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The Initial Domestication of Goats (*Capra hircus*) in the Zagros Mountains 10,000 Years Ago

Melinda A. Zeder^{1*} and Brian Hesse²

Initial goat domestication is documented in the highlands of western Iran at 10,000 calibrated calendar years ago. Metrical analyses of patterns of sexual dimorphism in modern wild goat skeletons (*Capra hircus aegagrus*) allow sex-specific age curves to be computed for archaeofaunal assemblages. A distinct shift to selective harvesting of subadult males marks initial human management and the transition from hunting to herding of the species. Direct accelerator mass spectrometry radiocarbon dates on skeletal elements provide a tight temporal context for the transition.

The fertile crescent region of the Near East was the center of domestication for a remarkable array of today's primary agricultural crops and livestock animals. Wheat, barley, rye, lentils, sheep, goats, and pigs were all originally brought under human control in the broad arc that stretches from the southern Levant through southeastern Turkey and northern Syria, to the high Zagros mountain pastures and arid lowland plains of Iraq and Iran. For more than 50 years researchers have sought to define the sequence, temporal placement, and social and environmental context of domestication (1). Central to addressing this process is the ability to identify early domesticates in the archaeological record, and to place them within a secure temporal context. Here we describe recent research that uses a study of modern wild goats (*Capra hircus aegagrus*) to develop an unequivocal marker of early goat domestication, which we apply to assemblages that lie both within and outside the natural range of wild goats in the eastern fertile crescent region—a region long thought to be the initial heartland of goat domestication (2).

Two markers have been used to identify domestication in goats. It has been proposed that changes in skeletal morphology, particularly population-wide reduction in body size, quickly follow human controlled breeding (3, 4). Uncertainty over the pace and causal connection between body size reduction and human control limits the utility of this marker, however, as does difficulty in distinguishing between human-in-

duced changes and those resulting from other biological or environmental factors (5). Alternatively, changes in age and sex profiles that resulted from controlled breeding and selective harvesting of young males have been proposed as providing a better early marker of domestication (6). Difficulty in distinguishing between various selective hunting strategies and those that reflect deliberate herd management and domestication has been the main perceived limitation of this demographic profiling approach (4). Until now a key obstacle has been an inability to construct the separate male and female age profiles necessary to detect the distinctive sex-specific harvest patterns of managed herds.

Recent metrical analysis of a skeletal collection of 37 modern wild goats, curated by the Field Museum of Natural History, from different habitats in Iran and Iraq provides an empirical basis for assessing the utility of these different markers of early goat domestication (7). In all measurements taken on nine different postcranial skeletal elements, sex was the single most significant factor influencing size (Fig. 1). Even the unfused bones of young males older than 1 year were absolutely larger than the fully fused bones of older, adult females. Environment also influenced body size, with a clear pattern of size reduction from the cooler, wetter regions in northern Iran and northwestern Iraq (Fig. 1A) to the arid, hotter, and sparser pastures of southern Iran (Fig. 1C). While the available sample of domesticated goats (*C. h. hircus*) from the region was too small to draw firm conclusions, domestic status does not appear to be a major factor influencing size in this modern sample, especially in female goats (Fig. 1, A and B).

This modern reference class of goat skeletons provides a baseline of comparison for analysis of goat bone assemblages

eight artifacts from the site were manufactured from the same material. Originally cataloged as "subfossil," their appearance and condition, especially in comparison to bone of other species from the cave, suggest that they had been "mined" from elsewhere, perhaps the nearby Redcliffs site, where moa bones were very common. The many artifacts found in 1889 [H. D. Skinner, *Rec. Canterbury Mus.* 2, 151 (1924)] included a few types that can be attributed to the Archaic [J. Golson, in *Anthropology in the South Seas*, J. D. Freeman and W. R. Geddes, Eds. (Avery, New Plymouth, New Zealand, 1959), pp. 29–74], including a fragment of a one-piece fish hook and 2 of the 17 adzes in the collection. However, most do not fit well into either the Archaic or Classic assemblages as currently understood. Monck's Cave is one of a group of northeastern South Island sites that are neither typically Archaic nor Classic in material culture, economic focus, or settlement pattern but appear to be transitional between the two [C. Jacomb, thesis, Department of Anthropology, Otago Univ., Dunedin, New Zealand (1995)]. Excavations in 1998 revealed extensive deposits of marine mollusk shell; some fish bone; sparse bird, seal, and Pacific rat bone; and a fragment of worked moa bone and three small pieces of moa eggshell.

