ANIMAL GENETICS

SHORT COMMUNICATION

Disclosing the origin and diversity of Omani cattle

Osman Mahgoub*, Hamza A. Babiker[†], I.T. Kadim*, Mohammed Al-Kindi[†], Salwa Hassan[†], W. Al-Marzooqi*, Yasmin E. Eltahir*, M. A. Al-Abri*, Aisha Al-Khayat[‡], Kareema R. Al-Sinani[‡], Homoud Hilal Al-Khanjari[§], Vânia Costa[¶], Shanyuan Chen[¶] and Albano Beja-Pereira[¶]

*Department of Animal & Veterinary Sciences, College of Agricultural & Marine Sciences, Sultan Qaboos University, PO Box 34, Al-Khod 123, Sultanate of Oman. [†]Department of Biochemistry, Faculty of Medicine and Health Sciences, Sultan Qaboos University, PO Box 34, Al-Khod 123, Sultanate of Oman. [‡]Department of Biology, College of Science, Sultan Qaboos University, PO Box 36, Al-Khod 123, Sultanate of Oman. [§]Rumais Animal Research, Ministry of Agriculture and Fisheries, PO Box 467, Muscat RB 100, Sultanate of Oman. [¶]Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO), Universidade do Porto, Rua Padre Armando Quintas 7, 4485-661, Vairão, Portugal.

Summary

Among all livestock species, cattle have a prominent status as they have contributed greatly to the economy, nutrition and culture from the beginning of farming societies until the present time. The origins and diversity of local cattle breeds have been widely assessed. However, there are still some regions for which very little of their local genetic resources is known. The present work aimed to estimate the genetic diversity and the origins of Omani cattle. Located in the south-eastern corner of the Arabian Peninsula, close to the Near East, East Africa and the Indian subcontinent, the Sultanate of Oman occupies a key position, which may enable understanding cattle dispersal around the Indian Ocean. To disclose the origin of this cattle population, we used a set of 11 polymorphic microsatellites and 113 samples representing the European, African and Indian ancestry to compare with cattle from Oman. This study found a very heterogenic population with a markedly *Bos indicus* ancestry and with some degree of admixture with *Bos taurus* of African and Near East origin.

Keywords admixture, Arabian cattle, genetic diversity, microsatellites, population structure

Modern cattle arose from at least three independent domestication events in the Near East, Africa and the Indian subcontinent, which resulted in European taurine (*Bos taurus*), African taurine (*B. taurus*) and zebu (*B. indicus*) cattle respectively (Troy *et al.* 2001; Beja-Pereira *et al.* 2006; Bradley & Magee 2006; Chen *et al.* 2010). After domestication, cattle spread through trade, theft, warfare and bride-dowry (Clutton-Brock 2000) as well as through the movements of pastoral societies (Cavalli-Sforza 1996; Diamond & Bellwood 2003). Widespread human population movement across the globe propitiated crossbreeding among cattle descending from the three different domesti-

Accepted for publication 10 July 2012

cation events. Associated with artificial selection imposed by the farmers and breeders, and the natural selection imposed by the vast range of environmental conditions, it resulted in a vast number of local breeds.

The last two decades have been quite rich in genetic studies concerning diversity, conservation and origins of modern cattle (Bradley & Magee 2006). Those investigations provided new insights into cattle origins, migrations and admixture. However, for several reasons, there are still many local populations that have never been assessed using molecular markers. For instance, although crossbreeds between taurine and zebu cattle in Africa have been widely documented in Africa, many regions in the continent still are not covered (e.g. Hanotte *et al.* 2010). So far, and to the best of our knowledge, no research has been carried out in the Arabian Peninsula regarding the origin of cattle in that region or its genetic diversity. Considering its strategic geographical position, between Africa and India and being south of the Near East, the study of the origins of cattle from

Address for correspondence

A. Beja-Pereira, Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO), Universidade do Porto, Rua Padre Armando Quintas 7, 4485-661 Vairão, Portugal. E-mail: albanobp@fc.up.pt

the Arabian Peninsula has great potential to improve our understanding about pastoral societies' expansion around the Indian Ocean. With the present study, we attempted to understand the origin of Omani cattle and its current genetic composition. This provides new insights into cattle migration and admixture processes on the Arabian Peninsula and agricultural dispersal through trade and human migrations around the Indian Ocean.

