Proc. Natl. Acad. Sci. USA
Vol. 91, pp. 2757–2761, March 1994
Evolution

Evidence for two independent domestications of cattle

(animal domestication/bovine evolution/conservation genetics/mitochondrial DNA)

RONAN T. LOFTUS, DAVID E. MACHUGH, DANIEL G. BRADLEY, PAUL M. SHARP*, AND PATRICK CUNNINGHAM

Department of Genetics, Trinity College, Dublin 2, Ireland

Communicated by John C. Avise, December 3, 1993 (received for review June 28, 1993)

ABSTRACT **The origin and taxonomic status of domesticated cattle are controversial. Zebu and taurine breeds are differentiated primarily by the presence or absence of a hump and have been recognized as separate species (*Bos indicus* and *Bos taurus*). However, the most widely held view is that both types of cattle derive from a single domestication event 8000–10,000 years ago. We have examined mtDNA sequences from representatives of six European (taurine) breeds, three Indian (zebu) breeds, and four African (three zebu, one taurine) breeds. Similar levels of average sequence divergence were observed among animals within each of the major continental groups: 0.41% (European), 0.38% (African), and 0.42% (Indian). However, the sequences fell into two very distinct geographic lineages that do not correspond with the taurine–zebu dichotomy: all European and African breeds are in one lineage, and all Indian breeds are in the other. There was little indication of breed clustering within either lineage. Application of a molecular clock suggests that the two major mtDNA clades diverged at least 200,000, and possibly as much as 1 million, years ago. This relatively large divergence is interpreted most simply as evidence for two separate domestication events, presumably of different subspecies of the aurochs, *Bos primigenius*. The clustering of all African zebu mtDNA sequences within the taurine lineage is attributed to ancestral crossbreeding with the earlier *B. taurus* inhabitants of the continent.**

Cattle have had a central role in the evolution of human cultures and are the most economically important of domesticated animal species (1). There are two major types, zebu (humped) and taurine (without humps), which are named as separate species (*Bos indicus* and *Bos taurus*), but which, due to complete interfertility, are more often considered as subspecies. Of the 800 breeds thought to exist, many are under threat of extinction, principally as a result of modern agricultural practices (2). An understanding of the extent and pattern of genetic variability among breeds may help in the development of more rational breeding programs (3) and is a prerequisite to the informed conservation of genetic resources (3, 4). Furthermore, determination of the genetic relationships among cattle breeds should complement and clarify archeological data on the origins of animal husbandry. Elucidation of the events surrounding bovine prehistory has proved quite difficult, since the distinction between wild and domesticated forms of a species is not always clear from the archeological record. In addition, data from sources such as rock paintings are often patchy and notoriously hard to date. These artifacts generally do not yield satisfactory information on the types or breeds of early domesticated cattle.

To address some of these issues, we have examined mtDNA from representative breeds (listed in Table 1) of European, African, and Indian cattle. Sequences of ≈900 bp comprising the entire displacement loop (D loop), the most variable mtDNA region (5), were determined for two animals from each breed.† The resulting data were subjected to phylogenetic analyses using a number of algorithms and the robustness of dendrograms was tested by bootstrapping. The data provide details on the population structure of domesticated cattle and give an indication of the levels of inter- and intrabreed variability. Here, the results are analyzed and interpreted in the light of data generated from other disciplines such as cytology, archeology, and allozyme studies. Taken together with these studies, estimated divergence times provide the strongest evidence to date for independent domestications of zebu and taurine cattle.

MATERIALS AND METHODS

Sample Collection. Fresh blood samples were collected from representative breeds of European, African, and Asian origin, the regions believed to contain the progenitors of most modern cattle populations (Fig. 1). Within each of these continents, typical breeds from the major breed groups were selected, taking into consideration other factors such as relative economic importance, geographic distribution, and amenability to sampling. With the exception of Jerseys, European breeds (Aberdeen Angus, Hereford, Charolais, Simmental, and Friesian) were sampled in artificial insemination centers throughout the Republic of Ireland. Jerseys were sampled from a large private herd comprised of animals from a number of countries. Indian samples (Tharparkar, Sahiwal, and Hariana) were collected from research herds at the National Institute for Animal Genetics (Karnal, Haryana State, India), and African breeds (Butana, Kenana, N'Dama, and White Fulani) were sampled at the National Dairy Research Centre (Shukaba, Wad Medani, Sudan) and the University of Ibadan (Nigeria). Samples of the outgroup species (*Bison bison*) were provided by W. Mann, Technical University of Munich. In all available cases, pedigrees were consulted to ensure that the animals sampled were unrelated. When pedigree details were unavailable, herdsmen with a knowledge of local breeds were consulted.