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24. Marine shell was cleaned, washed in 2 M HCl for 100 s, rinsed, and dried. Samples were not assessed by x-ray diffraction, because New Zealand marine shell very rarely exhibits significant recrystallization [T. Higham, *Quat. Geochronol.* 13, 163 (1994)]. Radiocarbon determinations were calibrated to calendar years using OxCal [C. Bronk Ramsay, *Radiocarbon* 37, 425 (1995); the marine curve was as modeled by M. Stuiver, P. J. Reimer, and S. Braziunas [*Radiocarbon* 40, 1127 (1998)]; *R* was set at -25 ± 15 years, according to T. F. G. Higham and A. G. Hogg [*Radiocarbon* 37, 409 (1995)]].
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from a number of archaeological sites, also curated by the Field Museum and by the Smithsonian's National Museum of Natural History, that bracket the transition from hunting to early herd management. This sample includes two sites widely accepted as providing the earliest evidence of domesticated goats—Ganj Dareh, an upland settlement located within the present-day geographical range of wild goats (8), and Ali Kosh, located in a lowland environment well outside the natural habitat of wild goats (9). In his initial study of the Ganj Dareh assemblage, Hesse proposed that domestic goats were present at the site on the basis of a demographic profile that indicated herd management (8). Subsequent researchers also concluded that the Ganj Dareh goats were domesticated, claiming these animals were considerably smaller than wild benchmark populations from Late Pleistocene/Early Holocene contexts (3, 4, 10). Flannery's identification of domesticated goats at Ali Kosh was based on a high percentage of young animals, on a gradual change in horn form, and on the abundance of goats despite the

site's location (9).

A reanalysis of the Ganj Dareh goats by Zeder (7) contradicts claims for a marked diminution in their size relative to wild populations, while supporting Hesse's original conclusions. In all postcranial elements examined in this analysis, there is an almost complete overlap in the size range, mean, and medians of the dimensions of the Ganj Dareh goat bones (Fig. 2C) when compared to wild goats from earlier nearby upland Zagros sites dating to the Middle and Upper Paleolithic (Fig. 2A). There is also no observed size difference between the Ganj Dareh goats and those from the nearby site of Asiab, a likely hunting camp occupied slightly earlier than Ganj Dareh (Fig. 2B) (3, 9, 10).

The apparent population-wide size reduction observed in the Ganj Dareh goats (3, 4, 10) is, in fact, an artifact of a long-standing practice of excluding the unfused bones of young animals from metric analyses. Very few of the large (male) Ganj Dareh goats survived to adulthood, and the exclusion of their unfused skeletal elements from size analysis skewed the resultant size profiles toward smaller adult females. When compared to goats in a hunted population, in which adult males are likely to be well represented, the Ganj Dareh assemblage can appear to indicate an overall reduction in body size. Methods that normalize the dimensions of a number of different skeletal elements into standardized species size profiles (3, 4) tend to exacerbate this bias, while combining assemblages from several different regions across the Near East to form broad temporal samples for comparison (3) further obscures actual patterns of size variation. When all bones, fused and unfused, are measured, and only direct element-by-element comparisons are made of assemblages from the highland Zagros region, the apparent differences in the size of these wild and domestic goat populations disappears.

There is a marked difference in the dimensions of postcranial elements of goats from all of these upland sites, however, when compared to the goats from the lowland settlement Ali Kosh (Fig. 2D). Yet the size difference of ancient goats from these different environmental zones is no greater than that noted between the modern wild goats from northern cooler and wetter upland areas and those from more arid southern regions (Fig. 1) (7). It is difficult to determine, then, whether the smaller size of the Ali Kosh goats is attributable to selective factors that favor smaller animals in managed herds, the response of colonizing populations of domesticated goats to harsher environmental conditions, or the original smaller size of a progenitor stock of wild goats.