A total of 36 samples collected from local Omani cattle were used together with 27 samples from the Libyan local Mahalli breed representing African taurine ancestry, 20 samples from a local cattle population from southern Indian representing the zebu gene pool and 30 samples from the Portuguese Friesian population selected to represent Near East taurine ancestry. DNA was extracted from a small piece of skin (<5 mm), using the DNeasy Blood & Tissue kit (Qiagen), according to the manufacturer's protocol. Eleven cattle microsatellite loci - ETH225, ETH10, SPS115, BM2113, TGLA227, TGLA053, ETH003, BM1824, INRA023, TGLA126 and TGLA122 - were chosen from the panel recommended by ISAG for parentage and population diversity studies (ISAG 2008). Each of the forward primers was labelled with a fluorescence dye at the 5' end and amplified in a single PCR multiplex reaction. Each reaction consisted of primer mix, Qiagen Multiplex PCR Master Mix, water and DNA. The multiplex products were added to a mix of denaturant formamide and size standard (Gene Scan 500LIZ size standard) and run in a 3130 XL Genetic Analyzer sequencer (Applied Biosystems). GENEMAPPER v4.0 software (Applied Biosystems) was used to analyse the microsatellites electropherograms and score the alleles. GENALEX v. 6.41 software (Peakall & Smouse 2006) was used to calculate allele frequencies per locus and populations; expected, observed and expected unbiased heterozygosities; and the number of populations' private alleles. The same software also was used to generate a genetic distance matrix and perform a principal coordinate analysis (PCoA) for calculating similarities and dissimilarities among populations and to calculate AMOVA. PCoA, also classically designated as multidimensional scaling (MDS), is a multivariate analysis used to explore and visualise individual and/or group differences. To analyse allelic richness per locus and pairwise populations F_{ST} (Pvalues achieved based on 1000 randomisations), FSTAT software v. 2.9.3 (Goudet 2001) was used. Significant deviation from Hardy-Weinberg proportions and linkage (gametic) disequilibrium were tested using GENEPOP software (Raymond & Rousset 1995). As Oman is a crossroads between the Near East, Africa and South Asia, the influence of cattle that originated in those three areas was investigated by estimation of the admixture proportions using LEADMIX software (Wang 2003). This analysis was carried out assuming the populations from India, Africa and Europe were representative of each of the gene pools originating from each putative domestication centre of cattle. The

statistical robustness of the admixture values was tested by bootstrapping (over loci) samples as described by Roberts & Hiorns (1965).

All loci were polymorphic, and the number of alleles per loci varied between eight (BM1824 and TGLA126) and 17 (TGLA053 and TGLA122). No considerable differences between breed-expected heterozygosities were found (Table 1). All populations had putative private alleles, with Mahalli being the one with highest number (12), followed by Europe (10), India (8) and Oman (7). Regarding linkage disequilibrium, only one pair of loci had significant results (P < 0.001), and populations from local India cattle and Libyan Mahalli deviated from Hardy–Weinberg proportions (P < 0.05). AMOVA showed that 80% of the variation occurred within populations, and only 20% of the data set variance was justified by differences among populations (data not shown).

Both the F_{ST} and the DA distances confirm the proximity of the two taurine populations, the African (Libya) and European populations (Table 2) and the marked distance between European and Indian populations (zebu ancestry). This differentiation also is denoted in the first axis of the PCoA analysis (Fig. 1). The second axis, representing 19.46% of the variance, roughly separates India from Omani populations, showing no separation of the taurine populations. Finally, the third axis differentiates European and African populations but does not distinguish between Indian and Omani populations. In fact, also the admixture analysis revealed that Omani cattle are a mixture of Indian zebu with African and Near East taurine (Table 3).

The higher levels of genetic diversity observed in the present study for Omani cattle (Table 1), compared with that found in Indian sub-continent zebu populations (e.g. MacHugh *et al.* 1997), can be indicative of gene flow from other regions, which perhaps is still ongoing. Interestingly, recent studies on mtDNA control region sequencing (Chen

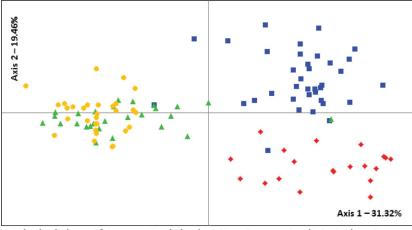
Table 1 Observed (H_o), expected (H_e) and respective standard deviation for the analysed populations.

