Hair and Fur Atlas of Central European Mammals

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1 Introduction

1.1. Preludes and mission

"Nature does nothing in vain."
(Aristotle)

The Nature has an extraordinary diversity of physical, chemical and biological structures. The hair is a synapomorphic and evolutionarily successful structure of the Mammalia, displaying highly variable functions as mediation of stimuli between the skin and their environment; maintaining the homeostasis, protection against mechanical injuries, and extreme temperature; insuring water repellence, camouflage; giving shape to the body; having important role in the intra- and interspecific communication.

The substance of the mammal hair is the keratin. There are no biogenic changes in the structure of the fully developed hairs after the process of keratinisation, and the physico-chemical and histological features of the hairs can be preserved for a very long time even when affected by variable external conditions. It means for example, that the microstructure of the hair, the pattern of the cuticle, the cortex and the medulla remain fundamentally unchanged going through the digestive system of a predator; resist the rather intense chemical and heat effects of the environment, so it can be fossilized within appropriate geochemical conditions.

The trichology, as a scientific discipline, is aimed originally at studying the anatomy and physiology of human hairs; the trichomorphology has derived from this discipline, targeting the structure and function of the hairs and fur of the wild and domesticated mammals. The trichomorphological patterns can be important taxonomic characters, and the analysis of their structure can be informative also about the life strategy and behaviour, the adaptations and the phylogenetic relationships of a given species or taxonomic group.

Hairs are frequently found in the nature and sometimes represent the only life signs of the hiding and/or rare mammals. This explains why many researchers use morphological characters of hair samples to identify and survey mammals. The macrostructure of the hairs visible to the naked eye like the shape, colouration, bends, etc. are also variable, and can be specific. The microstructures of the hairs visible only by high magnification using microscope (the patterns of the medulla, cuticula, cortex, pigments) are, however, much more diverse and much more specific; therefore, these micro-characteristics are appropriate to identify mammal species, at least at a certain level (species, genus or even higher taxa).

The base of this book is the "Handbook of trichomorphology of Hungarian mammals", the former monograph of the author published in Hungarian ("A magyar emlősfauna szőrtani kézikönyve"; Tóth 2015); the extension of the scope to all Central European species and the updated use of the most recent results enriched considerably the present issue. The Central European region is delimited in the present work with the following borders: the Rheine in Germany and the western border of Austria to the west; Ukraine and Belarus to the east; the northern areas of Poland to the north; the eastern and southern Carpathians in Romania; the southeast and the northern parts of Slovenia, Croatia and Serbia to the south. The selection of the 123 terrestrial and semi-aquatic wild mammal species is based on the

official homepage of the IUCN Red List of Threatened Species, the data of Mitchell *et al.* (2009) and the checklists of mammals of the Central European countries.

The handbook provides a general overview about the history and the recent state of art of trichomorphology. The discipline has no standardised nomenclature for the micro- and macro-structures yet, so a detailed, illustrated system of patterns and nomenclature was compiled. The synonymic, multilingual citations are provided for an easier understanding of the terms on morphological patterns used in the literature, where it was possible.

The main chapter is the Hair atlas. This chapter introduces the diagnostic features of hair and fur characters of all 123 species of Central Europe in a systematic order with plentiful illustrations, and followed by the Identification key. In some cases, the units might contain additional historical, cultural, physiological or forensic concerns.

The successful identification of mammals based on the macro- and microscopic characters of hairs often requires patience, long practice and extensive reference collection of hair samples.

The trichomorphological knowledge and skill are inevitable during the application of the research methods, which are based on the identification of the hairs (e.g. hair trapping, bird-nest analysis, identification hair as food remains). The identification of mammals based on the morphological hair characters can be useful in faunistics, mapping of distribution, but can help several other fields of researches. The investigation referring to a larger set of species and specimens will make the use of trichomorphology more reliable in the subsequent taxonomic analyses. The understanding of the physiological role of the different hair structures and modifications, the access to the molecular genetic information of the hairs and the integrative use of the classic morphological and the molecular taxonomic results can support a well-founded phylogenetical and evolutionary analysis.

I hope this handbook will serve as a firm basis for both the scholars and the experts of the trichomorphology and, on the other side, will provide the enjoyment of discovering this micro-world for the inquiring naturalists and readers, too. The content of the book addressed mainly to the potential users, biologists, wildlife biologists, conservation biologists, hunters, palaeontologists, archaeologists, wildlife forensic experts. Their future work will be essential in the development of this discipline.

1.2. Historical background

The trichomorphological studies include different sub-disciplines; a brief historical – and chronological – survey provided below demonstrates the interdependence of the differently aimed and executed studies and the importance of a synthetic approach.

The discovery of the microscopic and ultra-microscopic characters and the increasing number of the examined taxa resulted in an unexpectedly large diversity of morphological features, opening a new and diverse dimension within the trichomorphology. These results provided better identification keys that help considerably field studies, faunistical surveys and diet analyses. The investigations of the trichomorphological characters also have an

important role in taxonomy. The better understanding of the physiological aspects of the adaptive patterns of the hairs usually requires both the experimental work and the modelling. The results of genetic studies using hairs may help to clarify the phylogenetic relationships and, in an integrative taxonomic approach, the determination and identification of the closely related species.

1.2.1. Trichomorphology: the identification of mammal hair

World without the microscope

The recognition of the biological importance of the mammal hairs and pelage dates back to the ancient Greek ages, to the time of Aristotle. Aristotle (384 BC–322 BC), the great Greek philosopher and polyhistor is considered, besides others, as the father of biology. In his book series on the "History of animals", there are several more speculative than scientific descriptions on the animals, but all of them reflect the wide and detailed knowledge of Aristotle about the world in his era. In the volume "On the parts of animals" (350 BCE) the mammals were determined as red-blooded, four-legged and hairy animals. As a differential feature distinguishing the mammals from the other vertebrates, Aristotle mentioned the presence or absence of the eyelashes:

"All animals that have hairs on the body have lashes on the eyelids; but birds and animals with scale-like plates, being hairless, have none". It is really the truth, only the dolphins and whales have lost their eyelashes; certain birds and reptiles have "eyelash-like" structures but these ones are modified feathers or scales around their eyes.

The next milestone is the work of Conrad Gessner (1516–1565), the famous Swiss physician and polyhistor. His great series, the "Historiae Animalium" considered the first modern zoological work, as he synthesized the ancient, medieval knowledge on the nature with his own observations, so the book is a mixture of bestiaries, gods, monsters and real animals. The first book of the series describes the "Viviparous quadrupeds", the four-footed creatures that give birth to live young, what we name today mammals. This classification, using number of feet and method of birth was borrowed from Aristotle. In certain cases, Gessner neglected the importance of having hairs and, instead, emphasized on the importance of the lifestyle. Gessner considered bats ("De Vespertilione") "half way between a bird

Fig. 1. After Gessner (1551)

Fig. 2. After Gessner (1557)

and a mouse"; despite he acknowledged "bats viviparous, feed young milk, have hair", he referred the bats as birds because they can fly (Gessner 1557).

World with the microscope – the wonder of magnification

The recognition of the microstructure of the mammal hairs required the discovery and use of the microscope, a tool that can provide the necessary magnification. The exploration of the micro-world has begun with the use of the ingenious devices developed in the seventeenth century, the hand-made microscopes. The researchers used and continuously improved their tools and entered into a miraculous world of the often invisible entities of nature. The increasing knowledge of these microscopic structures helped considerably the understanding of the anatomical, physiological and evolutionary importance of mammal skin and its appendages.

Robert Hooke (1635–1703) was an English philosopher, architect and polyhistor. His famous book, the Micrographia (1665) opened a new window on the micro world of life. He was the first to recognize the cell as the basic unit of tissues. The magnificent book includes descriptions of samples with philosophic interpretation of their function and meaning, and his detailed drawings were realistic and showed the fine proportions that he could study with his microscope with about 30× magnification. He selected different kinds of hair samples for his studies like those of the hedgehog, deer, porcupine, pig, cat, horse and human (his own head hairs); he cut the hairs, compared them with the plant tissues, and tried to understand their structures. He mentioned earlier observations, that "…many have believed and asserted the Hairs of a man's head to be hollow, and like so many small pipes perforated from end to end", but he was the first, who published his own observation of the cellular and air-filled medulla, and in certain cross-sections of the hairs he studied the "large pitch in the middle, like the pitch of an Elder".

John Ray (1627–1705) was an English naturalist known as the father of English natural history, whose personal observations, and classification of plants and animals formed the basis of the modern botany and zoology. Ray wrote a work on "tetrapodes" and reptiles (Synopsis animalium quadrupedum et serpentini generis, 1693), where he emphasized the hair as basic character of mammals.

Anthony van Leeuwenhoek (1632–1723), the Dutch scientist, is often considered the "Father of Microbiology". His "animalcules" (tiny animals) were mainly microorganisms, but he also studied many other small things and discovered the microstructures of muscle fibres, spermatozoa, bone, blood flow, bees, lice, wood, etc., and studied the hairs from the tail of an elephant in 1674. His discoveries were published in letters of the Philosophical Transactions of the Royal Society. This fundamental work belongs also to these correspondences (cited in Yates *et al.* 2010):

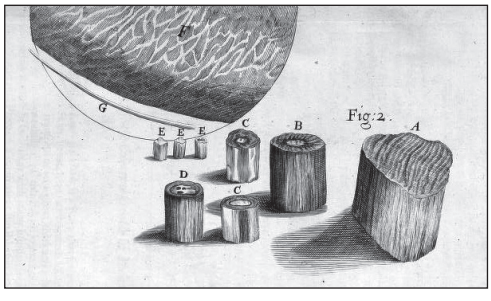


Fig. 3. After Hooke (1665)

"Having pull'd out of an Elephants-tayl a black Hair, and cut transversly from it a thin scale, I exposed it to my Microscope, which represented in the thick of that Hair about an hundred little specks somewhat whitish, and in each speck a black point, and in some few of those black points, a little hole; and this hair consisted withal of united Globuls, which yet I thought I should have found bigger in this thick hair of so bulky a Beast, than indeed they were. This Scale I keep still by me because of its curious and elegant appearance, not unlike (excepting the Colours) a Peacocks-tayl."

Carl von Linné (Carolus Linnaeus) (1707–1778) gave the name "Mammalia". The famous Swedish polyhistor published the 10th edition of Systema Naturae in 1758 and gave the diagnosis of mammals as "quadripedia, corpus pilosum, feminae viviparae, lactiferae".

David Brewster (1781–1868), the renowned Scottish physician (who was often called the "Father of the modern experimental optics") in the "A treatise on optics" (1835) and, later, John Quekett (1815–1861) English histologist and botanist in the "A practical treatise on the use of the Microscope" (1848) published diagnostic descriptions with nomenclature and fair illustrations about the microscopic structures of the hairs of bat and rodent species.

Alphonse Milne-Edwards (1835–1900), a French zoologist, described in 1867 an African rodent, the maned rat *(Lophiomys imhausi*; Cricetidae). In his extraordinarily detailed description, he illustrated the skull and the skeleton, the internal organs and the muscles, and, surprisingly, the microscopic structure of curious, spongy-structured hairs. The function of these hairs was probably obscure for him, but now, we know that this structure is an

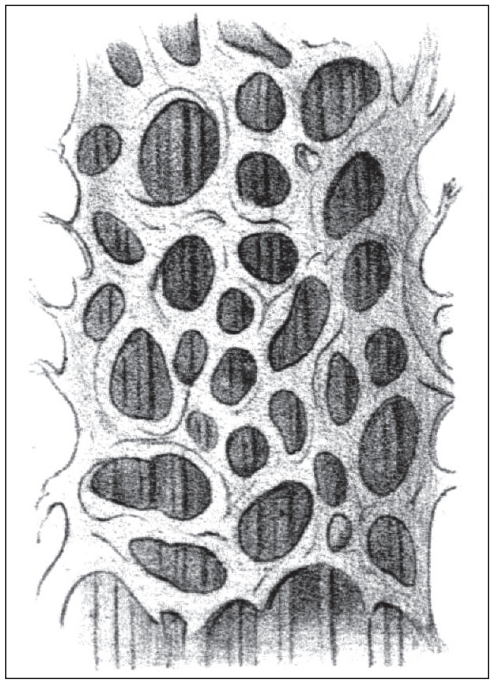


Fig. 4. After Milne-Edwards (1867)

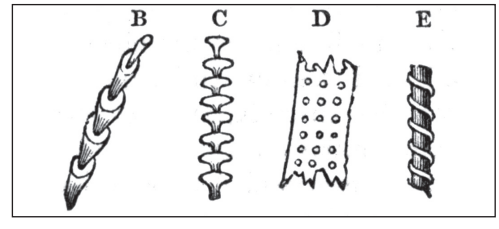


Fig. 5. After Brewster (1835)

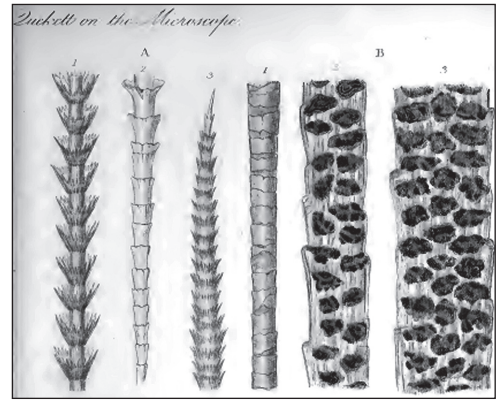


Fig. 6. After Quekett (1848)

autapomorphy of the species and the holes in the hairs accumulate the deadly poisonous sap of an Apocynaceae plant, which protects the maned rat from predators.

The embryological and anatomical investigations of the hairy skin started at the end of the eighteenth century, building up a firm base for both the morphology and the phylogeny. The first milestone in this field is the detailed treatise of Baldwin Spencer and Georgina Sweet (1899) about the ontogenesis of the hairs and spines of the Monotremata and Marsupialia species, describing the arrangement of follicles, bundles, and the different types of hairs. The forthcoming works of outstanding importance are the richly illustrated atlases of Karl Toldt (1910, 1935), Marcelle Lambert and Victor Balthazard (1910) and Hans Wilhelm Carl Friedenthal (1911). These handbooks pushed forward considerably the development of the entire discipline, displaying the immense diversity of the macroscopic and microscopic patterns of mammal hairs. It is important to mention the high quality of the illustrations: the drawings of these atlases are perfectly proportioned and detailed, and suitable for identification.

Leon Augustus Hausman (1888–1966), the American ornithologist and trichologist, was the founder of the scientific trichological research. He made the first systematization of the highly variable morphological characters and created the terminology of the discipline. His illustrations are unique, providing drawings from the visual angle of the ocular; the reader can see the same details of the hairs in the illustrations as if looking in the microscope. Using his skill and knowledge, Hausman (1920, 1924, 1930) was able to identify hairs from stomach remains.

The rapid development of the microphotography and the printing techniques during the first decades of the twentieth century promoted considerably the publication of the easily reproducible and editable, informative illustrations. The spreading of the modern electron microscopic (SEM, TEM) investigations facilitated remarkably the study and assessment of the micro-morphological patterns, thus, the basic knowledge and accuracy of the trichomorphology. In the following paragraphs, the main directions of development of trichomorphology and trichotaxonomy are shortly described.

Lochte (1938, 1954) published the first photo-microscopic images of the cuticular, medullar, cross-section and bulb characters. These "early" photographs are of excellent

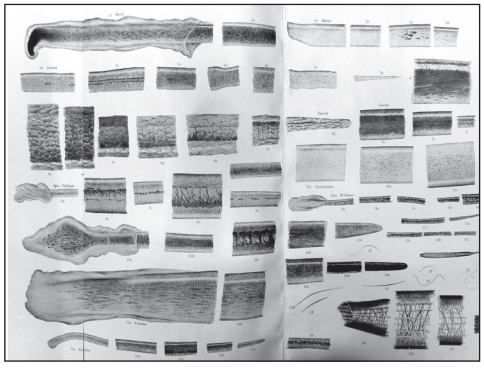


Fig. 7. After Friedenthal (1911)

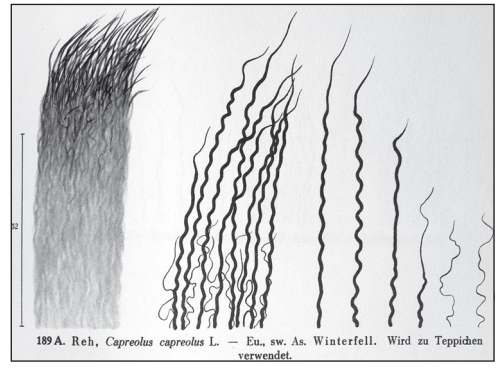


Fig. 8. After Toldt (1935)

quality; they are very informative and are appropriate for identification at species/genus level, especially with the help of the detailed descriptions and the additional explanatory drawings. Williams (1938) analysed the morphological patterns of the hairs of some mole and shrew species; Dearborn (1939) compared the hair microstructures of some North American rodents based on the cross section and medullar characteristics. Oyer (1946)

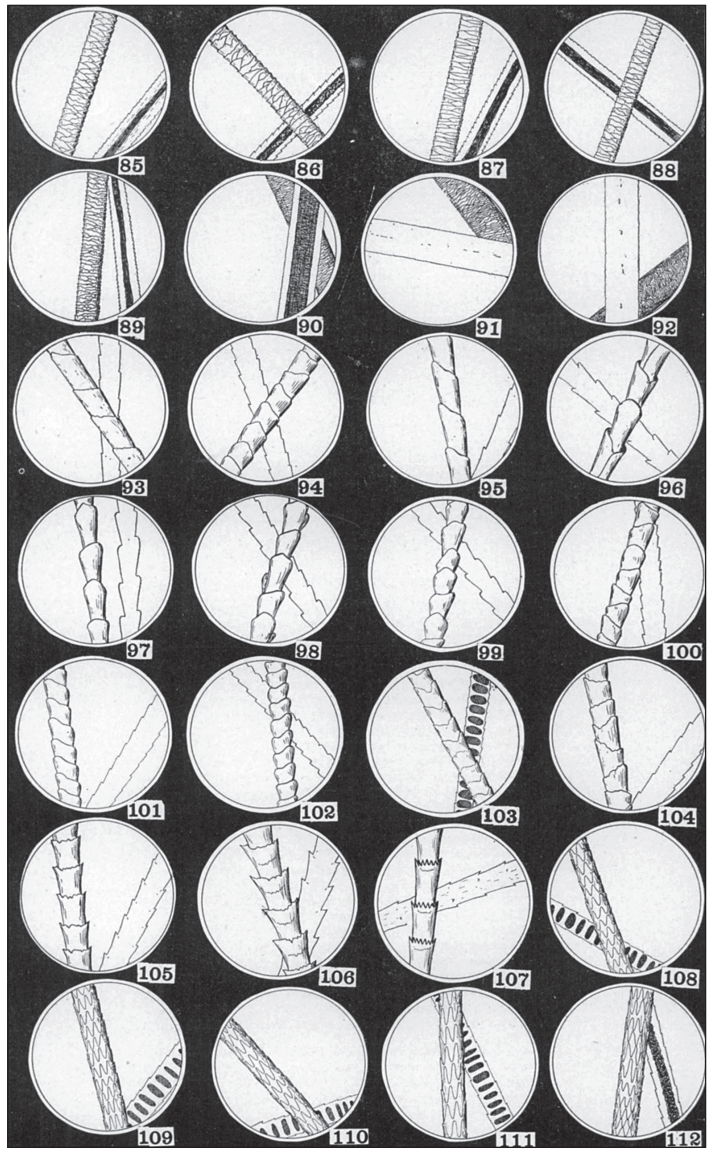


Fig. 9. After Hausman (1920)

investigated the hair structures of prey species that are "often found in the stomachs, faeces and pellets of their carnivores". His work includes a useful guide for the preparation of the hair samples and drawings of the cuticular patterns. In the same period, Williamson (1951) studied the hairs of the indigenous deer species (Cervidae) of the Ontario Lake region while Lyne and McMahon (1951) investigated the hairs of the Tasmanian monotremes and marsupials.

The first identification keys for the mammal hair characters were published by American scientists. The pioneer work was made by Mathiak (1938) who created an identification key for the hairs of the prey species of the carnivores living in Michigan. Subsequently, Mayer (1952) published the identification keys for the mammals of California, Moore *et al.* (1974) for Wyoming, and Wallis (1993) for the State of Ontario. Stains (1958) investigated the macroscopic features of certain Nearctic mammal species, pointing out the importance of the variability of the hairs in the different parts of the body as well.

The trichomorphological studies have extended to the faunas of the other continents, too. Day (1966) produced an identification key of hairs and feathers for the prey species of the two smallest European mesocarnivore species, the weasel and the ermine. Debrot (1982) selected 89 European potential prey species and provided their specific characters, considered as adequate for identification; this was the largest stock of species taken into consideration in that time. The trichomorphological characteristics of the Polish mammal fauna were described by Dziurdzik (1973), and those of the Swiss species by Keller (1981, 1984). Blazej *et al.* (1989) produced a numerical code system for the trichomorphological characters; this code system was partly applied in the computerised database of Galatík *et al.* (2011), who presented an online identification guide using SEM illustration material (http://www.furskin.cz).

