



Globaldiv

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Editorial - On crossbreeding and genetic purity: may we join what has been separated?

Breeds are our core business. They emerged by selective breeding and local adaptation, but are also irrevocably linked to the tradition and history of their region. According to the prevailing view in conservation biology, breeds are units of conservation and should be protected against extinction and genetic contamination. In this context, crossbreeding is seen as a threat of the genetic purity and should be avoided, at all costs. The use of bastard as invective is a trace of similar views, not so very long ago, on mixed descent of humans. Here I will defend a few heretic views. First, I speculate that by our education or instincts we are preconditioned against crossbreeding. Then, I put crossbreeding of livestock in a historic perspective. Next, I argue that crossbreeding does not need to affect the identity of a breed and may even be in its best interest.

Some dilettante philosophy, for the sake of argument. Remember our scientific education. In molecular life science we spent much effort on purification. From inorganic salts to enzymes and PCR products, pure it should be or our experiments fail. Did this contribute to our preconception of 'genetic purity'? Or does it have even deeper roots? Classes in society of medieval origin tried to remain of pure descent; even today a marriage of a royal with a common person is frowned upon. This way of thinking even found a practical use: agricultural production has benefited from a breeding strategy that avoided crossing of superior individuals with their less noble relatives. However, our

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preference of genetic purity is not wholly compatible with the diploidy of higher eukaryotes: offspring of parents that are too identical will suffer from homozygous gene defects.

Our ideas are further shaped in the biological classroom, where we learn about a strict hierarchical organization of the plant and animal kingdoms. Rather than a natural and widespread process, hybridization of species is seen as exception, which in a one-way process should precede complete divergence. As part of the canonical evolutionary process, subspecies are supposed to be adapted to their own environment. As a consequence, the 'splitters' among the conservation scientists advocate the conservation of all subspecies, as opposed to the 'clumpers' who do not mind combination of populations. I propose that by our education we are programmed to be splitters. Domestic breeds are perceived as being unique and we should be concerned about their genetic purity.

In fact, many of our colleagues were surprised to learn that breeds, like human races, share most of the polymorphisms. This should not have been unexpected, since most mutations that cause genetic variation occurred thousands of years ago, while most breeds are of much more recent origin. Several of the present types of livestock have medieval or even more ancient origins, but breeding became systematic only in the 18th century. Breeds started as incomplete samplings of the total diversity of the species and to date have kept a considerable part of their original diversity. Even after breeds became separate entities, genetic isolation was not strictly maintained. More often than not, the history of a breed, even if reputed to be unique, mentions upgrading by using sires of other breeds. For instance, in the 18th century Dutch dairy cattle has been used with British breeds, while in the next century British Shorthorns influenced several Northern European cattle and the Scottish Ayrshire became the ancestor of many Nordic herds. In Central Europe there is widespread influence of Swiss cattle. In sheep, Spanish Merinos as well as British breeds were exported to several countries. So there has always been a gene flow that is clearly incompatible with the above-mentioned conservation paradigm. 'Genetic purity' can be inferred from the pedigree, but has no clear molecular basis as long as gene variants that encode the breed-specific traits have not been identified.

However, even if crossbreeding was an integral part of the history of livestock, many breeds have become valuable for a variety of purposes and can be managed on their own. Crossbreeding may serve three purposes. First, breeders want to combine traits of different breeds. For instance, Heck cattle was created with material from several rustic and authentic breeds in order to approximate, most incompletely, the wild aurochs. In American crossbreeding created several synthetic breeds with an unique appearance, often by crossing an European production breed with zebu. Secondly, the productivity of a breed needs to be improved. Farmers will never maintain an authentic breed if their neighbors earn more money with more productive animals. Thirdly, a breed suffers from inbreeding. Closing the herdbook and a frequent use of top sires invariably cause a high prevalence of genetic diseases and loss of viability. Genetic purity, whatever it may be, then becomes incompatible with animal health and welfare. This applies especially to several horse, dog and cat breeds, but also to fancy breeds of livestock.