Amplification and Sequencing of mtDNA. Total mtDNA was isolated from fresh blood samples as described elsewhere (8) and D loops were amplified on a Perkin–Elmer DNA thermocycler. Primers, derived from the known bovine mtDNA sequence (5), were designed to lie in the conserved proline tRNA (5′-CTGCAGTCTCACCATCAACC-3′) and 12S rRNA (5′-GATTATAGAACAGGCTCCTC-3′) genes. Reactions were carried out using ≈10 ng of mtDNA, 50 pmol of primer, and 10 mM dNTPs in a reaction buffer containing 10 mM Tris·HCl (pH 8.3), 50 mM KCl, 1.5 mM $MgCl_2$, and 2.5 units of *Taq* DNA polymerase in 100 μl. Amplifications were carried out for at least 30 cycles as follows: 30 s at 94°C,

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

Abbreviations: Myr, million years; D loop, displacement loop.

*Present address: Department of Genetics, University of Nottingham, Queens Medical Centre, Nottingham NG7 2UH, U.K.

†The sequences reported in this paper have been deposited in the GenBank data base (accession nos. L27712-L27737).

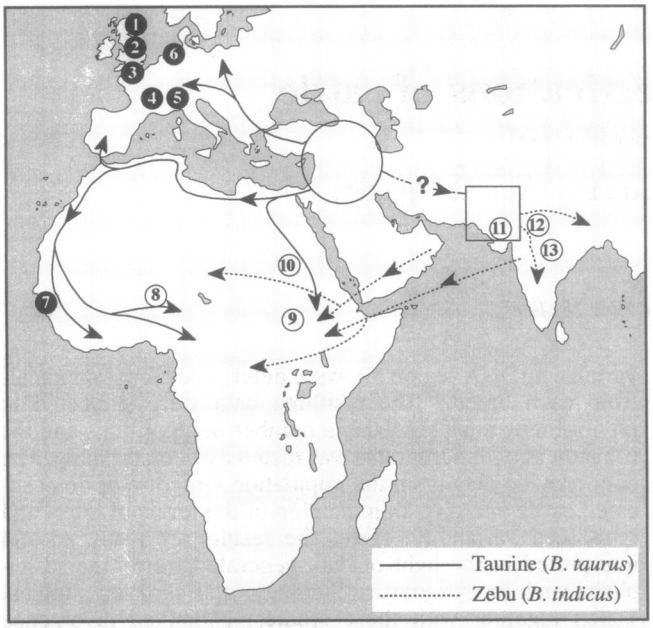

FIG. 1. Postulated migratory routes of cattle across western Asia, Africa, and Europe (6, 7). Geographical origins of the cattle breeds sampled in this study are indicated by numbered circles (taurine, black; zebu, white): 1, Aberdeen Angus; 2, Hereford; 3, Jersey; 4, Charolais; 5, Simmental; 6, Friesian; 7, N'Dama; 8, White Fulani; 9, Kenana; 10, Butana; 11, Tharparkar; 12, Sahiwal; and 13, Hariana. The large circle represents the original domestication event and the square represents the formation of Asian zebu. The dotted line between the two centers is an indication of the prevailing description of zebu origins as derivatives of migrating, domestic taurines.

30 s at 57°C, and 90 s at 72°C. Reaction products were electrophoresed using 1.5% low-melt agarose gels (NuSieve GTG FMC) to remove excess primer. The amplified fragment was isolated from the agarose slice using an anion-exchange column (Qiagen tip-5, Diagen, Dusseldorf, F.R.G.) according to the manufacturer's instructions. Sequencing was performed with a Promega sequencing kit using ≈250–500 ng of amplification product (9).

Phylogenetic Analysis. Phylogenetic trees were constructed using the neighbor-joining algorithm (10) incorporated into the CLUSTALV package (11), using distances corrected for multiple hits by the two-parameter method of Kimura (12). Sites representing a gap in any of the aligned sequences were excluded from the analysis. Bootstrap analyses (using 1000 replications) were used to assess confidence in the branching order of the phylogeny. Maximum parsimony trees were constructed using the heuristic search method in the PAUP package (13).

