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The characterization of goat genetic diversity: Towards a genomic approach

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ABSTRACT

The investigation of genetic diversity at molecular level has been proposed as a valuable complement and sometimes proxy to phenotypic diversity of local breeds and is presently considered as one of the FAO priorities for breed characterization. By recommending a set of selected molecular markers for each of the main livestock species, FAO has promoted the meta-analysis of local datasets, to achieve a global view of molecular genetic diversity. Analysis within the EU Globaldiv project of two large goat microsatellite datasets produced by the Econogene Consortium and the IAEA CRP-Asia Consortium, respectively, has generated a picture of goat diversity across continents. This indicates a gradient of decreasing diversity from the domestication centre towards Europe and Asia, a clear phylogeographic structure at the continental and regional levels, and in Asia a limited genetic differentiation among local breeds. The development of SNP panels that assay thousands of markers and the whole genome sequencing of livestock permit an affordable use of genomic technologies in all livestock species, goats included. Preliminary data from the Italian Goat Consortium indicate that the SNP panel developed for this species is highly informative. The existing panel can be improved by integrating additional SNPs identified from the whole genome sequence alignment of goats adapted to extreme climates. Part of this effort is being achieved

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by international projects (e.g. EU FP7 NextGen and 3SR projects), but a fair representation of the global diversity in goats requires a large panel of samples (i.e. as in the recently launched 1000 cattle genomes initiative). Genomic technologies offer new strategies to investigate complex traits difficult to measure. For example, the comparison of patterns of diversity among the genomes in selected groups of animals (e.g. adapted to different environments) and the integration of genome-wide diversity with new GIScience-based methods are able to identify molecular markers associated with genomic regions of putative importance in adaptation and thus pave the way for the identification of causative genes. Goat breeds adapted to different production systems in extreme and harsh environments will play an important role in this process. The new sequencing technologies also permit the analysis of the entire mitochondrial genome at maximum resolution. The complete mtDNA sequence is now the common standard format for the investigation of human maternal lineages. A preliminary analysis of the complete goat mtDNA genome supports a single Neolithic origin of domestic goats rather than multiple domestication events in different geographic areas.

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1. Introduction

Local breeds, well adapted to a range of agro-ecological conditions (different climates, diseases, local feed), grant the sustainability of animal farming in marginal and difficult areas in both developed and developing countries. They are source of meat, milk and skin and contribute to maintain livelihood in the harshest areas of the planet (Lampkin and Measures, 2001). Local genetic resources are threatened by a number of factors, including indiscriminate crossbreeding with cosmopolitan breeds and uncontrolled intermixing (Hanotte et al., 2010). However, among livestock species, goat is only marginally affected by crossbreeding. Rather, concerns about goat genetic diversity loss arise from the abandonment of marginal rural areas where goats are frequently reared. The consequent reduction of population size of local breeds increases the risk of inbreeding (Taberlet et al., 2008). Therefore, the molecular characterization of available genetic resources and information on diversity and genetic structure is desirable also in this species, to serve as a rational basis for the characterization and conservation of goat germplasm.

The investigation of genetic diversity at the molecular level has been proposed as a valuable complement to the evaluation of phenotypes and production systems, and sometimes as a proxy for phenotypic diversity of local breeds. This has expanded our insight into breed history, in order to guide breed development, utilization and conservation decisions. Characterization of breeds is presently considered by FAO as one of the strategic priorities to be undertaken in the development of a national plan for the management of animal genetic resources (AnGR). Therefore molecular characterization has a prominent role in Strategic Priority Area 1 – Characterization, Inventory and Monitoring of Trends and Associated Risks – of the Global Plan of Action for AnGR (FAO, 2007).

In the late 1990s, and later on in 2004, FAO has recommended the use of panels of selected microsatellite markers for each of the main livestock species. The assay of the same loci across projects facilitates the joining of molecular datasets and the combined analysis of independent investigations of genetic diversity that otherwise would remain local and fragmented. This initiative has only partially succeeded. Some projects have not considered FAO recommendations or have used different subsets of the recommended markers, not following the ranking order in the panel (Baumung et al., 2004). Even large-scale projects have sometimes not used the same set of microsatellites; therefore a worldwide picture of livestock diversity is yet to be drawn (Groeneveld et al., 2010).

2. Analysis of goat genetic diversity with classical markers

Several local studies have characterized the nuclear genetic diversity using molecular markers, mainly microsatellites, in European, African and American goats (Table 1). During the last decade, a number of international

research projects have also attempted to analyse the patterns of goat diversity at a broader scale (Table 2).

So far, the largest scale dataset published has been generated by the Econogene Consortium (<http://www.econogene.eu>) within a project funded by the European Commission during the 5th Framework Programme. The dataset describes the genetic diversity of 1426 goats from 45 traditional or rare breeds from 15 countries in Europe and southwest Asia, genotyped with the 30 FAO microsatellite markers. Results revealed the existence of four discrete groups of goat breeds in southwest Asia, central Mediterranean, western Mediterranean and northern-central Europe. Genetic diversity, measured as allelic richness, decreases from southeast to northwest, presumably as a consequence of repeated founder effects occurring during the colonization of Europe following domestication (Cañón et al., 2006).

The joint analysis of these data with those produced by the FAO/IAEA CRP (Coordinated Research Project of the International Atomic Energy Agency)/Asian Consortium has been attempted in the framework of the EU Globaldiv project (<http://www.globaldiv.eu>).

