plasma–mass spectrometry (ICP-MS). Other portions were used for noble gas and oxygen isotopic analysis. The analytical procedures were described in (*27–32*). Note that two oxygen isotopic analyses were performed with and without HCl wash to remove weathering products, and the two results are the same. This indicates that the oxygen isotopic composition of NWA011 was not changed during the weathering processes in the desert. This result is consistent with the very low Fe_2O_3 contents determined by wet chemical analysis (*7*).

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African Pastoralism: Genetic Imprints of Origins and Migrations

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The genetic history of African cattle pastoralism is controversial and poorly understood. We reveal the genetic signatures of its origins, secondary movements, and differentiation through the study of 15 microsatellite loci in 50 indigenous cattle breeds spanning the present cattle distribution in Africa. The earliest cattle originated within the African continent, but Near East and European genetic influences are also identified. The initial expansion of African *Bos taurus* was likely from a single region of origin. It reached the southern part of the continent by following an eastern route rather than a western one. The *B. indicus* genetic influence shows a major entry point through the Horn and the East Coast of Africa and two modes of introgression into the continent.

Cattle pastoralism is widespread in Africa today and still forms the basis of life for millions across the continent. Two hypotheses for the origins of African domesticated cattle are currently debated. The North African subspecies of wild cattle or aurochs *Bos primigenius* (*1*) may have undergone an indigenous African domestication around 10,000 years ago, possibly in the northeast of the continent (*2–4*). However, the archaeological evidence is disputed and the molecular data are not conclusive (*2*, *5*). Alternatively, domesticated cattle could have been introduced into Africa from the Near East where cattle domestication is known to have occurred (*6*).

The pattern and the chronology of subsequent domestic cattle dispersal within the continent are also unclear. The origin and history of the early dispersion of African pastoralism westward and southward in the continent remain largely unknown, as does the pattern of the introgression of *B. indicus*, which is known to have influenced the majority of cattle populations in Africa (*7*, *8*).

Pictorial representations and archaeological remains show that the earliest African cattle were humpless *B. taurus* (*9*, *10*). The earliest evidence for humped cattle on the continent, provided by Egyptian tomb paintings of the XIIth Dynasty, do not appear until the second millennium BC (*11*, *12*), which suggests that the Egyptian civilization may have played a role in the introduction of zebu into the continent. Today, most modern breeds have an appreciable zebu ancestry (*7*, *8*), which attests to a major secondary introduction.

We address these issues through a continent-wide sampling of indigenous African cattle. Fifty populations from 23 African countries spanning the present cattle distribution in Africa (*13–15*) were studied (Fig. 1A). The sample included 31 *B. taurus* (taurine) populations, generally found in more tropical regions in West, East, and Southern Africa, and 19 *B. indicus* (zebu) populations, restricted to the more arid zones of West and East Africa (*11*, *13*).

These samples were analyzed with 15 autosomal microsatellite markers (*14*). We observed 183 alleles whose frequencies were used to calculate the principal components (PC) values of the genetic variation (*14*). PC values of each population were then used to construct interpolation maps illustrating continent-wide genetic trends for the first three PCs (Fig. 1, B through D) (*16*). These allowed us to generate hypotheses, which were assessed statistically and in light of earlier mitochondrial and Y chromosome DNA results (*4*, *8*, *17*), as well as available archaeological and historic information.

The first principal component of the vari-

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ation, PC1, explains 38% of the total variation. The ranking of the PC1 values in our analysis shows East African *B. indicus* breeds at one extreme and the *B. taurus* breeds from both West and Southern Africa at the other (*14*), raising the possibility that PC1 values might be tied to the secondary zebu influx suggested by archaeological data. To assess this hypothesis, we estimated the level of *B. indicus* admixture in the African populations (*14*, *18*, *19*) and discovered an almost perfect correlation ($r = 0.98$, $P < 0.001$) with PC1, strongly supporting this interpretation (*20*).