RESULTS

mtDNA Variation. Complete mitochondrial D loop sequences, 910–920 bp in length, were determined for two animals from each of six European, four African, and three Indian breeds of cattle (listed in Table 1). Comparisons of these sequences revealed 24 mitochondrial types defined by polymorphism at 63 sites: one sequence was shared by two European animals and another by two African individuals. Of the 63 variable positions, 2 represented insertion–deletion events of a single base pair, 1 encompassed length variation in a poly(C) tract, and the remaining 60 were nucleotide substitutions. Only 1/60 of these substitutions was due to transversion, indicating a strong transitional bias. This is a characteristic of mammalian mitochondrial evolution and has been demonstrated in a variety of other species (especially between closely related sequences; ref. 14). An examination of the distribution of mutations in the D loop revealed two major hypervariable regions, one of ≈375 bp between the 5′ end and the central region, containing almost 58% of the overall number of substitutions, and a second, less variable, region toward the 3′ end (Fig. 2). Studies of human mtDNA D loops have revealed similar tracts of sequence. The first 400 bp of human control region DNA contain almost 64% of the total polymorphism (15) and a second, somewhat less polymorphic, region has been documented (16). The positions of these human and bovine hypervariable regions are similar if a known 66-bp insertion at the 3′ end of the bovine D loop (17) is taken into consideration.

The average pairwise sequence divergence estimates within breeds varied from 0.11% to 0.92% (Table 1). Similar average levels of divergence were seen among breeds within each of the three continental groups: 0.41%, 0.38%, and 0.42% among European, African, and Indian groups, respectively. Most surprisingly, there was no differentiation between African zebu and taurine breeds, which both exhibited low divergence from European (taurine) breeds (average 0.73%) but high divergence from Indian breeds (average 5.01%).

Phylogenetic Analysis. The apparent dichotomy between Indian and Afro-European breeds was confirmed by phylogenetic analyses, which indicate that these mtDNA sequences fall into two very distinct lineages. One contains all mtDNAs of European and African origin, and the other contains all those of Indian origin (Fig. 3*a*). Within each clade there is relatively little variability and no evidence of any breed or continental structure, except perhaps that European

Table 1. Interbreed variability estimated from total D loop sequences (above diagonal) and from the 375-bp hypervariable region (below diagonal) and intrabreed values from the total D loop (on the diagonal)

	Ang	Cha	Fri	Her	Jer	Sim	But	Ken	WFu	N'Da	Har	Sah	Tha
Aberdeen Angus	0.57	0.46	0.46	0.46	0.69	0.34	0.92	0.92	0.80	0.92	4.78	4.96	4.90
Charolais	0.28	0.11	0.23	0.23	0.63	0.17	0.63	0.57	0.46	0.57	5.03	5.22	5.15
Friesian	0.15	0.15	0.34	0.28	0.63	0.23	0.75	0.69	0.57	0.69	4.90	5.09	5.03
Hereford	0.29	0.29	0.15	0.34	0.63	0.23	0.63	0.63	0.57	0.63	4.78	4.96	4.90
Jersey	1.01	1.01	0.87	1.01	0.92	0.52	1.15	1.09	0.98	1.09	4.96	5.22	5.09
Simmental	0.15	0.15	0.00	0.15	0.87	0.23	0.68	0.63	0.52	0.63	4.84	5.03	4.97
Butana	1.01	1.16	1.01	1.16	1.90	1.01	0.23	0.46	0.52	0.63	4.59	4.77	4.71
Kenana	1.16	1.16	1.01	1.16	1.99	1.01	0.86	0.34	0.23	0.34	5.03	5.22	5.15
White Fulani	1.16	1.16	1.01	1.16	1.90	1.01	0.86	0.29	0.11	0.23	5.09	5.28	5.28
N'Dama	1.31	1.30	1.16	1.16	2.04	1.16	1.01	0.43	0.43	0.34	5.03	5.22	5.15
Hariana	7.05	7.38	7.21	7.05	7.88	7.21	6.72	7.71	7.54	7.21	0.34	0.46	0.34
Sahiwal	7.71	8.05	7.88	7.71	8.55	7.88	7.38	8.38	8.21	7.88	1.01	0.69	0.52
Tharparkar	7.38	7.71	7.55	7.38	8.21	7.55	7.05	8.04	8.04	7.55	0.86	1.16	0.11
Bison	10.68	10.85	10.85	10.68	11.21	10.85	9.64	10.68	10.68	10.16	9.47	10.34	9.99

All values were computed as average pairwise percentage sequence divergence estimates between individuals.