The FAO/IAEA CRP project (<http://www-naweb.iaea.org/nafa/aph/crp/aph-livestock-phase1.html>) genotyped 1629 samples from 43 local populations from 8 Asian countries (China, Bangladesh, Indonesia, Iran, Saudi Arabia, Sri Lanka, Pakistan, and Vietnam) with 15 microsatellite markers (Zein et al., 2012; Di et al., 2011; Afroz et al., 2010; Fan et al., 2008; Mburu et al., 2006; Vahidi et al., 2014). The highest number of alleles was observed in Iranian and Saudi Arabian native goats, followed by Chinese, Bangladeshi, Pakistani and Sri Lankan indigenous goat populations. Low genetic diversity was observed in Vietnamese and Indonesian local goats. Although genetic differentiation in all pairs of populations between countries was significant (pairwise F_{ST} estimates at $P < 0.01$), relatively close genetic relationships were found among most of the Chinese goat populations, Iranian and Saudi Arabian goats as well as among Bangladeshi, Pakistani and Sri Lankan goat populations, while the Vietnamese and most of the Indonesian goat populations loosely grouped together (Mburu et al., 2006).

Table 1

List of molecular marker based genetic diversity studies in goats. Indicated are breeds, the geographic area of origin of the breeds investigated, the type and number of molecular markers used, the main population genetics parameters investigated and the bibliographic reference..

No. of breeds	Breeds	Geographic area	Marker type	No. of markers	Parameters of diversity ^a							Reference	
					H _o	H _E	N _A	AR	Fst	Fis	PS		
1	Azpi Gorri	Spain	Microsatellites	29	•	•	•						Martínez et al. (2012)
8	Camosciata delle Alpi, Valdostana, Bionda dell'Adamello, Orobica, Grigia Molisana, Girgentana, Argentata dell'Etna, Sarda	Italy	Microsatellites	30	•	•	•	•				•	Negrini et al. (2012)
6	Algarvia, Bravia, Charnequeira, Preta de Montesinho, Serpentina, Serrana	Portugal	Microsatellites	25		•	•		•	•			Bruno-de-Sousa et al. (2011)
1	Capore	Albania	Microsatellites	30	•	•	•					•	Hoda (2011)
1	Croatian Spotted	Croatia	Microsatellites	20	•	•	•					•	Jelena et al. (2011)
6	Saanen, Anglo-Nubian, Alpine, Carpathin, White improved, Pygmy	Poland	Microsatellites	6	•	•	•						Sikora et al. (2011)
4	Girgentana, Derivata di Siria, Maltese, Messinese	Italy	Microsatellites	19					•			•	Siwek et al. (2011)
1	Guadarrama	Spain	Microsatellites	10	•	•			•	•			Serrano et al. (2009)
11	Swiss goat breeds	Switzerland	-	-		•			•				Glowatzki-Mullis et al. (2008)
45	Capore, Dukati, Hasi, Liqenasi, Mati, Muzhake, Pinzgauer, Tauern Pied, Swiss Alpine, Grisons Striped, Peacock, St. Gallen Booted, Valais Black Neck Makers, German Alpine, Thuringian Forest, Florida, Guadarrama, Malaguena, Payoya, Verata, French Alpine, Corse, Pyreneenne, Rove, Greek, Skopelos Hungarian Native, Argentata dell'Etna, Bionda dell'Adamello, Camosciata (Alpine), Girgentana, Grigia Molisana, Orobica, Sarda, Valdostana Polish Fawn Coloured, Brava, Carpathian, Beeshi, Najrani, Abaza, Angora, Gurku, Hair	Europe, SW Asia	Microsatellites	30		•	•	•	•	•		•	Cañón et al. (2006)
9	Sarda, Derivata di Siria, Ionica, Maltese, Garganica, Girgentana, Montefalcone, Saanen, Alpine	Italy	Microsatellites	15		•	•						Iamartino et al. (2005)
3	Maltese, Sarda, crossbred between Maltese and Sarda	Italy	Microsatellites	17	•	•	•						Sechi et al. (2005)
2	White Short-Haired, Brown Short-Haired	Czech Republic	Microsatellites	7		•							Jandurová et al. (2004)
7	Bionda dell'Adamello, Frisa, Orobica and Verzaschese, Val di Livo, Sarda, Saanen	Italy	AFLPs	-									Ajmone-Marsan et al. (2001)
11	Grison Striped, Chamois Coloured, Chamois Coloured from Grison, Verzasca, Peacock, Saanen, valais Blackneck, Toggenburg, Bezoar, Creole, Ibex	Switzerland	Microsatellites	20									Saitbekova et al. (1999)

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Table 1 (Continued)