A synthetic map constructed with the use of interpolated PC1 values allows us to show a gradient of zebu influence that peaks in the combined regions of the Horn and the East Coast of Africa (Fig. 1B). We observe a higher correlation between the PC1 values of the breeds and their distance from the Horn of Africa ($r = 0.79$, $P < 0.001$) than their distance from the Isthmus of Suez ($r = 0.48$, $P < 0.001$) (*21*). These suggest that the major process of *B. indicus* influence was centered in East Africa (*12*) rather than through the land connection between Egypt and the Near East. This is further supported by the much lower level of zebu admixture observed in the Egyptian taurine Baladi cattle compared with taurine breeds living further south (*14*). Moreover, the level of zebu genetic background within the Egyptian Baladi has been shown to be similar to those encountered in the Middle East (*22*), where higher *B. indicus* influence might have been expected in the case of a major zebu introgression from the Isthmus of Suez.

This major zebu immigration may have followed local Arabian contacts or it may have been part of the long-distance Indian Ocean trade that has left other domestic animal legacies, including chicken (*Gallus gallus*) and camel (*Camelus dromaderius*) (*23*). African domesticated cereals such as sorghum *Sorghum bicolor* and finger millet *Eleusine coracana* also appeared in India as early as the late 2nd millennium BC (*24*). The case for a predominantly sea-borne introduction is further strengthened by the admixture values (*14*) of the zebu cattle of Madagascar, which identify that population to be the most zebu-like in character of the African samples and by the presence of a zebu introgression pattern of coastal origin into taurine breeds of Mozambique and Zimbabwe as revealed by a Y-specific microsatellite locus (*8*).

Previous studies of mitochondrial DNA variation indicate that all African *B. taurus* and African *B. indicus* share the same African set of taurine mitochondrial DNA haplotypes (*4*, *17*). It suggests that the pattern of zebu influence on the African continent was a process of introgression rather than replacement of African taurine cattle with unmixed Asian zebu. Our data indicate that there were two different modes of *B. indicus* genetic introgression into Africa. When the PC1 values of *B. taurus* and *B. indicus* populations were plotted against the distance from the Horn of Africa, different regression lines ($P < 0.001$) were obtained for each type of breed (Fig. 2A). A sharp decrease of PC1 values with distance is clear amongst the taurine breeds, possibly a reflection of a slow introgression of zebu genetics into western and southern *B. taurus* populations (Fig. 2A). In contrast, the regression line is markedly shallower for the African *B. indicus* breeds (Fig. 2A), indicating less differentiation of PC1 values with distance from the Horn of Africa and maybe a more rapid dispersal of zebu genes.

These processes may have taken place over millennia, perhaps starting with the initial introductions of zebu to the continent (*11*, *12*). However, the introgression occurred after the initial migration of *B. taurus* herding into western Africa, as indicated by archaeological data showing an earlier presence of taurine cattle in this region (*9*) and as supported by the presence today of West African *B. taurus* breeds that lack any zebu ancestry (*7*, *8*, *14*). It is also thought that a major wave of *B. indicus* introgression may have started with the Arab settlements along the East Coast of Africa from about the end of the 7th century AD (*11*). Part of the subsequent inland dispersal of *B. indicus* probably fol-

