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Taphonomic, Avian, and Small-Vertebrate Indicators of *Ardipithecus ramidus* Habitat

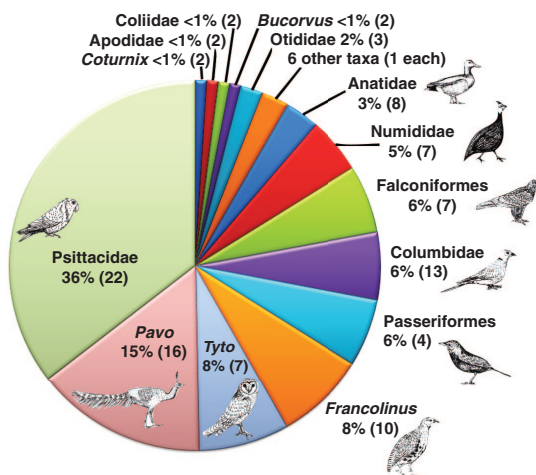
Antoine Louchart, Henry Wesselman, Robert J. Blumenschine, Leslea J. Hlusko, Jackson K. Njau, Michael T. Black, Mesfin Asnake, Tim D. White

The stratigraphic unit containing *Ardipithecus ramidus* was probably deposited rapidly, thus providing a transect through a 4.4-million-year-old landscape. To help reconstruct and understand its biological setting as thoroughly as possible, we recovered an assemblage of >150,000 plant and animal fossils. More than 6000 vertebrate specimens were identified at the family level or below. These specimens represent animals ranging in size from shrews to elephants and include abundant birds and small mammals that are usually rare in hominid-bearing assemblages. Many of these birds and small mammals are highly sensitive to environmental conditions and thus are particularly helpful in reconstructing the environment.

Accurate interpretation of fossil assemblages can be challenging. Even fossils from one layer can represent artificial amalgamations that might have originated thousands of years apart. Moreover, the remains of animals living in different habitats can be artificially mixed by flowing water or by shifting lake and river margins. Ecological fidelity can be further biased by unsystematic recovery if, for example, only the more complete, identifiable, or rare specimens are collected. Thus, interpreting the *Ardipithecus*-bearing sediments requires that we deduce the physical and biological conditions under which the fossils accumulated and the degree to which these biases operated at the time of deposition—a practice called “taphonomy.”

Both the large- and small-mammal assemblages at Aramis lack the damage that would result from transport and sorting by water, a finding consistent with the fine-grained sediments in which the bones were originally embedded. Many of the limb bone fragments of large mammals show traces of rodent gnawing and carnivore chewing at a time when the bones were still fresh. These bones were most probably damaged by hyenas, which in modern times are known to destroy most of the limb bones and consume their marrow. The actions of hyenas and other carnivores that actively competed for these remains largely explain why the fossil assemblage at Aramis contains an overrepresentation of teeth, jaws, and limb bone shaft splinters (versus skulls or limb bone ends).

As a result of this bone destruction, whole skeletons are extremely rare at Aramis, with one fortunate exception: the partial skeleton of *Ar. ramidus* excavated at ARA-VP-6/500. The relative abundance and



Abundance of birds (left) associated with *Ar. ramidus*. These distributions are consistent with a mostly woodland habitat. (Above) An example of the many small mammal and bird bones.

damage patterns of the fossils representing small mammals and birds suggest that they are derived from undigested material regurgitated by owls (owl pellets). Because of their fragility and size, bird bones have been rare or absent at most other eastern African fossil assemblages that included early hominids. However, we cataloged 370 avian fossils; these represent 29 species, several new to science. Most of the birds are terrestrial rather than aquatic, and small species such as doves, lovebirds, mousebirds, passerines, and swifts are abundant. Open-country species are rare. Eagles and hawks/kites are present, but the assemblage is dominated by parrots and the peafowl *Pavo*, an ecological indicator of wooded conditions.