But do we have to sacrifice the uniqueness of all local or inbred breeds? Not at all! Breed standards that have been achieved by selection can also be maintained in the same way, also after crossbreeding. Critical for conservation of a breed is not its genetic isolation. This maintains 'genetic purity', but is at best an easy way to keep out undesired traits. Deciding will be a clear definition of the unique breed features that can guide selective breeding towards the desired standards. For instance, crossbreeding the famous Friesian horse in order to alleviate their most problematic inbreeding would be first at the expense of their appearance and elegance, but this can be taken care of during later generations - if the breeders know what they want.

Inevitably, enhancing productivity of a breed will change its phenotype, but also makes it sustainable while conserving at least part of the original gene variants *in populo*. And only few people would mourn the loss of traits that directly affect animal health and well-being, like the facial deformations and eye problems of Pekinese dogs. But what about the adaptation of breeds to their environment that may be affected by crossbreeding? A clear example of adaptation is the trypanotolerance of African N'Dama cattle, while the zebu genes confer tolerance of hot and dry climates. However, for most breeds adaptation is only assumed implicitly and crossing of breeds from similar environments is not likely to give problems.

Our studies of European cattle have revealed one case in which only molecular data revealed the extent of crossbreeding. A typical authentic breed, the Portuguese Minhota cattle, has been upgraded with German Yellow bulls to the point that the local breed is now essentially German. However, for at least one breed cross-breeding would not be tolerable at all: Chillingham cattle, which during several centuries has been kept in strict isolation within a small population. Although this does not argue against the risk of inbreeding - the animals are small and have an average life span of only 15 years - their unique homozygosity is worth to be conserved.

Finally, we should mention one clear disadvantage of crossbreeding. For us scientists, genetic admixture confounds our attempts to analyze breed relationships and to reconstruct their history. So at least we should conserve our DNA samples!

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Article of the month - Goat domestication

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"Of all human inventions, none has had a more profound effect on our history - and on the biosphere as a whole - than agriculture" (Pääbo, 1999). Studying the domestication process allows to document a key step in human history. After the initial plant and animal domestications in the Near East,



ca. 11,500 and 10,500, respectively, years ago (1,2), agriculture diffused into Europe along two main routes: the Mediterranean route and the Danubian route. In complement to archaeological studies, genetics gives major insights for understanding key steps of the domestication process. Here we present the current knowledge about goat domestication, based on four main papers published on this topic, and following a chronological approach that shows our progresses according to genetic evidences gathered both from domestic goats (*Capra hircus*) and from its wild ancestors, the bezoar (*Capra aegagrus*).

Goats were one of the first domesticated ungulates. The archaeological evidence traces goat domestication as far back as ca. 10,500 years ago in the high Euphrates valleys, in Southeastern Anatolia (Peters *et al.*, 2005) and 9900 to 9500 years ago in the Zagros mountains (Zeder, Hesse, 2000). From their initial domestication areas, goats were introduced into Europe by following both the Mediterranean and the Danubian routes.

The initial large-scale study of mitochondrial DNA polymorphism (Luikart *et al.*, 2001)

For this first study, an extensive sampling of pure indigenous goats was carried out, spanning most of its Old World distribution, from Nigeria to Iceland, and Mongolia to Malaysia. The hyper variable region I of mitochondrial DNA (579 bp) was sequenced for 406 individuals, and appeared to be highly polymorphic, with 160 variable sites and 331 different haplotypes. The phylogenetic analysis revealed three highly divergent haplogroups A, B, and C with 316, 8, and 7 haplotypes, respectively. Mismatch distribution analysis for these three haplogroups revealed a genetic signature of a population expansion with different expansion dates. Assuming a domestication date of about 10,000 years ago for the haplogroup A, we obtained an expansion date of 2,130 and 6,110 years ago for haplogroups B and C, respectively. The sequencing of the whole mitochondrial cytochrome b from two representatives from each haplogroup indicated that they diverged at least 200,000 years ago, vastly predating the time of domestication suggested by the fossil record. These results were interpreted as three independent and sequential goat domestications, with a possible domestication of the B haplogroup in Asia.