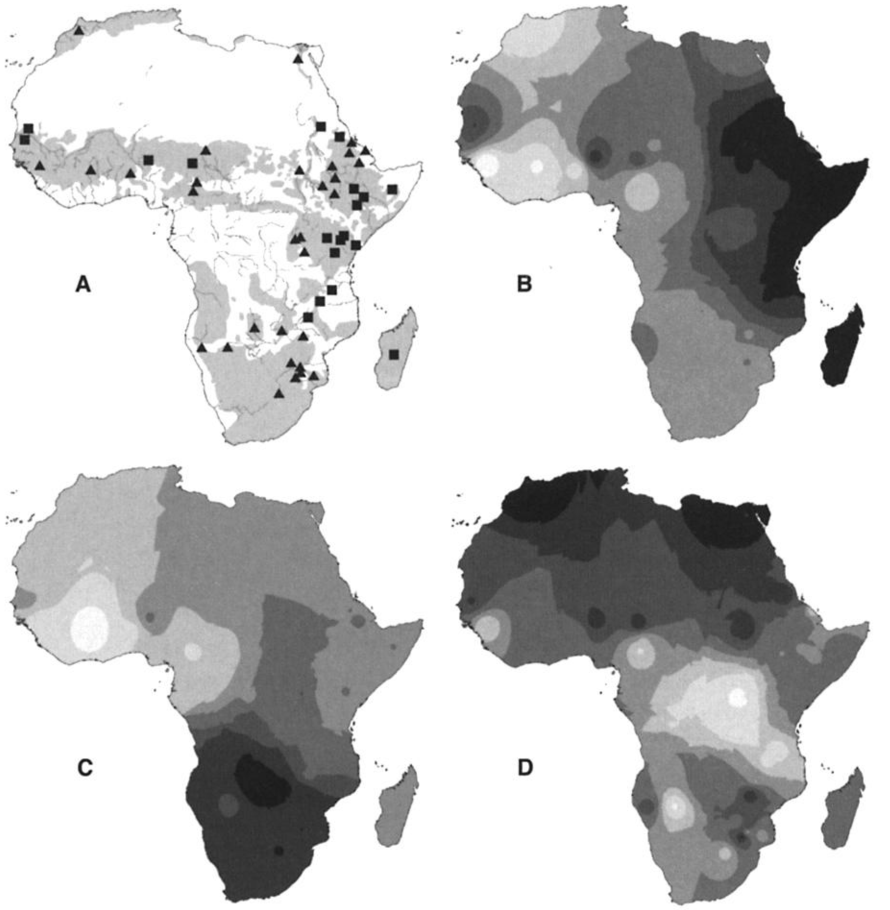

Fig. 1. (**A**) Cattle distribution on the continent of Africa (gray shaded area) (*15*) and locations of cattle populations sampled. The exclusion of cattle from large areas of the continent by desert and forest are obvious. *Bos indicus* breeds are denoted by solid squares (■) and *B. taurus* breeds are shown by solid triangles (▲). (**B**) Synthetic map illustrating geographic variation of the first principal component (PC1), which accounts for 38% of the total allelic variation. This obeys a gradient that peaks (shown by darkest shading) in East Africa and correlates with the level of *B. indicus* admixture, the result of a major secondary introduction to the continent. Madagascar also has a high value. (**C**) The PC2 variation (9.5%) is the major component of African *B. taurus* variation. It shows an arc of gradation extending from West Africa, passing through East Africa, and reaching the southern extreme of the continent. PC2 correlates with archaeological dates for the onset of herding in different regions, and it could represent the oldest major stratum of genetic differentiation within African *B. taurus*. (**D**) PC3 (6.6%) correlates with secondary *B. taurus* influence from Europe and the Near East. It shows a north-south gradient only in the northern part of the continent, with interesting exceptions in southern Africa. These are probably a more recent colonial legacy. The detection of this secondary influence in the minor *B. taurus* component of the variation lends support to an indigenous origin for the earliest African domestic cattle.

lowed more recent pastoralist movements such as those of the Maasai in East Africa and the Fulani throughout the Sahel (*25*). Zebu influxes may have been accelerated by the rinderpest epidemics in the late 19th century, which affected primarily the *B. taurus* populations of East and Southern Africa rather than *B. indicus* cattle, which possess an innate resistance (*11*).

Up to now, the substantial zebu background present in most African cattle has prevented unraveling the pattern of earlier *B. taurus* movements within Africa. Archaeological evidence suggests the eastern Sahara as a putative center for the earliest development of African pastoralism (*2*, *3*) with gradually more recent dates for the advent of herding as cattle moved west across the once-fertile Sahara, or south following an East African route (*9*, *12*, *26*, *27*). However, not all archaeologists agree with this scenario of origins and movements of African cattle (*2*, *28*). We therefore investigated if the next two principal components, PC2 and PC3, could provide insight into the history of early African *B. taurus*. Neither shows significant correlation with zebu admixture levels. PC2 explains 9.5% of the variation. Its ranking shows the *B. taurus* cattle of the West African river valleys at one extreme, intermediate values are found in East Africa, and the Southern African *B. taurus* are at the other extreme (*14*). This geographical coherence is well illustrated in the interpolation map (Fig. 1C). PC3 explains 6.6% of the variation. Its ranking shows North African taurines, northeast African zebu, and some southern African taurines at one extreme (*14*); West African *B. taurus* as well as taurine and zebu from the central and East Africa are at the other extreme (*14*).

