Human Evolution
DOI 10.1007/s11598-006-9010-0

How Did Domestication Change the Hair Morphology in Sheep and Goats?

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Received: 7 July 2005 / Accepted: 15 September 2005

Abstract We analysed macro-and microscopic features of dorsal guard hairs in 21 specimens of wild and domestic sheep and goats. We integrated and extended the available data on hair morphology of wild species and provide a first comparative analysis of hair structure of domestic forms. Domestic sheep and goats, probably due to a convergence process under artificial selection, show similar medullary features to each other and different medullary structures from their relative wild relatives. Different breeds show a diverse alteration of the medullary structure probably correlated to the duration of the domestication process. Domestic sheep have a cuticular structure different from the relative wild ancestor, while domestic goats do not show clear differences in the cuticle from the related wild species. The strong artificial selection for wool production may have transformed the hair structure of the sheep, but not that of the goat. We described the effects of age on the microscopic structure of hair, which have not yet been investigated. The medullary structure and the cuticular pattern in domestic forms do not change with age, as seen in wild species, because juveniles characters are retained in adults due to domestication.

Keywords bovids · guard hairs · medulla · cuticle · *Ovis* · *Capra*

Introduction

Several atlases and identification keys have been published on the hairs of wild sheep and goats occurring in Europe [8–10, 13, 14, 16–18, 24, 28, 32], Asia [13, 26] and North America [15, 21, 25]. Nevertheless, the hair of some species has not yet been described, i.e.

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the wild goat *Capra aegagrus*. The hair morphology of domestic sheep and goats has been extensively studied [1–3, 9, 10, 13, 16, 17, 26], but the domestication-related changes of the medullary and cuticular patterns are still poorly known [22]. The domestication process has caused several structural and functional modifications concerning general appearance, size of the body, shape of the skull and horns, dentition, skeleton and behaviour [5]. Artificial selection should also involve hair coats of domestic animals for characters that may be favoured for economic reasons.

The aims of the present paper are i) to integrate and extend the available data on hair morphology of wild sheep and goats, ii) to present the first comparative study of hair structure of wild and domestic sheep and goats, analysing also age variation, and iii) to evaluate the differences in medullary and cuticular morphology as domestication-related changes.

Material and Methods

We studied the hair structure of wild goat *Capra aegagrus* and mouflon *Ovis orientalis*. Wild goats sampled came from Montecristo Island and Crete while mouflons came from Sardinia and Corsica. The Montecristo wild goats shows a phenotypic polymorphism in the colour pattern of the coat. Five kind of coats has been described: agrimi, Montecristo, light brown, patched, and black [31]; three coat patterns are represented in our sample: agrimi, Montecristo and black. We compared the hair structure of these wild species with that of the domestic counterparts: goat (Saanen breed) and sheep (Gentile breed).

Terrestrial mammals are covered with two distinct types of hairs: long, thick, pigmented guard hairs, which determine the general colour of the coat, and short, thin, less pigmented and more numerous fine hairs, supplying insulation. Only guard hairs are important in species identification as they exhibit diagnostically reliable features. Since hair structure of fresh and tanned specimens is identical [21], we collected hair tufts from live and dry skins housed in Italian mammal collections (Natural History Museum, Zoological Section, Florence; Italian Wildlife Institute, Bologna). Hair samples were taken from 21 specimens (12 wild and 9 domestic). The hairs were collected from not less than five spots in the dorsolateral region of each specimen. Hairs of other body regions generally show similar characteristics but often they are less marked [32]. Previous studies reported that the first moult in young of wild ungulates of some European and North American species coincides with the development of adult hair characteristics (cf. [11, 12, 15, 29]. As far as we know, no data are available on domestic ungulates. To study the effect of age on hair structure of wild and domestic ungulates, we defined two age classes: young (prior to the first moult) and adult. We sampled 9 young of known age (< 4 months for wild species, < 2 months for domestic forms) and 12 adults. The guard hairs of ungulates do not show any expanded and flattened regions [15]. Therefore, we distinguished two general regions along the hair, each one corresponding to half a portion of the hair: lower and upper shaft [25]. Hair microstructure is described referring to these regions.