At the same time that this study shows that size reduction is not a good marker of early domestication, it also confirms and extends Hesse's original conclusion that the Ganj Dareh goats were domesticated on the basis of demographic profiling (6, 8). The marked bimodality in the size distribution of the postcranial skeletal elements noted by Hesse in his initial study is clearly evident in essentially all dimensions of postcranial skeletal elements measured in this analysis (Fig. 3). With the benefit of Zeder's recent study of size variation in modern goats (7), this bimodality can be securely attributed to the marked dimorphism in the size of male and female goats. Moreover, the study of the modern collections provides solid empirical support for Hesse's conclusion that the disproportionate number of unfused elements of large animals can be attributed to the early slaughter of young males. Finally, the

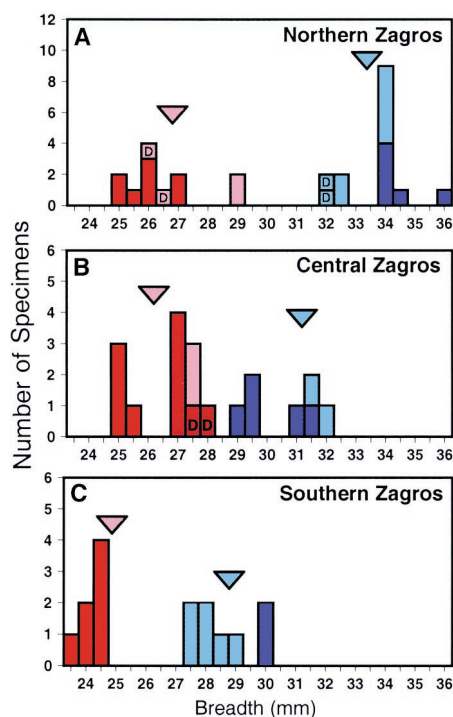


Fig. 1. Greatest breadth of distal metacarpal at epiphysis of modern goats older than 1 year of age (red, fused females; pink, unfused females; blue, fused males; light blue, unfused males; light blue triangle, male mean; pink triangle, female mean; D, domestic). (A) Northern Zagros: Caspian and Azerbaijan regions of Iran and Iraqi Kurdistan (individual animals = 17, specimens measured = 32). (B) Central Zagros: Kermanshah and Isfahan regions of Iran (individual animals = 12, specimens measured = 22). (C) Southern Zagros: southern Fars, Iran (individual animals = 10, specimens measured = 18).

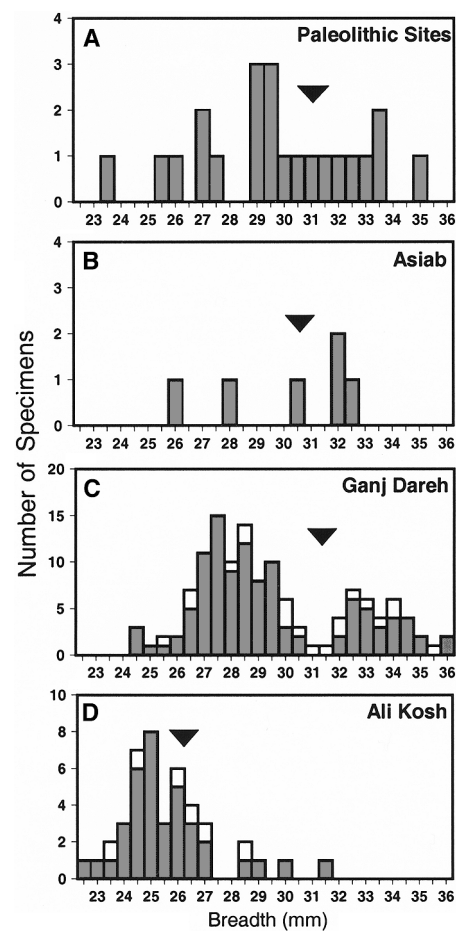


Fig. 2. Length of second phalanx of goats from Zagros sites (shaded, fused bones; unshaded, unfused and fusing bones; triangle, mean). (A) Paleolithic sites: Palegawra, Kunji, Kobeh, and Yafteh Caves, ~50,000 to 15,000 ¹⁴C yr B.P. (*n* = 23). (B) Asiab, ~10,000 ¹⁴C yr B.P. (*n* = 6). (C) Ganj Dareh, ~8900 ¹⁴C yr B.P. (*n* = 135). (D) Ali Kosh, ~8000 to 8400 ¹⁴C yr B.P. (*n* = 47).