No. of breeds	Breeds	Geographic area	Marker type	No. of markers	Parameters of diversity ^a							Reference
					H _o	H _E	N _A	AR	F _{st}	F _{is}	PS	
18	Shiba Southwest, Southeast West, East Luzon and Mindoro Kambing Katjang Bali, Kambing Katjang Java, Etawa	Japan Korea Taiwan Philippines Indonesia	Microsatellites	26	•	•			•	•		Nomura et al. (2012)
4	Black Bengal, Indian breed Zavkhan Buural, Zalaajinst White, Erchim Black, Ulgii Red, Bayandelger, Dorgon, Sumber	Bangladesh Mongolia										
4	Gembrong, Jawarandu, Peranakan Etawa	Indonesia	Microsatellites	13	•	•			•	•		Zein et al. (2012)
14	Tangshan, Liaoningcashmere, Nanjiangyellow, Chengde polled, Leizhou black					•	•			•		Zhang et al. (2012)
3	Alashan, Erlangshan, Wuzhumuqin, Liaoning, Chaidamu, Shanbei, Xinjiang, Hexi, Hegu											
3	Naini, Turki	Iran	–	–	•	•			•	•	•	Di et al. (2011)
6	Guinea Bissau Plateau-type Tibetan, valley-type Tibetan, Baiyu, Jianchang black, Meigu, Xinjiang	Africa Tibet	Microsatellites	10	•	•	•					Wang et al. (2011)
3	Black Bengal, Imported Indian, crossbred between Black Bengal and exotic breeds	Bangladesh	Microsatellites	15	•	•	•					Afroz et al. (2010)
1	Lori	Iran	Microsatellites	13		•	•					Mahmoudi (2010)
1	Vietnamese	Vietnam	Microsatellites	16	•	•			•	•		Berthouly et al. (2009)
22	Black Bengal, Ganjam, Gohilwadi, Jharkhand Black, Attappady, Changthangi, Kutchi, Mehsana, Sirohi, Malabari, Jamunapari, Jakhrana, Surti, Gaddi	India	Microsatellites	25	•	•	•		•	•		Dixit et al. (2012)
6	Marwari, Barbari, Beetal, Kanniadu, Sangamneri, Osmanabadi, Zalawadi, Chegu											
6	Attappady, Osmanabadi, Sangamneri, Malabari and Kanniadu, Ganjam	India	Microsatellites	25								Dixit et al. (2010)
3	Kutchi, Mehsana, Sirohi	India	Microsatellites	25								Dixit et al. (2009)
10	Shannan white, Shanbei white cashmere, Funiu, Huanghuai, Taihang, Guangzhong dairy, Xinong Saanen, Zhongwei, Tibetan, Inner Mongolia cashmere	China	Microsatellites	20								Qi et al. (2009)

Table 1 (Continued)

No. of breeds	Breeds	Geographic area	Marker type	No. of markers	Parameters of diversity ^a							Reference
					H_o	H_E	N_A	AR	Fst	Fis	PS	
1	Barbari	India	Microsatellites	21	•	•						Ramamoorthi et al. (2009)
5	Huai, Haimen, Yichang White, Suining White, Boer	China	Microsatellites	18	•	•	•	•				Fan et al. (2008)
3	Zalawadi, Gohilwadi, Surti	India	Microsatellites	18	•	•	•				•	Fatima et al. (2008)
7	Barbari, Jamunapari, Black Bengal, Pashmina, Jakhrana, Marwari, Sirohi	India	Microsatellites	17	•	•	•		•			Rout et al. (2008)
1	Jamunapari	India	Microsatellites	17								Rout et al. (2012)
			Milk protein loci	2	•	•	•				•	
			mtDNA control region sequences	-								
8	Bayandelger, Ulgi Red, Zavkhan Buural, Sumber, Zalaajinst White, Erchim Black, Dorgon, Gobi Gurvan Saikhan	Mongolia	Microsatellites	10	•	•	•				•	Takahashi et al. (2008)
7	Chinese goat breeds	China	mtDNA control region sequences	-								Wang et al. (2008)
1	Jamunapari	India	Microsatellites	23								Gour et al. (2006)
1	Marwari	India	Microsatellites	25								Kumar et al. (2005)
8	Liaoning Cashmere, Inner Mongolian Cashmere, Chengde Polled, Jining Grey, Chengdu Brown, Tibetan, Leizhou, Shannan White	China	Microsatellites	18								Li and Valenti (2004)
3	Korean goat, Chinese goat, Saanen	Korea, China	Microsatellites	9	•	•			•	•		Kim et al. (2002)
12	East Tibetan, Neimonggol, Liaoning, Taihang, Wu, Nanjiang Brown, Chuandong White, Black, Matou, South-east Tibetan, North Tibetan, Small-xiang	China	Microsatellites	25	•	•	•		•	•		Li et al. (2002)
NA	The indigenous goats of south-east Asia are not classified into breeds	SE Asia	Microsatellites	25	•	•	•		•	•		Barker et al. (2001)
5	Tibetan, Neimonggol, Liaoning, Taihang, Matou	China	Microsatellites	5								Yang et al. (1999)
5	Angora, Kilis, Honamli, Hair, Norduz	Turkey	Microsatellites	20	•	•	•		•	•		Ağaoğlu and Ertuğrul (2012)
3	Rousse de Maradi (Red Sokoto), Burkinabé Sahelian, Djallonké goat	Burkina Faso	Microsatellites	19		•	•	•	•	•		Álvarez et al. (2012)
6	Gumuz, Agew, Begia-Medir, Bati, Abergelle, Central Abergelle	Ethiopia	Microsatellites	15	•	•	•		•	•		Hassen et al. (2012)
1	Taleshi goat	Iran	Microsatellites	9	•	•	•					Mahmoudi and Babayev (2009)
6	Markhoz, Lori, Nadji, Tali, Raeini, Korbi Jonab Khorosan	Iran	Microsatellites	10		•	•					Mahmoudi et al. (2009a)
1	Markhoz goat	Iran	Microsatellites	13	•	•	•					Mahmoudi et al. (2009b)
3	Raeini, Korkijonub Khorasan, Lori	Iran	Microsatellites	13		•	•					Mahmoudi et al. (2011)

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Table 1 (Continued)