The interactive online identification key of Gaubert *et al.* (2008) introduced the hair and fur characters of the taxonomically difficult and hardly identifiable *Genetta* and *Poiana* species (http://lis.snv.jussieu.fr/apps/xper2/).

The trichomorphological studies have been extended to the faunas of the other continents. Detailed works were published about the mammals of Central- and South America by Chehébar *et al.* (1989), Ibara and Sánchez-Cordero (2004), Quadros & Monteiro-Filho (2006), and Pech-Caché (2009). The hair and fur characters of the Asiatic mammals were studied and published by Koppiker (1976), Chakraborty *et al.* (1996, 2010), De (1993), De *et al.* (1998) and Lee *et al.* (2014); those of the mammals of Africa by Keogh (1985), Seiler (2010), and Taru and Backwell (2014); while Brunner and Coman (1974), Taylor (1985), and Brunner and Triggs (2002) summarised the trichological knowledge of the Australian and Tasmanian mammal fauna.

The potential of the trichomorphological characters in the taxonomic and phylogenetic analyses was firstly put into the spotlight by the works of Cole (1924), Nason (1948) and Benedict (1957) based on the hair microstructure of different bat species, although they emphasized restricted suitability of hair characters in the taxonomic evaluation. In the excellent survey of Amman *et al.* (2002) about the cuticular patterns of North American bats, the authors found significant statistical differences between the quantitative SEM data while the other pattern characters showed only a limited taxonomic value. The studies of

Homan and Genoways (1978) on the cuticular characters of Heteromyidae indicated that the groove of the cuticular scales can appear more than once during the evolution of the family, and is supposedly an ancient feature of the Heteromyidae. Hess *et al.* (1985) compared the medullar patterns of Tayassuidae and Suidae and confirmed that the hairs with radial ribs and spongy areas are diagnostic characters of the Tayassuidae.

The trichomorphology and trichotaxonomy had a prosperous period in the last 25 years; the number of high quality publications shows a considerable increase, including monographs, hair atlases and identification guides for various taxonomic groups and geographical regions, as well as publications on taxonomic and physiological analyses of the cuticular and medullar patterns. The permanence of the hair morphological characters, and, thus, the suitability of their use for various disciplines, has been experimentally proved by Quadros and Monteiro-Filho (1998) who confirmed that the putrefaction and other chemicals or certain taxidermy processes do not change the microstructure of the hairs.

The last milestone of the twentieth century, the "Bible of trichomorphology", is the fundamental work of Teerink (1991) entitled "Hair of West-European mammals: atlas and identification key". This richly illustrated work provides a detailed historical survey about the discipline and the methodological overview; the identification of hairs is helped by extensive descriptions, nomenclatural account and identification keys. This book is actually the best handbook for all workers and students of the photo-microscopic trichomorphology.

Sokolov (1982) and Chernova (2002, 2006, 2016) established a consistent methodology using chemical treatment and SEM investigation to study the fine micro-and ultrastructure of the hairs. The information content of the high quality SEM studies form an excellent base for the taxonomic, comparative anatomical and even phylogenetic studies.

1.2.2. Molecular investigations

There are more and more sophisticated methods available for molecular investigations of the hairs; their use depends on several factors like the size and quality of the samples and the reliability of the identification at different taxonomic levels.

The keratin of hairs can accumulate various chemicals, mainly in the cortex and the medulla; the analytical study of the organic and non-organic compounds of the hairs may reflect the physiological condition of the individual; or the exposition of the animals to drugs and poisons (Báez *et al.* 2000, Wennig 2000). The quality and quantity of the different kinds of food taxa can be identified by values of stable isotopes (carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), sulphur ($\delta^{34}S$)) analysed from hairs (Ben-David & Flaherty 2012, Walter *et al.* 2014).

The MALDI-TOF (Matrix Assisted Laser Desorption/Ionization) method is based on the chromatographic differences of the molecular mass of the hair proteins. The MALDI-TOF mass spectrometry seems to be an accurate and reliable method to distinguish mammals (Hollemeyer *et al.* 2007), even at species level.

The neutron activation analysis (NAA) is a particularly useful technique that can identify different elements in the hair. The hair is placed in a nuclear reactor and bombarded with high-energy neutrons. The different elements give off gamma-radiation with differ-

ent signals, which can provide the concentrations of elements in the sample. Elements, like arsenic, argon, bromine, copper, gold, manganese, silver, sodium, zinc, etc., can be identified and quantified. This method is used mainly in forensic investigations, archaeology and environmental sciences (http://ngl.cengage.com/assets/downloads/forsci_pro0000000541/4827_fun_ch3.pdf).

The molecular genetic analyses of hairs can provide important data for phylogenetic and evolutionary studies and conservation genetics. The amount of nuclear DNA in hairs is typically low compared to other tissues, as hair cells undergo dehydration and catabolic breakdown of nucleic acids and organelles during keratinisation. The requirements concerning quantitative and qualitative conditions of hair samples are often hardly fulfilled, due to the fragmentation, contamination which can make the DNA extraction more limited. Meanwhile the cornified cells of the hair contain only very low quantity of nuclear DNA, the hair bulb always contains keratinocytes, which are ideal for the extraction of nuclear DNA. One of the most frequently used molecular approach is the sequencing of mitochondrial DNA (mtDNA), in particular the mitochondrial gene COI (Cytochrome Oxidase subunit 1) (barcoding) which is appropriate in most cases for species identification, although for many mammals, the Cyt*b* (Cytochrome b gene) is more appropriate and more frequently used for identification and taxonomic studies. Other markers (such as the Control Region) or other methods, like the microsatellite genotyping, the Rad-Seq (Restriction-site associated DNA sequencing) are used for population studies or individual identifications.

The mitochondrial DNA has been extracted successfully from degraded and old hair samples, thanks to PCR and, more recently, using NGS (Next Generation Sequencing), providing data from DNA molecules preserved in fossils and museum specimens. Many protocols are now commonly used to study ancient DNA from different kinds of samples, including the hairs of mammals, found in various embedding (e.g. mineral, wood, or amber) (Shapiro & Hofreiter 2012).

In former times, the old museum specimens, treated by several harmful chemicals and exposed to disadvantageous light and heat effects, were not good source of DNA but recent technologies showed that the tough keratin of the hair shaft actually protects a significant quantity of mtDNA. Kurihara (2013) made the comparisons of extractions from fresh and burnt alum-fixed hair shafts and showed that burnt alum, which is commonly used in taxidermy, had no harmful effect on the amount of total DNA and length of the mtDNA fragments. He analysed hair samples of series of specimens of *Paguma larvata* dated from 1924 to 2011 and found that hair shafts were rich sources of mtDNA. These investigations proved that the museum specimens are rich source of DNA.

1.2.3. Range of applications of morphological hair identification

The rapid development on trichomorphology and the increasing use of its results in the other disciplines require extending the aspects of studies, to grow the number of the target taxa and use/test the different modern techniques as well as the establishment of precise morphological descriptions, identification keys and available databases. The synthetic ap-

proach reinforces the trustworthiness of the identifications which is essential for collaborative scientific studies.

Fossils – "hirsute" remains

The keratin preserved itself well and, consequently, the hairs are theoretically well-fossilized objects. There are, however, only very few fossils known containing hairs. Fossilized or preserved hairs might be in amber, coprolites, frozen remains of animals, or might appear only as their physical shape, like the impressions of the cuticula on the surface of the sediment. The taphonomic (post-mortem) degradation processes relevant to mammalian hairs mean microscopic changes resulting in from the actions of biological agents that digest and degrade hairs. The most prevalent agents responsible for the destruction of hair structure are fungi, but certain other environmental factors, keratinolytic bacteria and insects can also damage the hair structure and/or DNA content (Tridico *et al*. 2014).

Altogether, the identification of the fossil hair remains is always difficult; require the use of different methods and carefulness in the interpretation of the results, due to the lack of comparative material and to potential structural damages and deformations. The stratigraphical, palaeoecological, palaeoenvironmental knowledge may help in the proper identification of the samples, but without comparative materials, the results cannot be confirmed. The trichomorphological and genetical database both on extant and the ancient, extinct mammals would be fundamental, to confirm the identification of taxa, to interpret the function of the morphological patterns, to understand their role in the adaptation, and help to reconstruct the origin and evolution of mammal hair (Shapiro & Hofreiter 2012, Gharu & Trevedi 2016).

The *Morganucodon* (Therapsida, Cynodontia) was discovered in limestone crevice fillings in Wales, aged 200 million years; these tiny mammals were most probably insectivores. There is no data about the microstructure (medullar and cuticular patterns) of these Mesozoic hair samples, but, supposedly muscles, nerves and sebaceous gland could be attached to them on the basis of the fine structure of the fossils (Benton 1991, Gould 1993).

The oldest hairy mammal fossil remains are known from Mesozoic, Jurassic and lower Cretaceous ages, from China and Spain. The ancient, extinct species represent a diverse fauna with different lifestyles, early adaptations to the diverse habitats in the shadow of the late dinosaurs. Their coats appear to be heterogeneous, dense, with differentiated, heteronomous hairs, like guard and under hairs. *Castorocauda lutrasimilis* was a supposedly semi-aquatic mammal, aged around 164 million years, and lived in Mongolia, China (Yi *et al*. 2006). *Volaticotherium antiquum* seems to be the earliest known flying mammal aged 135–160 million years old, it had fur-covered skin membranes that stretched between the fore and hind limbs of the creature; this species is comparable in size and shape to modern-day flying squirrels (Meng *et al*. 2006). *Eomaia scansoria* was a small Eutherian-like animal, ca 125 million years old, it had scansorial skeletal adaptations; hairs are preserved as carbonized filaments and impressions around most of the body (Yi *et al.* 2002). *Spinolestes xenarthrosus* seems to be a mixture of an armadillo and a hedgehog, aged 127 million years, and was discovered in Spain. The mineralized fossils conserved perfectly the external ear lobe, soft tissues of the liver, lung and diaphragm, dermal scutes and individual hair fol-

licles and bulbs, as well as the microstructure of individual hair shafts, could be identified using a scanning electron microscope (Martin *et al.* 2015).

The Messel pit is an Eocene assemblage of fossils conserved in oil-shale bed, 47–50 million years old. This material of finds is often mentioned as the "Pompeii of the palaeontology" or a "Konservat-Lagerstatte" as Messel has yielded abundant fossils with soft tissue preservation including hairs, feathers, and stomach and intestine contents. The *Clostridia*, an anaerobic heterotrophic bacterium, could have been responsible for the mapping of the soft tissues. They were petrified (turned to mineral) by their own CO_2 production combined with precipitated Fe (iron) from nearby weathered rocks. This fauna tells us about the feeding habits, the ecology and the environment of the Messel floras and faunas. The well-preserved and intact remnants of mammals represent ca 2% of the entire findings. *Pholidocercus hassiacus* was a primitive spiny insectivore with scaled front, head and tail; *Macrocanion tupaiodon* appeared as an early long-tailed hedgehog without spikes; *Ailuravus macrurus* was a squirrel-like ancient rodent, while *Eomanis waldi* was a kind of pangolin, having hair remnants on the entire body surface except the tail (Hoffmann 2000).

The phylogenetic relationship of the Pleistocene mammoth *(Mammuthus primigenius*), the Indian elephant (*Elephas maximus*) and the African elephant (*Loxodonta africana*) have been tested by morphological (including trichomorphological), serological, histological and immunological methods. The results showed the closer relationship between the mammoth and the Indian elephant (Valente 1983, Mayer *et al*. 2017).

There are successful DNA extractions from the hairs of the fossils of the extinct steppe bison *(Bison priscus*) dated as 64 800 years old (Zazula *et al*. 2009), and from the 9800 years old remnants of the Nevada sheep (*Ovis canadensis nelsoni*) (Bonnichsen *et al.* 2001).

Skeleton and hair remains of the Siberian cave lions (*Panthera spelaea)* were found from frozen soil in Chukotka, Russia. The morphological features, the mtDNA and the isotope study on the hair samples were discussed by Chernova *et al*. (2016); they pointed out that the hairs of the cave lion were similar but not identical to those of the present-day lion, having different colouration, a thicker and denser undercoat, and slightly higher scales than in the living relatives. Supposedly, the differences may be due to adaptations of cave lions to the harsh climatic and environmental conditions of the Pleistocene Ice Ages.

Coprolites

Coprolites are fossilised faeces of mammals, and regurgitalites are fossil pellets of raptor birds. These fossils can include hairs of prey mammals that might be identifiable. The extraction and preservation of the embedded hair samples require special opening methods, depending on the chemical composition of the fossil.

A rich accumulation of fossil excrements from the Late Palaeocene aged 60 million years beds of Inner Mongolia in China contained mammalian carnivore coprolites and raptorial bird regurgitalites. The fossil hairs occurred as impressions in the calcareous matrix and the shape of the cuticular scale patterns were SEM analysed. Hairs from at least four mammalian taxa, most notably the multituberculate *Lambdopsalis bulla*, have been identified (Meng & Wyss 1997).

Pleistocene aged (195,000–257,000 years ago) coprolites were found in the latrines of South African Brown hyena (*Parahyaena brunnea*). The fossils highlight that the latrine-making behaviour observed in extant *P. brunnea* is an ancient behaviour of this species. The hairs from the coprolites were identified as prey of the hyena and included warthog, zebra, impala, kudu and humans (Berger *et al.* 2009, Taru & Blackwell 2009).

Mylodon darwinii is an extinct ground sloth representing the only species of Mylodontidae; it lived in Patagonia (Argentina and Chile) 10–13,000 years ago. The well-preserved remains including the skin and coprolites were discovered in very good condition thanks to the extreme cold and stable conditions in the caves where they were found. Clack *et al.* (2015) could separate hair samples from a coprolite believed to belong to a Darwin's ground sloth and amplified 12S and 16S rDNA sequences. The sequences obtained from the coprolitic hairs matched well with the sequences of the hair remains of *M. darwinii* originating from the skin remains.

These studies proved that hairs selected from the coprolites might be effective sources of ancient DNA.

Amber

The mammal hair seems to be rare in amber but there are a few very interesting assemblages of hairs, arthropods, and plants. The exceptional preservation circumstances allow to study of the cuticular structure of these hairs.

The oldest mammalian hairs embedded in amber were discovered in association with an empty puparium (Diptera) in 100-million year-old (Early Cretaceous) amber from France (Vullo *et al.* 2010).

Poinar (1988) analysed the hairs from amber of the lower Miocene to upper Eocene that contained fragments of hair without cuticula but with fragmented medulla and bulb. This information were insufficient for the identification of the species but the amber contained two fossilized ectoparasites that feed on rodents, which supported the idea that these hairs belong to a rodent species.

Peñalver and Grimaldi (2006) published rich assemblages of mammal hairs and blood-feeding midges (mainly *Lutzomya* spp.) in other Dominican ambers. The fossil hairs were usually not identifiable but comparisons were made between the cuticular patterns of fossil and potential recent relatives inhabiting this region from the Miocene to the Holocene. Based on this, the authors proposed that a part of the hairs might belong to a small mammal endemic to Antilles, *Nesophontes,* which is an extinct solenodontid genus of the Caribbean.

Mummies and clothing

Humans are using the furs as clothes for a long time; the first archaeological finding is dated back to several thousand years. The ancient burial sites and the clothes of the mummies often contain hairs and feathers; the studies of their morphological characters can help identify the domesticated and wild animals that the human tribes lived with.

There are exceptionally well-preserved 4–5,000 years old mummies found on the Kagamil islands in Alaska which were buried with their clothes and jewels. The study of the clothes revealed that the Kagamils used the fur of seals (Phocidae), otters (*Lontra* and *Enhydra* species), bears (*Ursus*), foxes (*Alopex* and/or *Vulpes*), and caribou (*Rangifer tarandus*) in the burial rituals (Dove & Peurach 2002). The Tyrolean Iceman, the oldest known natural European human mummy is 5,300 years old and was discovered in South Tyrol in the Ötztaler Alps in 1991. The clothes of Iceman were made of furs of domestic animals (goats, sheep, and cows), deers and bears according to mtDNA analyses (O'Sullivan *et al.* 2016).

Taxonomy, phylogenetics

A phylogenetic tree or evolutionary tree is a branching diagram showing the inferred evolutionary relationships among various biological species or other higher taxonomic entities. The phylogeny is based on shared morphological and/or genetic characters. The morphological characters of the mammal hairs and pelage can provide relevant information to such analysis.

The phylogenetic relationships of the giant panda (*Ailuropoda melanoleuca*) and the red panda (*Ailurus fulgens*) have long been disputed until molecular, genetic and trichotaxonomic analyses proved in parallel that the giant panda is closely allied and belong to the bears (Ursidae) while the red panda is related to the Procyonidae and Mustelidae) (Dziurdzik & Nowogrodzka-Zagórska 1991, Sato *et al.* 2009).

An integrated taxonomic revision of the Viverridae genus *Paradoxurus* (palm civets) was carried out by Veron *et al.* (2015) based on molecular taxonomic (mitochondrial and nuclear genes) and classic morphological features (e.g. teeth, fur colouration, and hair characters). The results supported the division of the formerly common species *Paradoxurus hermaphroditus* into three distinct species, *P. hermaphroditus*, *P. musangus* and *P. philippinensis*.

Forensic research

The morphological study and the molecular analysis of hairs both can be useful in forensic investigations, as the mtDNA sequencing provides information about the genotype while the microscopic examination evaluates physical characteristics and provides information about the phenotype. It is important to note that microscopy is not a "screening test" and mtDNA analysis is not a "confirmatory test" (Houck & Budowle 2002) but their combination can help the identification providing different and independent kinds of information about the same species. The forensic genetic methods use three main techniques: the DNA nucleotide sequencing, the SNP (single nucleotide polymorphism) typing, and the microsatellite genotyping. The results of these analyses might be suitable for the identification of the species, the population, the geographical origin, or even the individual identity, depending on the type, quality, and quantity of samples and the applied methods (Ogden *et al*. 2009).

Criminology – The first case of a murder said to have involved the investigation of hairs found at the scene took place in Paris in 1847; then the next reported use of forensic hu-

man-hair comparison was by Rudolf Virchow in 1861 (cited in Bisbing 1982). The classic book on forensic science "The Principles and Practice of Medical Jurisprudence" by Alfred Swaine Taylor and Thomas Stevenson (1883) contains a chapter on using hair in forensic investigations. This chapter includes drawings of various parts of human hairs under magnification. The comprehensive study of the human and animal hairs entitled as "Le Poil de l'Homme et des Animaux" (The Hair of Man and Animals) was published by the French forensic scientists Victor Balthazard and Marcelle Lambert in 1910.

Wildlife forensic – The increasing destruction of natural habitats and the senseless and unstoppable destruction of wildlife are attendant consequence of the human activity of the modern ages. The illegal hunting of protected species for their fur, claws, horns and other organs, or simply for their meat, runs in such an extent that it can lead to their extinction. The structure of the furs entered into the illegal trade are often intentionally modified by distorting methods (cutting, stretching/racking, use of various chemicals); therefore, the morphological studies are most often insufficient for the species level identification, so combined molecular and morphological methods required.

The wildlife forensic is an applied science that synthesise the methodology, technology of conservation genetic and forensic genetic researches, with the aim to enforce the protection of endangered species, fight again the illegal trade and poaching, and promote the functioning of the international (the CITES – *Convention on International Trade in Endangered Species of Wild Fauna and Flora*) and national legislation (Ogden *et al*. 2009, Cooper & Cooper 2013).

Asian elephants (*Elephas maximus*) are protected under Appendix I of CITES, while populations of African elephants (*Loxodonta africana*) are protected under Appendix I and II. The Asian elephant is also listed as endangered on the US Endangered Species Act (ESA), while the African elephant is listed as threatened. In contrast, giraffes (*Giraffa camelopardalis*) are not protected under CITES or the ESA. Overall, commercial trade in elephant parts is highly regulated and forensic methods for distinguishing elephant and giraffe tail hairs are critical to wildlife enforcement efforts. The thick, coarse, black tail hairs of elephants (African and Asian) and of giraffes are easily confused macroscopically. While elephant tail hairs are generally thicker than those of giraffe, the size of an individual hair alone cannot be used to distinguish these species. Yates *et al.* (2010) presented methods for distinguishing tail hairs of African and Asian elephants and giraffes. Such hairs are commonly used to manufacture jewellery artefacts that are often sold illegally in the international wildlife trade. The authors proved that tail hairs from those three species can be identified based on differences in cross-sectional shape, pigment placement and pigment density as well.

The hunting of the marine mammals was an essential part of the life of the ancient tribes, as the fur and meat of these animals was indispensable for their life. Later, the fur trade (seals, mesocarnivores, etc.) has become a massive killing of hundreds of thousands of animals yearly, pushing several formerly abundant species close to the extinction. The Sea mink (*Neovison macrodon*) was probably the first mammal species that was extirpated by the fur hunters; it became extinct in the last decade of the nineteenth century (Helgen & Turvey, 2016).