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strong regularity of the proportional relation between the size of male and female animals in the modern sample allows the separation of the ancient goat assemblage into male and female subpopulations. Sex-specific age profiles can then be constructed for each of the different size-separate subpopulations.

When this is done for the Ganj Dareh assemblage (Fig. 4A), there is a clear pattern of selective kill-off of subadult males and delayed slaughter of females that matches culling patterns in modern domesticated herds managed for meat (11). In contrast, the sex-specific age profiles of goats from nearby Asiab (Fig. 4B) are more consistent with a hunted population in which there is a focus on fully adult males, with females and young taken when encountered. Preliminary examination of the size and fusion patterns of the Ali Kosh

goats also shows the distinctive demographic profile of a managed herd, although both subadult males and adult females seem to have been slaughtered at somewhat older ages than the Ganj Dareh goats.

Previous efforts to date these sites have been problematic (12). An early date for the initial occupation of Ganj Dareh suggested that the settlement was established about 11,000 years ago, whereas four subsequent levels were dated to about 9500 years ago. At Ali Kosh, a number of laboratories, using different extraction techniques on different types of organic materials, have produced several nonconforming series of dates. On the basis of site stratigraphy, material culture, and some of the dates obtained, excavators identified three different phases of occupation, from 9500 to 7500 years ago (10).

Accelerator mass spectrometry (AMS)

dating of four samples of charred barley at Ganj Dareh (13), and 12 bone collagen samples that span all five levels at the site obtained as part of this study (Table 1), clearly indicate that Ganj Dareh was occupied briefly, for perhaps no more than 100 to 200 years, at about 10,000 calendar years before the present (yr B.P.). While the seven new AMS dates obtained for Ali Kosh provide the most consistent age determinations obtained for this site, there are still some internal inconsistencies, possibly stemming from the different material dated—collagen and carbon extracted from charred bone. It is clear, however, that the occupation of Ali Kosh was much briefer than previously thought, perhaps lasting only 500 years. Moreover, whether the date of initial occupation was 8900 calendar yr B.P. (14), as indicated by the date derived from bone collagen, or 9500 calendar yr

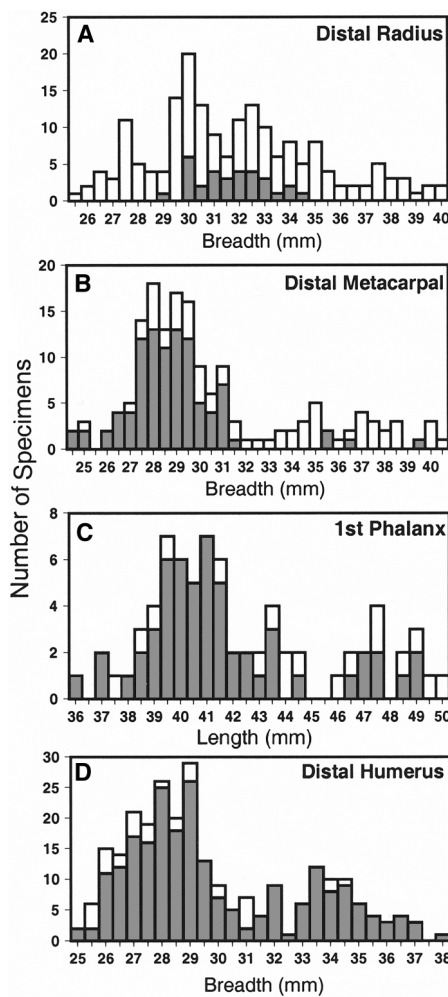


Fig. 3. Ganj Dareh postcranial bone dimensions (shaded, fused bones; unshaded, unfused and fusing bones). (A) Breadth of distal radius (fusion ~36 months, *n* = 186). (B) Breadth of distal metacarpal (fusion ~24 months, *n* = 165). (C) Length of first phalanx (fusion ~16 months, *n* = 83). (D) Breadth of distal humerus (fusion ~10 months, *n* = 292).