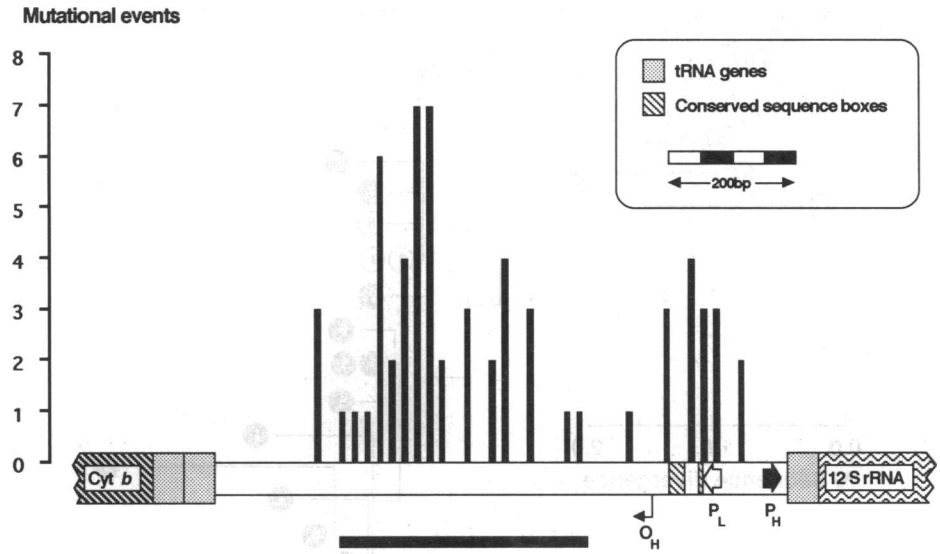

FIG. 2. Distribution of base substitutions in the bovine mtDNA D loop. Numbers of sequence variations in the data set were examined in consecutive blocks of 20 bp and plotted as a histogram. P_L, P_H, and O_H refer to the transcriptional promoters for the light and heavy chains and the origin of heavy strand replication, respectively. The heavy line underneath the D loop highlights the region sequenced in the American bison.

breeds, as a group, fall within the African radiation. Bootstrapping revealed little robustness in branch topology apart from the major division. This lack of mitochondrial population subdivision contrasts with that found in many natural populations, which generally appear to be highly structured (18). However, studies of human and mouse populations have demonstrated a similar lack of phylogeographic structure (19, 20), consistent with the view that highly mobile species exhibit little population differentiation (18). Livestock, as exchangeable units of wealth, are expected to have dispersed at least as thoroughly as their herders. The results do not appear to be an artifact of small sample size, since analysis of a shorter (but highly informative; see Fig. 2) 375-bp region of the D loop from five additional animals per breed, and restriction fragment length polymorphism analysis of an even larger sample size, produce essentially identical results (21).

Estimation of Divergence Times. Two independent approaches were employed to estimate the divergence time of the two major mtDNA clades. First, we utilized a one-lineage evolutionary rate estimate of 0.118×10^{-6} substitution per site per year, calculated from human D loops (22), which, when applied to our data, suggests a divergence time of 210,000 years B.P. This rate is derived from the most variable regions of the human D loop and is therefore likely to give an underestimate of the actual lineage bifurcation time. However, there is also an implicit assumption that rates are similar in humans and cattle, which may not be strictly valid. Therefore, for a second approach we incorporated a close outgroup, American bison (*B. bison*), for which the date of common ancestry with cattle has been estimated at 1.4 million years (Myr) ago [from allozyme studies (23)], or at least 1 Myr ago from palaeontological evidence (A. W. Gentry, personal communication). The sequence of a shorter (375 bp), more variable and, hence, more informative, region of the D loop defined from the information presented in Fig. 2 was determined for bison (two animals, American and European, differed in only 3 nucleotide positions). Considering this region, the average pairwise distance between Afro-European and Asian mitochondria is 7.86% and that between bison and domesticated cattle is 10.62%. Hence, the extent of divergence between Indian and Afro-European mtDNAs relative to the divergence between *Bos* and *Bison* is 74.0% (Fig. 3*b*), leading to estimates in the range of 740,000 to 1.04 Myr ago for the common ancestry of the two *Bos* lineages. Finally, the small divergence between African and European breeds, if taken as having accumulated largely since domestication, ≈10,000 years ago, provides an internal standard that further highlights the magnitude of the split between the two major lineages.