An AMOVA analysis showed that most of the mitochondrial DNA variation was within breeds (~80%), leaving only ~10% of the variation among breeds within continents, and ~10% among continents. On the opposite to what has been found for cattle and sheep, goats only exhibit a very weak phylogeographic structure, which was interpreted as high gene flow among continents related to human trade (human travelling much more with goats than with sheep and cattle!).



Ancient DNA challenged the first interpretation of goat domestication (Fernández *et al.*, 2006)

We had the opportunity to analyze goat fossil samples from an archaeological site (Baume d'Oullen) located in Southern France, dating from about 7,500 years ago, and corresponding to the front of the Neolithic expansion in this region. Such fossils allowed us to test the sequential domestication process

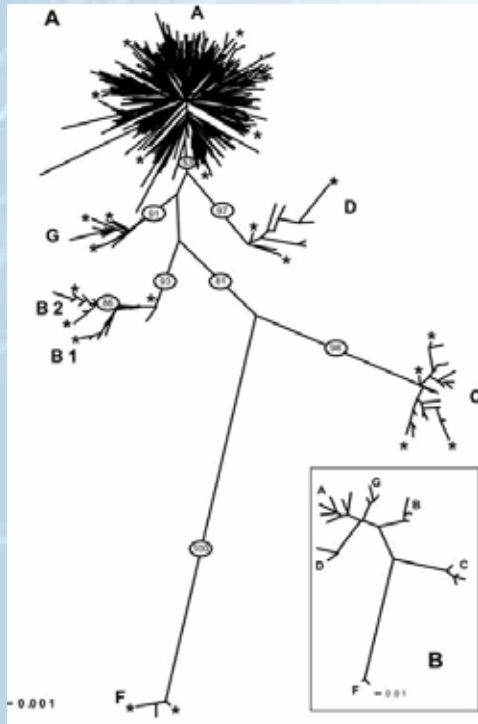


Figure 1. Neighbor-joining trees of domestic goat based on 1540 mtDNA haplotypes (A) and on the 22 reference mtDNA haplotypes (B) from Naderi *et al.* 2007. On the (A) tree, the numbers on the branches represent bootstrap values out of 1000 replications, and the stars point out the position of reference individuals for each haplogroup used to construct the (B) tree.

Table 1. Proportion of goat mtDNA haplogroups (in % of individuals and of haplotypes) and geographic distribution of these haplogroups.

Haplogroup	% of individuals	% of haplotypes	Geographic distribution
A	90.86	93.51	Global
B	5.92	2.99	Asia
C	1.44	1.49	Global
D	0.54	0.65	Asia
F	0.12	0.19	Sicily
G	1.11	1.17	Mainly fertile crescent



suggested by Luikart *et al.* (2001): if the hypothesis of a sequential domestication is true, according to the expansion dates found previously, we only expect to find the single A haplogroup in Baume d'Oullen. Furthermore, the level of diversity found can give information about the timing of the extensive mixing that has been observed (weak phylogeographic structure).

Two separate mtDNA segments, 130 bp of the control region and 110 bp of cytochrome b, were successfully amplified and sequenced from 19 of the 24 ancient samples tested. These 19 samples corresponded to at least 6 individuals based on the dating and on the haplotypes found. Sequencing of several clones obtained from each PCR product validated the sequences obtained. Moreover the results were confirmed by independent analyses in separate laboratories.