The small-mammal assemblage includes up to 20 new species, including shrews, bats, rodents, hares, and carnivores. Extant counterparts live in a variety of habitats, but their relative abundance in the fossil assemblage indicates that *Ardipithecus* lived in a wooded area. Avian predators most probably procured the much rarer squirrels and gerbils from drier scrub or arid settings at a distance. Most of the bat, shrew, porcupine, and other rodent specimens are compatible with a relatively moist environmental setting, as are the abundant fossils of monkeys and spiral-horned antelopes.

The combination of geological and taphonomic evidence, the assemblage of small-mammal and avian fossils, and the taxonomic and isotopic compositions of remains from larger mammals indicate that Aramis was predominantly a woodland habitat during *Ar. ramidus* times. The anatomical and isotopic evidence of *Ar. ramidus* itself also suggests that the species was adapted to such a habitat.

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Taphonomic, Avian, and Small-Vertebrate Indicators of *Ardipithecus ramidus* Habitat

Antoine Louchart,¹ Henry Wesselman,² Robert J. Blumenshine,³ Leslea J. Hlusko,⁴ Jackson K. Njau,⁴ Michael T. Black,⁵ Mesfin Asnake,⁶ Tim D. White^{4*}

Thousands of vertebrate specimens were systematically collected from the stratigraphic interval containing *Ardipithecus ramidus*. The carcasses of larger mammals were heavily ravaged by carnivores. Nearly 10,000 small-mammal remains appear to be derived primarily from decomposed owl pellets. The rich avifauna includes at least 29 species, mostly nonaquatic forms. Modern analogs of the most abundant birds and of a variety of rodents are associated with mesic woodland environments distant from large water bodies. These findings support inferences from associated geological, isotopic, invertebrate, and large-vertebrate assemblages. The combined results suggest that *Ar. ramidus* occupied a wooded Pliocene habitat.

In an effort to characterize the environment inhabited by *Ardipithecus ramidus*, between 1994 and 2000 we repeatedly collected fossils from the surface of all known hominid-bearing exposures of the 4.4 million-year-old Lower Aramis Member (1). All fossils encountered in systematic “crawls” (2), excavations, and two quarries were collected; this avoided biases introduced by selective collection, a practice that can confound ecological analysis (3).

Most of the recovered macrofaunal specimens (approximately 135,000 fossils from mammalian families in which most species exceed 5 kg in adult body weight) were pieces of bone or tooth that could not be taxonomically identified below the family level (Fig. 1). Most were long bone shaft splinters, and many teeth were represented by less than half of a crown. These less identifiable specimens were pooled into locality-specific bulk samples (such as “bulk equid dental” and “bulk mammal bone” from ARA-VP-6). The other >6000 collected specimens from this interval were taxonomically more precisely identifiable and were assigned individual numbers (such as ARA-VP-6/1356). These

specimens represent mammals ranging in size from shrews to proboscideans (2).

Taphonomy. Crania, horn core fragments, and postcranial elements identifiable to family level are rare in the total Lower Aramis Member collection. For example, not a single cranium, or even partial cranium, is present among 733 cataloged tragelaphine bovid specimens. Bovid postcranial samples include just 6 proximal metapodials, 17 distal metapodials, 7 calcanei, 19 astragali, 84 phalanges, and 8 distal humeri. Only a few mammals are represented by associated elements, the most complete being the primarily in situ ARA-VP-6/500 *Ar. ramidus* skeleton (1).

Fossils from larger mammals show no rounding or abrasion associated with hydraulic transport. This is consistent with the sedimentology of the deposits (1), as well as with the abundance and preservation of small specimens. The assemblages have therefore not been water-transported or -sorted. Surface exfoliation from subaerial weathering and chemical corrosion has obscured the original surface of some pieces and varies by locality. Only 66 of 157 limb bone shaft fragments retain original surfaces adequate for confident identification of perimortem modifications in the most affected bulk bone collection from an *Ardipithecus*-bearing sublocality (ARA-VP-1 SHF). In the more representative bulk sample quantitatively analyzed for this variable (ARA-VP-1 SRG), 40 of 64 specimens had good surface preservation. Fragments from smaller taxa tend to show less weathering across all localities where present, suggesting more rapid burial.