No. of breeds	Breeds	Geographic area	Marker type	No. of markers	Parameters of diversity ^a							Reference
					H_o	H_E	N_A	AR	Fst	Fis	PS	
19	Gubu/Bissau	Guinea Bissau	Microsatellites	11	•	•			•		Muema et al. (2009)	
	Boran Galla	Kenya										
	Small East African	Kenya, Tanzania										
	Maure	Mali										
	Pafuri, Landim	Mozambique										
	Red Sokoto, Born White, West African Dwarf	Nigeria										
	Grison Striped	Switzerland										
2	Maasai, Ugogo, Ujiji	Tanzania	Microsatellites	13		•	•				Sadeghi et al. (2009, 2010)	
	Karamoja, Teso, Kigezi, Sebei	Uganda										
3	Tali goat, Raeini	Iran	Microsatellites	27	•	•	•		•	•	Traoré et al. (2009)	
5	Djallonké, Mossi, Sahelian	Burkina Faso	Microsatellites	7	•	•	•		•	•	Agha et al. (2008)	
7	Egyptian Baladi, Barki, Zaraibi	Egypt	Microsatellites	6	•	•	•		•	•	Missohou et al. (2006)	
4	Maltese, Montefalcone	Italy	Microsatellites	18					•	•	Els et al. (2004)	
	Casamance goat, Labe Goat, Sahel Goat, Red sokoto, Guera	W Africa										
20	Ovambo, Caprivi, Kunene, Kavango	Namibia	Microsatellites	19							Chenyambuga et al. (2004)	
	Maasai, Kigezi, Mubende, North West Highland, Arsi Bale, Ndebele, Pafuri, West African Dwarf, Maure, Djallonke	Africa										
6	Grisons Striped, Toggenburg	Europe	Microsatellites, asl-Casein alleles	5	•	•	•		•		Ouafi et al. (2002)	
	Mongolian Cashmer indipur	Asia										
-	Arab	SWAsia	Microsatellites	12	•	•	•		•	•	Calvo and Gonzáles (2012)	
	Draa, Noire-Rah alii	Morocco										
12	Alpine, Saanen, Poitevine, Pyre'ne'enne	France	Microsatellites	15	•	•	•	•	•	•	Ribeiro et al. (2012)	
	626 goat individuals from 14 localities	Colombia										
9	Algarvia, Bravia, Charnequeira, Preta de Montesinho, Serpentina, Serrana	Portugal	Microsatellites	13	•	•	•		•	•	Oliveira et al. (2007)	
	Azul, Caninde', Grauna, Marota, Moxoto, Repartida	Brazil										
2	Anglo-Nubian crossbred, Moxot6, Caninde', Alpine-German Alpine, Saanen, Toggenbourg, Anglo-Nubain, Undedined breed, Grauna	Brazil	Microsatellites	20	•	•	•	•	•	•	Oliveira et al. (2010)	
	Moxot6 breed	Brazil										
3	Serpentina	Portugal	Microsatellites	11	•	•	•		•	•	Araújo et al. (2006)	
3	Alpine, Saanen	Europe	Microsatellites	11	•	•	•		•	•	Araújo et al. (2006)	
	Brazilian Moxot6goats	Brazil										

^a Parameters of diversity: H_o = observed heterozygosity; H_E = expected heterozygosity; N_A = number of alleles; AR = allelic richness; Fst = fixation index; Fis = inbreeding coefficient; PS = population structure.

Table 2
Research projects cited in the text and reference websites.

Project name	Website
Econogene	http://www.econogene.eu
Globaldiv	http://www.globaldiv.eu
FAO/IAEA CRP	http://www-naweb.iaea.org/nafa/aph/crp/aph-livestock-phase1.html
International Goat Genome Consortium	http://www.goatgenome.org
Italian Goat Consortium	http://www.goatit.eu/
ADAPTmap	http://bioinformatics.tecnoparco.org/adaptmap/
FeedtheFuture	http://www.feedthefuture.gov
NextGen	http://nextgen.epfl.ch/
3SR	http://www.3srbreeding.eu/
1000 genome project	http://www.1000genomes.org
Genome 10K project	http://genome10k.soe.ucsc.edu
1000 bull genomes project	http://www.1000bullgenomes.com/

A total of 11 markers and a few populations of Mediterranean goats were shared by Econogene and FAO/IAEA datasets, but no sample was genotyped in both projects. Therefore around 200 samples from the Econogene project were re-genotyped by the FAO/IAEA CRP project in the Chinese Academy of Agricultural Sciences (CAAS)–International Livestock Research Institute (ILRI) joint lab in Beijing, China and the ILRI laboratory in Nairobi, Kenya, to calibrate the allelic size calling methods implemented by the two projects. A preliminary joint analysis with the 11 shared markers indicates the clear genetic partitioning of goats into large geographic regions and continents and suggests separate ancient migration routes to Asia and Europe. However, a limited genetic differentiation is observed among indigenous goats within most of the countries, an indication of a relatively high gene flow across local goat populations, at least until recently. A clear phylogeographic partitioning of goat diversity was also observed by Pereira et al. (2009) that investigated the distribution of Y-chromosomal haplotypes in European and North African goat breeds.

Traditionally, the molecular phylogeny of livestock species has been based on the characterization of short fragments of the mitochondrial DNA (mtDNA) control region (d-loop). In goats, the first studies based on this region highlighted the existence of several well differentiated maternal lineages, whose variability has a lower geographic structure compared to other livestock species. This evidence was first interpreted as indicating separated and independent domestication events in the Fertile Crescent and in Asia (Luikart et al., 2001; Chen et al., 2005), but more recently, by comparing the mtDNA genetic variability of domestic and wild goats, Naderi et al. (2007, 2008) showed that, most probably, the domestication of *Capra hircus* took place in a wide geographic area centred around Southwest Asia, and was a large-scale phenomenon both from the temporal and numerical point of view. These results largely agree with archaeological evidence, which already suggested that goat domestication took place about 10,000 years ago in an area between the Zagros mountains and the Fertile Crescent, placed between the present day boundaries of Iran, Iraq and Turkey (Zeder and Hesse, 2000; Zeder, 2008).