Taking into account the nomenclature currently used to describe microstructure (cf. [15, 32], we selected only a few, easily identifiable without misunderstandings, descriptive categories, [7]. Hair microstructure is composed of three layers of keratin: medulla, cortex and cuticle, from the innermost to the outermost. The medulla is composed of loosely packed cells with air spaces in the cells themselves or between them. It is described by composition (unicellular irregular and multicellular), structure (uniseriate, multiseriate, filled lattice and partially filled lattice), pattern (continuous and fragmental) and margin form (irregular and scalloped) (Fig. 1). The cortex, composed of cells coalesced into a hyaline mass, does not exhibit characters that could be used as criteria for identification

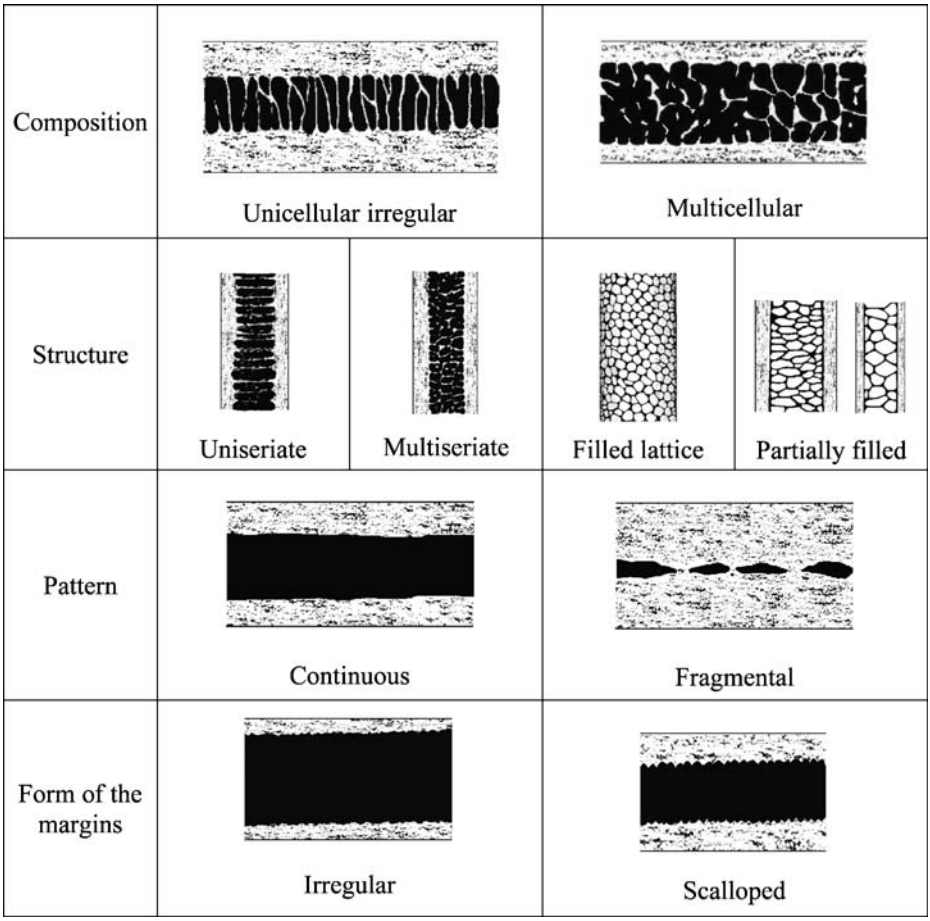


Figure 1 Medulla classification system used in the present work.

because of its nearly homogeneous structure. However, there is a considerable interspecific variation in the cortex width. The cortex width was estimated by eye, taking the width of the medulla as a reference unit. The cuticle consists of overlapping scales. We considered the position of the scales in relation to the longitudinal axis of the hair (transversal and intermediate), the structure of scale margins (smooth and rippled), the distance between scale margins (distant and near) and the scale pattern (regular mosaic, "Ω" shaped, regular and irregular wave) (Fig. 2).

Microscopic hair preparations were made following De Marinis and Agnelli [6]. Microphotographs were taken using a light microscope fitted with a digital camera.