Recens hairs – "mammals tracked by hairs on the spot"

The trichomorphological knowledge on the recent mammal fauna is useful for the field researchers as the identification of the hair samples collected in the field are proofs of the presence of the given species, in the given studied area and period. The random collecting of hairs may also produce important information about the presence and distribution of species but the systematic and regular hair collecting provides hair samples of better quality and sufficient amount for a more detailed analysis and more reliable identifications. The non-invasive methods are fundamental for the study of the rare and protected species, and can be applied in the faunistical, nature conservation, wildlife management and ecological studies; and the hair samples obtained from the field can be adequate for DNA extraction (Kendall & McKelvey 2008). The potential advantage of hair collecting is that the plucked hairs usually have the bulbs contain more cells with DNA than shed hairs; the potential disadvantage might be the cross-contamination between individuals because multiple individuals can be sampled before hairs are recovered from the snare (Beja-Pereira *et al*. 2009).

The successful identification of these hair samples requires the presence of suitable atlases and identification keys and, often also, a reference collection concerning on the given taxa and/or geographic area. The literature has become very rich on this topic in the last decades; the next paragraph is only a brief survey about the main fields of application.

Hair as life sign

Hairs can be found in the field due to the seasonal or occasional moulting, and the spontaneous loss of hairs; the scratching and rubbing behaviours produce often a remarkable quantity of hairs. Hairs can be spread over by the wind, the rain or entangled on smaller or larger bundles on branches of shrubs usually along the regular pathways of the animals, or accumulate on resting places.

Hair as food remain

The diet studies are usually based on the study of the remains of the digested food, including hair samples from faeces, stomach remnants and pellets (Day 1966). The knowledge obtained from such studies is essential for biological and ecological research as the stock of prey species can be identified, and the structure and the seasonal changes of the food chain can be clarified in this way. The microstructures of hairs are well preserved during the digestion process but may be contaminated, broken or entangled; the shape of the bulbs can be distorted, so the identification of the hairs originating from such sources needs experience and practice.

Hairs by trapping

The hair collecting methods, called as "hair trap", "hair snare", or "hair tube", combine the trapping, the tracking experience and some trichomorphological knowledge. The main target of the method is to gain hairs from the targeted mammals. Hair samples will be trapped

on an adhesive or spiky surface when the animal rub on it or go through the hair-collecting instrument; then these hairs can be identified. The structure of hair-collecting instruments depends on the size, behaviour, diet, habitat of the target taxa but the crucial and expected requirement is that they do not change the natural behaviour of the animals. Thus, this method provides hairs and data for distribution, ecology, genetics, conservation and population studies. The effectiveness of this method has been confirmed by synchronous camera trapping surveys and live-trapping investigations.

The hair trapping method has been started using a PVC tube with an adhesive inner surface in which the hairs get trapped; this type of trap was done for a study of two tree-climbing marsupials, the insectivorous Brown Antechinus (*Antechinus stuartii*) and the Sugar Glider (*Petaurus breviceps*), and the hairs were fairly well-preserved and suitable for documenting the presence and the distribution of the species (Suckling 1978). This simple, effective and inexpensive method was then rapidly distributed and utilised in the field studies and, several methodological and synthetic works provide detailed information about the use and careful planning of these samplings.

The distribution patterns and the genetic variability of the populations of the endangered Northern Hairy-nosed Wombat (*Lasiorhinus krefftii*) were studied by collecting and analysing the hairs trapped at the openings of their tunnels. These hair samples were suitable for DNA extraction; microsatellite markers analyses provided the identification of the individuals (Sloane *et al.* 2000).

MacDaniel *et al.* (2000) distinguished the sympatrically occurring Canada Lynx (*Lynx canadensis*) and the Bobcat (*Lynx rufus*) by the DNA samples extracted from the bulbs of hairs collected by hair snares. The estimation of the population size and the genetic variability of Grizzly Bear (*Ursus arctos horribilis*) (Mowat & Strobeck 2000) and American Marten (*Martes americana*) (Mowat & Paetkau 2002) populations were evaluated by using hair-trapped samples.

Hairs from bird nests

The "Bird nest analysis" method (Tóth 2003, 2008) is based on the nest constructing activity of birds which frequently use mammal hairs for building and lining their nests. These birds (like certain species of tits, finches, etc.) collect hairs from their surroundings, visiting the hiding, resting sites, scratching and rubbing places used by mammals, finding hairs and tufts hanging on shrubs or barks or spread by the wind, sometimes also taking hairs from corpses, or attack and pluck directly on the mammals. The hairs can be collected from the nests after the breeding season. The identification of hairs collected from the bird nests can provide a detailed picture about the mammal fauna of the given area, including also the temporary presence of migrating ones; there might be hairs of the secondary nesting species (like Gliridae) or even the hairs of the predators raiding the nest. The method proved to be successful both in natural and urban environment (Tóth & Heltai 2010, Ondrusova & Adamík 2013).

2 Evolution of the mammal hair and the adaptive patterns

2.1. Evolution of the mammal hairs

The study of ancient hair can assist in establishing the origin of hairs in mammals. Most of the early mammal fossils were preserved with a so-called "halo of fossil fur", a print and/or very small fragments of hairs. There are several theories about the emergence and evolution of the different kinds of hairs might be supported or rejected by the newest fossils and the results of the modern methods. The lack of the informative fossil evidence, or surviving proto-mammals or any primitive hair-like organs prevent a comparison with hairs of extent taxa. The most promising opportunity within such conditions is the histological study of ontogeny of the recently living descendants. However, the emergence of hair is a crucial innovation in the amniote lineage leading to mammals. The hairy skin of the mammals (Mammalia) is a multifunctional organ, having important role in the protection against the heat and cold and the dangerous radiation of the sunshine; it is an insulating organ, which is waterproof and protective from mechanical effects, and is able to perceive and transmit stimuli, helps in the sexual selection and in the camouflage. The macro- and microstructural modifications promote the evolutionary adaptations of the animals. There are only a few, generally accepted but well supported theories the evolution of the mammal hairs, as follows.

- Endothermy appeared earlier in the reptile-like ancestors of birds and mammals than the insulating function of the feathers and the fur (Meng & Wyss 1997, Quick 2013).
- The vibrissae, most probably, emerged earlier than body hairs, and originated from mechanoreceptors; the body hairs were the derivatives of the vibrissae. The first hair-like outgrowing mechanoreceptors might have appeared between the (partly) overlapping horny scales of the *Cotylosaurus* sauropods, and the sensory hairs of the mammals could have developed from these mechanoreceptive hairs in the Cynodontia–Theria evolutionary lineage. Surprisingly, the sensory hairs are absent in the Cynodontia–Prototheria lineage, and humans have completely lost the vibrissae but not the sensory function of body hairs. The vibrissae reflect, therefore, the primitive condition and might have appeared long before an insulative pelage had evolved. Supposedly the dense body hair covering became advantageous with the smaller body size, as the nocturnal lifestyle required to keep a constant, higher metabolism (Pocock 1914, Lyne 1959, Maderson 1972, Bennett & Ruben 1986, Maderson 2003). Chernova (2006) has outlined a logical and well-supported process of diversification of the different hair types: a hypothetical ancestral hair gave rise to two types, the vibrissae with blood sinuses connected with sensory nerves and the hairs, without them. The evolution of vibrissae resulted in two further types, the "active" and "passive" vibrissae, depending on if have or not circular blood sinus. The hairs evolved into cover hairs (spines, bristles, and guard hairs) and downy hairs.
- The subsequent differentiation of the mechanoreceptor cells could lead to the formation of the hair follicles (dermal papillae). The evolutionary importance of these organs is that they regulate and maintain the differentiation process of the keratinisation throughout the life under hormonal control (Gould 1993). A main difference exists during morphogenesis of scales in lepidosaurs and in crocodilians and in avian scuta, feathers or

hairs; only in the latter three is the placode individualized, followed by the formation of a dermal papilla (Dhouailly 2009).

– The origin of the regular body hairs is explained by two different hypotheses. The scaling hypothesis states that the hairs came from a scaled reptilian integument (Spearman 1964, Maderson 1972, Alibardi 2004). These "sensory protohairs" might then have evolved secondarily into an insulative pelage as mammals became endothermic. The body hair still retains a sensory function in all modern mammals (Bergman 2004). The other alternative is the glandular hypothesis of hair evolution (Stenn *et al.* 2007, Dhouailly 2009, Alibardi 2012). This hypothesis postulates that, after the dichotomy of Amniota (ca 310 million years ago), the Synapsida branch preserved the glandulous skin, which is characterised by the presence of dermal glands and filiform hair-like appendages of the dermal papillae, while the Sauropsida branch almost completely lost the glandulous features of the skin. Thus, the hairs built up from α-keratin might have derived from the amphibian glandulous skin while the feathers of the birds originated directly from the β-keratin horn-scales of the Sauropoda ancestors, in a later period of the evolution.
– There are two theories explaining the evolution of the protecting-defending spines, too. The first hypothesis states that the spines are modified hairs, and are formed by the fusion of several follicles so that developing hairs become later enlarged and produce spines; in ontogeny, spines are formed as a result of heterochrony of a group of follicles (Sokolov & Chernova 2006). The second hypothesis states that spines precede hairs in ontogeny and evolution of hairs derived from the smaller size of later generations of spine bulbs in Echidnas; it appears that the size of the dermal papilla determines the output of the epidermal derivative and that large papillae give rise to spines or to large hairs, while the remaining small follicles growing into hairs (Alibardi & Rogers 2015).
– The structure of the vertebrate integument is predominantly defined by the presence or absence of the two keratin types (α-keratin and β-keratin), or their rate in the skin and appendages. Molecular investigations highlighted that the vertebrate skin appendages are made of keratins produced by multigene families, and while α-keratins are found in all vertebrates, the β-keratin can be found exclusively in sauropsids (reptiles and birds). Moreover, the cystein-rich α-keratins are not restricted to mammals, so supposedly the last common ancestor of all extant amniotes had it too, thus, the classic notion of 'hard' and 'soft' keratins/keratinized tissues has been refined by the realization that corneous tissues may consist on either α- or β-keratin proteins (Maderson 2003, Eckhart *et al.* 2008, Greenwold *et al.* 2014). Other studies indicate that in the medulla of hairs, the keratinocytes express both keratins typical of hard-cornifying epithelia (i.e. follicular or trichocytic keratins) as well as keratins typical of soft-cornifying epithelia (i.e. interfollicular epidermal keratins) (Bragulla & Homberger 2009). So, the structure of the hairs of the recent mammals seems to be unique and complex, having (like scales of pangolins) both the β-keratin and α-keratin in all three layers of the hair, the medulla, the cortex and the cuticula (Spearman 1966, Bragulla & Homberger 2009, Hill *et al.* 2010, Alibardi 2012, Wang *et al.* 2015).

– The independent co-evolution of the successful Wnt/β-catenin pathway gave rise to protruding keratinized filaments both in mammals and in the birds. The β-catenin is very important in the development of the hairs, as stem cells of the skin require β-catenin signalling in order to differentiate into hair follicles. It regulates the production of certain proteins and fixes the complex structure of the keratinocytes (Dhouailly 2009, Alibardi 2012).

2.2. Adaptive patterns

The evolution and function of the different trichomorphological patterns is primarily explained by physical laws and knowledge on the life strategy and behaviour of the animals. These processes, however, cannot be simply generalised as the direct connection between the presence or absence of the "advantageous" morphological characters and the life strategy or habitat (or the phylogenetic relations) of species is often missing or hardly detectable. It seems more probable that certain trichomorphological patterns could appear more than once, independently and spontaneously during the evolution of mammals. The structural and functional modifications of the hairs make possible the adaptation and survival of the mammal species in very different habitats and physical conditions, and the understanding of these modifications is inevitable for the study of the adaptive evolution.

There are two well-known climate-dependent rules which recognise correlation between the parameters of the hair and fur structure (density, length and thickness) and colouration, and the climatic factors. Both rules are typically gradual (referring to the climate zones of the Earth) and applicable for the widely distributed taxa but with numerous exceptions.

The "Rensch's hair rule" states that the adaptation to a cooler climate require longer and thicker hairs in denser fur for a better thermal insulation; therefore the mammal species living in the cold zones have such pelage. In the cold and temperate zones, the winter fur is much denser and the hairs are significantly longer and thicker than in the summer pelage, the medulla is broader, containing large air inclusions, and the frequent undulating structure also increases the insulative capacity. The size of the cuticular scales and the cortex may also be connected with the heat insulation, as the broader and more keratinised scales with relatively larger surface and the thicker cortex provide stronger pillars to the thinner hairs, too (Meyer *et al.* 2000).

Gloger (1883, in Zink & Remsen 1986) recognised that the colours of the feathers are related to climatic factors: they are darker in humid, warmer habitats while lighter in cooler, drier habitats. Against the numerous exceptions, the "Gloger's rule" proved to be true in relation of the endotherm vertebrates, the birds and the mammals, as the climate has an influence on the quantity and type of the pigments providing the colours of the feathers and hairs.

Game of the evolution – playsuits: concealment, camouflage, mimicry, attraction, aposematism, sexual dimorphism

The colouration of mammals is informative although they are much less colourful than many other groups of animals, including vertebrates. The basic colours of the hairs and the fur are the brown, red, white and black, with several shades, and a remarkable number of species possess characteristic, often striking, patterns. They might reflect the sexual dimorphism, the fitness, and the age of the specimen but the functions of these patterns are not always clear and are possibly multilateral, and the generalised interpretations have numerous exceptions. Altogether, the main functions of colourations and markings of the pelage are concealment, communication, and regulation of physiological processes. Their evolutionary and ethological significance is indisputable and diagnostic tool for identifying mammals.

Both hiding and/or warning patterns vary on a large scale. Shading in the environment can be advantageous to avoid attacks and predation and stalk the prey (like mammals with spotted and striped fur live in forests, high undergrowth or canopy). The cryptic colourations can be achieved through mechanism including background matching, disruptive colouration, and countershading. Advertising the unprofitability (e.g. having armoured defences, like spines, odours) scare the predators. The information content of aposematic patterns is very diverse: might help to avoid the attack of the visually oriented predators (e.g. masquerade: the masked face, the contrasted stripes around the eyes, in several species of Viverridae, Mustelidae, and Procyonidae); advantageous and informative during territorial fights; reflects the motivational state, the courtship intention (Ortolani 1998, Caro 2009, Santana *et al*. 2011, Caro *et al*. 2012), etc.

The hiding is often helped by the marbled pattern, which is based on the "Moiré-effect": the shifting of the hairs of different length, colour and structure produces this effect which is typical of certain canids and felids and some rodents; the intensity of the Moiré-effect is changing with the movement of the animals.

The possible role of the hair characters in the identification of the age, fitness, and condition of the individuals is still poorly investigated but observations unambiguously show that certain macro- and microscopic features of the fur refer to these physiological conditions and states (e.g. the texture, the changing reflection of the cuticular scales, the atypical moulting/shedding, the greying, etc). The gradual development of the adult hairs and fur during the moulting/shedding cycles gives the opportunity to distinguish the age-groups within the populations. The appearance of pigmented patches on the surface of the skin is typical during the maturation of the follicles, before the hatching of the hair and the shape and size of these patches is connected with the density of the fur and the intensity of the shedding (Stein 1960). The development of the macro- and microstructural characteristics of the hairs comes to the end until the maturity and the adult fur patterns (spotted, banded, manes, etc.) are fixed.

Alfred Russel Wallace (1823–1913), a British naturalist and explorer, summarized the knowledge and theories of his age and categorized the types and roles of colours in his publication "The colors of animals and plants" (1877). Sir Edward Bagnall Poulton (1856–1943), a British evolutionary biologist, Darwinist, published the large review on animal

colouration entitled: "The colours of animals, their meaning and use, especially considered in the case of insects" (1890). He lead and defined the terms aposematism' as warning colouration; used the 'protective colouration' for the camouflage; surveyed in detail several examples of the mimicry and the sexual dimorphism.

Hairlessness and the sensory hairs (vibrissae)

The hairlessness is always a secondary phenomenon in the modern mammals that is strongly connected with adaptive evolution. It is important to note that certain parts of the body remain sparsely hairy in small patches (lips, genital organs, bends, back) or, at least, some sensory and/or underhairs remain. The degree of hairlessness is also variable within mammals, with strongly reduced hair cover are, for instance, the Hairless Bat (*Cheiromeles torquatus*), all elephants (Elephantidae) and hippos (Hippopotamidae), the Walrus (*Odobenus rosmarus*), and the armadillos (Dasypodidae); the Cetacea are almost hairless, as well as humans.

Vibrissae have a wide range of functional roles like, for example, object detection, fine texture discrimination, hydrodynamic or air drift perception; vibrissae contribute to the existence of mammals in large variety of environments. The presence of the vibrissae is restricted mainly to the face (Pocock 1914) but several species like bats, hyraxes, manatees, dugongs, are exceptions (Sarko *et al*. 2011).

Possibly the most curious of hairless mammal is the fossorial Naked Mole-rat (*Heterocephalus glaber*) which has only very few tactile hairs, most of them on the head, and a few covering the body.

The green mammals are not green (coloured)

The green-coloured mammal species has no green pigments or green physical colours; their greenness comes from the green algae and cyanobacteria, which live occasionally on or sometimes inside their hairs.

The pelage of the tropical southeast Asiatic, fruit-feeding flying fox species, the Pallas's Tube-nosed Bat (*Nyctimene cephalotes*) often changes into green due to the algae living in the fur of the animal in the rainy seasons.

The rough-coated, water-repellent skin of the sloths (Folivora) protects the slowly climbing animals from the mechanical injuries in the dense and often spiky branches and foliage of the rainforests. The sloth hair is extremely specialized for living in a wet tropical environment.

The guard hairs grow in a direction opposite from that of other mammals, as their hairs grow away from the extremities to the body to provide protection while they hang upside down. Moreover, this dense, coarse fur is the host of several commensalistic, mutualistic and parasitic creatures, including caterpillars of tineid micromoths, cockroaches, nematodes, diatoms and other different algae, cyanobacteria and microfungi. A part of them are specific to the sloth fur and appear as symbiotic organisms (Higginbotham *et al.* 2012); while certain arthropods among them are vectors of arthropod-borne viruses (Gilmore *et al*. 2001). The algae and the microscopic fungi live on the surfaces of the cuticular scales

on the growing hair, but will breed in the partly deteriorated cortex and the medulla of the fully developed hairs; this modified section of the cortex appears as a straggly web of hyphae using microscope. Other characteristic feature of the guard hairs of the sloths is the flattened and deeply grooved medial section; these grooves can drain the rain, which could be abundant in the rainforests.

The fur of the Polar Bear (*Ursus maritimus*) consists of fine, dense, insulating hairs; each hair is pigment-free and transparent; the medulla is narrow, there are smaller-larger air-sacs between the medullar cells; so the hair scatters and reflects visible light, much like what happens with ice and snow. Optical studies of the Polar Bear fur proved that the keratin of hairs has UV-absorbing properties (Koon 1998).

Polar Bears look usually white and whitest just after the moulting period; later on, oils from the seals they eat can make them look yellow. In zoos, polar bears have been known to

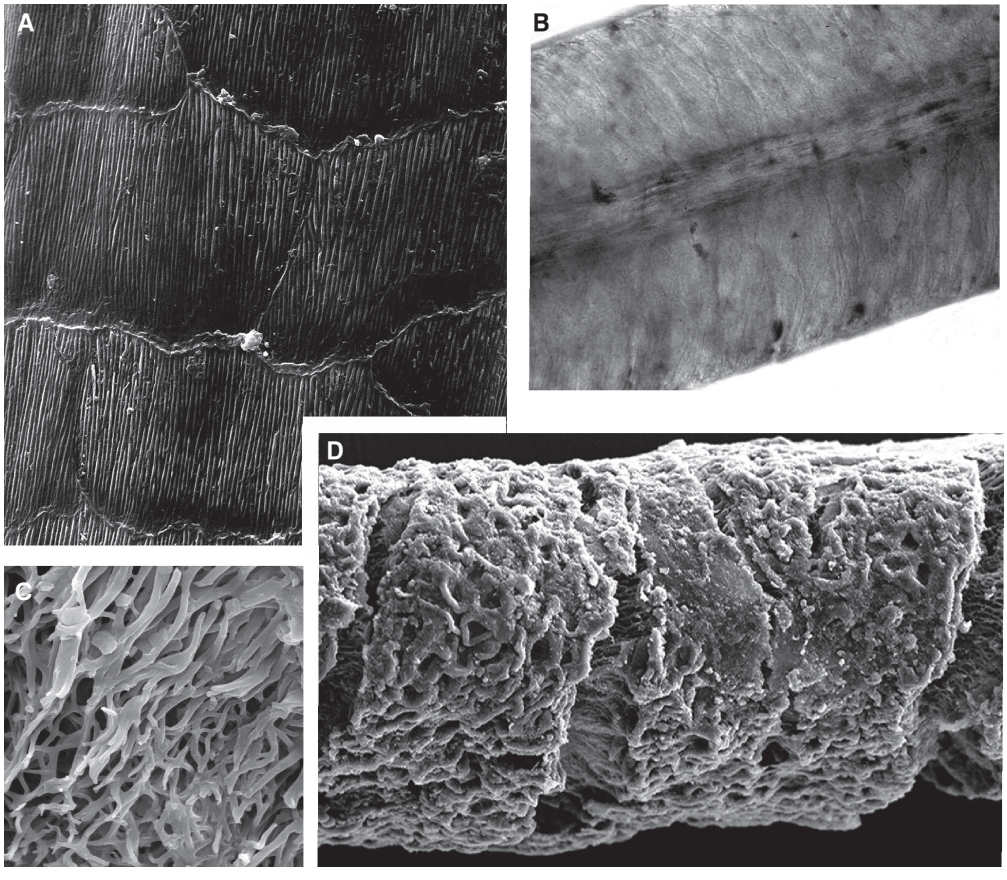


Fig. 10. *Bradypus tridactylus* GH (SEM): A = grooved scales on the shaft, B = channelled shield, C = spongy-like cortex, D = shield and apical section whithout cuticula

turn green due to colonies of algae growing in their hollow hair shafts; these algae colonize the hair during the bath of the bears, which take place into too warm and unsalted water.