Where assessed on preserved original surfaces, limb bone shaft fragments from large mammals display a wide range of marks (Fig. 1). Tooth marking by mammalian carnivores is evident in 21 of 24 bulk bone samples from different localities (each sample typically containing hundreds of specimens). Tooth marks attributable to crocodyles (4) are rare, and were found in only three

of nine bulk samples assessed. Rodent gnawing (mouse- to porcupine-sized) and insect-derived marks are present in all bulk samples. Root etching is extremely rare. The paucity of trampling marks corresponds to a lack of sand in the substrate (1).

Although raptors can account for over 80% of deaths in some modern primate assemblages (5), the distinctive signature of such predation is missing from the cercopithecoid assemblage. Instead, the damage and breakage patterns are more consistent with a mammalian carnivore [supporting online material text S1]. A full demographic range is represented, and it is likely that the cercopithecoid assemblage is attritional, with heavy postmortem ravaging by carnivores (6, 7). This pattern also holds for the bovid remains.

Large mammal carnivores represent the dominant agent of perimortem bone breakage, as evidenced by the ubiquity of ancient spiral fractures. There are high rates of tooth marking on limb bone fragments (47 to 75% in three bulk assemblages quantitatively assessed; $n = 155$ specimens) and tooth notching of bone fragment edges (27% of tooth-marked pieces; $n = 30$). Proportions of limb bone shaft fragments with tooth marks and/or tooth notches are within ranges produced by modern spotted hyaenas, which have been observed to deflesh and extract all marrow while consuming whole limbs (8, 9). There is nearly complete destruction of limb bone ends (98% in one bulk assemblage assessed quantitatively; $n = 166$). Digestive etching by stomach acids is rare but widespread (including a hominid molar exemplar). This pattern of destruction parallels that seen in instances of complete marrow consumption by modern spotted hyaenas.

The hyaenids *Ikelohyaena abronia* and cf. *Crocota* cf. *dietrichi*, as well as the ursid *Agriotherium* and four suid taxa are likely suspects for the destruction of the larger bones. The canid *Eucyon* was also present. Degreased, subaerial, pre-fossilization fragmentation appears to have been relatively insignificant. Postfossilization fracture resulting from breakage upon erosional exposure is ubiquitous (between 33 and 63% of limb bone shaft fragments examined).

The overall *Ardipithecus*-bearing locality and sublocality assemblages indicate that the competition for large mammal carcasses must have been intense. Abundant shaft fragments, rare epiphyseal portions, and the extremely low representation of axial postcrania as compared to those of the appendicular and craniocentral skeletons, combined with the high tooth-marking rates, suggest that the Aramis ecosystem may have matched highly competitive modern settings such as Ngorongoro Crater (10). The rarity of late-stage weathering damage characterized by deep cracking and exfoliation (<3% of total specimens at stages 4 and 5) suggests that exposure to subaerial conditions before burial was brief and/or buffered by tree cover and/or leaf litter.

Exceptions to this taphonomic pattern associated with *Ardipithecus* are the SAG-VP-1 and

¹Iziko South African Museum, Natural History Department, Cenozoic Palaeontology Collections, Box 61, Cape Town 8000, South Africa; and Institut de Génétique Fonctionnelle de Lyon, Team “Evo-devo of vertebrate dentition,” Ecole Normale Supérieure de Lyon, Université Lyon 1, CNRS, INRA, 46 Allée d’Italie, 69964, Cedex 07, Lyon, France. ²Post Office Box 369, Captain Cook, HI, 96704, USA. ³Center for Human Evolutionary Studies, Department of Anthropology, Rutgers University, 131 George Street, New Brunswick, NJ 08901-1414, USA. ⁴Human Evolution Research Center and Department of Integrative Biology, University of California, Berkeley, 3010 Valley Life Sciences Building, Berkeley, CA, 94720, USA. ⁵Phoebe A. Hearst Museum of Anthropology, 103 Kroeber Hall, Number 3712, University of California, Berkeley, CA 94720-3712, USA. ⁶Ministry of Mines and Energy, Post Office Box 486, Addis Ababa, Ethiopia.