The interpolation map of PC3 (Fig. 1D) suggests that PC3 could represent non-African *B. taurus* genetic influence from Europe and/or the Near East in the north and the northeast area of the continent and, in localized areas, in the southern part of the continent. This is supported by the estimated levels of Near East–European admixture in indigenous African cattle, which correlate significantly (r = 0.59, $P < 0.001$) with PC3 (*14*, *18*, *19*, *29*). The distribution of this exogenous and minor *B. taurus* component of the variation, which is geographically restricted to some areas of the continent, suggests that it must have been secondary to the origin of African cattle pastoralism and its dispersion westward and southward (Fig. 1D). Therefore, PC3 results support local domestication rather than Near East introduction as plausible origin for African cattle.

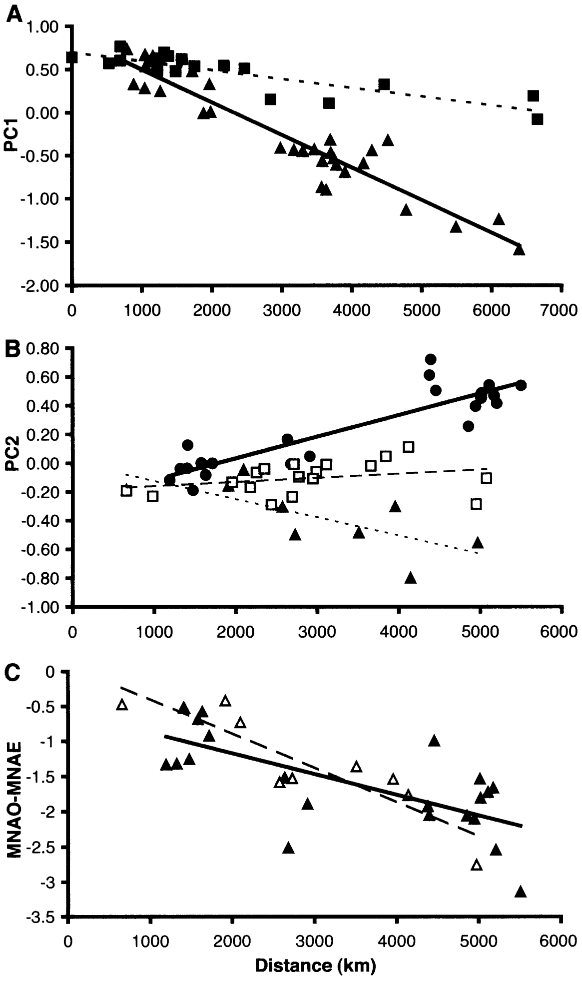

Fig. 2. (**A**) Regression of PC1 versus distance from the Horn of Africa (represented by the distance from the most continental easterly population sampled) conducted separately for populations denominated as *B. indicus* (■) (r = −0.86, $P = 0.000$) and those denominated as *B. taurus* (▲) (r = −0.95, $P = 0.000$). Two separate relations ($P < 0.001$) of this component, which strongly correlates with the level of zebu genetic background in today's African breeds, are clearly visible. They indicate the presence of two different patterns of zebu introgression. (**B**) Regression of PC2 versus the distance from a putative North Eastern centre of origin of African pastoralism (calculated as the middle point between the two most northeastern African breeds sampled). Differentiation with distance is clearly visible in *B. taurus* breeds for the two postulated migratory routes of the initial cattle dispersal, westward through the Sahara (▲) (r = −0.72, $P < 0.05$) and southward towards the Cape (●) (r = 0.89, $P < 0.001$). No strong relation is apparent for the *B. indicus* breeds (□) (r = 0.296, $P = 0.116$), indicating that their dispersal was a separate process. (**C**) Regression of the loss in genetic diversity (*33*) observed in African *B. taurus* breeds versus the distance from a putative northeastern center of origin of African pastoralism. The loss of diversity was represented along the two main routes of the initial African *B. taurus* dispersal. The two regression lines, westward (△, dashed line) and southward (▲), are similar ($P = 0.630$). They support a pattern of dispersal in both directions from a single region of origin.