In a Bubble: insulation, hydrophobicity, flotation

There are several adaptive modifications of the hairs and fur that help the maintenance and improvement of the insulation and thermoregulation, such as, for instance, the stratification and density of the fur, the length and colouration, and certain microstructural features of the hairs. They have an outstanding importance in the case of the flying, the semi-aquatic or aquatic and the subterranean mammals, as well as in the hibernating species. These characters are more advantageous in these mammal groups but evolved in certain other, less specialised taxa.

The main types of the air preserving and thermoregulative modifications are:

- the flattened hairs: the toughly touching, overlapping hairs, having flattened shields, make the fur waterproof and maintain an air layer (e.g. beaver, muskrat, seals);
- the channelled hair, which has deep channel(s) along the hair, and characteristic shape of cross section (e.g. H, tetrangular); it can be a diagnostic and/or taxonomic feature of semiaquatic shrews and rodents;
- the dense under hair: one of the most typical features of the semi-aquatic mammals is the very dense and tough under hair while the guard hairs are more sparse and heterogeneous, sometimes even absent.

The large amount of air carried in the dense, waterproof fur of semi-aquatic mammals like the otters confers protection against heat loss in water and also contributes to the positive buoyancy of the animals, but requires more energy from the animal to dive and remain submerged. Moreover, the waterproof fur is subject to water infiltration can be compressed in water, thus, the maintenance of the air layer in the fur requires a remarkable plus energy, mean longer and more frequent scratching (Fish *et al*. 2002).

Hairs to fly

Among the mammals, only the bats (Chiroptera) have an active flying; the other species, for example the flying squirrels (Pteromyini), the Feathertail Glider (*Acrobates pygmaeus*) or the flying phalangers (*Petaurus* sp.) only glide. Their entire body is highly adapted to the flying behaviour, and the flight is supported by the special microstructural modifications of the hairs, too. The hair characteristics of the flying and gliding species are generally different, but the shared features might be the remarkably larger cuticular scales and/or the presence of protruding scales with frilled edges. These enlarged scales function like minute sails which can capture the air turbulences, create turbulence around the animal, so reducing the specific gravity and facilitating the flight. For example, these kinds of adaptations produce an effective support for the flight of the nectar-feeding bats (Glossophaginae), which can hover during the licking the nectar, like hummingbirds (Meyer *et al*. 1995).

The fur structure of bats is mostly uniform over the entire head and body, except for sensory whiskers. There is a grid of microscopically small hairs found on both dorsal and

ventral surfaces of the bat wing. Most of them protrude from "hair domes" and are associated with a variety of tactile receptors. The hairs on the wing membrane are too sparsely distributed and too short to be involved in heat insulation or influencing the airflow over the wing surface. On the other hand, they can percept the air current and can help in the coordination of the flight and the regulation of the speed. These small and thin, terminally tapering and sometimes apically hooked sensory hairs are often called the "sixth sensory organ" of the bats (Bullen & McKenzie 2008, Sterbing-D'Angelo *et al.* 2017).

Osmetrichia – the scent dispersing hairs

The "osmetrichia" means modified scent dispersing hairs (Müller-Schwarze *et al*. 1977) that grow and function mainly around or near the glands. These hairs differ in their structure and function from the regular guard hairs and underhairs covering the body; for example, the edges of the cuticular scales may be protruding, with smaller or larger cavities between them and the deeper groove may be present on the scent hairs. These modifications promote the draining, storage and dispersion of the species-specific and sex-specific secretion produced by glands, helping the chemical communication between individuals. The osmetrich patches can be found in both sexes, in diverse appearance and location of the body. Such osmetrich patches are, for instance, the erectile, fringe-like tufts in the hyrax (*Procavia*); the sexual secretions are accumulated on the hair-brushes in the knee and the inner surface of the tarsus in certain ungulates (e.g. *Odocoileus hemionus*); on the breast and the neck in Phyllostomidae, Molossidae, Pteropodidae and in certain marsupials (e.g. *Antechinus stuartii*); on the hypogastric area in some shrews (e.g. *Suncus murinus viridescens*); while there are modified quills on the dorsal section of the rump in the North American Porcupine (*Erethizon dorsatum*).

The Crested Rat (*Lophiomys imhausi*) has an extraordinary defensive strategy, making its fur as deadly poisonous. This species gnaw the roots and bark of *Acokanthera schimperi* (Apocynaceae) then salivate onto the flanks the mucus, where the modified, perforated hairs wick up this like a spongy. The drug of this plant is a cardenolide; it closely resembles ouabain, one of the active components in a traditional African arrow poison that can kill even elephants. These osmetrich hairs have fenestrated cortex and trabecular medulla and the shaft sections develop a thin but strong outer cylinder perforated by abundant vacuoles (Kingdon *et al.* 2012).

The hard keratin arsenal

Several mammals have rows, patches, partly or total covering of remarkably modified elements of the integument, like scales, quills, or spines. Their primary function is the protection against physical stress by predators, aggressors or the environment, but the palette of other functions is surprisingly variable: communication by intonation, camouflage, thermoregulation, storing water or providing specific odours. These structures can be rigid and stable but most of them are connected to muscles and movable or riseable.

The scaly armour

The "scaly" integument is the characteristic of the armadillos (Dasypodidae) and pangolins (Pholidota). These flattened and tiled-roof-like, tightly closed structures are similar but phylogenetically convergent organs (Rose & Gaudin 2010): the armadillos (Dasypodidae have the bony carapace is a complex unit of the osteodermes (dermal bone); the dermal bones covered by thin, polygonal epidermal scales, without hairs or with only very few coarse, short hairs in-between; the pangolins (Pholidota) have the strong, thick, overlapping, triangular shaped, movable epidermal scales, with only very few, longer coarse hairs in-between. The origin of the scales of the pangolins is explained by three different hypotheses; either these epidermal scales derived from thickened and flattened hairs, or they are considered as homologous to the scales of the ancient reptiles, or even homologous to nails (Spearman 1966). In the pangolins, the presence or absence of dorsal hairs is a diagnostic feature: the Asian species have three or four hairs at the base of each scale, while the African species lack hairs at the base of the scales (Atkins 2004).

The spiky armour

The "spiky" integument is characteristic of the Echidnas (Tachyglossidae), Tenrecs (Tenrecidae), Hedgehogs (Erinaceidae), Cricetidae, Muridae, Old World porcupines (Hystricidae), New World porcupines (Erethizontidae), Spiny rats (Echimyidae), Cane rats (Thryonomyidae), and the Spiny dormice (Platacanthomyidae).

The spines (like in hedgehogs) and quills (like in porcupines, echidnas) are different in many aspects: they have different microstructure and physical quality and ability. Their common primary function is the protection, but there are other functions related to the adaptive modifications of the macro-(e.g. tip, bulb) and microstructural elements of the hairs (e.g. cuticula, medulla). Obviously, the spines and quills evolved independently several times through the evolution of mammals. The quills are stronger than spines, have spongy medulla and inverted cuticula on the tip region, and are perfect against aggressors. The spines (e.g. in hedgehogs) are much more elastic, having medulla sectioned by air holding septas. The bulb keeps the spine stable, so this structure is perfect to avoid they get hurt when they fall down, as well as protect them from aggressors (Vincent & Ower 1986, Chernova 2002). The fine structure of the spines might hold fluids and probably this character was the basement of the self-anointing behaviour of certain hedgehog species. Self-anointing is a special behaviour of animals that produce a mixture of fluids for its own defence; in case of certain hedgehog species, a mixture of the saliva and of secretions of other animals is spread on the dorsal-lateral spines by the tongue of the animal.

The Lowland Streaked Tenrec (*Hemicentetes semispinosus*) is the only mammal that can communicate by echolocation (producing ultrasound calls) by rubbing together specialised quills on its back. A group of 7 to 16 specialized quills arranged in three rows on the medio-posterior dorsum, which, together with the underlying dermal musculature, form the stridulation organ (Petter & Petter-Rousseaux 1963, Gould 1965).

The Old World porcupines (Hystricidae) can vibrate the hollow structured quills of their tail resulting in a special "rattling" sound, similar to the rattling of tail scales of the rattlesnakes. This kind of alarm-signal is called acoustic aposematism.

Human altered changes – the domestication

Domestication is the human directed selection of wild creatures for human purpose. It will result genetic modification, exhibiting morphological, physiological and behavioural characteristic of the animals. The volume of changes depends on several factors like the aim of the domestication, the duration of this process, or the isolation of the breeding gene pool. The appearance of the pet or/and the quality of fur, especially in case of fur-animals, are basic aspects of selection, thus the domestication has influenced the macro- and microstructure of the hairs. There are sometimes significant differences between certain quantitative and qualitative characters (e.g. surface area of cuticula, medullar index, diameter of medulla, length of hairs, pattern types) of the wild and the domestic animals; there are accepted domestication-induced defects of patterns of the hair and the hair-producing follicle system (Short 1978, Meyer *et al*. 2000, Meyer *et al.* 2002). The medullary and the cuticular pattern in domestic forms do not change with the age as seen in wild species but the juvenile characters are retained in adults due to domestication (De Marinis & Asprea 2006). The reduction or absence of the bands on the hairs of the domestic animals and the homogenisation of fur structure appear as very frequent consequences of domestication, as well. The trends of morphological changes are hardly comparable in a wider scope as rather different micro- (e.g. cuticular, medullar) and macroscopic (e.g. shape, colour) characters being typical of the different taxa are changing in different scales and rates (Kennedy 1982, De Marinis & Asprea 2006).

Notwithstanding that the descriptions on hairs of domesticated animals is quite rich in the literature of fur-industry, anthropology, and wildlife-forensic, still the identification is difficult or less reliable. The identification usually problematic in cases where the domesticated animals preserving the characters of the "wild forms", or the hybrids are hardly or not separable by microscopic studies from those of their wild relatives, or there are high number and diversity of phenotypes. Sometimes the trichomorphological characters of rather remotely related animals are remarkably more similar, then the closely related ones like, for instance, in case of certain domesticated goat and sheep forms (De Marinis & Asprea 2006). As the hairs of domesticated animals occur frequently in the Nature, their morphological and parallel molecular investigations will help the work of field biologists and forensic experts, too.

Anatomy of the mammal skin and hair and the ontogeny of the hair

3

3.1. Anatomy of the mammal skin and hair

3.1.1. Anatomy of the mammal skin

The skin and its appendages consist of two distinct components: surface epithelium, which develops from the embryonic ectoderm, and connective tissue which develops from the mesoderm. The epidermis maintains a physical and chemical barrier between the interior of the body and the environment. The five layers of the epidermis are, from the base towards the surface, the stratum basale, stratum spinosum, stratum granulosum, stratum lucidum, and stratum corneum. The life cycle of the epithelial cells consists of three phases: mitosis, keratinisation (differentiation) and exfoliation.

The *stratum basale* (germinativum cell layer) is a single layer of cells where the keratinocytes divide, differentiate and start their transformation from the basal layer to the surface; keratinocytes synthesise the keratin proteins; this layer contains the melanocytes producing melanin; melanin accumulates in melanosomes that are transferred to the adjacent keratinocytes where they remain as granules.

The *stratum spinosum* (spinous cell layer) is formed of several layers of larger, oval-shaped cells with nuclei but with limited mitotic activity. Intercellular, spine-like desmosomes connect the cells; this layer contains the Langerhans cells derived from the bone marrow which play a significant role in immune reactions of the skin.

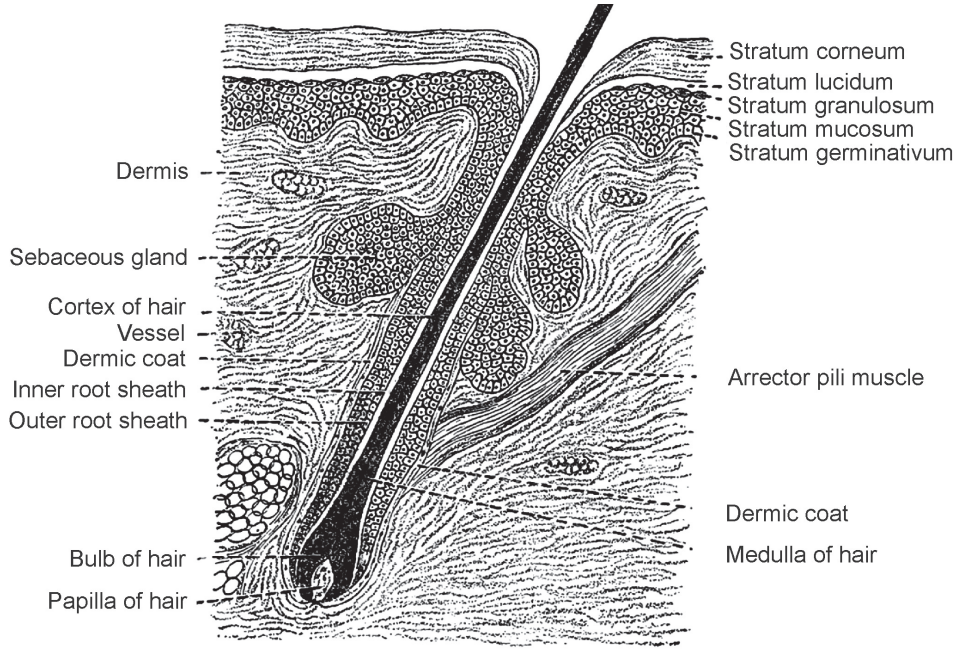


Fig. 11. Fine structure of the epidermis (after Gray 1918)

The *stratum granulosum* (granular cell layer) is composed of a few layers of cells containing keratin fibres, their nuclei are reduced or absent and their cytoplasm appears granular. The *stratum lucidum* (transculent layer) is a thin layer that exists only in lips, paw pads (palms and soles in Primates). The *stratum corneum* (horny layer) consists of several layers of dead, cornified, polygonal, flattened corneocytes – typical rhomboid or hexagonal shaped and overlapping scales; these cells are surrounded by a protein and filled with water-retaining keratin proteins while the extracellular space contains lipids, so the stratum corneum provides the natural physical and water-retaining barrier of the skin. The dermis forms the resistant layer of the skin, and contains structural proteoglycans and proteins like elastin and collagen, which give the skin its elasticity. The subcutis is made up of connective tissue and fat (Parakkal & Alexander 1972, Sokolov 1982).

3.1.2. Anatomy of the mammal hair

The hairs belong to the appendages of the skin (like nails and glands) and can be found in various densities over the entire surface of the body, except on the paw pads, penis and glands. The physical proprieties of hair involve the resistance to stretching, elasticity and hydrophilous power.

The hairs have two main parts, the root (radix pili) which is embedded into the dermis and the hair – called as hair shaft or stem (scapus pili) – protruding from the surface in a given angle. The hair follicle (folliculus pili) is a sac-like component of the skin; the cells are derived from the epidermis and its function is to produce the hairs. The bulb (bulbus pili) is the deepest part of the follicle lined by germinative cells and melanocytes.

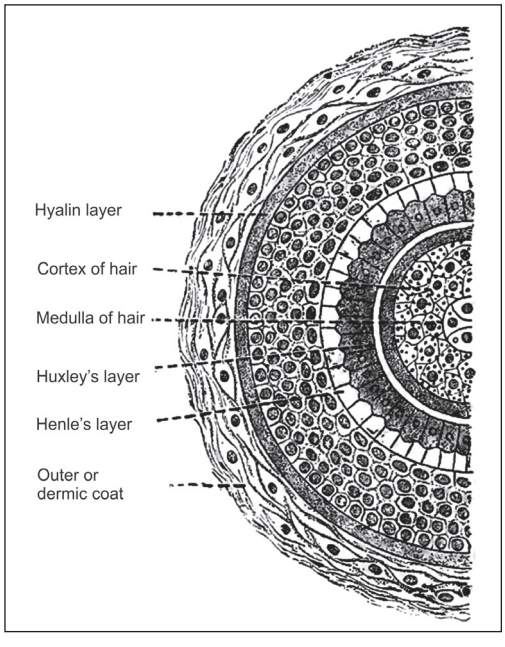


Fig. 12. Structure of the hair (after Gray 1918)

The epidermic coat of the hair follicles is the outer and inner layers of the root sheath. The dermal papilla is situated in the uppermost layer of dermis and its role is to provide nutrition and oxygen by extending from the dermis into the hair bulb. An erector pili muscle (musculus arrector pili) is associated with the hair shaft and contracts with cold, fear and emotion to pull the hair erect. Sebaceous glands (glandula sebacea), also unique to mammals, are connected with the hair follicle and produce oil secretion (sebum) that moves outward along the hair shaft and spreads on the surface of the epidermis.

The hair consists of an outer cuticle, a middle cortex and an inner medulla. The cuticula is derived from the outermost cells of the papilla dermalis. It consists of dead, strongly keratinised, flattened cells which do not contain pigments or cellular organs. The three main layers of the cuticula (the epi-, exo- and endocuticula) form together a very complex system, which constitute a substantive hydrophobic and protective surface against physical and chemical stress because of their lipid and protein content.

The cortex is developed from the medial part of the dermal papilla and the cells of the inner inner root sheath; statically, it is the most important structural element of the hair. The cortex covers the entire hair; it consists of tightly joining and strongly keratinised, fusiform cells, often with desmosomes in between them. These fusiform cells somewhat transformed during their maturation, slightly drifted from each other and move towards the apex, while fine cavities appear between them which is filled with interstitial liquid in the basal region, and air in the upper parts of the hair. These fusiform cells are filled densely with macrofibrilles, the pigments appear between the macrofibrilles, most often as granules; sometimes also remnants of nuclei can be recognised. The cortex can be divided into three parts, the para- (compact), meso- (transitional) and orthocortex (transparent).

The medulla develops from the keratinocytes located above the medial part of the dermal papilla; its structure is most often rather intricate. The medullar cells might contain pigments but when they become dehydrated, their spaces often filled with air, which affects both colour and shine (Spearman 1966, Parakkal & Alexander 1972, Krstić 1997, Homan & Genoways 1978, Chernova 2003, Lillywhite 2006, Velasco *et al.* 2009).

3.2. Ontogeny of the hair

The ontogeny of the hairs having diverse structure and function, it is regulated by both internal and external factors. Hair polymorphism is due to the several generations of hair follicles in ontogeny regulated by the genes and hormones of the species, the age of the specimen and some environmental factors (Chernova 2002). The sequence of the three major phases of development (anagen, katagen, telogen) is constant during the ontogeny but the duration and intensity of the three phases is variable due to the age and physical conditions of the animal and the location of the hairs on the body.

The first phase of the ontogeny of the hair is the *anagen* phase. The epidermis invaginates into the cutis and the movement of the secondary matrix cells into the depth leads to the emergence of the bulb (bulbus). The increasing mitotic activity of the bulb cells and the keratinisation start the longitudinal growth of the scapus. The size and quantity of the keratin microfibrilles and the amorphous proteins increase towards the surface of the body during this process and, with the entire filling of the cells with these substances, appears the keratin pattern. The proportion of the keratin microfibrilles and the amorphous proteins is different in the layers of the hair: this ratio is 1 : 1 in the cortex while the cuticula and the medulla contain a much higher proportion of amorphous proteins.

The second phase, the *katagen*, is a regressive phase. The cells lose their mitotic activity, and the hair starts its movement towards the surface of the skin with the surrounding cells of the dermis and the cutis, and its nutrition and pigment accumulation ceased. The bulb and the hair together get their characteristic clubbed shape. The secondary germ cells develop under these hairs. The lowest layer of cells dips down while the others are destructed by lysosomal enzymes (autophagy).

The third phase, the *telogen*, is a resting phase. One of the main functions of the telogen is to hold in place the hair during the preceding anagen, and can also regenerate the next generation of anagen hairs. The new structures of this stage are the club and the surrounding germ. The club is attached to the hair shaft at one end and to the germ at the other end. The club is responsible for anchoring the hair in position, and the germ cells give rise to the next generation of anagen hair. The emerging newly developed hair pushes out the older hair; this is the process of moulting or exfoliation (Parakkal & Alexander 1972, Banks 1981, Wennig 2000).