	H _o	H _e
India	0.69 ± 0.04	0.69 ± 0.03
Oman	0.73 ± 0.05	0.73 ± 0.02
Africa	0.74 ± 0.03	0.74 ± 0.02
Europe	$\textbf{0.70}\pm\textbf{0.04}$	0.73 ± 0.03

Table 2 Pairwise F_{ST} values (below the diagonal) and D_A distances (above the diagonal) among the analysed populations.

	India	Oman	Africa	Europe
India		21.76	22.91	23.46
Oman	0.1152		21.91	22.34
Africa	0.1508	0.1148		19.83
Europe	0.1653	0.1265	0.0722	

© 2012 The Authors, Animal Genetics © 2012 Stichting International Foundation for Animal Genetics, 44, 336-339



◆ Zebu (India) 🔺 African taurine (Libya) 🔸 Near East taurine (Friesian) ■Oman

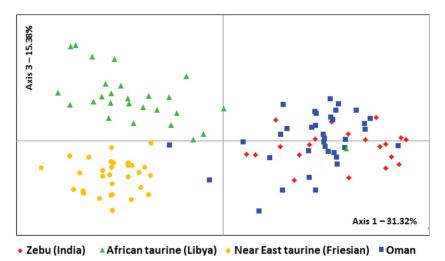


Figure 1 Graphical plotting of the (a) first and second and (b) first and third axes of the PCoA based on individual genetic distances of the 11 microsatellite loci and respective representation of the variation justified by each axis.

et al. 2010) and Y-specific chromosome microsatellites diversity (Perez-Pardal *et al.* 2010) also have found zebulike haplotypes. Therefore, the closer F_{ST} values (Table 2) and the grouping of Omani and Indian cattle together in the PCoA analysis (Fig. 1) indicate that the Indian zebu cattle played a major role in the genesis of this local population. Nonetheless, the moderate contribution of Africa taurine gene pool to this breed (Table 3) cannot be ignored. Omani people have a long history as seafarers with close ties to the

 Table 3
 Contribution of the parental populations for the current composition of Omani cattle, respective standard variation (SD) and confidence interval.

Parental populations	Point estimate	SD	-95%	95%
India	0.4625	0.0796	0.3145	0.6265
Africa	0.3009	0.0863	0.1499	0.4891
Europe	0.2365	0.0559	0.1154	0.3244

East Africa region and southern Asia. Owing to its geographical equidistance between the Indian subcontinent, the centre of origin of zebu cattle (Joglekar & Thomas 1992; Chen et al. 2010) and East Africa, the Arabian seafarers were strategically positioned to play a key role in the expansion of zebu cattle from its domestication centre. Indeed, the involvement of the Arabian seafarers in the long distance trade between India and Africa is well documented (e.g. Boivin & Fuller 2009). It is not surprising that the south-east Arabian Peninsula, where the Sultanate of Oman is located, may have served as a distribution platform for domesticated plant and animal species originating on both sides of the Indian Ocean. As a consequence, modern Omani cattle are a living legacy of a trading corridor's cosmopolitan past, incorporating both African taurine and Indian zebu genes in its current genetic pool. Finally, the influence of Near East cattle also can be explained by the dispersal of the Neolithic pastoralists southward into the Arabian Peninsula (e.g. review by Boivin & Fuller 2009) as

well as by trading activities that obviously included the region around the Persian Gulf, particularly Iraq, from where cattle is known to be mainly derived in the Near East (Loftus *et al.* 1999).

In conclusion, the Omani cattle breed is a very interesting population that inhabits one of the hottest regions of the globe. The adaptation to the extreme environment of the region might have been the result of this peculiar admixture between the three main lineages of domestic cattle across the time.

Acknowledgements

We thank the staff of Biochemistry Department, SQU, Oman, for technical support. This paper resulted from a project on the characterisation of Omani livestock resources, which was funded by Sultan Qaboos University HM Fund (SR/AGR/ANVS/08/01). S.C. is supported by a postdoctoral research grant from FCT (SFRH/BPD/46082/ 2008) and A.B.P by a project grant from FCT (PTDC/CVT/ 117851/2010).