*To whom correspondence should be addressed. E-mail: timwhite@berkeley.edu

Fig. 1. Bone modification of medium and large mammalian remains from the Lower Aramis Member. The central panel shows limb bone shaft splinters that are ubiquitous in the assemblage and were collected by the thousands during the 100% recovery operation. Scale bar, 2 cm. (A) Termite damage. (B) Inner conchoidal scars from carnivore gnawing. (C) Carnivore tooth marks on an *Ardipithecus* mandible corpus. (D) Stomach acid etching on an artiodactyl phalanx and bone splinter of a medium-sized mammal. (E) Carnivore tooth punctures. (F) Gnawing damage by a small-to-medium carnivore on cercopithecoid limb bones. (G) Similar damage on an *Ardipithecus* metacarpal. (H) Damage from gnawing by a small rodent on a large-mammal limb bone shaft fragment.



SAG-VP-3 localities, 0.5 and 2.0 km southeast of the easternmost *Ar. ramidus* occurrence. Here, different assemblage composition (table S1) and modification signatures are present. Micromammals, birds, and primates are absent from the Lower Aramis inter-tuff horizon within these spatially extensive but faunally depauperate localities ($n = 5$ and 3 identified specimens, respectively). Sublocalities with the most surface bone were circumscribed within each of these localities, and fossils were collected by identical methods for comparison with the faunally richer *Ardipithecus*-bearing localities to the northwest. The resulting assemblages are dominated by poorly preserved (highly weathered) remains of large, mostly aquatic animals, which is consistent with their more axial location in the

depositional basin (as evidenced by structural and sedimentological considerations) (*I*).

Small mammals. Micromammals and birds closely related to extant taxa (and therefore presumed to be ecologically sensitive indicators) are found at all *Ardipithecus*-bearing localities (table S1). However, the large majority of these primarily small fossils (both individually cataloged and pooled bulk samples) were recovered by water-sieving at two widely separated quarries. The more productive quarry (located <100 m from the ARA-VP-6/500 partial *Ar. ramidus* skeleton) yielded about 10,000 total specimens. Of these, more than 1000 are micromammal teeth or jaw fragments, or small bird fragments identifiable at or below the ordinal level. In con-

trast to the intensive destruction of large-mammal bones described above, micromammal and small avian postcrania are well preserved and abundant in these quarry assemblages.

All microvertebrate remains from the two quarries were analyzed taphonomically [according to the protocol in (*II*)]. The dense concentration of remains, consistently high-quality preservation, abundant postcranial elements, and mostly intact jaws suggest that these small mammals were protected from trampling and sunlight. Thus, they probably experienced no postmortem transport, beyond perhaps bioturbation and/or emplacement in desiccation cracks during alluvial flooding (based on the in situ vertical alignment of many rodent limb bones in the alluvial silty clay in both quarries).