The moulting provides the continuous regeneration of the fur following the seasonal changes. In the seasonal moulting, the density and the colouration of the fur are usually changed, as well as the air content and certain quantitative parameters (e.g. length, diameter) of the individual hairs. The season(s) and the span of the moulting are variable, depending on the species, the individuals and the different parts of the body and is regulated by a number of intrinsic and environmental factors. The most important environmental factors that regulate the moulting are the intensity and length of the natural light, the photoperiodism, and the changes of the temperature. The physiological regulation and the internal stimuli represent a complex system. The hormone of the pineal gland (epiphysis cerebri), the melatonin is the principal neuro-endocrinological factor which has a key role in the seasonal regulation of the biological rhythms (the circadian and the yearly rhythms), the body mass, the normal function of the thyroid gland, the sexual activity, and also the moulting. There are correlations between the production and release of the melatonin and the levels of the hypophyseal prolactin (LTH), luteinizing hormone (LH), and follicle stimulating hormone (FSH). The photo-impulse inhibits the production of the melatonin via/through the retino-hypothalamic tract, therefore there is a direct relation between the melatonin production (and release) and the moulting and the daily and seasonal intensity of the light and the length of the daylight. The hairs always contain tryptophan, the precursor amino-acid of the moulting-regulating hormone, the level of which is correlating with the age and the sex and, according to some studies, also with the colouration (Bertazzo *et al*. 2000).

Structure of hairs and fur 4

4.1. Ultrastructure of hairs

4.1.1. Keratin

Keratin is one of the most important structural proteins in the integument of vertebrates. The basic macromolecules that form keratin are polypeptide chains. Fibrous proteins and amorphous matrix proteins are found in the mammal hair. Keratin extracted from hair is classified into three main types: the α-keratin has helical structure, is flexible, cysteine rich and sulphur poor (mostly in the cortex of hair); the β-keratin has plated sheets structure, is rigid, and cystein poor (forms the majority of cuticula); and the globular γ-keratin has high sulphur content (forming amorphous matrix components).

When stretched or heated, the α-keratins give a β-diffraction pattern, due to the disintegration and reorganisation of the disulfid bridges; the various curling and painting technics of hairdressing are based also on this phenomenon. The keratin is insoluble in water but can be converted into proteins soluble in alkaline or acidic medium, with a definite optimum pH of flocculation and digestible by trypsin or pepsin after breaking the disulfide bonds of the protein. The keratins have a wide variety of morphostructures and properties related to different functions. The major components of hair are the α-keratins (called as hard, or mammal-keratin) and the keratin associated proteins, each of which are encoded by two multigene families.

The molecular microstructure of the hair is rather complex. Its basic unit is the dimer in which two right-handed α-helix keratin molecules coil into a left-handed superhelix. These dimers arranged into protofilaments; two protofilaments form a protofibrillum, four protofibrilla produce a microfibrilla, and 9+2 microfibrilla create the macrofibrilla. The main components of cortical cells are the macrofibrilla (Wu *et al*. 2008, Hill *et al.* 2010, McKittrick *et al*. 2012).

4.1.2. Pigments

The melanin is the most frequent pigment in the animal kingdom which has several important physiological functions. In the mammals, the melanins are part of the immune system. The mammal skin has three major systems for the protection against ultraviolet (UV) radiation: the blood, the dermal/epidermal melanosomes, and the keratin. These protecting systems have different sensitivity and photo reflecting capacity due to their different substance structures, therefore their common effect is a complex, broad spectrum of protection. The absorption spectrum of the blood is mostly between 400–425 nm (blue light) and 500–600 nm (green light), the melanosomes protect against the UVA 300–700 nm ultraviolet light while the keratin absorbes in the UVB 280 nm spectrum (Nielsen *et al*. 2008, Sebetić *et al*. 2008).

The colouration of the fur and the hairs can be highly variable due to the genetic polymorphism and the sexual dimorphism, the adaptive selection pressure, and the changes during the ontogeny. The colour of the hair is defined mostly by the melanin content of the medulla and the cortex. The phaenotypical variability of the colouration is a consequence of the genet-

ic regulation of two proteins, the melanocortin 1 receptor (MC1R gene) and the Agouti protein (Slominski *et al.* 2004). The inheritance traits of the colouration may be variable in the different mammal species but are principally dominant-recessive. The genesis of the melanin in the follicles is cyclical, similarly to that of the ontogeny of the hair. The melanin granules are synthetised in the melanocytes located diffusely in the basal layer. The melanin consists of polymerised precursor molecules and is built up into the hairs in various oxidative stage and density. It has two major types, the eumelanin and the phaeomelanin. The precursor of eumelanin is the dihidroxi-phenylalanin (DOPA), which develops from the tyrosine amino-acid. The absence or deficiency of the tyrosine hydroxylase causes the albinism, as the precursor of eumelanin cannot develop. Eumelanin is water soluble and has a key role in the protection of the body against the UV-radiation. It can be found at the highest density in the retina and the dark hairs. The eumelanin can be considered as evolutionarily more ancient than the phaeomelanin if the UV-protection is considered as the main function of the melanins.

The phaeomelanin is soluble in alkaline and is concentrated in the blond and red hairs. The red, orange and ochreous-brown colours are given by trichosiderine proteins containing iron; the synthesis of the trichosiderine pigments differ from those of the dark brown and black pigments (Flesch 1968). In the white-coloured hairs, the medulla contains keratinocytes but they lack melanin. The situation is different in the greying process in which the medulla is filled up with air sacs, the melanocytes stop the production of melanin and the keratinocytes are lacking. The greying is connected strongly with the age via the destruction of the cells induced by the reactive oxydative compounds and the UV-radiation; sometimes the process is correlated with the disruption of the homeostasis of the organism (Tobin & Paus 2001, Geyfman & Andersen 2010).

There are some infrequent colour variations which differ remarkably from the typical individuals of a given taxon. The melanistic specimens are darker in colouration, most often dark brown of blackish, the erythristic ones have reddish, rusty or yellowish-brownish hairs, while the leucistic animals are rather similar to the albinistic ones but are more ochreous shaded and their eyes are not red. The albinism is caused by the partial or total absence of melanin which is based on the defective production of the tyrosinase enzym. Such colour variations may appear in the native and domestic populations of several species (Imes *et al*. 2006).

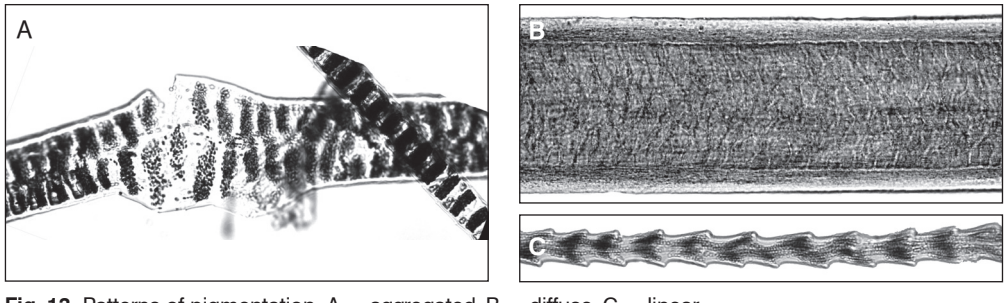


Fig. 13. Patterns of pigmentation. A = aggregated, B = diffuse, C = linear

4.1.3. Types of pigment distribution and their examination

The distribution of the pigments defining the colours of the hairs can be studied using photomicroscopes. The distribution of the pigments can be even or uneven, and the arrangement of the pigment granules can be diffuse or aggregated (isolated or linear) in both main types. There are some parts of the hairs, which may lack pigments, but these depigmented areas are often hardly visible by the naked eye (e.g. the apical region).

"The iridescence is widespread among birds and arthropods but rarely been reported in mammals, although non-iridescent blue skin colours produced by organized collagen fibres have been described. The fur of the golden moles (Chrysochloridae) shows shining colours ranging from purple to green. The SEM and TEM based analysis provided interesting information on the fine structure of the hairs of the golden moles. Complex adaptive morphological features contribute to this coloration: the flattened hair shape increases the surface area available for reflection; the compressed cuticular scales provide a smooth reflective surface that enhances specular reflectance; the layers of light and dark materials in the cuticle act as multi-layer reflectors that produce colour through thin-film interference" (Snyder *et al*. 2011).

Specimens of striking colouration and/or pattern may appear due to spontane and inherited mutations. As a curious case, similarly coloured and striped Roe Deer (*Capreolus capreolus*) and Red Squirrel (*Sciurus vulgaris*) specimens (see p. 283) were observed in North Tyrol in Austria, in different places and time. This white patched-striolate pattern was inherited but as these specimens had an adaptive disadvantage, they rather quickly disappeared from the natural populations.

4.2. Microstructure and patterns of hairs

The hair consists of three layers: the cuticle, the cortex and the medulla (Fig. 14). The quantitative and qualitative features of the patterns of these layers, their composition and sequence along the hair represent taxonomic characters that can serve as key features for the identification of the different mammal taxa. The definitions of these patterns and their classification in this book are based on the most important literature sources. The nomenclature of these very variable patterns is rather difficult and complex, therefore the creation of a practical and concise system was a crucial point of this book. The different pattern types are named using geometrical and natural conformations, and adopting the terms used most frequently in the former publications, like Hausman 1920, Wildman 1954, Benedict 1957, Day 1966, Brunner & Coman 1974, Moore *et al.* 1974, Hutterer-Hütter 1981, Keller 1981, Debrot 1982, Teerink 1991, Blazej *et al*. 1989, Meyer *et al*. 2002, Chernova 2002, 2003, Ibara *et al*. 2004, Pech-Caché *et al*. 2009).

The nomenclature and system of the trichomorphological hair characters are based only on the Central European mammal species. The major aim of this classification was to produce a consistent morphological system in which the higher taxonomic categories can be

characterised by simple and unequivocal basic structures. Furthermore, this system can be completed with the insertion of the new patterns missing from the basic system.

The study and analysis of the light microscopic patterns are sufficient in most cases for the identification of the hair samples, on the other hand, the investigations of the ultra-structures provided by the SEM could be essential for the taxonomic and physiological studies. Thus, in this book, I used exclusively the light microscopic trichomorphological features, visible with maximum 1000× magnification; certain ultra-structures, seen only by using SEM, are included in the diagnoses of the given taxa but are excluded from the identification keys.

4.2.1. The cuticula

The cuticular scales are best comparable to the tiles; they are usually partly overlapping and are directed apically, with the exception of certain spike-like hairs/spikes, towards the tip of the hair. The cuticula can be a monolayer but is usually multi-layered; for instance, there are 6–10 layers in the human hairs while the bristles of the wild boar can be composed from even 35 cellular layers (Blazej *et al*. 1989). The cuticular scales can be divided up by their shape, direction and position, and their marginal structures. The direction of scales can be closed or divergent from the axis. The position of scales can be transversal (when the longer axis of the scale is rectangular with the axis of the hair; they are shorter than broad), medial

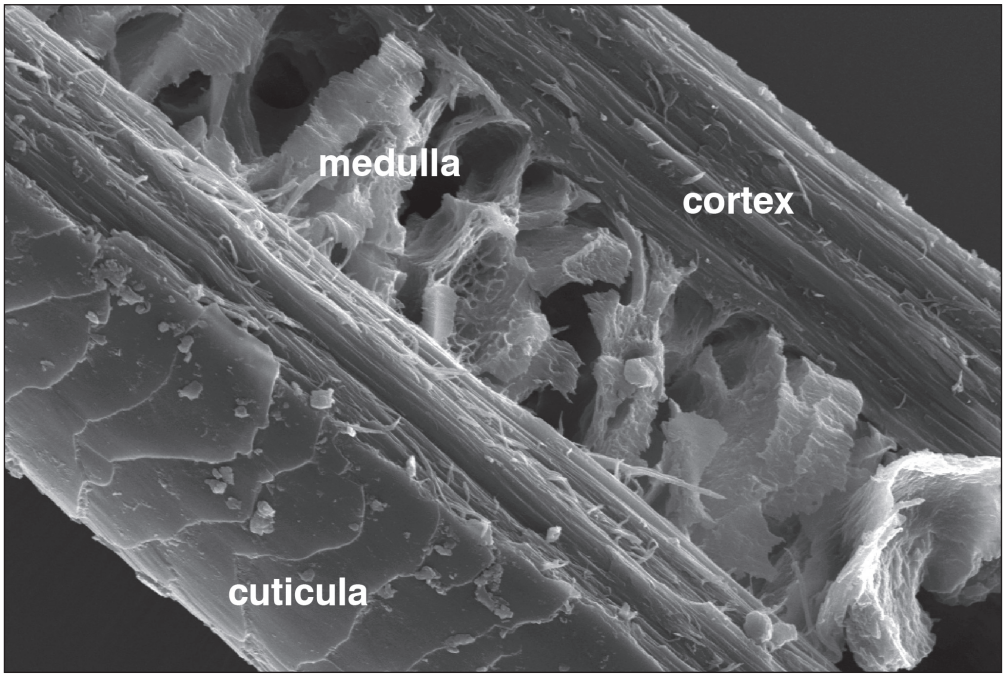


Fig. 14. Microstructure of hair (SEM)

or longitudinal (the longer axis of the scale fits with the axis of the hair, they are longer than broad). The apical margins of the scales can be smooth, crenate, rippled or dentate; the distance between the scales, as units, could be distant, near or close. The contour of the hairs, embedded into gelatine has two main types, the spiky and smooth transparent view, depending on the arrangement of the scales.

The surface of the cuticular scales can be informative: the fine scratches on the surfaces of the scales which are visible with 200–400× magnification are most often the consequences of certain physical damages (e.g. in case of fossorial mammals, caused by grains of sand); the grooves and grains, which can be seen usually only by the SEM, are genetically fixed pattern of the scales which could be taxonomic features (Teerink 1991, Chernova 2002).

The qualitative and, in certain cases, some quantitative characters of the cuticular scales can be taxonomic features which are suitable for the identification of a given species. The most common qualitative characters are the scale index, which is the rate of the length and width of the scales; the number of the scales of a given length and section of the hair (e.g. 100 micron length of the middle-shaft section); and the average area of the surface of a scale; these values are often significantly different and are characteristic of a given taxon.

The most important cuticular features can be found mainly in the basal and the shaft sections of the hair but in certain species, the study of the shield and the apical section of the hair are also necessary.

The cuticular patterns

Coronal. This pattern resembles mostly joint coronets or funnels. This pattern is variable in its appearance and is typical of the Chiroptera but occurs also in the basal parts, the nodes and the arches of some other mammal taxa.

The coronal pattern is uniserial; the apical edges of scales overlie on the axis or straddle gently. The angle of the scales and the axis of the hair may be variable along the length of the hair and can be changed in the nodes. The arrangement of the scales forming the coronal pattern could be regular (and monotonous in its dip angle with the axis or with the margin parallel with the axis), alternate or irregular.

- coronal, zigzag (Fig. 15A): scales symmetrical or somewhat asymmetrical, non-overlapping; their arrangement alternate with the long axis; apical margins usually smooth; the transparent view of this pattern is slightly spiky.
- coronal, corniculate (Figs 15B, C): apical parts of scales stepwise or abruptly broadened, somewhat divergent from the axis and partially overlapping; transparent view is smooth or spiky.
- coronal, spiked (Fig. 15D, E): scales tightly arranged, symmetrical and slightly overlapping; margins smooth; transparent view smooth or slightly spiky.
- coronal, hastate (Fig. 15F, G): basal parts of coronets somewhat broader, lateral margins of scales not touching, alternate coronets forming a characteristic lanceolate print; transparent view spiky.
- coronal, K-shaped (Fig. 15H, I): lateral margins of scales touching in a clearly visible line; two small and a large scale form a repetitive K-shaped unit; transparent view smooth.

– coronal, compressed (Fig. 15J, K): a monotonous pattern consisting of tough, flattened scales; the shape of scales can be cup-, crown- or cornet-like; apical margins of scales are divergent, dentated or crenated; transparent view spiky.
– coronal, mosaic (Fig. 15L, M): a pattern appearing usually on the shield; the print of scales is irregularly mosaic-like; the scales might be deeply scalloped or conical shaped and the edges are divergent from the axis; the ultrastructure can be studied only by the SEM; transparent view smooth or spiky.

Figureless. The cuticula consists of irregularly shaped scales of hardly visible arising and indistinct contours; scales most often transversally elongate and tightly closed.
– figureless, waved (Fig. 15N): a dense pattern of irregularly or parallel arranged scales; apical margins of scales often indented;
– figureless, sketched (Fig. 15O): an irregular pattern with indistinctly contoured scales.

Mosaic. The cuticula consists of polygonal scales lacking pronounced apical parts.
– mosaic, meshed (Fig. 15P): a reticulate system of more or less equally sized, transversal, isodiametric or polygonal and often differently orientated scales;
– mosaic, transversal, regular (Fig. 15R): transversally elongated, rather angular scales; their arrangement may be perpendicular or waved;
– mosaic, irregular (Fig. 15P): transversally elongated, or isodiamaetric scales arranged alternately in dip angles.

Chevron. The typical chevron pattern is composed from variably strongly elongated, apically pointed, often biforked scales.
– chevron, cuneate (Fig. 15T): scales rather broad, apically usually dilated; apical margins often rippled, "M"-shaped;
– chevron, lanceolate (Fig. 15U): a pattern of narrower and elongated, apically pointed scales; their apical margin often characteristically "V- or W"-shaped;
– chevron, galeate (Fig. 16A): helmet-like scales arranged into the middle line of the hair; the lateral view of this pattern shows usually petal-like pattern.

Petal. The typical petal pattern is composed of scales with arched edges.
– petal, broad (Fig. 16B): from one to three rows of mostly isometric, distant scales; apically smooth or rippled;
– petal, transversal (Fig 16C): one row of transversal, regular, narrow, near, scales; typical on the channelled shield; scales reaching the entire diameter of the hair, apically smooth;
– petal, combined (Fig. 16D): an atypical, asymmetrical petal pattern in which a large and longitudinally elongated rhomboidal scale encompasses 2–3 smaller broad petal scales.
– petal, rhomboidal (Fig. 16E): a transitional pattern between the petal and the rhomboidal type; consisting of regular or irregular, isometric, intermediate scales.

Rhomboidal. A tight, reticulate pattern of more or less rhomboidal scales arranged into regular, parallel rows.

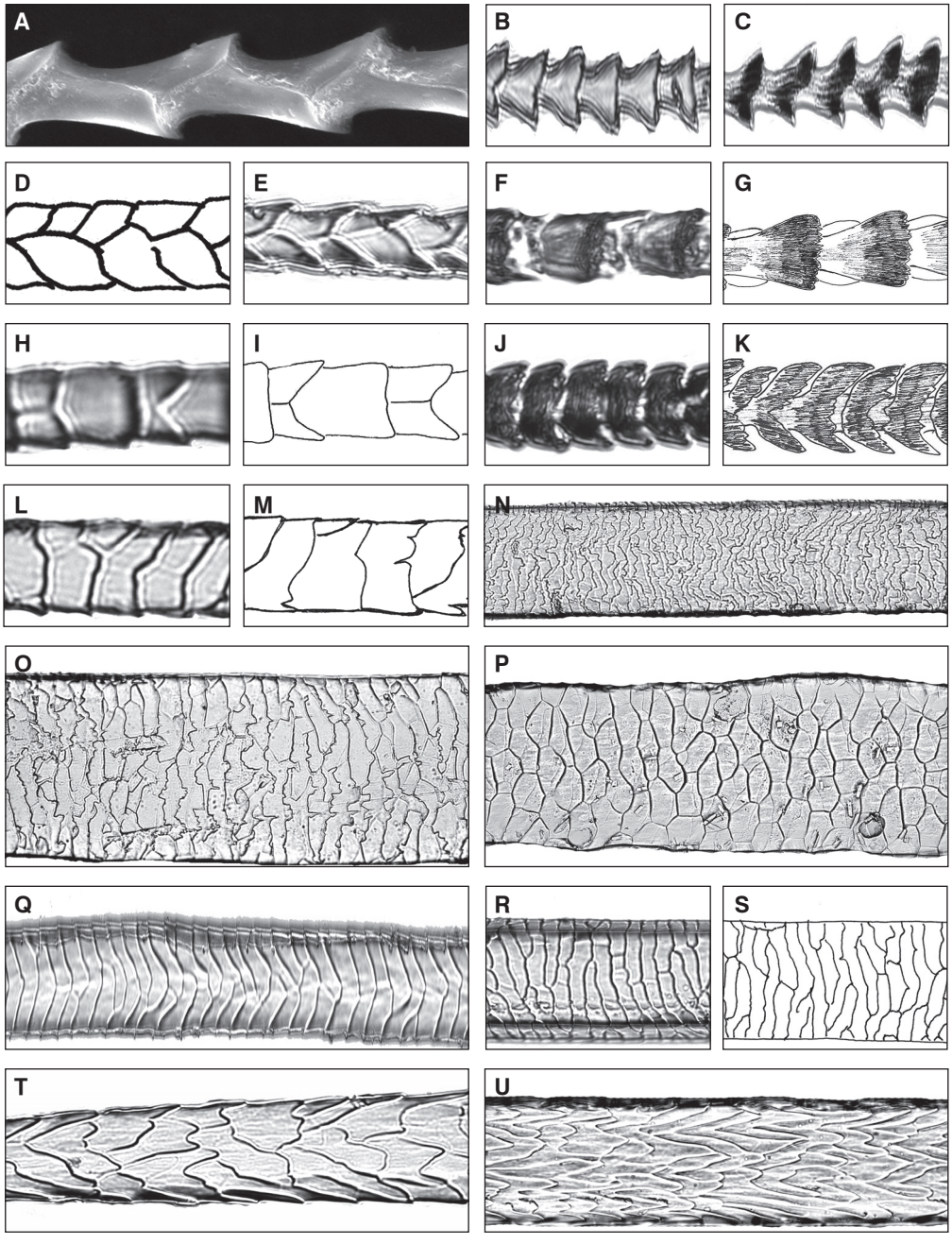


Fig. 15. Cuticular patterns. **Coronal**: A = zigzag, B–C = corniculate, D–E = spiked, F–G = hastate, H–I = K-shaped, J–K = compressed, L–M = mosaic; **Figureless**: N = waved, O = sketched; **Mosaic**: P = meshed, Q = irregular, R = transversal, regular; **Chevron**: T = cuneate, U = lanceolate

– rhomboidal, elongated (Fig. 16G): scales longitudinally somewhat elongated, apically finely pointed;
– rhomboidal, broad (Fig. 16H): scales more or less isodiametric, apically arcuate;
– rhomboidal, pine-cone (Fig. 16I): scales strongly elongated, apically dentate.