Results

Macroscopic Hair Description

Wild sheep and goats can be macroscopically distinguished from domestic forms because of their shiny appearance and undulated profile (Table 1). Hairs of young other than sheep

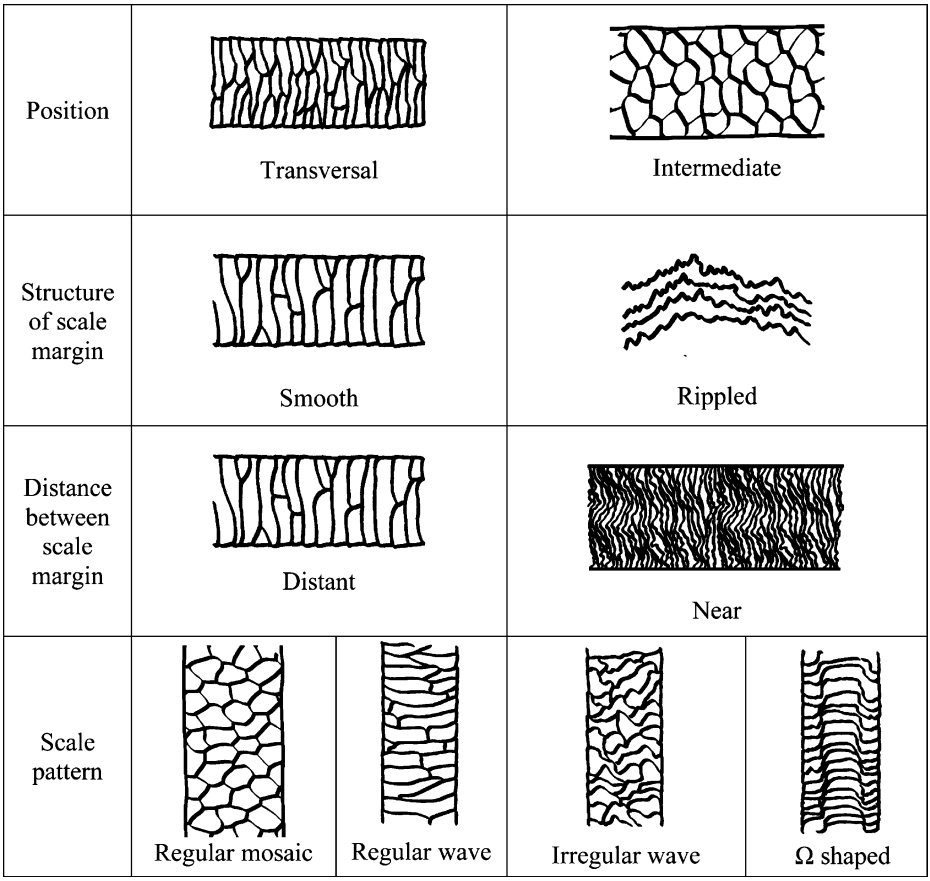


Figure 2 Cuticle classification system used in the present work.

can be distinguished from those of adults because they are thin and straight, in wild and domestic forms as well (Table 1). However the hair of young of wild species has a shiny appearance as in the adults. Adults and young of sheep showed undulated and dull hairs (Table 1). We did not observe any macroscopic differences among them.

Microscopic Hair Description

Medulla Features Mouflons and wild goats showed filled lattice and partially filled lattice structures, respectively, while domestic forms had multiseriate and uniseriate structures (Table 2 and 3). Domestic goats showed the medullary structure of the related wild species

Table 1 Macroscopic characters distinguishing hairs of wild and domestic sheep and goats.

Sheep and goats	Age class	Profile	General appearance
Wild	Adult	Undulated	Thick and shiny
	Young	Straight	Thin and shiny
Domestic	Adult and young	Straight (undulated in sheep)	Thick (thin in young) and dull

Table 2 Features and microphotographs of the medulla of *Ovis orientalis* and sheep.

Taxon	Medulla				Cortex width	Microphotograph
	Composition	Structure	Pattern	Form of the margins		
Ovis orientalis young	Multicellular	Partially filled lattice with polygonal and elongated cells	Continuous, fragmental at the base	Scalloped	Narrow, but clearly visible	
adult	Multicellular	Filled lattice with polygonal cells	Continuous, fragmental at the base	Medulla fills the entire width of the hair	Very narrow or not visible	
Sheep (young and adult)	Multicellular	Multiseriate	Continuous	Scalloped	Narrow, above all in the adults, but clearly visible	

Table 3 Features and microphotographs of the medulla of *Capra aegagrus* and goat.