The fraction of the ancestral mitochondrial variability which was captured at those early times constituted the starting gene pool of domestic goats which subsequently

spread all over the world during the migration waves of Neolithic farmers. The analysis of the relationships existing between mitochondrial haplotypes and haplogroups, therefore, may reveal how the diffusion of domestic goats occurred and shed light on the dynamics of past human migrations.

Interestingly, nuclear DNA shows a remarkable level of geographic structuring that is not detected in mtDNA. Complex demographic dynamics may explain this pattern, however, a simpler reason can be identified comparing goats to other livestock species, as cattle. In *Bos taurus* the geographic structure of the maternal lineage is due to differences in the frequency of distinct haplogroups in different geographic areas (e.g. T3 in Europe and T1 in Africa; Troy et al., 2001). Conversely, in goats a single haplogroup (haplogroup A) largely predominates the world, likely masking the existence of a geographic structuring of the maternal genetic diversity, evident only in the case of rare haplogroups (Naderi et al., 2007).

3. Development of high-throughput SNP assays for the analysis of goat genetic diversity

Being highly polymorphic, microsatellites are very informative markers and have been extensively used in diversity studies. A large number of these hypervariable markers is available in goat (Seki et al., 2012), however, their genotyping and scoring are labour intensive, and allele size calling is difficult to be calibrated across apparatus and laboratories, in the absence of a substantial number of shared samples.

Recently, the whole genome sequencing of livestock species, and the development of panels of 50,000 to 1 million SNPs, allow the use of genomic technologies in all livestock species, goats included. A drawback of SNPs is ascertainment bias (Nielsen, 2004; Albrechtsen et al., 2010), depending on the strategy and the animals used for their discovery. SNPs are also inefficient to capture some relevant genome polymorphisms, such as certain types of copy number variation (e.g. Kijas et al., 2011; Fontanesi et al., 2012). Nevertheless, they are quickly replacing microsatellites in paternity testing and genetic diversity studies, due to their robustness, low cost and automatic allele calling. In addition, high-density SNP panels permit the investigation of the goat genome at very high resolution. This is a clear advantage for the

investigation of population structure, reconstruction of demographic history and detection of recent and historical admixture, identification of selection sweeps and of marker–trait associations in genome-wide association studies (GWAS) of non-experimental populations. A number of these approaches are either unfeasible or at least imprecise using low-density markers, even if highly informative as microsatellites. In addition, SNP panels are applied in breeding programmes as a support to traditional selection and for genomic selection, presently implemented on a large scale in dairy cattle.

A 50k goat SNP panel has been recently developed (<http://www.goatgenome.org>; Tosser-Klopp et al., 2014) by the combined sequencing of whole genomes and reduced representation libraries from eight different breeds/populations from Europe and Asia through the cooperation of the French INRA Institute, Utrecht University (The Netherlands), the Malaysian Agricultural Research and Development Institute, and the DNA Landmark laboratory (Canada). The current panel comprises 53,347 SNPs (Illumina 50k Infinium iSelectHD Custom Bead Chip), which have been mapped on goat scaffolds/contigs produced by a joint effort of the Beijing Genomics Institute, Kunming Institute of Zoology and Inner Mongolia Agricultural University (China).

The status of goat genome has improved since the release of the reference genome that was made available by the IGGC in 2012 (Dong et al., 2013). In particular, additional Illumina new-generation short reads sequencing and the optical mapping technology of large DNA molecules permitted the assembly of 349 super-scaffolds with N50 reaching as high as 18.2 Mb. The current assembled base pairs total 2.66 Gb, which is about 92% of the estimated goat genome size (~2.9 Gb). Data is assembled into 30 pseudo-chromosomes, with high colinearity between cattle and goat.

PacBio sequences (72× sequence read depth coverage) from a highly inbred San Clemente buck are being used to create a de novo caprine reference genome assembly model to enhance identification of important adaptive variants (Sonstegard et al., 2013, 2014). The long-term goal of these efforts is to develop genomic tools for goats that can be used to breed genetically superior adapted goats and help meet rising global demands for animal protein based food.

Moreover, within the EU FP7 project Nextgen, populations of domestic goats (*C. hircus*) and their wild ancestors (bezoars, *Capra aegagrus*) were sequenced and genotyped. In particular, 164 domestic goats from Morocco were whole genome sequenced. Their sampling was based on a grid system to investigate adaptive variation by a landscape genomics approach newly developed within Nextgen. An evaluation of the potential of wild ancestors and traditional breeds, as reservoirs of neutral and adaptive genetic diversity was also conducted, by analysing the whole genome of about 40 individuals (bezoars and local Iranian domestic goats), sampled in Iran. The genome of the wild ancestors was assembled de novo and resulted in 6676 scaffolds with N50 reaching 1.75 Mb and a total length of 2.58 Gb.

Conversely, to our knowledge only a few goat transcripts have been sequenced to date, e.g. within the 3SR project, whole blood, mammary gland and milk somatic

cells from 10 alpine goats have been sequenced in a differential expression experiment targeting mastitis.

4. Detection of selection signatures in the goat genome

The availability of dense marker panels throughout the genome marked a paradigm shift in the way livestock populations are investigated and analysed genetically, either for studying the population genetic structure (McKay et al., 2008), searching for QTL controlling complex traits (Kolbehdari et al., 2008), performing genome-wide marker-enhanced selection of young animals (VanRaden et al., 2009; Hayes et al., 2009), identifying patterns of recent and past selection (Luikart et al., 2003; MacEachern et al., 2009) or addressing other objectives.

