areas of chronostratigraphy and dating made critical advancements over the efforts by Patterson and colleagues in the 1960s. The present results are generally consistent with prior findings about the relative age, paleoecology, and depositional environments of Lothagam (see Patterson *et al*., 1970; Behrensmeyer, 1976; Smart, 1976), in retrospect a remarkable achievement, considering how much less information earlier researchers had at hand.

The second section of the book provides carefully revised and newly calibrated information about the stratigraphic, chronological, and depositional contexts of the site, and draws sound paleoclimatic inferences from the analysis of paleosol formation at Lothagam. This is a considerable improvement on the original, simple stratigraphic schema of Lothagam 1–3 (Behrensmeyer, 1976), and the age of the lowermost fossiliferous beds is shifted back in time a few million years. Those whose studies incorporate fossils from both the Patterson era and Leakey collections will appreciate the volume's alignment of old and new stratigraphic terminologies. The most important units now recognized in the Lothagam succession are the late Miocene Upper and Lower Members of the Nawata Formation, constrained between 9.1 and about 5.0 Ma, though most of the fossils from this formation are thought to derive from a more restricted span of 7.4–5.0 Ma, and the superjacent Pliocene-aged Nachukui Formation, the most fossiliferous subunits of which are the Apak Member (from about 5.0–>4.2 Ma), and Kaiyumung Member (<3.9 and >1.88 Ma). Lithostratigraphic analyses re-affirm earlier findings that the Nawata Fm. is depositionally fluvial, with a shift occurring to lacustrine sedimentation during the Apak Mb. interval (Behrensmeyer, 1976). Study of paleosols suggest a relatively dry phase of soil formation in the Upper Nawata, from 6.7 to 5.0 Ma, in mostly dry savanna conditions, preceding a return to tree savanna environments after 5.0 Ma. These results will be useful for refining biochronological correlation with sites lacking radiometric dating controls, such as latest Miocene-early Pliocene Manonga Valley, Tanzania, Sahabi, Libya, Langebaanweg, South Africa, and a wide array of Western Rift localities in Uganda and the Democractic Republic of Congo, as well as for comparison with well-dated faunas from sites such as Lukeino and Kanapoi, Kenya. In addition, they add data vital to understanding the interplay between changes in local ecological circumstances and shifts in faunal composition over time.

The third section of the book focuses on description and systematic paleontology of the animals from successive units. Each chapter can stand alone, with individual overviews of taxa and separate bibliographies. Chapters proceed in a "scala naturae," from invertebrates (crabs) to "lower" vertebrates (fish, reptiles, and birds), to mammals (lagomorphs and rodents, primates, carnivores, proboscideans, tubulidentates, rhinos and horses, hippos and suids, and giraffes and bovids). They are comprehensive in their coverage of taxa, and many are exhaustive in their tabulation of specimen measurements. Given the experience of the contributors, it is no surprise that most are admirably crafted and current in their discussion of the taxonomy, biogeography, and systematic issues of their constituent taxa.

Together, the faunas these chapters depict, particularly from the Nawata Fm., are spectacularly diverse, speciose, and form unique assemblages separated by multiple episodes of

turnover. Imagine rivers and backwaters filled with crabs, lungfish, birchirs, eel-like gymnarchids, perch, catfish, side-necked and soft-shelled turtles, multiple species of hexaprotodont hippos, and *five* contemporaneous species of crocodiles (ranging from highly piscivorous forms to specialists in hunting large mammals), and plied by a host of waterbirds, alongside landscapes inhabited by an extraordinary mix of older Miocene mammals and an abundance of new taxa that were precursors to the familiar species of modern Africa. For example, Lothagam was cohabited by the last of the old listriodont pigs and some of the first of a new suid cohort derived from invading Eurasian tetraconodontines; the archaic rhino genus *Brachypotherium*, at the end of its lineage, co-existed with precursors to modern white and black rhinos; among bovids, boselaphines, of ancient pedigree in Africa, become increasingly rare upwards in the sequence from Lower Nawata Fm. to the Apak Mb., but were joined by a wave of newcomers—some representing the first of bovid tribes characteristic of Africa today.