DISCUSSION

All modern domesticated cattle breeds (excluding Bali cattle and mithan) are believed to be derived from the now extinct wild ox or aurochs, *Bos primigenius* (6, 7, 24–26). This formidable animal had a range incorporating most of the Old World, and three continental races have been identified: *B. primigenius namadicus* (Asia), *B. primigenius opisthonomus* (North Africa), and *B. primigenius primigenius* (Europe). Only the latter survived into the Christian era, the last one reputed to have been killed in Poland around 1627. The most widely accepted view holds that taurine cattle were domesticated from *B.p. namadicus* in civilizations of the Near East 8000–10,000 years ago (7, 24–26) (Fig. 1). Early remains of *Bos*, judged to be domestic because of their small size, have been found in Anatolia dating to 7800 B.P. (27). The arid-adapted physiology and hump of *B. indicus* are described as having developed on the eastern fringes of the Great Salt desert of Iran, prior to eastward migration (6, 7, 24). Fossils indicating the presence of both zebu and taurine cattle have been found at Mohenjo Daro and Harappan sites of the Indus valley from 4500 B.P. Additionally, early representations of zebu animals, which predate similar finds further East, may be found in Mesopotamia (6). Consequently, many authors have concluded that zebu breeds developed from taurines subsequent to the original domestication event. However, the mtDNA data presented here are clearly not consistent with a single origin for all cattle breeds within the 10,000-year history of animal husbandry. Estimated divergence times point to independent primary events leading to the establishment of each of the two bovine subspecies.

Because of the relative importance of the dual domestication hypothesis, the possibility that the large observed divergence could be the result of some other phenomenon must be considered. Indeed, there have been an increasing number of incidences in the literature of discordances between mtDNA