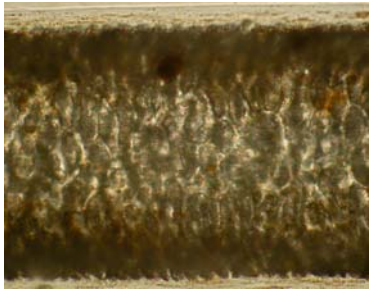
Taxon	Medulla				Cortex width	Microphotograph
	Composition	Structure	Pattern	Form of the margins		
Capra aegagrus (young and adult)	Multicellular	Partially filled lattice with elongated cells	Continuous, fragmental at the base	Scalloped	Narrow, but clearly visible	
Goat (young and adult)	Multicellular and unicellular irregular	Uniseriate and multiseriate	Continuous or fragmental	Scalloped and irregular	Very narrow but well recognizable if medulla is multicellular, wider than medulla if medulla is unicellular	

Table 4 Features and microphotographs of the cuticle of *Ovis orientalis* and sheep.

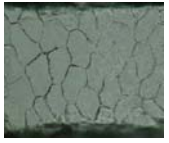
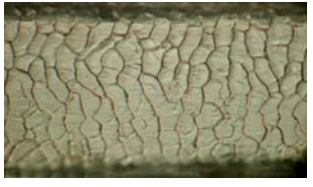
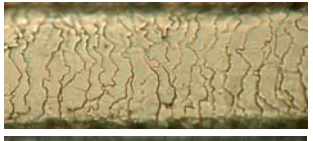
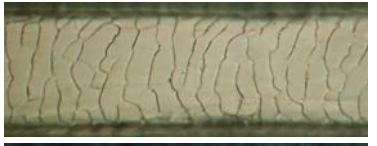
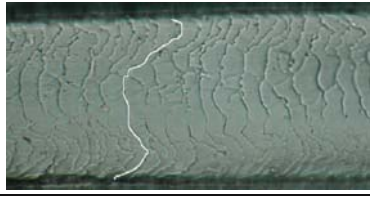
Region of the hair	*Taxon*	Scale position	Scale margin	Scale margin distance	Scale pattern	Microphotograph
LOWER SHAFT	*Ovis orientalis* adult	Intermediate	Smooth	Distant	Regular mosaic	
	young	Transversal	Smooth	Distant	Irregular wave	
	Sheep (young and adult)	Transversal	Smooth	Distant	Irregular wave	
UPPER SHAFT	*Ovis orientalis* adult	Transversal	Generally rippled	Distant	Regular wave	
	young		As in the lower shaft			
	Sheep (adult and young)	Transversal	Generally rippled	Distant	Irregular wave and "Ω" shaped	

Table 5 Features and microphotographs of the cuticle of *Capra aegagrus* and goat.

Region of the hair	*Taxon*	Scale position	Scale margin	Scale margin distance	Scale pattern	Microphotograph
LOWER SHAFT	*Capra aegagrus* young	Transversal	Smooth	Distant	Irregular wave	
	Goat (adult and young)					
UPPER SHAFT	*Capra aegagrus* adult	Transversal	Generally rippled	Distant	Regular wave and "Ω" shaped	
	Goat (adult and young)	Transversal	Smooth and rippled	Distant and near	Regular wave and "Ω" shaped	

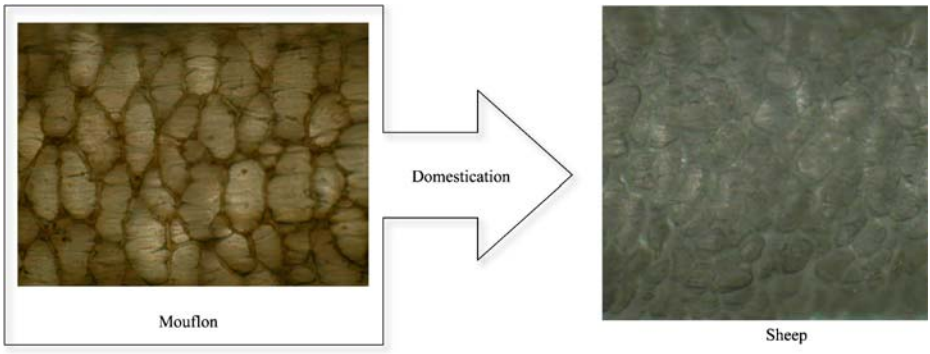


Figure 3 Domestication-related changes in medullary structure of mouflon and sheep.