Genomic regions under selection have a relevant importance both in conservation and in the analysis of complex traits. For conservation, loci under selection reveal functional adaptation, complementing the information collected from neutral genomic regions (Bonin et al., 2007). In addition, they permit to investigate the genetic control of traits extremely difficult, costly or even impossible to measure in experimental conditions. Among these are adaptation to extreme climates and low-quality feed, and disease resistance. These traits may very well be relevant for the sustainability of livestock husbandry in times of rapid and unpredictable climate change. Projections, in fact, indicate a rapid trend towards a warmer planet and shorter growing seasons in a large part of the world.

Positive directional selection rapidly fixes advantageous alleles in a population. If fixation is rapid, relative to the rate of recombination, neutral alleles around the selected locus are fixed as well, creating a long invariant haplotype block around the selected locus as signature of recent directional selection.

Rapid fixation of new alleles by selection also increases the divergence between selected and non-selected (or divergently selected) populations in the region around the selected locus, compared to other genomic regions. In contrast, balancing selection actively maintains diversity in a population for longer than expected under neutral genetic drift. Hence, regions under selection can be detected by searching for outlier markers or haplotypes in either the distribution of allele frequencies within or between populations (or groups of populations), or the patterns of linkage disequilibrium along the genome. This is based on the assumption that selection hits specific genomic regions (the selected locus and linked genetic markers), while drift and inbreeding influence the entire genome. These and similar methods for the identification of selection signatures have been reviewed in more detail by Oleksyk et al. (2010).

Given the earlier availability of SNP markers, genome-wide selection signatures have been mostly searched in humans, using both sequence and genome-wide marker data (Oleksyk et al., 2010). In farm animals, they have been investigated in the framework of the HapMap project and re-sequencing projects (e.g. The Bovine HapMap Consortium, 2009; Stella et al., 2010). In chicken, whole genome re-sequencing of wild and domestic animals

identified 58 genomic regions under selection containing genes likely involved in the domestication process. One of the most interesting signatures was found in domestic chickens at the locus for thyroid stimulating hormone receptor (TSHR), which has a pivotal role in metabolic regulation and photoperiod control of reproduction (Rubin et al., 2010). However, inferring the cause of sweeps (i.e. the selection force) and identifying the genes under selection are still difficult tasks, and require proper experimental design, particularly when studying the complex traits involved in adaptation.

An interesting approach has recently been proposed by Gautier et al. (2009). A system biology strategy was used to identify the physiological functions controlled by the genomic regions involved in adaptive genetic divergence in West African cattle. By contrasting genome-wide scans of nine cattle breeds, and using a Bayesian method, they identified 53 selective sweeps. The genes closest to the peaks of signature were submitted to functional and network analyses and found to be involved in three main physiological functions: immune response, nervous system and hair and skin development. This approach is presently limited, however, by the difficulty in identifying the right genes to include in system biology analyses, since the precision with which selection signatures are localized is relatively low, and by the present incomplete knowledge of gene functions. These limitations may be partially overcome by recently designed methods that use a composite of multiple signals to detect selection signatures, greatly increasing the resolution of detection (Grossman et al., 2010).

Selection signatures specific for adaptation have been identified in humans (e.g. Harris and Meyer, 2006; Lappalainen et al., 2010) and in wild organisms (Bonin et al., 2006; Poncet et al., 2010) but their discovery will be most useful in livestock species, in which they might very well become targets of marker assisted or genomic selection. This highlights the need for strengthening the collaboration among scientific communities on the use of emerging technologies and new analytical approaches (Joost et al., 2011).

A different approach to identify genomic regions associated to environmental variables is based on the combined use of genomics and GIScience. GIScience permits to depict, explore and compare variables according to their geographic coordinates. This allows the detection and description of spatial synchrony, identification of data combinations associated with effects specific to a geographic area, calculation of synthetic indicators and, most importantly in this case, of hidden relationships between variables (Joost et al., 2010). Recently a spatial analysis method (SAM) based on GIScience has been developed to assess the level of association between molecular markers and environmental parameters (Joost et al., 2007, 2008). SAM is based on the spatial coincidence concept to connect genetic information with geo-environmental data. Logistic regression provides a measure of the association between the frequency of molecular markers and the environmental parameters at sampling sites. The proof of concept of the method was obtained in the pine weevil (*Hylobius abietis*) and in sheep (Joost et al., 2007). Interestingly, in sheep the DYMS1 microsatellite marker, previously shown

to be involved in parasite resistance (Buitkamp et al., 1996) was found to be associated to the number of wet days, an environmental variable greatly influencing parasite load. A few other interesting examples of the application of SAM recently appeared in the literature (Pariset et al., 2009; Parisod and Joost, 2010). The interest in this method stems from its independency on population genetics models and complementarity to the population genomics methods previously described (Pariset et al., 2009). Indeed, SAM appears to be more sensitive compared to Fst-based approaches and able to link significant genomic regions to specific environmental variables, rather than identifying signatures caused by selection forces not easy to identify.