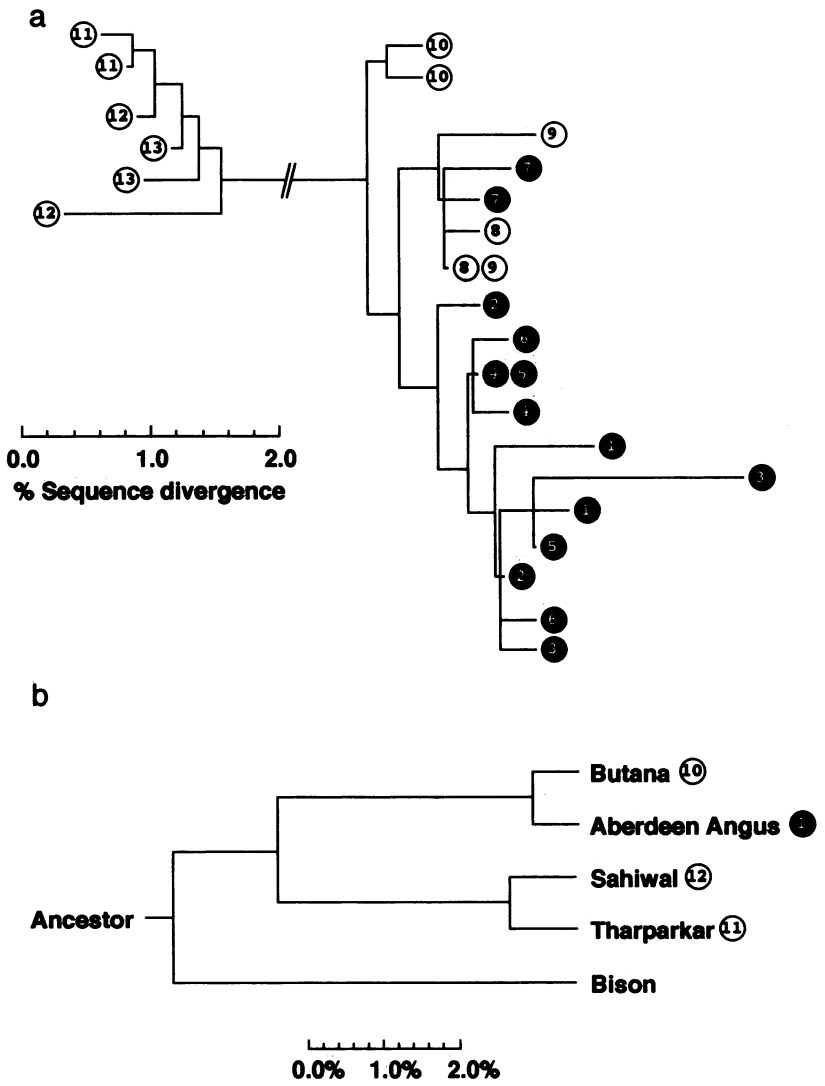

FIG. 3. (*a*) Phylogenetic relationships among European (nos. 1–6), African (nos. 7–10), and Indian (nos. 11–13) cattle derived from complete mtDNA D loop sequences. Each node is an individual animal; numbered circles are used to denote breed and these correspond to those used in Fig. 1. The full magnitude of the split between Indian and Afro-European lineages is not shown. Bootstrapping gave a replicate value of 100% for this major split. The branch grouping the two Tharparkar (breed 11) sequences occurred at a frequency of 51% in trees from 1000 resamplings and all other branches at 15% or less. (*b*) Rooted tree from a highly variable 375-bp region in the D loop, illustrating the large dichotomy between mtDNA of Indian and Afro-European origin, relative to the small divergence within each cluster and relative to the divergence of *Bos* and *Bison*. The tree is rooted at the midpoint between the latter.

and population phylogenies (28). These discrepancies usually result from one or a number of the following factors: evolutionary rate heterogeneity, secondary introgression from another species, or the stochastic loss of mitochondrial lineages. A study of East African jackals has indicated gross differences in intraspecific evolutionary rates of mtDNA (29). However, this is considered an unlikely explanation of the findings presented here, as both *B. indicus* and *B. taurus* are approximately equidistant from the outgroup species (Fig. 3*b*), indicative of internal rate consistency.

Secondary introgression of mtDNA from related species such as banteng (*Bibos banteng*), bison (*B. bison*), gaur (*Bibos gaurus*), or yak (*Bos grunniens*) into *B. indicus* populations could also account for the large divergence. Indeed, banteng and gaur, which possess humps, have each been suggested as a wild ancestor for *B. indicus*. Extensive reciprocal crossing to improve indigenous cattle populations is known to take place with wild banteng in Indonesia (7). However, each of these candidates may be discounted using mtDNA sequence comparisons. Sequences (in some cases partial) of D loops from bison (Fig. 3*b*), yak (30), gaur, and banteng (D.G.B., unpublished results) are all more divergent from both *B. indicus* and *B. taurus* than the latter are from each other.

A further alternative might be that the original source population possessed two deep mtDNA lineages that subsequently partitioned into the modern continental groups (28). However, this interpretation seems quite unlikely, given the magnitude and distribution of lineage divergence. Furthermore, it is difficult to reconcile with a large body of evidence from protein polymorphisms illustrating a considerable (if undated) genetic divergence between European and Indian cattle breeds (31–33). The observations of gross cytogenetic dimorphism of the Y chromosome and of significant morphological and physiological differences are also consistent with a pre-domestic separation between the ancestors of modern *B. taurus* and *B. indicus* (24, 34).

Archeological remains that show the presence of the Asian aurochs, *B.p. namadicus*, at early agricultural sites in Shahr-i-Sokhta, Sistan (Iran-Afghanistan), may represent the progenitor of *B. indicus* and give some indication of an alternative domestication center (35). Also, the site of Mehrgarh in Pakistan has yielded evidence for cattle herding, probably of

zebu, from 7000 B.P. at the latest and may also represent a potential Eastern domestication site (36).