in some parts of the hair, but this pattern was not clearly identifiable. The medulla features per species did not vary with age, except in mouflon (Table 2). We did not detect any differences among coat phenotypes of the Montecristo goat.

Cuticle Features We observed a clear differentiation in the cuticle features of lower and upper shaft between wild and domestic sheep (Table 4). Scale pattern was diagnostic for the identification. We could not use the cuticle to distinguish between wild and domestic goats, because of the high overlap among cuticular patterns (Table 5). Coat phenotypes of the Montecristo goat did not show any differences in the cuticle features. The cuticle was a useful tool, only in wild species, to distinguish between young from adult animals.

Discussion

Our hair samples of *Ovis orientalis* and *Capra aegagrus* came from animals living respectively in Corsica and Sardinia, and in Montecristo and Crete. Generally speaking Mediterranean islands often represent natural enclosures where goats and sheep have been

Figure 4 Domestication-related changes in medullary structure of wild and domestic goat.

kept and bred in a free ranging state since prehistory [19]. Therefore, our samples are not representative of the true wild ancestor of sheep and goats and at the same time they cannot be considered true domestic forms. They come from populations of animals that were introduced on the Mediterranean islands at an early stage of domestication and now live as wild populations [5, 20]. These populations show the morpho-phenotypic characteristics of their relative wild species [20]. Moreover *Capra aegagrus* and *Ovis orientalis* have the same medullary structure of species of the same genus, which have never been domesticated, i.e. *Capra ibex* and *Ovis canadensis* [7]. Different patterns of medullary cells might express the evolutionary history of the species [4, 30], although ecological factors almost certainly play an important role in determining hair morphology (cf. [27]).

During the domestication process important structural modifications in the architectonics of medulla were induced by artificial selection influenced by economic, cultural and aesthetic factors [5, 24]. Indeed, domestic sheep and goats have different medullary structure from their relative wild counterparts, while showing similar medullary features to each other. In general, the medulla of domestic forms seems to derive from the disgregation of the medullary structure of the related wild forms (Figs. 3 and 4). The resulting structural homogeneity in the medullary features can be interpreted as a convergence process under the same artificial selection. However in some tracts of the hair of the Saanen breed it is possible to recognize a medullary structure similar to the related wild form. On the other hand, in the Gentile breed, the medullary structure is clearly different from that of the mouflon. The Saanen breed can be considered a primitive breed of domestic goat, while the Gentile breed has undergone a long domestication process [20].

Domestic sheep have a cuticular structure different from their relative wild ancestor, while domestic goats do not show clear differences in the cuticle from their relative wild form. According to Meyer et al. [23] there is a relationship between the cuticle scale parameters and the coat structure and function. Therefore the strong artificial selection for wool production may have transformed the hair structure of the sheep but not that of the goat.

The medullary structure and the cuticular pattern as the general appearance of the hairs change with age in the wild species but not in the domestic forms. The retention of juveniles characters into adult life is one of the main effects of domestication visible in different group of mammals [5].

Acknowledgments We wish to thank curators of the museum collections, colleagues and friends who kindly supplied hair samples for this study: P. Agnelli (Natural History Museum, Zoological Section, Florence University); P. Montanaro (Italian Wildlife Institute, Bologna); P. Di Pirro, G. Lippa, S. Monti and L. Zorn. Special thanks are extended to all the staff of Servizio Scientifico of the Abruzzo Lazio and Molise National Park with particular reference to L. Gentile, R. Latini and C. Sulli for technical and logistical assistance. M. Masseti (Dept. Animal Biology and Genetics, University of Florence) gave critical and helpful suggestions to the manuscript.

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