As well, the composition of the Lothagam faunas suggests tremendous environmental heterogeneity at the close of the Miocene, a factor that would have been important for promoting species richness: among carnivores, for instance, forest-dwelling amphicyonids, with phylogenetic roots extending back into the Eocene, were contemporaries of newer, cursorial, open country forms like the giant mustelid *Ekorus* and hyaenid *Ictitherium*. This ecological diversity is echoed among the equids, with species adapted both to closed woodland, and for more sustained, swift locomotion, presumably in open habitats. Terrestrial features in the postcrania of both cercopithecine and colobine monkeys further signal the availability of open country at Lothagam (and parenthetically shows that colobines in fossil faunas of this age should not be used as automatic indicators of woodland conditions), while the occurrence of giant squirrels provides additional evidence for forested areas. The carrying capacity of the region must have been astounding to support the diverse communities of micromammals (including the first porcupines, hares, and cane rats), bovids, suids, and multiple types of large proboscideans enumerated in the book.

Indeed, the most important aspect of the volume is the correlation between this biotic wealth and the substantial spread of C_4 plants (grasses and sedges) throughout the Old World tropics in the late Miocene, mediated by increased fragmentation and productivity of habitats. Studies of isotope paleoecology in the fourth section of the book indicate that the Lothagam landscape at the end of the Miocene was a mosaic of wooded grasslands, grassy woodlands, and riparian forests, and that significant grass forage was available, though not in pure grassland conditions. This work is especially valuable for demonstrating the substantial availability of C_4 (grass and sedge) plants to help sustain such a large and diverse herbivore biomass. $\delta^{13}C$ analysis of bioapatites shows that elephants and anancine gomphotheres, some rhinos, numerous bovids, and equids all became primary C_4 consumers by the beginning of the Pliocene (some before), with suids and hippos also incorporating some C_4 forage into their diets. Competition within novel, grass-dominated habitats, and ecological niche partitioning apparently helped lead to rapid species turnover and taxonomic differentiation between the late Miocene and early Pliocene, and this is now nowhere better documented than for Lothagam. In the final, summary section of the book, hominid origins and the emergence of bipedal abilities are plausibly linked inextricably to these changes in environmental conditions.

As with any large edited volume, all is not perfect. For such an expensive book, the washed-out appearance of photographs is regrettable, and the figures range too much in

quality; there is simply too much contrast between the beautiful stipple drawings in the turtle chapter and the poorly executed photographic cutouts and artwork of the hominid chapter. The hominid chapter, which should have been a centerpiece, is strangely perfunctory, and the chapter on birds is basically just a list of taxa. The proboscidean chapter departs from the format for the rest of the faunal section in lacking diagnoses, which unfortunately invalidates a newly erected species of elephant, *Elephas nawataensis*, putatively the first of its genus in the Miocene. It would have been interesting to know just how the hypodigm differs from the typical late Miocene elephant taxa *Primelephas* and *Stegotetrabelodon*. In the chapter on rhinos, non-experts should have been provided with a diagrammed, notated molar (some readers will want to know what an "antecrochet" is), and figures should have been labeled "A," "B," and so on, to avoid confusion. Every chapter would have benefitted from having a chart depicting the temporal distribution of taxa in the sequence, following the example in the carnivore chapter. The claim in the equid chapter that Lothagam and the Middle Awash have the only long, well-dated sequences in East Africa oddly disregards the Tugen Hills, Olduvai, and the Omo. *Palaeotragus* is misspelled as "*Paleotragus*" in places throughout the chapter on giraffes. In the bovid chapter, the heading for the tribe Neotragini is omitted.

Does the volume meet its expectations? In spite of these few imperfections, yes. While its heavy emphasis on description, at the expense of synthesis and interpretation (except in the closing chapter), may limit its appeal to specialists, the weight given to morphological minutiae in each chapter should bestow on the book a long and useful life as a research reference. Furthermore, its technical formality is softened somewhat by the wonderful reconstructions of fossil vertebrates by Mauricio Antón, which bring the animals alive again (imagine if they were in color!). Anyone seriously engaged in the study of the evolution of Neogene Afro-Arabian biotas will want to add this valuable new resource to their library.

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