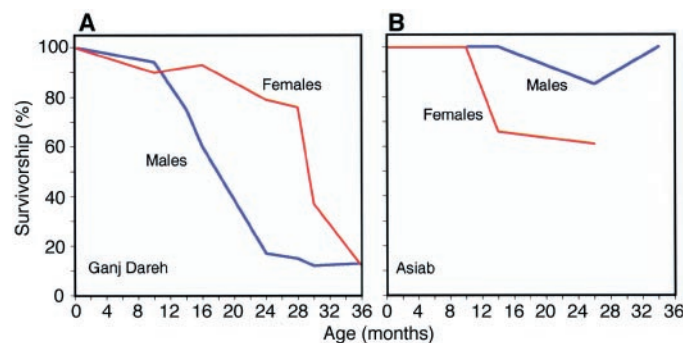


Fig. 4. Sex-specific survivorship curves, displayed as a percentage of animals living beyond a certain age for each fusing element (red, females; blue, males). (A) Ganj Dareh (females = 783, males = 367). (B) Asiab (females = 19, males = 24).

Table 1. AMS ¹⁴C dates on animal bones from Ganj Dareh (GD) and Ali Kosh (AK).

Site	Level	Depth (mm)	Beta Analytic number	Material	Age (radiocarbon yr B.P.)*	Calibration curve intercept (yr B.P.)†	Dendro-calibrated 2σ age range (yr B.P.)‡
GD	A	180–200	B-108238	Collagen	8780 ± 50	9850	9910–9585
	B	165–180	B-108239	Collagen	8930 ± 60	9940	10,005–9870
	B	220–240	B-108240	Collagen	8780 ± 50	9850	9910–9585
	B	240–260	B-108241	Collagen	8720 ± 50	9650	9875–9525
	B	280–300	B-108242	Collagen	8940 ± 50	9945	10,000–9890
	C	460–480	B-108243	Collagen	8920 ± 50	9935	9990–9875
	D	430–460	B-108244	Collagen	8840 ± 50	9890	9945–9820
	D	580–600	B-108245	Collagen	8940 ± 50	9945	9765–9665
	E	580–585	B-108246	Collagen	8870 ± 50	9905	10,000–9890
	E	665–675	B-108247	Collagen	8830 ± 50	9880	9960–9845
AK	MJ	70–80	B-118719	Carbon	8130 ± 70	8995	9725–9695
	MJ	130–140	B-118720	Carbon	8140 ± 70	9000	9940–9805
	AK	210–230	B-118722	Carbon	8110 ± 80	8985	9780–9660
	AK	280–300	B-118723	Carbon	8490 ± 90	9465	9940–9805
	AK	380–400	B-118724	Carbon	8340 ± 100	9375	9780–9660
	BM	635	B-122721	Carbon	8540 ± 90	9485	9980–9865
	BM	546	B-108256	Collagen	8000 ± 50	8945	9945–9820
	BM	546	B-108256	Collagen	8000 ± 50	8945	9765–9665

*Uncalibrated conventional ¹⁴C age of specimens in ¹⁴C yr B.P. (±1σ). †Intercept between the conventional ¹⁴C age and the dendrocalibrated calendar time scale, in calendar yr B.P. (Pretoria calibration procedure program, Beta Analytic). ‡2σ dendrocalibrated age range for specimens, in calendar yr B.P.

B.P., as indicated by the earliest carbonized bone date, these new dates confirm that the site is chronologically more recent than Ganj Dareh by at least 500 years, and perhaps by as much as a millennium.