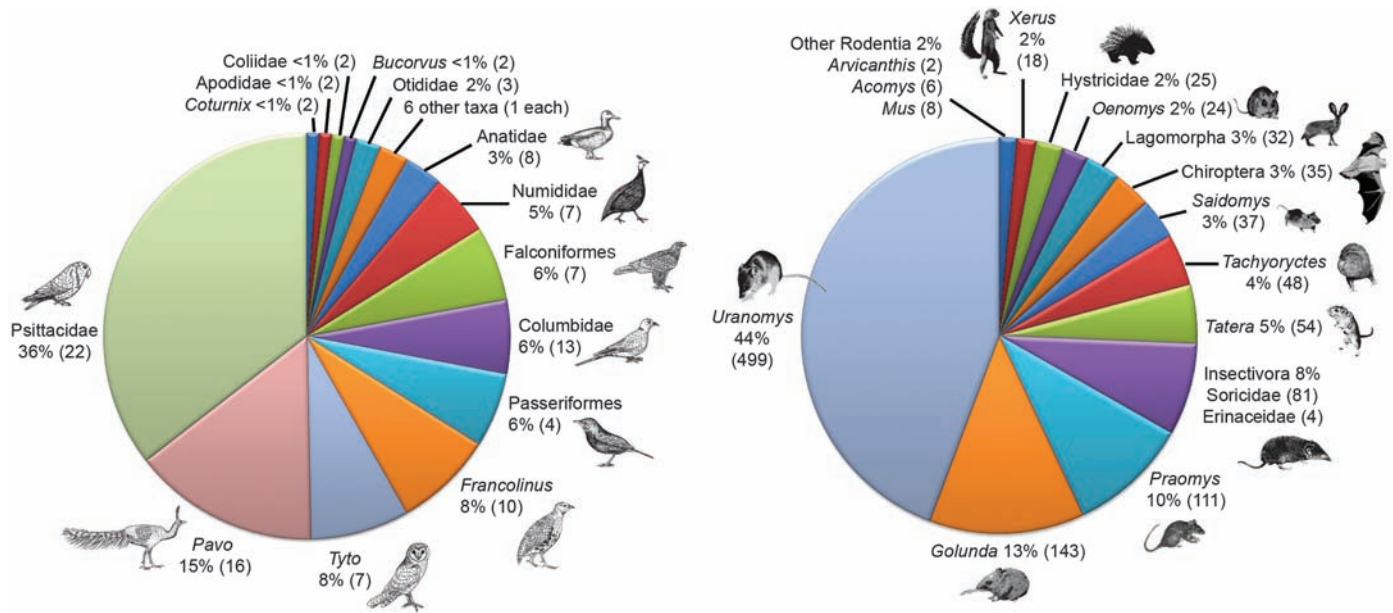


Fig. 2. Relative abundance of avian and small-mammal taxa. For each bird taxon, the pie slice and first number apply to the number of identified specimens ($n = 263$); the second (in parentheses) is the minimum number of individuals

represented in the overall sample. For small mammals, the numbers apply to the number of identified specimens only ($n = 1127$), but closely reflect the minimum number of individuals because only craniodental specimens are included.

The lack of digestive traces on micromammal molars (0.9%, all in the “slightest” category), the low percentage and degree of such traces on incisors (10.7%; 9.9% in the “slightest” category), and the avian assemblage composition (Fig. 2) combine to suggest that many of the microvertebrate remains may have been disaggregated from barn owl (*Tyto*) pellets (11). Aside from one strigid specimen, *Tyto* sp. nov. is the only owl recorded at Aramis and is relatively abundant. Barn owls are well-known micromammal accumulators that produce the lowest levels of digestion and modification among avian predators. Their pellets are known to provide a sample of the micromammal fauna within several kilometers of the roost (11, 12), but the assemblages they create may be biased by prey availability and vulnerability.

The Aramis collection (Fig. 2) includes up to 20 new species among a total of 32 small-mammal genera within the orders Insectivora (two families), Chiroptera (five families), Hyracoidea (one family), Rodentia (six families), Lagomorpha (one family) and Carnivora (one family) (2). These taxa indicate that the drainage basin contained a variety of biotopes, but the distribution of fossils and sediments implies that the *Ardipithecus*-bearing locales were wetter. Drier environments were present at some distance (1, 13).