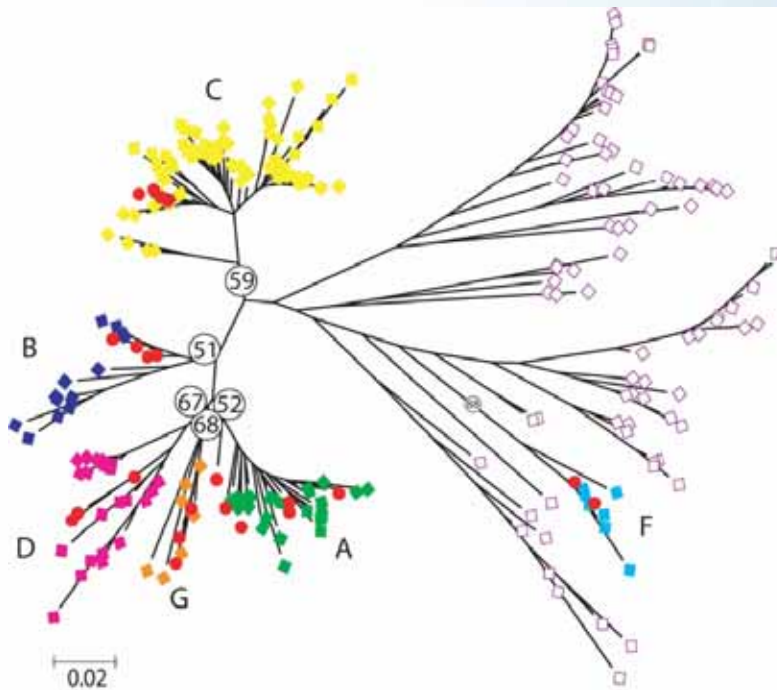


Figure 2. Phylogenetic relationships of the 243 haplotypes from the 473 *Capra aegagrus* studied (neighbor-joining) method (from Naderi *et al.* 2008). To identify shared mtDNA haplogroups, the 22 modern goat haplotypes from tree B of Figure 1 have also been included in the analysis (in red). The different colors correspond to the haplotypes from the different mtDNA haplogroups found in domestic goat (A, green; B, dark blue; C, yellow; D, purple; F, light blue; G, orange). The other *Capra aegagrus* haplotypes are represented in white.