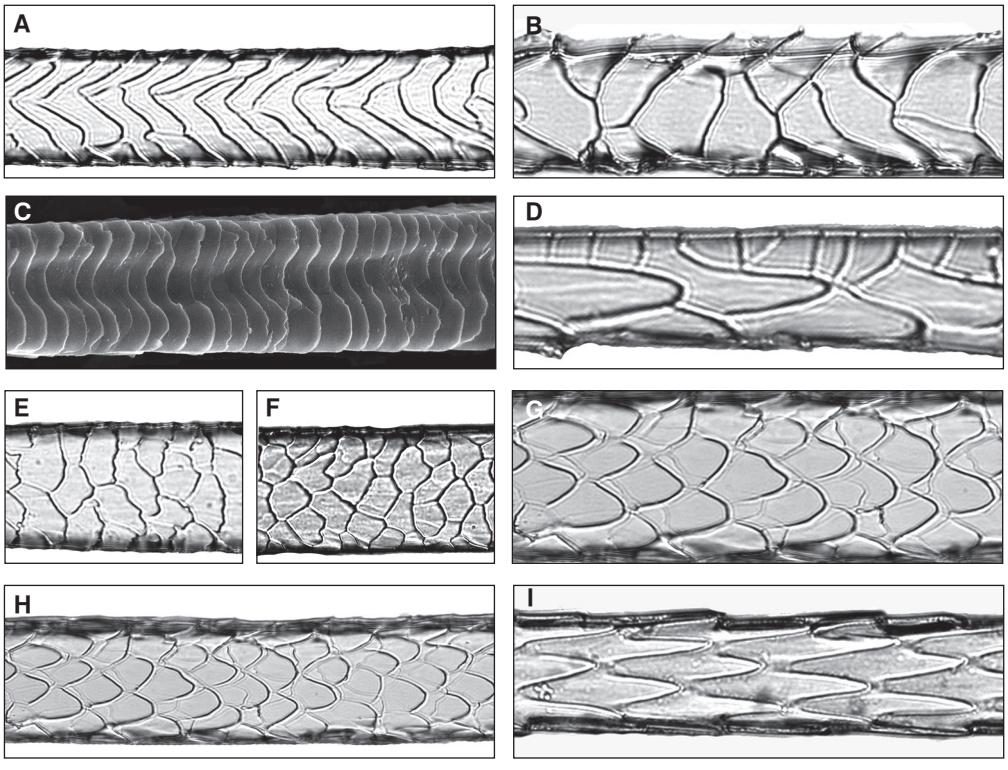


Fig. 16. Cuticular patterns. **Chevron**: A = galeate; Petal: B = broad, C = transversal, D = combined, E = rhomboidal, F = rhomboidal; **Rhomboidal**: G = elongated, H = broad, I = pine-cone

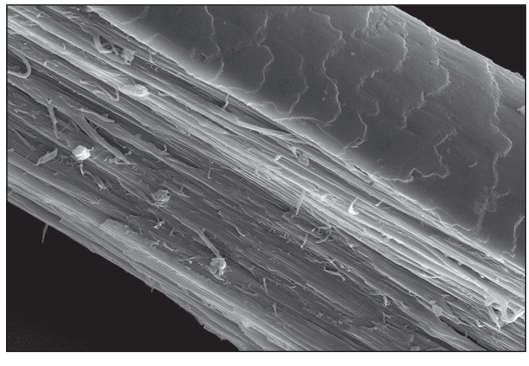


Fig. 17. Structure of the cortex (SEM)

4.2.2. The cortex

The cortex is an important supporting element of the hairs. Its basic structure is a regular cylinder with evenly thick walls within the hair but this regular structure is usually discontinuous as, in certain parts of the hair, the cortex is fused with the cuticula while in other sections, it may penetrate into the medulla (Alibardi 2012). The structure and thickness of the cortex correlates also with the natural shape of the hairs, therefore, it is very thin in most Artiodactyla while it can fill up the entire hair forming either medullaless sections within the hairs (in case of the strong bristle hairs) or even medullalesshair types (underhairs; guard hairs in certain families of Chiroptera).

The cortex, because of its nearly homogeneous structure, was not found to exhibit characters which could be used as criteria for identification. On the other hand, the width and transparency of the cortex, in connection with the density and colour of the pigments accumulated in the cortex, could be important diagnostic characters. The microstructure of the cortex becomes visible in the macerated hairs using chemicals or the physically injured, cut hairs where the cortex teased out to show the distorted, elongated cortical cells (Fig. 17).

4.2.3. The medulla

The cells of the medulla are variable in shape, size and arrangement. The medulla is usually well separable from the cortex; the volume of the medulla is in inverse ratio to the volume of the cortex. The margin between the cortex and the medulla depends on the arrangement of the medullar cells. The main types of the margin of the medulla are the straight**,** the fringed (needle-like tiny intrusions between the cortex and medulla) and the crested (regular, semicircular intrusions of medullar cells into the cortex). The thickness of the medulla increases with the number of the layers of medulla cells, and with the volume of the air sacs. The thermal insulation capacity is directly proportional to the thickness of the medulla but the flexibility and strength of the hair is decreasing with the thickness of the medulla. The volume of the air sacs of the medulla might be related to the environmental factors (e.g. temperature, humidity) and the life style of the animals; it can be changed during the shedding and the winter fur always contains a larger amount of air. The mature hairs usually lack the medulla from the basal and apical sections but the sequence of the medullar patterns from the shaft towards the apex are characteristic.

The medulla is absent from the hairs of certain chiropterans (Rhinolophidae, Vespertilionidae and Miniopteridae), from the underhairs of some Artiodactyla families (Bovidae, Cervidae), and in some sensory hairs. The medulla of the guard hairs is most often continuous but can be fragmented, like the hairs of humans, beavers, badgers, etc.

The qualitative and quantitative medullar features are also appropriate for the identification. One of the important quantitative characters is the medullary index (m/d_x) which is the rate of the width of the medulla measured at the thickest part of the hair (m_{max}) and the maximum diameter of the hair (d_{max}). The specific patterns of the medulla can be found most often at the thickest sections of the hair, like the transit or the shield.

The medullar patterns

Nummiform. The medullar cells are oblong or elliptical-ovoid discs arranged into one or two rows; the cells are usually contiguous; the cortex is usually transparent (hyaline); the width of the air sacs fits with the width of the medullar cells; the margin type of the medulla is always fringed.

- nummiform, uniserial, regular (Fig. 18A): medullar cells arranged into a single row; this row is perpendicular to the axis of the hair, often filling the entire medulla;
- nummiform, uniserial, chromosomal (Fig. 18B): medullar cells variably oblique and partially fused, displaying "X", "Y", or "V" shaped patterns;
- nummiform, biserial, regular (Fig. 18C): medullar cells smaller, arranged into two parallel rows without fusions.

Multiserial. The medullar cells are angular or rounded, arranged into a multiserial reticulate pattern.

- multiserial, cob-like (Fig. 18D): medullar cells polygonal or rounded, arranged into regular and parallel rows filling (almost) the entire width of hair; margin of medulla straight or crested.
- multiserial, twisted (Fig. 18E): the typical feature of the pattern is the larger number of rows of cells separated by septums; the size of the cells in the rows are irregular, the rows are locally constricted, displaying a braided pattern; margin of medulla crested.
- multiserial, chambered (Fig. 18F): medullar cells variably shaped (polygonal, rounded, fusiform) and sized, with air sacs of different size in between them; both the air sacs may span the entire width of the medulla; margin of medulla straight or crested;
- multiserial, spongoid (Fig. 18G): medullar cells rounded or polygonal; cortex usually very thin; margin of medulla straight;
- multiserial, foamy (Fig. 18H): medullar cells small, mostly rounded, close; neither the cells nor the air sacs span the entire width of the medulla; margin of medulla straight or fringed.

Tubular. Medullar cells variably shaped and sized; the air-filled (not prepared) medulla is tubular shaped and not transparent; the maximum width of the medulla does not exceed the half diameter of the hair, $m/d \leq 5$; margin of medulla straight.

- tubular, colonnade (Fig. 18I): this pattern is characterised by the large, fusiform, rounded or oblong medullar cells which often span the entire medulla; medullar cells arranged into 1–3 rows, with large air sacs between them;
- tubular, globulose (Fig. 18J): medullar cells rounded or amorph, different sized, arranged rather tightly to each other;
- tubular, fragmented (Fig. 18K): medulla is structureless and discontinous;
- tubular, amorphous (Fig 18L): medulla is amorphous, the structured cells and septae are mostly absent.
- tubular, porous (Fig. 18M): medullar cells and air sacs are very small, arranged closely; the fine structure (SEM) is porous-like; margin of medulla straight.

Medullaless hairs (Fig. 18N). The absence of the medulla is typical in the basal and apical parts of the guard hairs, it may appear also in the intermediate region between the shield and the shaft, or in the nodes of the zigzagged hairs; it can be an important taxonomic character.

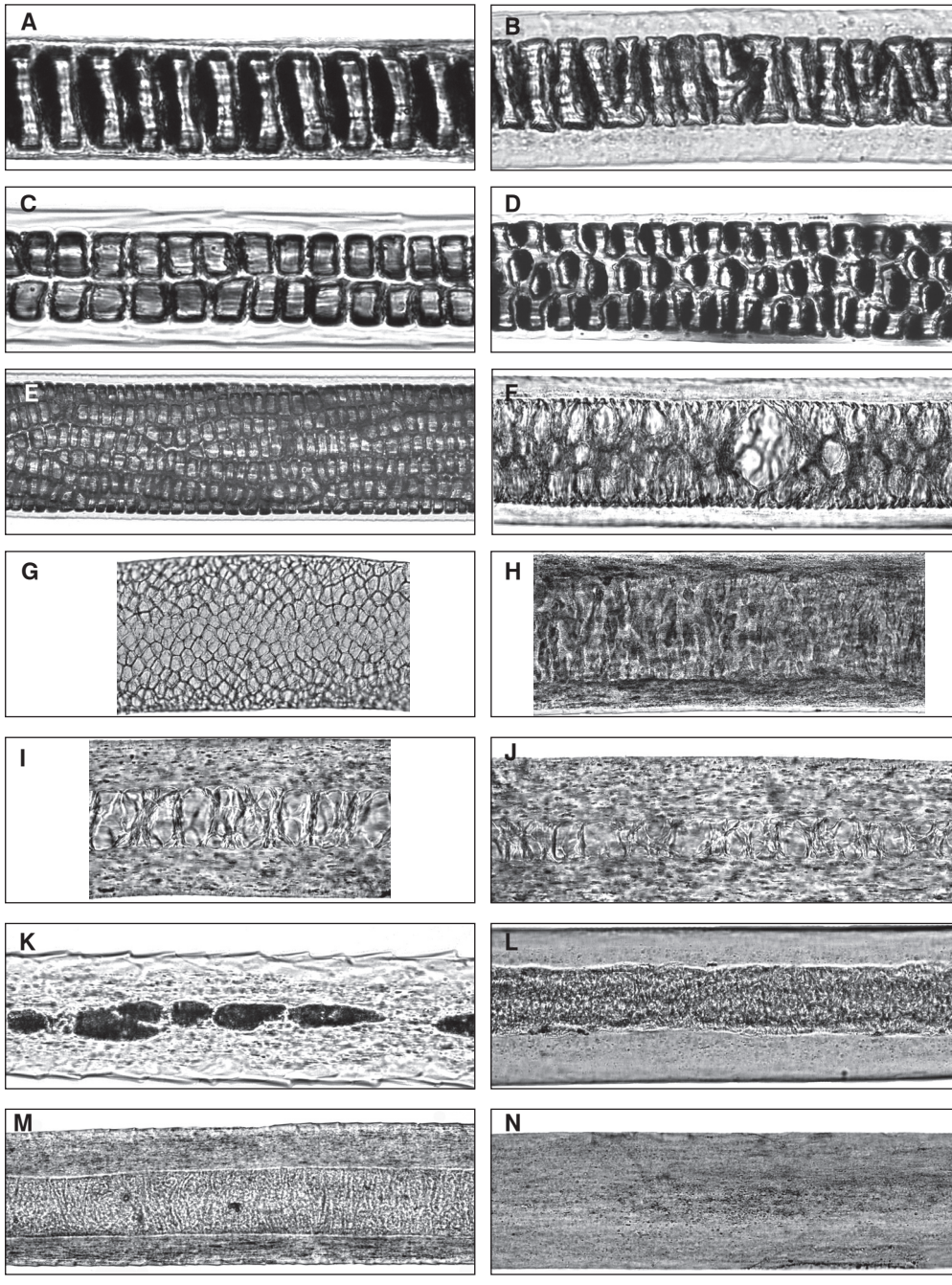


Fig. 18. Medullar patterns. **Nummiform**: A = uniserial, regular, B = uniserial, chromosomal, C = biserial; **Multiserial**: D = cob-like, E = twisted, F = chambered, G = spongoid, H = foamy; **Tubular**: I = colonnade, J = globulose, K = fragmented, L = amorphous, M = porous, N = medullaless

4.2.4. The types of cross-section

The cross-sections of the entire hair and the contour of the medulla differ in the different planes of section along the hair; the characteristic patterns are found most often in the shaft and the thickest section of the hair. The grooves and channels, their shape, depth and numbers are best studied by the sections of these areas. This information has often a great taxonomic importance; cross-section studies are made principally using SEM. The trichomorphology adopted the terminology of the geometry and the optical lenses despite that the hairs, as natural objects, display often deformations and transitional conformations, and their edges and apices are not sharp as in the geometric forms but rounded. The cross-section shape types mentioned in this book are as follows: circular, oval, oblong, convex-concave (reniform), biconvex ("eye"), biconcave ("diatom"), plano-concave, quadri-concave (amoeboid), triangular, H-shaped and U-shaped (Fig. 19).

4.2.5. Channels on the hairs

The channel is a depression on the surface of the hair. The location of the channel is typical for a given taxon as it may run along only the shield and/or the apical section, may extend onto the full length of the hair and, rarely, there might be more than one parallel channels. The channel is recognisable on both the cuticular print (Fig. 20A) and the medullar preparation (Fig. 20B) having blurred contour because of variable depth of focus. The channels might be wide or narrow, shallow or deep; in the latter type the inner surface of the channel usually shows charcteristic lamellate structure, which is best studied by SEM (Fig. 20C).

4.3. Macrostructure and patterns of hairs

The macrostructure of the hairs that can be studied by eyes or a stereomicroscope (e.g. the shape, colouration, striature, and wave) is often characteristic to a taxonomic group but, in the overwhelming majority of cases, the hairs can be identified at a supraspecific level. The basic parameters of the identification keys are the quantitative characters of the macrostructure.

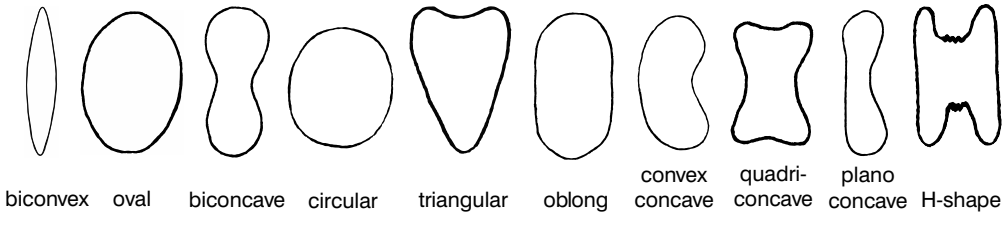


Fig. 19. Cross-section shapes of hairs

Bulb. The shape of the bulb can be characteristic for some taxa and in these cases it can be used for identification. Its shape is slightly variable due to the phase of maturation of the hair and remains on the hair only rarely after the maturation. It can be found more frequently on the hairs of the freshly moulting specimens, the samples of the hair traps or in the museum specimens preserved in alcohol. It has two main types, the ball bulb (Fig.) and the knobby bulb (Fig. 22).

Hair (Stem). The stem or flag of the mature hair can be divided usually into five sections (Fig. 21); there are also more simplified hairs having more or less equally wide stem and homogeneous microstructure along the entire hair (e.g. the underhairs and the guard hairs of some Artiodactyla groups).

1. The base or basal section is connected to the bulb; it grows partly towards the epidermis. Its shape can be tubular (Fig. 22) which is evenly thick; bulbous (Fig. 22), which is thickened in a short part forming a bulb; and bottleneck-shaped where the thin and tubular stem distally abruptly dilated (Fig. 22).

2. The shaft (partie proximale) is most often the thinnest and longest section of the stem, with diverse cuticular pattern; this pattern is usually very important for the identification.

3. The transit is the transitional section where the cuticular, and often the medullar patterns change on the stem; this section may be gradually or abruptly dilated distally.