PC2, the major taurine component of the variation did not correlate with the level of European–Near East admixture (r = −0.17, $P > 0.130$) nor, as indicated above, with the level of Asian zebu admixture. We suggest that it represents an African *B. taurus* genetic component.

Because wild cattle were not native to sub-Saharan Africa (*1*), there must have been a taurine colonization process from a center of origin. Accordingly, the pattern of PC2 differentiation observed between the west and the south of the continent (*10*) (Fig. 1C) could then correspond to genetic differentiation of two groups of cattle after their dispersal from their populations of origin. Population bottlenecks, due to attrition from tropical livestock diseases (*26*), could have also contributed to the observed differentiation pattern.

Colonization processes have been shown theoretically (*30*) and through simulation (*31*, *32*) to result in genetic differentiation. Also, they may be tested through the calculation of the correlation between geographic distances from one putative region of origin and PC2 values (Fig. 2B). We took the eastern Sahara (*3*, *21*) as the putative region of origin for dispersion west and south. Significant correlations were obtained for the westward (r = −0.72, $P < 0.05$) and the southward (r = 0.89, $P < 0.001$) routes. These regressions were linear; i.e., there was no significant quadratic component to the relationships. Moreover, when archaeological dates of the earliest advent of cattle pastoralism were used as estimates for the timing of these migrations, a one-way analysis of variance (ANOVA) of geographical distance on archaeological date demonstrated significant associations westward and southward ($P = 0.08$ and $P < 0.001$, respectively). When the variation in PC2 across archaeological date southward was compared by analysis of covariance (ANCOVA) with that among breeds of an archaeological date, a significant curvilinear association persisted between PC2 and archaeological time depth corrected for geographical distance ($P < 0.05$). The converse was not true; there was no significant correlation between PC2 and geographical distance when corrected for archaeological date. The stronger association of PC2 with archaeological time depth than with geographical distance suggests that PC2 represents the oldest component of genetic differentiation of African *B. taurus*. There were too few breeds

($n = 8$) in the western direction to undertake a similar analysis.

To assess if the earliest *B. taurus* patterns of migration westward and southward routes had the same region of origin, as had been assumed for the other observations here, we calculated a sensitive index of sample genetic diversity: the mean number of alleles per locus (MNA), which was corrected for the effects of *B. indicus* admixture and sample size (*22*, *33*). During the migration of cattle from a center of origin, neutral genetic diversity would be expected to decline, with the lowest loss of genetic diversity closest to the center of origin. This was observed here with a strong negative correlation between distance from the putative eastern Sahara center of origin and genetic diversity for both the westward ($r = -0.70$, $P < 0.001$) and the southward route ($r = -0.89$, $P < 0.001$) (Fig. 2C).

Southern Africa was the last region of the continent to acquire cattle pastoralism, and alternative models have been proposed for first arrival of domestic stock in the region (*34*). The most commonly held view is that herding spread southward from the Great Lakes region, in what is now Uganda, which 2000 years ago was the site of an eastern Bantu core area with confluence of agriculture, pastoralism, and iron technology (*24*). Bantu-speaking farmers ultimately came into contact with San hunter-gatherers, around the Caprivi strip and northern Botswana, who acquired livestock from them. Some groups of these hunters later became the Khoi Khoi herders of the western and southern Cape.

Alternatively, a western Bantu route for the southern dispersion of livestock has recently been suggested (*35*). It invokes movements of livestock that followed Bantu dispersal and migration from their heartland in the Niger-Cameroon region, along the Atlantic coast, or through the rainforest basin. We argue here that the sharp differentiation in PC2 values between West and Southern Africa (Fig. 1C), which contrasts with the more graduated contours along an eastern route, is not consistent with a major introduction along a western route. Accordingly, the transfer of cattle pastoralism to the south of the continent appears to have been subsequent only to the southward migration, through the eastern part of the continent, of pastoralist or crop-livestock farmers.

The history of African pastoralism explains the contemporary genetic composition of African cattle revealed in this study. Domesticated within the continent but genetically influenced by the centers of cattle domestication in the Near East and the Indus Valley, the modern African cattle breeds represent a unique genetic resource at a juncture when there is an urgent need to improve livestock productivity for the benefit of the present and future human generations.

References and Notes

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