References

- Beja-Pereira A., Caramelli D., Lalueza-Fox C. et al. (2006) From the cover: the origin of European cattle: Evidence from modern and ancient DNA. Proceedings of the National Academy of Sciences 103, 8113–8.
- Boivin N. & Fuller D.Q. (2009) Shell middens, ships and seeds: exploring coastal subsistence, maritime trade and the dispersal of domesticates in and around the ancient Arabian peninsula. *Journal of World Prehistory* 22, 113–80.
- Bradley D.G. & Magee D.A. (2006) Genetics and origins of domestic cattle. In: *Documenting Domestication New Genetic and Archaeological Paradigms* (Ed. by Zeder. MA, Bradley. DG, Emshwiller. E & Smith. BD), pp. 317–28. University of California Press, Berkeley, California.
- Cavalli-Sforza L. (1996) The spread of agriculture and nomadic pastoralism: insights from genetics, linguistics and archaeology. In: *The Origins and Spread of Agriculture and Pastoralism in Eurasia* (Ed. by Harris. D). Smithsonian Institution Press, Washington.
- Chen S., Lin B.Z., Baig M. *et al.* (2010) Zebu cattle are an exclusive legacy of the South Asia neolithic. *Molecular Biology and Evolution* **27**, 1–6.

- Clutton-Brock J. (2000) Cattle, sheep, and goats south of the Sahara: an archaeozoological perspective. In: *The Origins and Development of African Livestock - Archaeology, Genetics, Linguistics and Ethnography* (Ed. by Blench. RM & Mac.Donald. KC), pp. 30–7. University College of London, London.
- Diamond J. & Bellwood P. (2003) Farmers and their languages: the first expansions. *Science* **300**, 597–603.
- Goudet J. (2001) FSTAT, a program to estimate and test gene diversities and fixation indices. Available at: http://www2.unil. ch/popgen/softwares/fstat.htm.
- Hanotte O., Dessie T. & Kemp S. (2010) Ecology. Time to tap Africa's livestock genomes. *Science* **328**, 1640–1.
- ISAG (2008) Cattle Molecular Markers and Parentage Testing Workshop. In: *ISAG - International Society for Animal Genetics* 2008, Amsterdam, The Netherlands.
- Joglekar P.P. & Thomas P.K. (1992) Ancestry of Bos species: myth and reality IV. The origins of humped cattle. *Man and Environment* 17, 51–4.
- Loftus R.T., Ertugrul O., Harba A.H., El-Barody M.A., MacHugh D.E., Park S.D. & Bradley D.G. (1999) A microsatellite survey of cattle from a centre of origin: the Near East. *Molecular Ecology* 8, 2015–22.
- MacHugh D.E., Shriver M.D., Loftus R.T., Cunningham P. & Bradley D.G. (1997) Microsatellite DNA variation and the evolution, domestication and phylogeography of taurine and zebu Cattle (*Bos taurus* and *Bos indicus*). *Genetics* 146, 1071–86.
- Peakall R.O.D. & Smouse P.E. (2006) GENALEX 6: genetic analysis in EXCEL. Population genetic software for teaching and research. *Molecular Ecology Notes* 6, 288–95.
- Perez-Pardal L., Royo L.J., Beja-Pereira A. *et al.* (2010) Multiple paternal origins of domestic cattle revealed by Y-specific interspersed multilocus microsatellites. *Heredity* 105, 511–9.
- Raymond M. & Rousset F. (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *The Journal of Heredity* 86, 248–9.
- Roberts D. & Hiorns R. (1965) Methods of analysis of the genetic composition of a hybrid population. *Human Biology* 37, 38–43.
- Troy C.S., MacHugh D.E., Bailey J.F., Magee D.A., Loftus R.T., Cunningham P., Chamberlain A.T., Sykes B.C. & Bradley D.G. (2001) Genetic evidence for Near-Eastern origins of European cattle. *Nature* **410**, 1088–91.
- Wang J. (2003) Maximum-likelihood estimation of admixture proportions from genetic data. *Genetics* 164, 747–65.