Fossils of the porcupine *Atherurus*, the murid *Oenomys*, and the emballonurid *Taphozous* found at *Ardipithecus*-bearing localities suggest that forests and/or well-developed mesic woodlands were at least locally present in the paleodrainage basin. Such flora, supported by a high water table or high rainfall due to a higher altitude (1), may have graded into deciduous woodlands. Other associated woodland animals

include the shrews *Crociodura*, *Myosorex*, and *Suncus*; the bats *Rousettus* and possibly *Hipposideros*; the porcupine *Xenohystrix*; the mice *Dendromus*, *Praomys*, and *Mus*; and the dwarf mongoose *Helogale*. The existence of mesic settings is supported by the strong presence of the Asiatic murid *Golunda* (~13%), whose contemporary species *G. ellioti* is today typically found in thickets and bush on densely vegetated plains. The absence of the cane rat *Thryonomys* suggests that local suitable aquatic environments were absent, although it is also missing from the more aquatic, primate-free assemblages to the southeast of Aramis. The absence of small hyracoids and galagos is notable and unexplained.

The murid *Uranomys* is abundant, large and small species together representing 44% of small-mammal specimens. In association with *Praomys* (10%), the two genera constitute about 50% of the micromammalian specimens. Today, *Uranomys* is almost always found in abundance and in association with *Praomys* in two biotopes: (i) *Borassus* palm savanna characterized by a wet *Hyparrhenia* grassland with dense thickets, and (ii) Mbuga mesic grassland characterized by dense, long grasses (14). Combined with the taphonomic findings, this numerical predominance may reflect predator bias, because barn owls would be expected to have focused their predation in open islands of palm-thicket grassland within the larger woodland setting, as indicated by the many “wooded-habitat” mammalian and avian indicator taxa.

Rarer species in the *Ardipithecus*-bearing assemblages indicate that more xeric and open savanna woodlands were regionally present. These include the bats *Rhinolophus* and *Cardioderma*, the squirrel *Xerus*, the gerbil *Tatera*, the

mice *Acomys* and *Saidomys*, and the rat *Arvicanthis*. Still dryer scrub or even arid steppe settings must have also been present (and probably sampled by avian predators), as rarely attested to by the hare *Lepus*, the hedgehog *Atelerix*, and the bat *Coleura*. The Lower Aramis Member localities are today at an elevation of about 600 m, but *Tachyoryctes* and *Myosorex* have contemporary counterparts typically found at higher altitudes, in mesic montane forests and uplands.

Birds. Rich avifauna (Fig. 2 and table S2) provides additional understanding of the Aramis environment. The 370 cataloged specimens comprise a minimum of 29 different taxa representing at least 16 families in 13 orders. Most taxa are terrestrial rather than aquatic (the latter make up only 3.8% of identified specimens). Small taxa such as doves, lovebirds, mousebirds, passerines, and the swift are abundant. These were mostly recovered from the two quarries and are interpreted as deriving from owl pellets. Open-country taxa such as two bustards (Otididae) and the quail *Coturnix* sp. are exceedingly rare. Waterfowl are rare and include ?*Platalea* (ibis or spoonbill, $n = 1$ identified specimen), Anatidae (geese and ducks, $n = 9$), and *Anhinga* (darter, $n = 1$). These indicate the presence of open water, presumably a river or lake distal to the focus of deposition.

In addition to the barn owl, we recovered fossils of the diurnal predators *Aquila* (eagle, $n = 11$) and smaller raptors (the size of hawks or kites). These prefer to hunt in open or ecotonal conditions and presumably roosted in tall emergent trees (15). The Aramis galliform assemblage (35% of identified specimens) is dominated by the abundant ecological indicator species *Pavo* sp., a peafowl ($n = 39$), signaling forested conditions (16). The lovebirds *Agapornis* ($n = 88$) the parrot

Poicephalus sp. ($n = 1$), and guineafowl ?*Guttera* sp. ($n = 2$) are known from woodlands and forests, ranging into wooded savanna.

Collectively, the large-mammal taphonomy of *Ardipithecus*-bearing localities indicates a landscape where carcasses were almost always rapidly and intensively ravaged and the resulting fragments soon buried without transport. The small-mammal and avian assemblages combine with other geological and paleontological data to indicate that mesic woodlands dominated the *Ardipithecus*-bearing landscape 4.4 million years ago.

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Supporting Online Material

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