4. The shield (partie distale) is the upper, usually wider and sometimes flattened section of the stem, which is continued in the apical section. The medullar patterns of the shield

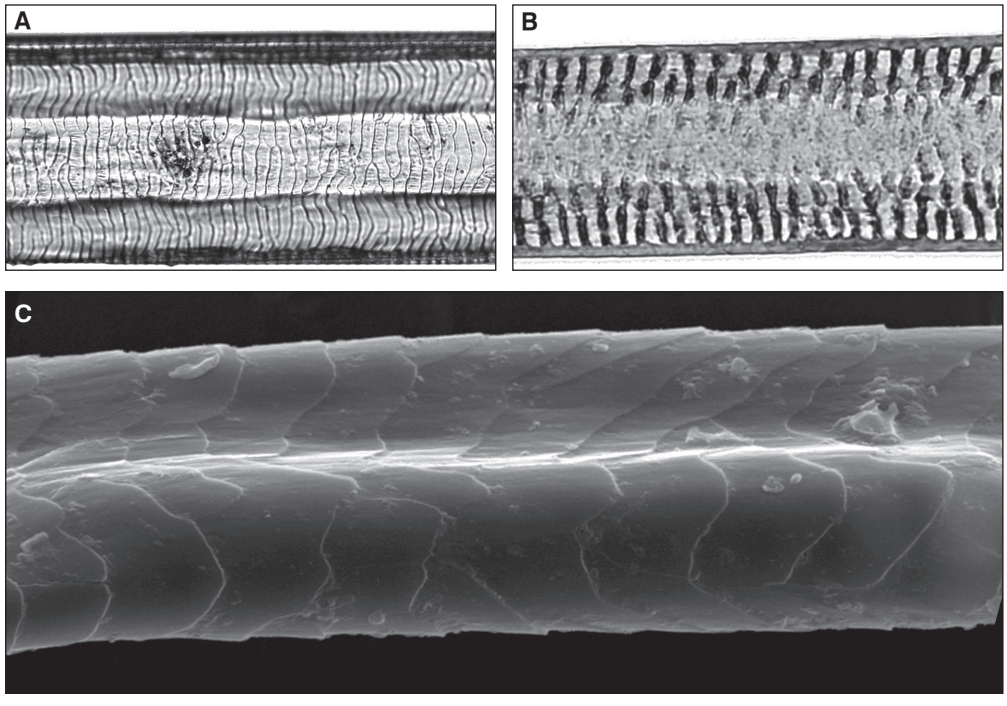


Fig. 20. Channel on cuticular print (A), medullar view (B) and scanning electronmicroscope images (C)

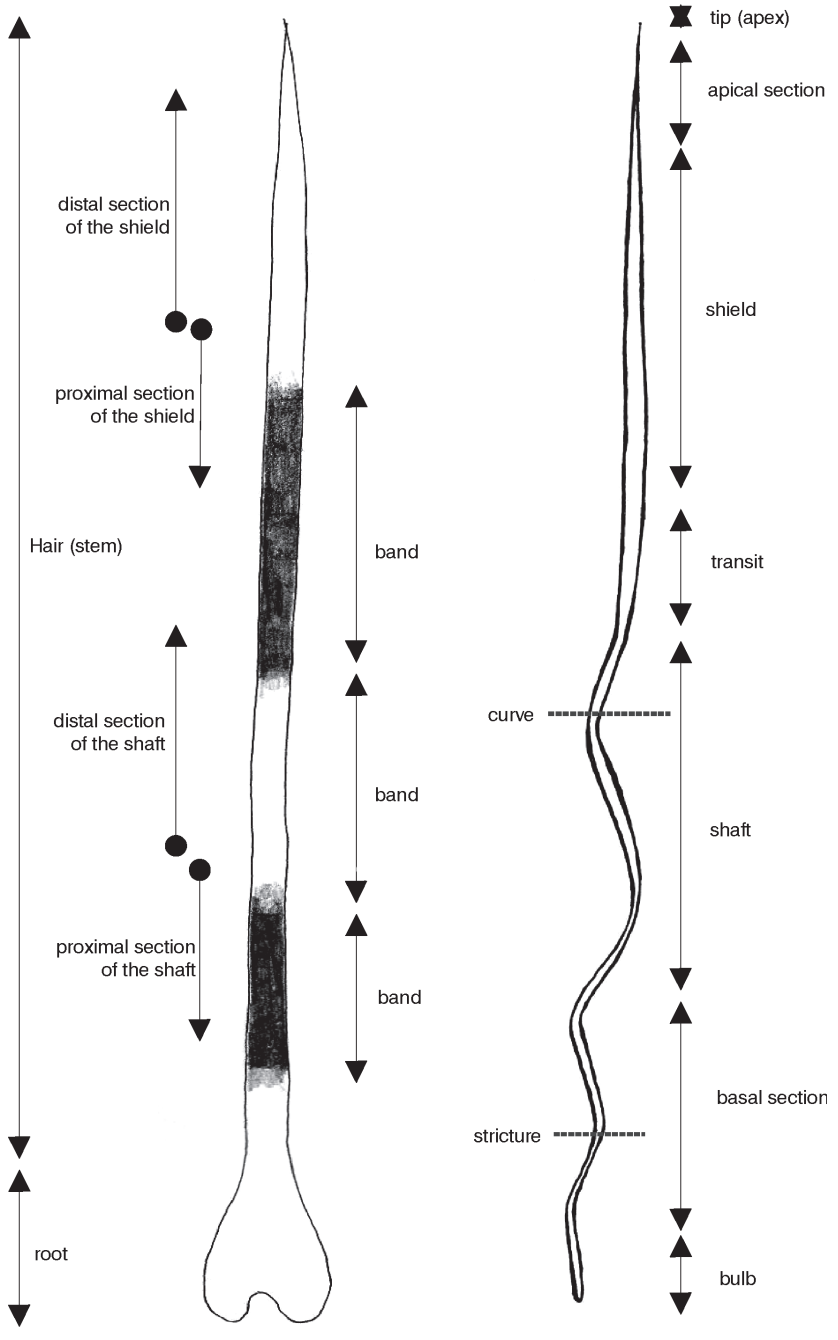


Fig. 21. Sections of the hair

are diverse and characteristic of a given taxon; therefore they are important features for the identification.

5. The apical section and the tip represent the distal end of the hair; their cuticular patterns are frequently irregular, figureless waved or sketched; in this part of the hair the medulla is absent or fragmented; and the pigmentation is mostly reduced. The length of the apical section is hardly defined but this part of the hair is characteristically tapered towards the tip and the microscopic patterns tend to be homogeneous. The asymmetrical and alternate arrangement of the apical scales produces the branching pattern (Fig.) while the symmetrical arrangement results in the telescopic pattern (Fig. 22).

The tip could be gradually tapering (Fig. 22), abruptly tapering (Fig. 22), straight, or gently arched. The tip is characteristically splitted (or barbate) (Fig. 22) in some taxa; this form is possibly linked to the rigid structure of the hair and/or the mechanical erosion due to some environmental conditions (bushy habitats, fossorial, etc.). The colouration of the tip also could be a diagnostic character.

4.3.1. Hair shape categorisation

The shape of the hairs and the evenness or the changes of its thickness from the base to the tip are important macroscopic features.

The shape of the hair could be straight, curved, wavy, crispy, undulate and combined: combined wavy or zigzag, when the shaft is wavy or zigzag-like but the shield is straight. Along the zigzagged shaft, very characteristic, short and thin strictures (Moore *et al*. 1974) can be seen. The orientation of the cuticular patterns can change in these strictures by the twists around the main axis but the patterns between these strictures are generally the same (Fig. 23).

The main types concerning the variation of the thickness along the length of the hair (before becoming thin at the tip section) are as follows: tube-shaped (uniformly thick), spine-shaped (evenly tapered from the transit towards the tip), cornet-shaped (thickened at the shield), and spatula-shaped (flattened at the shield).

4.3.2. Categories based on the colouration of the hairs

The colouration of the hairs can be categorised by the evenness and the type of changes along the full length of the hair. The main groups are as follows:

- unicolorate: the hair is unicolorous in its full length;
- polychrome: the colouration gradually changes from the base towards the apical section;
- bicolorate: the colouration of the hair distinctly and abruptly changes;
- banded: there are differently coloured sections (bands) on the hairs. The band is a unicolorous section bordered by differently coloured parts in both sides (proximally and distally); the differently coloured tip on an unicolorate hair cannot be considered as a band.

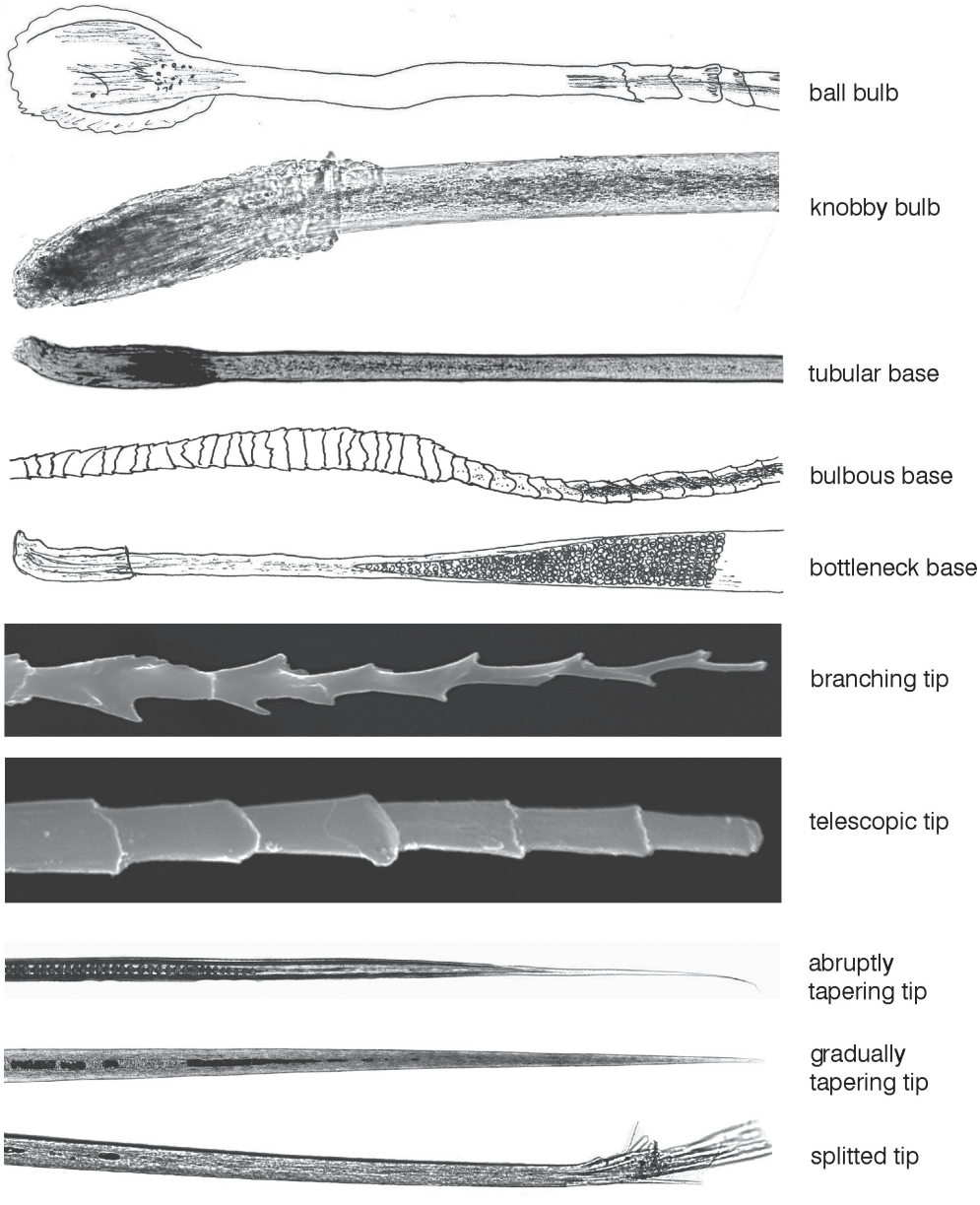


Fig. 22. Typology of hair bulb, base and tip

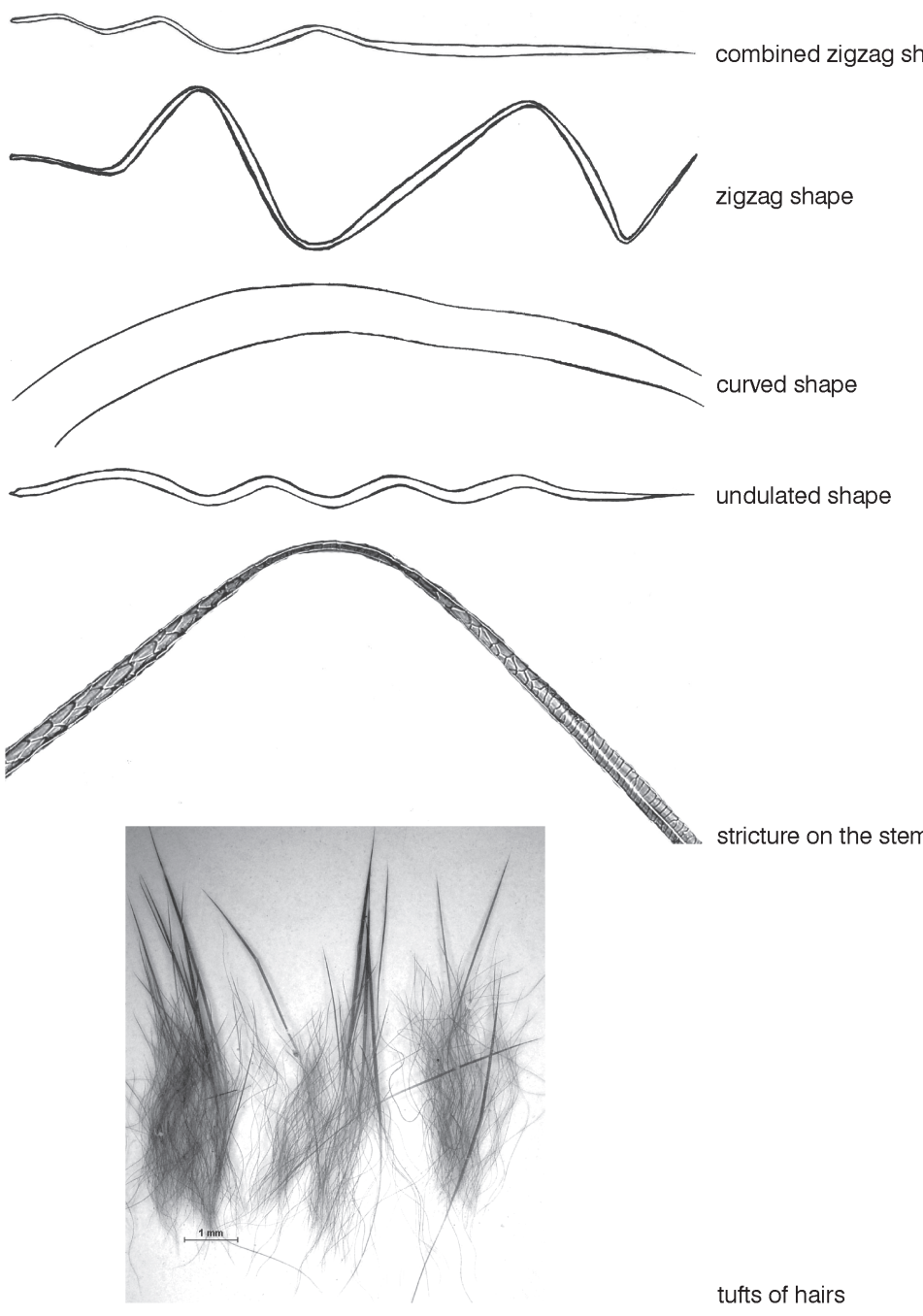


Fig. 23. Typology of shapes of hairs and tufts

4.3.3. Categorisation of the hairs by their structure and function

The former large trichomorphological works defined a number of hair types, for instance, Hausman (1930) classified the hairs by the structure and thickness of the medulla; Brunner and Coman (1974) by the structure and the function of the hairs, while Teerink (1991) used principally morphological features for its categorisation. He distinguished three main types of the hairs, the rarest, often solitary or patchy, sensory hairs named as vibrissal hairs (VH); the thicker, stronger, protective hairs, the guard hairs (GH); and the fine, dense, insulating hairs, the underhairs (UH). The present work introduces a modified system based mainly on the categorisation of Teerink, distinguishing the sensory hairs and the body hairs as the main categories.

Sensory hairs

VH (vibrissal hair) (pili tactili): The sensory or sinus hairs can be found in different parts of the body (e.g. the muzzle, the neck, the foot, or the belly); they are longer than the body hairs; they are generally straight and stiff; the best known sensory hairs are the whiskers. The follicles of the sensory hairs include tiny cavities of blood, the sinuses, in which the quantity and the pressure of the blood can be regulated by the nervous system. If the sinus is uploaded by blood, the receptor-rich walls of the follicle pressed close to the hair and, therefore, the smallest movement of the hair can be intercepted. The vibrissal hairs show most often no specific microscopic characters, and they are unsuitable for identification.

Body hairs

UH (underhair) (pili lanati): The underhairs are light and soft to the touch. In most mammal groups, the underhairs are the thinnest, shortest and most dense hairs which have a crucial importance in the thermoregulation of the body. The field samples (e.g. tufts, faeces, pellets, beddings, etc.) contain a remarkably larger amount of underhairs than guard hairs. Their shape could be curved, wavy or crispy; the shield may be dilated or evenly thick. The underhairs and the guard hairs are easily distinguished by their macroscopic and microscopic features as well, with only a few exceptions (e.g. in certain bats). The microscopic structures of the underhairs are less diverse and characteristic than those of the guard hairs therefore they are usually unsuitable for the separation of the species or generic level taxa, but the higher taxonomic categories (e.g. orders) sometimes can be defined also by the features of their underhairs.

Special hair types are the lanugo and the vellus. The lanugo appears intra-uterine on the embryo and the animals most often lose it prenatally or soon after the birth. The term vellus is used generally for the humans, indicating those depigmented, very thin and soft, medullaless hairs, which have an important role in the mechanical perception and the thermoregulation. It is worth to note that the vellus is not identical with the underhairs. In the *Homo sapiens*, the vellus is typical of the infancy but remains also throughout the life as less visible, short and sparse hairs.

GH (guard hair) (pili tectori). The guard hairs are longer and stronger hairs defining the colouration and patterns of the fur, as well as its consistency and thickness. The guard hairs develop in the primary follicles, and in certain cases, more guard hairs or underhairs can grow up from the same follicle; this structure is called as club-hairs. The diagnostic morphological features are best visible on the catagen and telogen hairs.

The guard hairs have three main types as follows:

- GH0 (bristle hair): straight and strong hairs; the longest and thickest guard hairs which are the rarest types of hairs in the fur. These ones are grow most frequently on the back, dispersedly or grouped in larger patches. The touch of the GH0 can be silky and soft, or rough, strong, often modified bristle hairs, like the spines. The GH0 hairs are less suitable for the identification, with a few exceptions, like the bristles of the wild boar.
- GH1 (primary guard hair): most often straight, less frequently curved, wavy or undulating hairs with characteristic microscopic structures which provide well-defined diagnostic features for the identification;
- GH2 (secondary guard hair): the thinnest guard hairs; their shape could be curved, wavy or undulating, sometimes combined, wavy or zigzag on the shaft and straight on the shield; this type of guard hairs might possess the best identification characters.

4.4. Structure and typology of furs

Structure of the fur

The term "fur" refers to the body hairs of the mammals; it is called in the different literature sources as pelage, pelt, coat or skin, but with slightly different meaning: for instance, the term "skin" is used in anatomy and for the fur of museum specimens; the term "pelt" is used mainly for the fur used for industrial purposes. The fur includes all the body hairs of different structure and function covering the body of the animal, consequently it is rather heterogeneous and the distribution of the different hairs is uneven on the body surface. The hairs are directed in the majority of the mammal species from the backbone to the belly and from the head to the bottom/tail. The density of the fur can be strongly variable in the different parts of the body; there are entirely hairless areas like the paw pads, nipples, lips, genital organs, etc. The structure, colouration and density of the fur depend on the age, the environmental and the physiological conditions, and may also show seasonal changes. In a given taxon, the fur can display special morphological features related to the life strategy and behaviour, the seasonal and macroclimatic conditions, and the physical fitness.

The dense, fine and homogeneous fur is characteristic of the infants and of the belly of terrestrial mammal species.

The structure of the fur, the thickness, colours of GH and UH layers can be studied by laying hairs in the fur, using a small comb. The tuft (Fig. 23) is a small bundle of hairs which usually represents well the different types of hairs; tufts are frequent natural field samples because of the scratching, rubbing and during the seasonal moulting of mammals.

Colouration of the fur

The colouration results from the reflection or emission of light from the different surfaces. The physical colours of the hairs are given by the pigments (presence and rate of eumelanin and phaeomelanin) while the colouration of the fur is the result of the complex general effect of the mass of variably coloured hairs. The objective description of the furs and their unit hairs is very difficult, with a lack of possible standardisation. The impression about the colouration of the fur is highly dependent on the observer and the circumstances influenting the observer (brightness, background colours, etc.). The colouration of the fur of the examined specimens depends strongly on the conditions of the collecting/observation; in the case of museum specimens, it also depends on the preparation methods, techniques and conditions of storage.

The knowledge of the polymorphism of the colouration and pattern of the fur in a given taxon helps the identification of the individuals that, therefore, require the study of the intra-populational and intraspecific variation, the recognisation of the geographical distribution of the different pattern types, and also phylogeographical analysis of a given taxonomic group. The morphometric studies, the statistical analysis of the digital images and the three-dimensional graphic programmes (3-D computer matching system) provide an immense help in the identification and characterisation of the patchy, striolate and masked patterns (Kelly 2001).

There are different objective colour measuring methods. One of them is the reflective spectrophotometry which can be used also for the measuring and the comparative analysis of the colours of the hairs (Vaughn *et al*. 2009).

The photo documentation of the furs in natural daylight conditions, using less reflective (dull) background can be ideal for the comparative studies. In order to preserve the natural colours, the use of the flashlight or a strong direct sunshine should be avoided.

Typology of furs

The structure and the basic colouration of the fur are defined by the general effect of the different hair types. The furs can be characterised by their density (compact or loose), touch (velvety, silky, coarse, greasy), colouration and pattern. Due to the different characters of the fur on the different parts of the body, the categories provided below refer to the back and the lateral side.

Colouration types of the fur (Fig. 24):

- unicolorous fur: the fur is rather uniformly coloured. It is important to note that there are no really unicolorous furs as the shafts of the guard hairs and the underhairs always have somewhat different colour or shade; for instance, in case of the unicolorous fur of the otter;
- grizzled fur: the fur has numerous longer and more densely mixed white(ish) or light striolate hairs which provides a grizzled appearance; this type of fur is typical, for instance, of the certain canids and rodents;

– marbled fur: the shades of the different colours and the contours of the fur patterns are blurred due to the long guard hairs with differently coloured shafts and/or the dense underhairs; the moiré effect is often remarkable; this type of fur is characteristic of some canids, felids and bats;
– mottled fur: differently shaped and coloured spots, patches, stripes, etc. are found on the given part(s) or on the entire body of the animals; this pattern is typical of different Artiodactyla and Carnivora groups, some rodents, etc.