Goat breeds adapted to sustainable production systems in extreme and harsh environments will play an important role in this since response mechanisms to environmental challenges have been evolving for millions of years, in the wild ancestor and in derived domesticates. The post-domestication global colonization, along with agriculture expansion and human migrations, has taken goats well outside the agro-climatic range of adaptation of wild ancestors. Nowadays goats count thousand local populations adapted to environments as different as sub-Saharan Africa and Norway. A single example of the SAM method applied to goats has to date appeared in the literature (Pariset et al., 2009). These authors analysed some 500 animals from 16 Mediterranean breeds with 27 SNPs in functional genes. The combined use of SAM and an Fst-based method identified three alleles under environmental selection at a very high confidence level. Two SNPs are in the *alpha S1 casein* (*CSN1S1*) gene. The first SNP (*CSN1S1.ex9*) is associated to seven and the second (*CSN1S1-5*) to three environmental parameters. The third SNP, in the *lipase* gene, is also associated to three environmental parameters. A second investigation used the Econogene goat dataset (1228 animals belonging to 43 European and Near Eastern goat breeds spanning from Jordan to Poland) to look for association between environmental variables and 96 AFLP markers. A total of four markers were found to be significantly associated with environmental variables and confirmed to be under selection by at least one other test implemented in either MCEZA (Antao and Beaumont, 2011) or BAYESCAN (Gaggiotti, 2010) software (Colli et al., 2014) to search for association between environmental variables and AFLP markers.

The identification of genes, causative mutations, and ultimately the biologic mechanisms involved in adaptation remain a challenging undertaking, requiring the integrated approach of different expertise and the difficult task of designing proper experimental design for validation experiments. However, the availability of the goat 50k SNP panel and of exome/whole genome sequences will permit the testing and exploitation of SAM and other methods detecting selection sweeps at their full potential, bypassing the limits of low density of microsatellites and AFLPs.

5. Landscape Genetics projects in goats

The ADAPTmap (<http://bioinformatics.tecnoparco.org/adaptmap/>) is an International effort planned in collaboration with the International Goat Genome

Consortium (IGGC) (<http://www.goatgenome.org>) and with the FeedtheFuture programme of the USAID agency (<http://www.feedthefuture.gov>) to improve coordination among otherwise independent projects for genotyping and re-sequencing of goat breeds. The aim of ADAPTmap is to use both traditional and novel approaches to explore diversity of breeds and populations around the world. Population studies are targeted to assess variability based on mutation classification, analysing the effects of mutations on protein structure as a tag for adaptation.

Methods used for efficiently storing, querying and retrieving large-scale genomic, phenotyping and environmental data have been developed and an on-line questionnaire distributed to collect and summarize information on the various genomic initiatives on goats worldwide. Information has been so far collected from 14 projects, most of which coordinated at the national level. The number of sampled breeds ranges from 3 to 15 and covered in total 31 countries and a wide variability of environments and breeding systems. Most breeds are autochthonous (80%) and mostly bred for meat production (63%). In most cases (about 70%), sampling and genotyping/re-sequencing activities are planned to be completed in early 2013. Collection of FAO production environment descriptors (PED) is foreseen for about 40% of the populations.

A few large international projects, as FeedtheFuture and NextGen (Next Generation methods to preserve farm animal biodiversity, <http://nextgen.epfl.ch/>) are disentangling the diversity of the breeds/populations investigated, by recording and relating genomic diversity, morphological traits and several geo-climatic parameters, for characterizing the breeding environment. In these projects, Global Positioning System (GPS) coordinates are available for each flock, allowing for application of Geographical Information Systems (GIS) and spatial analysis (Joost et al., 2007; Joost et al., 2010).

A few national and international projects, as 3SR (Sustainable Solutions for Small Ruminants; <http://www.3srbreeding.eu/>), plan large-scale genotyping efforts to characterize commercial populations of goats and investigate marker–trait associations. The result of linkage and genome-wide association analyses are used to select individual animals for whole genome re-sequencing.

Genomic analyses comprise a large amount of genotyping with the Illumina 50k SNP panel. However, re-sequencing and genotyping by sequencing techniques will be applied on some of the same populations and de novo sequencing approaches will be applied to wild ancestors. Integration of data from various sources will allow for the comprehensive application of population genomics, for example, to identify selection signatures in groups of breeds that share common phenotypes.

Preliminary data from the recently established Italian Goat Consortium indicate that the SNP panel developed in this species is highly polymorphic. Results on Orobica, Bionda dell'Adamello and Valpassiria breeds reared in the Central and Eastern Alps in Northern Italy and on Grigia Ciociara from Central Italy, analysed with the 50k SNP chip, indicate that 98.25% SNPs are polymorphic

(rare allele observed at least once), 1.1% monomorphic and 0.5% give no results. In addition 97.6% has MAF > 1%. The existing goat SNP panel can be partially improved by integrating additional whole genome sequences produced by the previously described international projects, targeting populations from different geographic localities representing the areas of the domestication event(s) and potential agro-climatic adaptability. Hence, the contribution of a larger number of samples (i.e. as in the recently launched 1000 cattle genomes initiative) is needed to achieve a comprehensive representation of the global diversity in goats.

6. Reconstruction of goat evolutionary history

The first researches on the evolutionary systematics of the genus *Capra* and on the identification of the domestic goats wild relative were mostly based on the analysis of mitochondrial DNA. These studies showed that the bezoar *C. aegagrus*, the markhor *Capra falconeri*, the Kuban tur *Capra caucasica*, and the eastern tur *Capra cylindricornis*, are the wild species more closely related to domestic goats (Pidancier et al., 2006).

Contrasting hypotheses regarding the wild ancestor of domestic goats have been suggested, proposing either the bezoar (Zeuner, 1963) or the markhor, or both (Harris, 1962) as candidates. In the case of the Girgentana goat breed (native to Sicily in southern Italy), for example, the presence of screw-shaped horns similar to those of the markhor and of some highly divergent mtDNA haplotypes (Sardina et al., 2006) seemed to suggest an Asian origin (Portolano, 1987) and a direct descent from *C. falconeri*.

Although some cases of introgressive hybridization between the wild species and the domestic goats have been reported (Giacometti et al., 2004; Hammer et al., 2008; Alasaad et al., 2012), several evidence based on mitochondrial control region variation (Takada et al., 1997; Mannen et al., 2001; Naderi et al., 2007, 2008) finally challenged the contribution of markhor and confirmed the bezoar as the wild ancestor of *C. hircus*.