The origins and history of African cattle are complex, local varieties often emerging from a background of nomadic movements, pastoralist migrations, and successive introductions of Asian animals. An African origin from the African aurochs (*B.p. opisthonomus*), although still controversial (37), has not gained general acceptance, due to the lack of supporting archeological evidence (6, 7, 24). Consequently, African cattle are thought to have originated from successive migrations from the Middle East, Arabia, and the Indian subcontinent (Fig. 1). Our studies have found only taurine mitochondrial genomes in the African breeds surveyed. This is surprising given the distinctly zebu character of three of these four African breeds, and, indeed, morphological analyses (6) and allozyme data (31–33) point toward a considerable input of Asian zebu genes into African animals. Archeological evidence indicates that Asian *B. indicus* were introduced prior to, and especially during, the Arab invasions of A.D. 670, giving rise to typical East African zebu such as the Kenana and Butana breeds (38, 39). The apparent lack of Asian *B. indicus* mitochondria in these cattle may be taken as strong evidence for their crossbred origins and suggests that most zebu gene flow must have been through male transmission. As most early exotic imports into Africa either crossed the Red Sea or came through the isthmus of Suez (Fig. 1), the introduction of small numbers of males would have been the most effective way of disseminating desirable phenotypes. Also, given that male animals are favored for meat and draft, as well as ceremonial purposes, they may have been introduced selectively. Our ongoing studies point to the presence of the Asian *B. indicus* Y chromosome in African cattle populations and support this view (40). Furthermore, populations that go through bottlenecks may lose extensive mitochondrial genetic variability while retaining nuclear variability (14), and since African animals have been regularly subjected to famines and epidemics (for example, rinderpest killed 90% of the cattle in sub-Saharan Africa at the end of the last century), any rare Asian mtDNA lineages could have been lost by this process.

In conclusion, we provide convincing molecular evidence supporting independent domestication of *B. indicus*; together with recent archeological studies, these data point toward the origin and development of cattle husbandry in two separate locations. The data also demonstrate the exclusive presence of taurine mitochondria in the physiologically zebu background of African *B. indicus*, illustrating a striking discordance between phylogenetic relationships based on morphology and mtDNA and reinforcing the need for caution when undertaking studies based on a single genetic marker. Finally, the study provides an indication of the rather low levels of population structuring within domestic species that are likely to be detectable from mtDNA analysis.

We acknowledge the assistance of the following in the collection of blood samples: D. S. Balain and V. J. Shankar (National Institute for Animal Genetics, Karnal, Haryana, India), A. M. Badi, J. Rizgalla, and A. Hassan (Animal Production Research Administration, Khartoum, Sudan), L. O. Ngere (University of Ibadan, Nigeria), and W. Mann (Technical University of Munich). We are also grateful to A. T. Lloyd and C. J. Burgess for their assistance and J. Clutton-Brock and A. W. Gentry for comments on an earlier version of the manuscript. Data analytical support was provided by the Irish National Centre for BioInformatics. This work was funded by the European Economic Community Tropical Agriculture Programme.