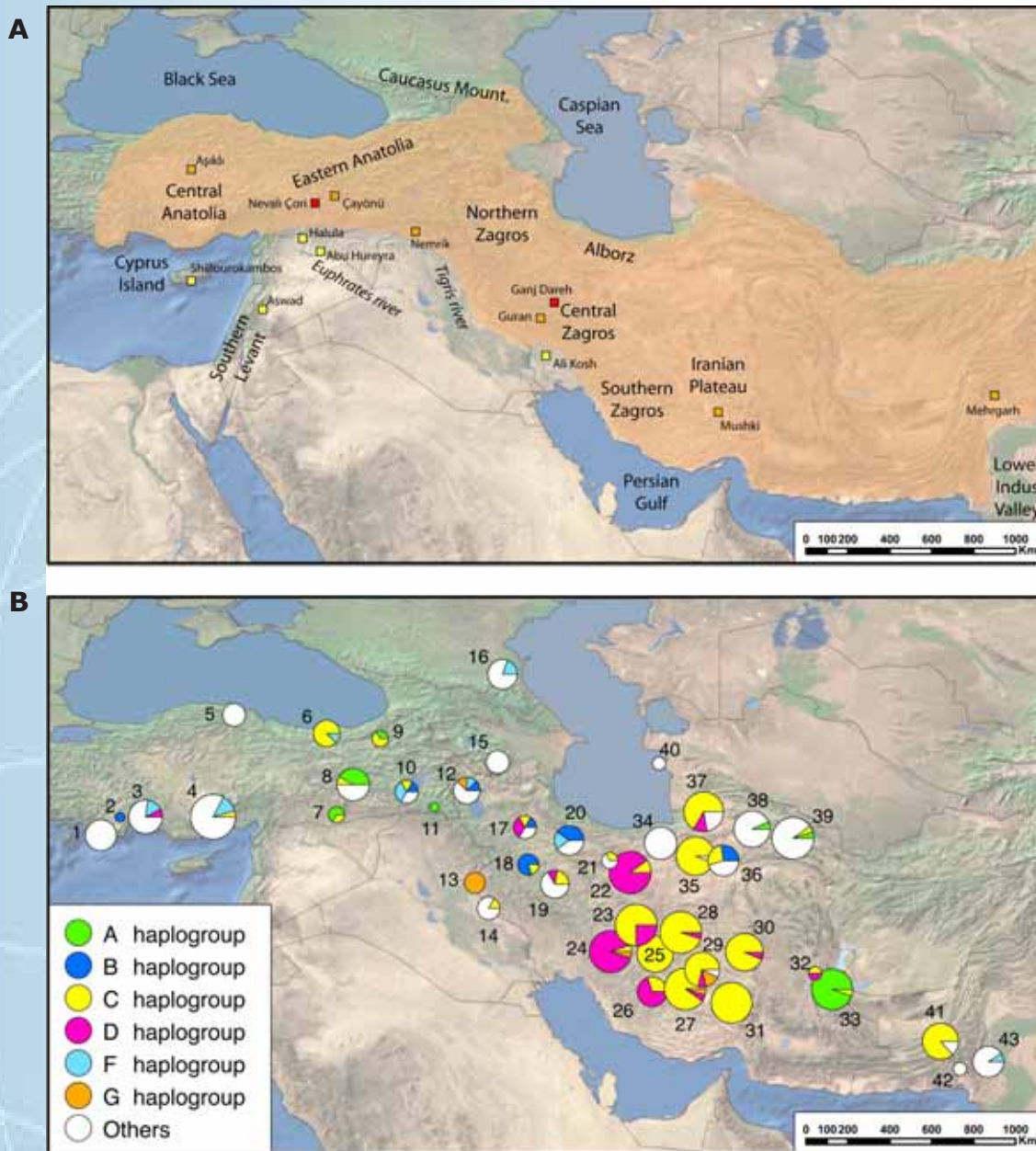


Figure 3. Study area and geographic distribution of the mtDNA haplogroups in *Capra aegagrus* (from Naderi *et al.* 2008). (A) Natural distribution of the bezoar. This distribution may not have changed since the beginning of goat domestication, and stops at the eastern limit of the map. The archaeological sites that give evidence of local pre-Neolithic goat domestication are represented in red. The sites that suggest either local goat domestication or early prepottery Neolithic transfer of domesticated goat are represented in orange. Finally, the sites that provide evidence of transfer of domestic goats out of the original geographic range of *Capra aegagrus* just after the domestication are represented in yellow. (B) Geographic distribution of the mtDNA haplogroup of *Capra aegagrus*. The size of the circles is proportional to the number of individuals analyzed. The different *Capra aegagrus* haplogroups are color-coded as in Fig. 2. The different localities are identified by numbers.



First, we were surprised to find a high diversity, showing that the extensive mixing observed today in domestic goats traces back as far as the Neolithic expansion in Europe. Second, we were also surprised to find both haplotypes A and C in the two layers analyzed (layer 1: 7,700-7,500 years ago; layer 2: 7,500-7,000 years ago). The attested presence of the C haplogroup in Southern France 7,500 years ago was not consistent with the domestication scenario proposed by Luikart *et al.* (2001) and suggesting that the C haplogroup has been integrated in the goat gene pool only 6,110 years ago.

Recent large-scale mitochondrial DNA analysis (Naderi *et al.*, 2007)

After the initial global survey by Luikart *et al.* (2001) several regional studies describing more precisely the genetic diversity of goat breeds have been carried out. The existence of three new haplogroups have been found, haplogroup D in Pakistan (Sultana *et al.*, 2003), haplogroup E in India (Joshi *et al.*, 2004), and haplogroup F in Sicily (Sardina *et al.*, 2006). Naderi *et al.* (2007) compiled all the available goat mitochondrial DNA, and added 946 new individuals from regions poorly studied previously, mainly from the Fertile Crescent. The combined analysis of all these samples lead to the discovery of a new haplogroup (G) located mainly in the Fertile Crescent, and to the conclusion that the haplogroup E was not valid (it clusters without any doubt within the haplogroup A). Naderi *et al.* (2007) also proposed standard criteria for the definition of haplogroups. The proportion of the six goat haplogroups and their geographic locations are presented in Table 1. The phylogenetic tree with 1540 haplotypes (2430 individuals) is given in Figure 1. This study of the genetic diversity of domestic goats also concluded that the knowledge of phylogenetic relationships between wild and domestic haplotypes was necessary to fully understand the domestication process.