Recent evidence, both in livestock and wildlife, showed that molecular phylogenies based on a short and fast-evolving portion of mtDNA, such as the control region, can be heavily affected by the effects of NUMTs (NUclear Mitochondrial Transpositions, also called pseudogenes; Hassanin et al., 2010; Moyle et al., 2013) and homoplasy (McCracken and Sorenson, 2005; Bonfiglio et al., 2012), which may mask the actual extent of divergence/similarity between mitochondrial lineages. mtDNA control region analysis in cattle proved to be inadequate for a thorough characterization of maternal lineages, and a far more precise picture has been obtained from complete sequences of mitochondrial genomes (Achilli et al., 2008; Bonfiglio et al., 2010, 2012). Next generation sequencing technologies now permit the high throughput/low cost analysis of entire mitochondrial genomes at the maximum resolution, and have become the common standard for the investigation of the human maternal lineages. The analysis of complete mitochondrial genomes has been recently extended also to goat, to provide a more comprehensive molecular phylogeny of the species. A first study by Nomura et al. (2013) focused upon partial mitogenomes to reappraise

goat domestication dynamics through the analysis of about 10 Kbp of mtDNA protein-encoding genes. Further (and still unpublished) analyses of more than 70 complete mtDNA sequences representative of *C. hircus* from western Eurasia and one wild goat (*C. aegagrus*) from Iran confirmed a restricted number of mtDNA haplogroups. The topology of a maximum parsimony tree, based on complete mtDNAs and rooted with a *C. falconeri* sequence, revealed well defined monophyletic clades corresponding to haplogroups A, B, C and G, all including at least one individual of southwest Asian origin. Haplogroup A is confirmed as the most frequent in western European goats (including more than half of the analysed samples). Its star-like shape suggests the occurrence of a recent bottleneck followed by a population expansion which likely represents a single domestication event occurred in southwest Asia and dating back to Neolithic times. The structure of such a clade closely resembles that of the mtDNA haplogroup T3 of taurine cattle (Achilli et al., 2008, 2009), thus suggesting strong similarities between the domestication processes of these two livestock species.

7. Perspectives

The cost of DNA sequencing has recently decreased by orders of magnitude. This trend will likely continue and open the door for very affordable whole genome sequencing in all livestock species, goats included. As a consequence, the amount of genomic information is expected to grow exponentially. Research focus is now shifting from the sequencing of a single individual to hundreds or even thousands of individuals. The “1000 genome project” in humans (<http://www.1000genomes.org>), and the “Genome 10K project” (<http://genome10k.soe.ucsc.edu>), targeting the whole genome sequencing of 10,000 vertebrate species are paradigmatic examples of the present trend, recently extended to cattle (<http://www.1000bullgenomes.com/>) and in the near future hopefully to goats.

Sequencing will extend our knowledge of SNP variation, enhancing the discovery of rare alleles and alleles confined to particular breeds or geographic areas, and on other polymorphisms potentially relevant for animal phenotypes, as insertions, deletions and copy number variations (CNVs) (e.g. Beckmann et al., 2007). A recent example of the potential of whole genome sequence analysis is the inference of human population size changes occurred during the last 10 Kya–1 Mya (Li and Durbin, 2011). This reconstruction was based on a pairwise sequentially Markovian coalescent model that allows to infer the past demographic history of species or populations from the sequence of single diploid genomes.

Sequencing will also be applied to identify patterns of methylation along the genome (Lister et al., 2009) and to quantify levels of gene expression and detect alternative splicing in different tissues, developmental and environmental conditions, hence permitting the investigation of genome functioning in a given environment.

It is expected that these new tools will facilitate the identification and understanding of variation underpinning important traits, including phenotypes relevant for

adaptation and sustainable exploitation. With regard to conservation, whole genome sequencing will also provide more objective indications of uniqueness than any marker panel and avoid the ascertainment bias presently affecting SNP panels developed from a few breeds not fully representing the genetic variation existing within a species. In addition, adaptive variation will be included in prioritization protocols in order to ensure conservation of unique adaptive variants, thus optimizing conservation efforts both in vivo and in vitro.

It is also envisaged that breeding and selection will be more and more guided by molecular analysis. Models are to be developed and customized to populations with different genetic structure (small vs. large breeds) and to different purposes (e.g. genetic improvement, control of inbreeding, maintenance of diversity).

We conclude that we are facing a challenging and stimulating time. Although the revolutionary development of low cost genomic analysis methods has created tremendous opportunities for genetic analysis, it has also created particular challenges. Tools for producing genomic information about livestock breeds have advanced faster than our capacity to process and understand this information. Storing, organizing, analysing, and interpretation of these data will be the future challenge for researchers and will more than ever benefit from networking and integration of expertise in different disciplines. In addition, full exploitation of the knowledge resulting from this research, through its application in breeding and conservation programmes, is also hindered by the lack of infrastructure and technical capacity, especially in developing countries. Under these circumstances, any loss of biodiversity before characterization risks to turn into a loss of invaluable opportunities for both science and agriculture.

Conflict of interest

None of the authors (P. Ajmone-Marsan, J.L. Han, A. Achilli, H. Lancioni, L. Colli, S. Joost, P. Crepaldi, F. Pilla, A. Stella, P. Taberlet, P. Boettcher, R. Negrini, J.A. Lenstra) has a financial or personal relationship with other people or organizations that could inappropriately influence or bias the paper entitled “The characterization of goat genetic diversity: towards a genomic approach”.

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