1. Cunningham, E. P. (1992) in *Selected Issues in Livestock Industry Development* (The World Bank, Washington, DC), pp. 1–12.
2. Loftus, R. T. & Scherf, B. (Eds.) (1993) *World Watch List for Domestic Animal Diversity* (FAO, Rome), pp. 32–34.
3. Kidd, K. K., Osterhoff, D., Erhard, L. & Stone, W. H. (1974) *Anim. Blood Groups Biochem. Genet.* **5**, 21–28.
4. Kidd, K. K. (1974) *Proc. World Congr. Genet. Appl. Livstk. Prod.* **1**, 321–328.
5. Anderson, S., DeBruijn, M. H. L., Coulson, A. R., Eperon, I. C., Sanger, F. & Young, I. G. (1982) *J. Mol. Biol.* **156**, 683–717.
6. Epstein, H. (1971) *The Origin of the Domestic Animals of Africa* (Africana Publishing Cooperation, New York), Vol. 1.
7. Payne, W. J. A. (1991) *Cattle Genetic Resources*, ed. Hickman, C. G. (Elsevier, Amsterdam), 51–72.
8. Lindberg, G. L., Koehler, C. M., Mayfield, J. E., Myers, A. M. & Beitz, D. C. (1992) *Biochem. Genet.* **30**, 27–33.
9. Murphy, G. & Kavanagh, T. A. (1988) *Nucleic Acids Res.* **16**, 5198.
10. Saitou, N. & Nei, M. (1987) *Mol. Biol. Evol.* **4**, 406–425.
11. Higgins, D. G., Bleasby, A. J. & Fuchs, R. (1992) *Comput. Appl. Biosci.* **8**, 189–191.
12. Kimura, M. (1980) *J. Mol. Evol.* **16**, 111–120.
13. Swofford, D. L. (1989) PAUP, Phylogenetic Analysis Using Parsimony (Illinois Natural History Survey, Champaign, IL), Version 3.1.
14. Wilson, A. C., Cann, R. L., Carr, S. M., George, M., Gyllensten, U. B., Helm-Bychowski, K. M., Higuchi, R. G., Palumbi, S. R., Prager, E. M., Sage, R. D. & Stoneking, M. (1985) *Biol. J. Linn. Soc.* **26**, 375–400.
15. Di Rienzo, A. & Wilson, A. C. (1991) *Proc. Natl. Acad. Sci. USA* **88**, 1597–1601.
16. Vigilant, L., Pennington, R., Harpending, H., Kocher, T. D. & Wilson, A. C. (1989) *Proc. Natl. Acad. Sci. USA* **86**, 9350–9354.
17. Saccone, C., Pesole, G. & Sbisa, E. (1991) *J. Mol. Evol.* **33**, 83–91.
18. Avise, J. C., Arnold, J., Ball, R. M., Bermingham, E., Lamb, T., Neigel, J. E., Reeb, C. A. & Saunders, N. C. (1987) *Annu. Rev. Ecol. Syst.* **18**, 489–522.
19. Vigilant, L., Stoneking, M., Harpending, H., Hawkes, K. & Wilson, A. C. (1991) *Science* **253**, 1503–1507.
20. Ferris, S. D., Sage, R. D., Prager, E. M., Ritte, U. & Wilson, A. C. (1983) *Genetics* **105**, 681–721.
21. Loftus, R. T. (1992) Ph.D. thesis (University of Dublin).
22. Stoneking, M., Sherry, S. T., Redd, A. J. & Vigilant, L. (1992) *Philos. Trans. R. Soc. London Ser. B* **337**, 167–175.
23. Hartl, G. B., Goltenboth, R., Grillitsch, M. & Willing, R. (1988) *Biochem. Syst. Ecol.* **16**, 575–579.
24. Epstein, H. & Mason, I. L. (1984) in *Evolution of Domesticated Animals*, ed. Mason, I. L. (Longman, New York), pp. 6–27.
25. Grigson, C. (1980) *J. Arch. Sci.* **7**, 3–32.
26. Clutton-Brock, J. (1989) in *The Walking Larder: Patterns of Domestication, Pastoralism and Predation*, ed. Clutton-Brock, J. (Unwin Hyman, London), pp. 200–206.
27. Perkins, D., Jr. (1969) *Science* **164**, 177–179.
28. Avise, J. C. (1989) *Evolution* **43**, 1192–1208.
29. Wayne, R. K., Meyer, A., Lehman, N., Van Valkenburgh, B., Kat, P. W., Fuller, T. K., Girman, D. & O'Brien, S. J. (1990) *Proc. Natl. Acad. Sci. USA* **87**, 1772–1776.
30. Miyamoto, M. M., Tanhauser, S. M. & Laipis, P. J. (1989) *Syst. Zool.* **38**, 342–349.
31. Manwell, C. & Baker, C. M. A. (1980) *Anim. Blood Groups Biochem. Genet.* **11**, 151–162.
32. Naik, S. N. (1978) *J. Hum. Evol.* **7**, 23–30.
33. Graml, V. R., Ohmayer, G., Pirchner, F., Erhard, L., Buchberger, J. & Mostageer, A. (1986) *Anim. Genet.* **17**, 61–76.
34. Halnan, C. R. E. (1989) *Cytogenetics of Animals* (CAB, Wallingford, U.K.), pp. 235–256.
35. Bökönyi, S. (1985) *East and West* **35**, 426–429.
36. Meadow, R. H. (1984) in *Animals and Archaeology: 3. Early Herders and Their Flocks*, eds. Clutton-Brock, J. & Grigson, C. (BAR International Series, Oxford), **202**, 309–354.
37. Grigson, C. (1991) *African Archaeol. Rev.* **9**, 119–144.
38. Boyns, B. M. (1947) *Empire J. Exp. Agri.* **15**, 27–41.
39. Maule, J. P. (1990) *The Cattle of the Tropics* (Centre for Tropical Medicine, University of Edinburgh).
40. Bradley, D. G., MacHugh, D. E., Loftus, R. T., Sow, R., Hoste, C. H. & Cunningham, E. P. (1993) *Animal Genetics* **25**, 7–12.