The domestication process inferred from the combined analysis of wild and domestic individuals (Naderi *et al.*, 2008)

In order to solve the question of the number of domestication events, Naderi *et al.* (2008) sampled and analyzed 473 *Capra aegagrus*, the wild ancestor, from its whole geographic range. The same mitochondrial DNA region was sequenced. Figure 2 presents the phylogenetic tree of the 243 *Capra aegagrus* haplotypes found, together with representatives of each of the haplogroups of domestic goats. Figure 3 shows the geographic distributions of the *Capra aegagrus* haplogroups. All the haplogroups found in domestic goats have also been found in *Capra aegagrus*. These haplogroups all occur in Eastern Anatolia (Turkey) and in Northern Zagros (Iran), suggesting a single large-scale domestication process in these areas. This result fit well with archaeological data identifying Eastern Anatolia as an important domestication centre. It clearly demonstrates that another more eastern domestication centre is not necessary to explain the current mitochondrial DNA polymorphism of domestic goats. These data also



suggest that the weak phylogeographic structure of domestic goats result at least partly from the weak phylogeographic structure of its wild ancestor, and not only from more recent commercial trade among continents.

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A Tibetan farmer with a ram of Peng Bo sheep. It is suspected to have some genes from the wild Argali sheep found in the region due to their similar phenotypes.

A newly developed breed of semi-fine wool sheep, the first in the Tibetan Autonomous Region, China but could also be the latest in the world



A flock of Peng Bo sheep.

The Peng Bo semi-fine wool sheep has recently been verified and granted by the Chinese Committee on Animal Genetic Resources with a certificate to be considered as a newly developed breed in 2008. This is the first ever but could also be the latest new livestock and poultry breed being developed in Tibet, China, where the Everest, the world's highest mountain, is located.

Peng Bo sheep is a composite breed being developed from crossing the valley type of

indigenous Tibetan ewes with rams of Xinjiang Merino (another composite breed being developed in 1980's through crossbreeding the local sheep) and Tsigai sheep (a semi-fine wool breed) since 1975. An "open nuclear flock" breeding scheme was applied following three phases of upgrading, within flock breeding for fixation and selection within flocks for further improvement. There are around 69,000 sheep being considered as and kept in the nuclear flocks in Linzhou county of Tibet, a homeland of the breed. So far a total of 3000 top quality rams have been supplied to the region for production of up to half of a million crossbreds.

Peng Bo has been developed under tough ecological conditions at altitudes around 2600 to 4200 metres above sea level. It adapts well to rough feeding, grazing and management systems and also shows a very strong disease resistance.





A marvelous tail of the Large tailed Han sheep in China.

a number of minority tribes live together with similar cultural and religious values of such products.

In the current local market, a Peng Bo sheep can be sold at 380 Yuan, 200 Yuan more than a local Tibetan sheep. Its wool also values double of its maternal parent.

Performance of Peng Bo: wool lengths and weights of the first grade, adult males and females are 10.4 cm and 3.1 kg, and 10.3 cm and 3.1 kg, respectively. The fineness is 25-40 μm in fiber diameter and clean wool percentage 62.35%. Body weights of adult males and females after shearing are 37.5 kg and 33.0 kg, respectively. Adult castrates weighs at 44.43 kg with a carcass at 20 kg. The mutton is top quality, in particular rich in Selenium content.

The development of Peng Bo has been considered very successful in genetic improvement of the productivity while maintaining the super adaptability of the local Tibetan sheep and very important to provide unique mutton and wool products to regional markets where

Calendar

- 16th International conference KRMIVA 2009 in the field of animal nutrition and feed. Opatija, Croatia. 1-3 June 2009. www.krmiva.hr/index-en.htm
- XXXIII CIOSTA-CIGR Section V International Conference "Technology and Management to ensure Sustainable Agriculture, Agrosystems, Forestry and Safety". DISTAFA, Università Mediterranea di Reggio Calabria, Reggio Calabria, Italy. 17-19 June 2009. www.ciosta.unirc.it
- Joint International Agricultural Conference 2009. Wageningen, NL. 6-8 July 2009. www.jiac2009.nl
- Practical strategies and tools for the genetic management of farm animal populations - Session 13 of the 60th EAAP Annual Meeting Monday, 24 August 2009 -Barcelona, Spain



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