By resolving the temporal placement of these two sites, it is possible to place the initial domestication of goats in the highland Zagros region well within the natural habitat of this species. The long-term concentration on the hunting of wild goats in this upland region seen in assemblages stretching as far back as the Middle Paleolithic (2) suggests that the eventual domestication of goats grew out of a long-term process in which hunting strategies evolved into the actual management of captive animals. Ganj Dareh represents an early stage in herd management, in which the feeding, movement, and other environmental circumstances of these animals was little changed. Although the Ganj Dareh goats may not yet be morphologically, or even genetically, distinguishable from wild goats, however, the distinctive profile of young male slaughter and prolonged female survivorship documented here marks the goats of Ganj Dareh as a managed, and therefore domesticated, population.

The subsequent establishment some 500 to 1000 years later of settlements like Ali Kosh, outside this natural habitat zone, represents a break with the environmental, biological, and social context of initial domestication. This move seems to have necessitated some adjustments in management strategies from those developed in the upland zone. It also allowed the expression of morphological traits not widely seen in either wild or domesticated goats in upland habitats, such as the gradual alteration in the shape of horns identified by Flannery and, possibly, the reduction in the size of the Ali Kosh goats seen in this study.

Such morphological changes, if related to the process of domestication at all, are only delayed, and possibly indirect, artifacts of human management. Instead, it is the transformation of strategies that seek to maximize off-take from wild herds into those that seek to control the productivity of captive herds that lies at the heart of the process of animal domestication. The method for computing sex-specific age profiles developed here provides the most sensitive tool to date for monitoring this transformation and should be applicable not only to goats, but to any sexually dimorphic species. Combined with high-precision small-sample AMS dating, it promises a much finer understanding of the timing and trajectory of the origins of animal domestication across the Near East and beyond.

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 15. Funded by a Smithsonian Predoctoral Fellowship awarded to B.H. in 1976, and by grants from the Smithsonian's Research Initiative and Scholarly Studies Programs awarded to M.A.Z. Acknowledgment is given to the staff of the Field Museum of Natural History; to A. Aisen, S. Arter, N. Cleghorn, M. Hiers, H. Lapham, S. McClure, C. McLinn, A. Shapiro, and S. Stackhouse; and to M. J. Blackman, B. D. Smith, P. Wapnish, and three anonymous reviewers.

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Molecular Linkage Underlying Microtubule Orientation Toward Cortical Sites in Yeast

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Selective microtubule orientation toward spatially defined cortical sites is critical to polarized cellular processes as diverse as axon outgrowth and T cell cytotoxicity. In yeast, oriented cytoplasmic microtubules align the mitotic spindle between mother and bud. The cortical marker protein Kar9 localizes to the bud tip and is required for the orientation of microtubules toward this region. Here, we show that Kar9 directs microtubule orientation by acting through Bim1, a conserved microtubule-binding protein. Bim1 homolog EB1 was originally identified through its interaction with adenomatous polyposis coli (APC) tumor suppressor, raising the possibility that an APC-EB1 linkage orients microtubules in higher cells.

The orientation of microtubules toward defined cortical sites in eukaryotic cells is a common theme in the regulation of nuclear position, the targeting of secretion, the navigation of growth cones, and the alignment of mitotic spindles. However, identification of the molecular means by which microtubules associate with spatially defined sites on the cortex has remained elusive. Budding yeast must align the mitotic spindle in parallel to the mother-bud axis to segregate one nucleus to each progeny cell. It is thought that cytoplasmic microtubules are selectively oriented toward the bud and that the forces generated by microtubule motors and microtubule

shortening produce the movement and alignment of the spindle (1–5). The budding yeast *KAR9* was genetically defined as being required for spindle alignment (6, 7), and the Kar9 protein localizes to the tips of buds and mating projections, two positions toward which microtubules become oriented (7). No microtubule binding has been shown for Kar9.

To determine the mechanism by which microtubules are oriented toward the bud tip in yeast, a two-hybrid screen was performed with Kar9. One interacting protein was Bim1, which was isolated in a two-hybrid screen against α -tubulin (BIM, binds to microtubules) (8). Bim1 exhibited strong and specific interactions with Kar9 (Fig. 1A). Although direct binding of Bim1 to microtubules has not yet been reported, Bim1 does associate with the microtubule cytoskeleton and affects microtubule dynamics in

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