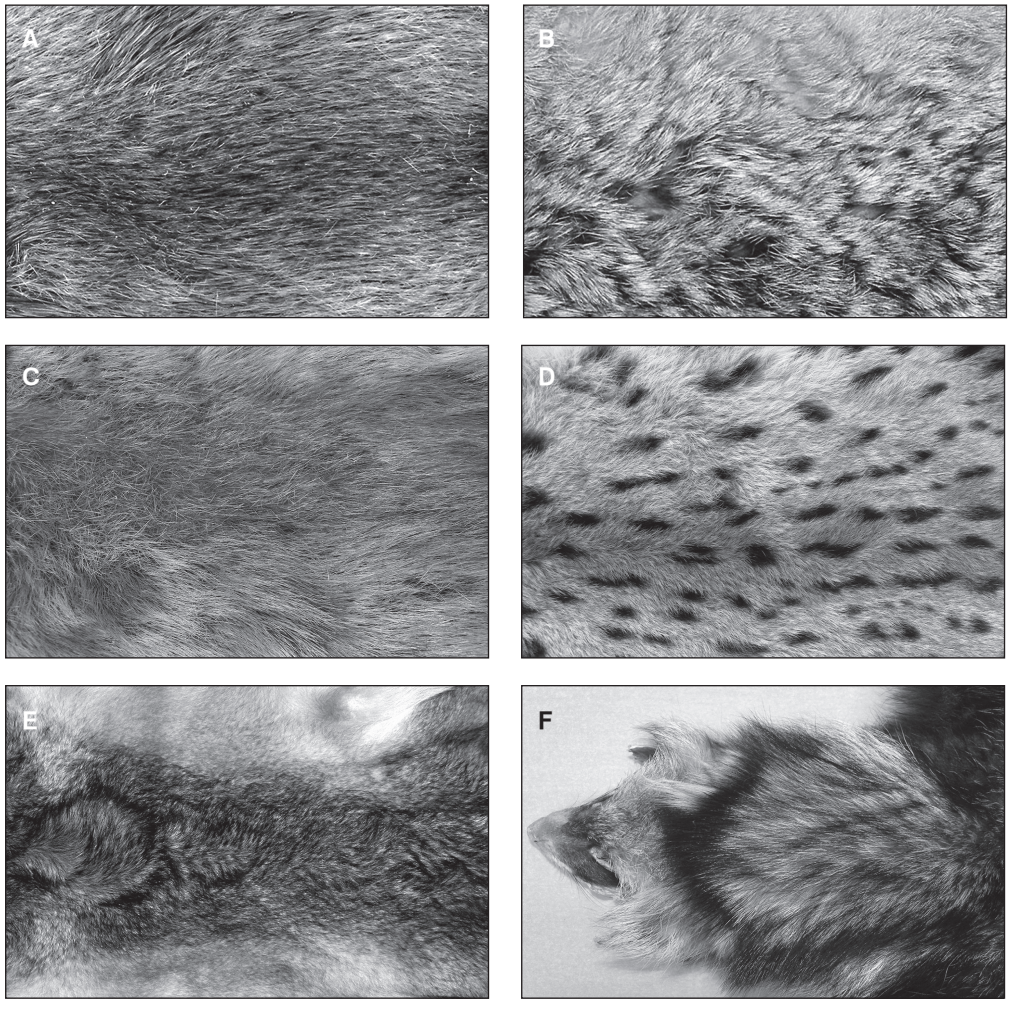


Fig. 24. Fur pattern types. A = unicolorate, B = grizzled, C = marbled, D = mottled, E = black-backed, F = masked face

Contoured patterns of the fur (Fig. 24):

- masked-face pattern: this type of pattern on the face composed from distinct and contoured, often aposematic stripes or patches arranged crosswise or lenghtwise around the eyes;
- black-backed pattern: a pattern where the darker backside fur expands towards the rump and the sides of the remarkably paler coloured body, becoming stepwise or abruptly lighten downwards;
- contoured body patterns: the breast, the rump, the undertail, the shoulders, the legs might show sharp-cutted, different colouration and/or pattern;
- ringed-tail pattern: distinct dark and light, full or incomplete rings on the tail.

Methods of investigation 5

5.1. Reference collection of hairs

Building up a reference collection of hairs

The different populations of the widely distributed mammal taxa may show a considerable variability in their hair and fur characteristics. This variability may be linked to the environmental factors like the climatic and other physical conditions of the habitats, or nutrition, genetic, etc. reasons, which can be clarified by the study of this variability.

The major aim of the reference hair collections is to assort a representative stock of hair samples of as many taxa and their different populations as possible. The treatment and register of this collection should be in conformity with that of the museum specimens. The basic data for each sample (if available) are the name of the taxon, the locality, the date of the collection of the specimen, the origin and/or sampling method of the hair sample (e.g. plucking, hair-tapping, feces, bird nest, etc.), the sampled part of the body, the sex and the known or estimated age (age-group) of the specimen.

The reference hair collection requires the proper identification of the species at species (or genus) level and only adult specimens with healthy and fully developed fur are chosen to collect the hairs. Thus, the reference hair collection used for the preparation of this book includes only hair samples of museum specimens. However, the morphological study of the furs has been completed by the investigations of living specimens (in the Nature or in zoos), and photodocumentations as the colours of the fur of museum specimens are frequently change (most often faded) during the treatments and the storage.

Fig. 25. Hair sampling with adhesive tape

The sampling of the fur of the museum specimens require practice and care, due to the potential damages of the old, dry and often rigid skin, though there are remarkable differences between the executions of the procedure. An adhesive tape (appr. 1 cm × 2 cm), or a small, fine-tooth comb are the most recommended tools to get the necessary hairs; certain featured guard hairs were removed using forceps; this collecting method will not cause visible loss of hairs even in the very old specimens (Fig. 25).

The sampling areas on the furs were the dorsal spinal and lateral regions, mainly around the shoulders. The offered standard sample size requires 30–50 hairs; this sample size is fairly enough for the morphological investigations, for the preparations and the subsequent statistical analyses.

The parameters provided in the Atlas for each species are the quantitative and qualitative hair characters.

The quantitative features of the guard hairs (GH):

- the maximum length of the hair (l_{max});
- the maximum width (diameter) of the shield (d_{max});
- the average value of the medullar index (m/d_x): rate of the average of the width of the medulla at the maximum width of the shield and the average of the maximum diameter of the shield.

The qualitative features of the guard hairs (GH):

- the shape and colour of the hair;
- the cuticular and medullar patterns of the proximal section of the hair (bulb, basal part and shaft);
- the cuticular and medullar patterns of the transit section of the hair;
- the cuticular and medullar patterns of the distal section of the hair (shield, apical section) at the thickest part of the hair;
- the shape of the cross section (primarily on the shield).

5.2. Preparation techniques

5.2.1. Preparation of the hair samples

The preparation of the hair samples requires a careful and thorough cleaning of the hairs from the pollutions, in all cases, even the hairs originate from skin samples from museum stored specimens, or are fresh samples from living mammals or random, moulted samples from the field. The hairs are often very dirty due to the behaviour of the animals or certain weather conditions; the furs and museum specimens are treated with different chemicals (e.g. arsenic, naphthalene, other insect repellent or poisoning chemicals, aluminium compounds, etc.); and variable thick deposits appear on the hairs during the long storage.

The most frequently used solvents for the chemical cleaning are the concentrated acetone and the min. 70% ethanol, which can dissolve both the hydrophilic and the hydrophobous pollutions from the surface of the cuticular scales and from the smaller grooves and cavities. The hairs can be stored in glasses containing 1:1 mixture of the two solvents; the manual shaking promotes better and quicker cleaning but the use of bolter or ultrasonic cleaner (e.g. Bandelin Sonorex RK31) provides the best results. The well-cleaned hairs are then suitable for the light and the scanning microscopic studies; the cleaned samples are recommended to store in 70% ethanol before the studies or storage in the reference collections.

5.2.2. Preparation of the cuticula

The study of the cuticular patterns requires special microscopic techniques. The prints can be prepared with different celluloid-based compounds, nail varnish or gelatine, all such

compounds having both advantages and disadvantages. The preparation of the gelatine prints is more time consuming than the use of the other print mediums but the quality of the print is the best. The 10% gelatine solution (10 vv% gelatine powder and 90 vv% distilled water), preserved by some thymol crystals, should be boiled up with continuous stirring. As in the freshly made gelatine solution, the tiny air bubbles remain for a long time and may distort the contours of the cuticular pattern, it is recommended to prepare the gelatine solution a few days before and only warm up before making the prints. The well-prepared and thymol preserved jelly of gelatine solution will be bubbleless, easily manageable and several times utilizable; it can be stored for months until the first warming up. The warming up of the jelly-like gelatine is best in a microwave oven (in a plastic or glass tube standing in a cup of water; on 750W, ca 10–30 seconds) or by putting it into a boiling water-bath until it becomes fluid. The gelatine liquid should be evenly dispersed on the glass slide and when the shrinking begins (1–3 minutes, depending on the temperature of the room and the thickness of the gelatine layer), the hairs can be embedded onto the gelatine layer. The hairs are proposed to put into the gelatine in the same position and parallel to the longer edge of the slide. It is important to note that if the gelatine is not dense enough then the cuticular patterns of the immersed hairs cannot be studied or only in little parts, due to the continuous sinking in the medium. The gelatine will be solid after some 30 minutes and the hairs can be removed using a forceps, a stronger brush or by hands. The hairs themselves will not be damaged, so this method can be used even for the study of the hairs of type specimens or very rare species, and small crucial samples collected in the field. The removed hairs can be put back into the reference collection or used for the subsequent studies (e.g. the investigation of the medullar patterns by preparing the cross sections). For the permanent slides, the embedded hairs must be covered by cover glass, which prevent the hairs from damages and pollution. The corners of the cover glass are better fix with some glue or Canada balm. This fixing should be done carefully as, if the glue runs over the inner surface of the cover glass, the print (which is a depression in the solid gelatine) will be filled with the glue, shadowing the fine cuticular patterns.

5.2.3. Preparation of the medulla

The hairs prepared for the study of the medulla should be fixed on the microscopic slide which can be easiest produced by putting drops of Canada balm along the left edge of the slide. The hairs have to be laid in these drops, parallel to the longer edge of the slide and in the same direction (from base to tip). After the small drops dried, the hairs are better fixed in a few other points with the same way. The hairs have to be cut with sharp blade between these fixed points. The most informative part is the thickest part of the shield but sometimes the shaft and the transit could be also necessary for the studies.

For the temporary studies, we can drop paraffin oil or glycerine on the cutted surfaces of the hair samples; for the preparation of permanent microscopic slides, the use of Canada balm (a special turpentine, which does not crystallize with age, its optical properties do not deteriorate), or euparal (NBR: Nitrile-caoutchouc) are recommended.

A longer incubation in the above-mentioned mediums pushes out the air sacs and bubbles, therefore, the entire hair becomes more transparent and the characteristic medullar patterns will became better visible. The medullar structure of the thinner, pale or transparent hairs sometimes visible with light microscope without cutting or saturation.

5.2.4. Sectioning

The sectioning has three major types depending on the angle of the cut. The most frequent is the cross-section of which the cut is perpendicular to the main axis; the two other types are the longitudinal and the oblique direction of the cut.

Every section may provide new, additional information about the microstructures, which may be crucial for the taxonomic studies or the proper identification. The embedding and cutting of the thin, elastic and slippery hairs is difficult. If the aim of the study is only to investigate the contour of the cross section of the hair, the cutting is rather simple. The cork method (Heyn 1954) is a practical, clever method: we have to roven the hairs into the cork by sewing machine needle and then cut them by blades. We can use, similarly to the plant histological work, kerria, using or elderpith and the imbedded hairs can be cut by blade into short pieces. These tiny fragments can be washed out by distilled water and take out by a fine brush. Another simple method is to glue the hairs on a microscopic glass with celluloid or euparal ointment and cut the hair at the selected points. The slices of hair have to be placed directly into gelatine, Canada balm, Euparal; or in case of SEM studies, onto the carbonised, electrically conductive, double-sided adhesive tape. The imbedded slices can be studied by light miscroscope and the 200–400× magnification is often suitable for the recognisation of the contour characters. The preparation of much more thinner slices requires the use of microtom or vibratom.

5.2.5. General habit preparation

The general habit preparations are very useful for the study of the shape of the hairs, the basic structure of the medulla, the polarity of the cuticular scales, margins of the scales and the distribution of the pigments. This method requires the examination of the intact hair using low magnification by light-microscope; the intact hair can be imbedded into gelatine, nail varnish, immersion oil or can be layed without fixing, but must be covered by a cover glass. The view we got is called as the "transparent view", which will not present the microstructure of the hair, but might help the identification.

5.3. Microscopy and photography

The hairs are transparent, low-contrast biological objects; their structure and patterns can be investigated by stereo-, light- and scanning electron microscopes.

The general habit preparations placed on millimetre squared paper were investigated using stereomicroscope. The shape and colouration of hairs were registered and their length was measured. The optimal domain of magnification, in correlation with the size and transparency of the hair samples, was between 1–10×; a LEICA MZ95 stereomicroscope was used for these studies.

The permanent preparations of hairs are mounted on glass slides. Such slides are suitable for the study of the cuticula, the medulla and the cross section and were investigated by light microscope. The optimal domain of magnification, in correlation with the size and transparency of the hair samples, was 200–400×. Nikon Eclipse 80i photomicroscope with Nikon DS-Fi1 digital camera and Axio Imager.A2 microscope, AxioCam MRc 5 (Zeiss) digital camera with Axiovision software were used for these studies.

The scanning electron microscopy opened a new window for the micro- and ultrastructures thanks to the imagery technique and high magnification. This aspect provides details on the configuration of the fine structure of the cuticula, cortex, pigments and medulla. The method requires precise cleaning of hair samples otherwise the remnants of the small pollutive particles can cover the information to be studied. Chernova (2003) used to perform thermal chemical hydrolysis on the hair samples for her SEM investigations. The hair fragments were placed in a 10-15% solution of NaOH and maintained at a temperature of 50–90°C for maceration. The careful cleaning is very important as the maceration can led to the collapse of the keratinous cells resulting in the loss of information. This kind of maceration method was not applied in this book.

The dry biological samples are most often non-conductors therefore the ultra-thin covering of the sample surfaces with a good conductor metal are usually indispensable. Therefore, the hair samples were cleaned, dried and positioned on the adhesive tape placed on the stubs. The samples were coated with platinum, gold, gold-palladium, or carbon using a sputter coater (LEICA EM SC540) mostly at 30mA and 5×10^{-2} mbar and scanned with an electron microscope (ZEISS EVO-LS-IOSEM, FEI-XL-30-ESEM, TESCAN-VEGA-II-LSU, JEOL JSM 6610LS) and FEI Quanta 3D dual beam scanning electron microscope (SEM/FIB), usually at 15–17 kV. The magnifications used in the SEM depend on the aims of the investigations, the information content of the sample and the possibilities allowed by the available physical parameters.

The furs were photographed by a Samsung WB5000 camera, using mat, light background and natural light, avoiding the flashlight whenever it was possible.

6 Checklist of the Central European mammal species

Erinaceomorpha

Erinaceidae

Erinaceus roumanicus Barrett-Hamilton, 1900 – Northern White-breasted Hedgehog
Erinaceus europaeus Linnaeus, 1758 – Western European Hedgehog

Soricomorpha

Soricidae

Neomys anomalus Cabrera, 1907 – Miller's Water Shrew
Neomys fodiens (Pennant, 1771) – Eurasian Water Shrew
Sorex alpinus Schinz, 1837 – Alpine Shrew
Sorex araneus Linnaeus, 1758 – Common Shrew
Sorex arunchi Lapini & Testone, 1998 – Udine Shrew
Sorex coronatus Millet, 1828 – Crowned Shrew
Sorex minutus Linnaeus, 1766 – Eurasian Pygmy Shrew
Crocidura leucodon (Hermann, 1780) – Bicoloured white-toothed Shrew
Crocidura russula (Hermann, 1780) Greater white-toothed Shrew
Crocidura suaveolens (Pallas, 1811) – Lesser white-toothed Shrew

Talpidae

Talpa europaea Linnaeus, 1758 – Common Mole

Chiroptera

Rhinolophidae

Rhinolophus blasii Peters, 1867 – Blasius's Horseshoe Bat
Rhinolophus euryale Blasius, 1853 – Mediterranean Horseshoe Bat
Rhinolophus ferrumequinum (Schreber, 1774) – Greater Horshoe Bat
Rhinolophus hipposideros (Bechstein, 1800) – Lesser Horseshoe Bat
Rhinolophus mehelyi Matschie, 1901 – Mehely's Horseshoe Bat

Vespertilionidae

Eptesicus nilssonii (Keyserling and Blasius, 1839) – Northern Bat
Eptesicus serotinus (Schreber, 1774) – Serotine
Pipistrellus kuhlii (Kuhl, 1817) – Kuhl's Pipistrelle
Pipistrellus nathusii (Keyserling and Blasius, 1839) – Nathusius' Pipistrelle
Pipistrellus pipistrellus (Schreber, 1774) – Common Pipistrelle
Pipistrellus pygmaeus (Leach, 1825) – Soprano Pipistrelle
Nyctalus lasiopterus (Schreber, 1780) – Greater Noctule
Nyctalus leisleri (Kuhl, 1817) – Leisler's Bat
Nyctalus noctula (Schreber, 1774) – Noctule
Myotis alcathoe Helversen and Heller, 2001 – Alcathoe Whiskered Bat
Myotis aurascens Kuzjakin, 1935 – Steppe Whiskered Bat
Myotis bechsteinii (Kuhl, 1817) – Bechstein's Bat
Myotis blythii (Tomes, 1857) – Lesser Mouse-eared Bat
Myotis brandtii (Eversmann, 1845) – Brandt's Bat

Myotis capaccinii (Bonaparte, 1837) – Long-fingered Bat
Myotis dasycneme (Boie, 1825) – Pond Bat
Myotis daubentonii (Kuhl, 1817) – Daubenton's Bat
Myotis emarginatus (Geoffroy, 1806) – Geoffroy's Bat
Myotis myotis (Borkhausen, 1797) – Greater Mouse-eared Bat
Myotis mystacinus (Kuhl, 1817) – Whiskered Myotis
Myotis nattereri (Kuhl, 1817) – Natterer's Bat
Plecotus auritus (Linnaeus, 1758) – Brown Long-eared Bat
Plecotus austriacus (Fischer, 1829) – Grey Long-eared Bat
Plecotus macrobullaris Kuzjakin, 1965 – Mountain Long-eared Bat
Hypsugo savii (Bonaparte, 1837) – Savi's Pipistrelle
Barbastella barbastellus (Schreber, 1774) – Western Barbastelle
Vespertilio murinus Linnaeus, 1758 – Particoloured Bat

Miniopteridae

Miniopterus schreibersii (Kuhl, 1817) – Schreiber's Bent-winged Bat

Molossidae

Tadarida teniotis (Rafinesque, 1814) – European Free-tailed Bat

Lagomorpha

Leporidae

Lepus europaeus Pallas, 1778 – European Hare
Lepus timidus Linnaeus, 1758 – Mountain Hare
Oryctolagus cuniculus (Linnaeus, 1758) – European Rabbit

Rodentia

Sciuridae

Sciurus vulgaris Linnaeus, 1758 – Red Squirrel
Eutamias sibiricus (Laxmann, 1769) – Siberian Chipmunk
Spermophilus citellus (Linnaeus, 1766) – European Ground Squirrel
Spermophilus suslicus (Güldenstaedt, 1770) – Speckled Ground Squirrel
Marmota marmota (Linnaeus, 1758) – Alpine Marmot

Gliridae

Eliomys quercinus (Linnaeus, 1766) – Garden Dormouse
Dryomys nitedula (Pallas, 1778) – Forest Dormouse
Glis glis (Linnaeus, 1766) – Edible Dormouse
Muscardinus avellanarius (Linnaeus, 1758) – Hazel Dormouse

Dipodidae

Sicista betulina (Pallas, 1779) – Northern Birch Mouse
Sicista subtilis (Pallas, 1773) – Southern Birch Mouse

Muridae

Apodemus agrarius (Pallas, 1771) – Striped Field Mouse
Apodemus alpicola (Heinrich, 1952) – Alpine Field Mouse
Apodemus flavicollis (Melchior, 1834) – Yellow-necked Field Mouse
Apodemus sylvaticus (Linnaeus, 1758) – Wood Mouse
Apodemus uralensis (Pallas, 1881) – Pygmy Field Mouse
Micromys minutus (Pallas, 1771) – Eurasian Harvest Mouse
Mus musculus Linnaeus, 1758 – House Mouse
Mus spicilegus Petényi, 1882 – Steppe Mouse
Rattus norvegicus (Berkenhout, 1769) – Brown Rat
Rattus rattus (Linnaeus, 1758) – Black Rat

Spalacidae

*Nannospalax (*superspecies) *leucodon* Nordmann, 1840 – Lesser Blind Mole Rat
Spalax antiquus Méhely, 1909 – Mehely's Blind Mole Rat
Spalax zemni (Erxleben, 1777) – Podolian Blind Mole Rat
Spalax graecus Nehring, 1898 – Balkan Blind Mole Rat

Cricetidae

Cricetus cricetus (Linnaeus, 1758) – Common Hamster
Arvicola amphibius (Linnaeus, 1758) – Eurasian Water Vole
Arvicola scherman (Shaw, 1801) – Montane Water Vole
Myodes glareolus (Schreber, 1780) – Bank Vole
Chionomys nivalis (Martins, 1842) – European Snow Vole
Dinaromys bogdanovi (Martino, 1922) – Balkan Snow Vole
Microtus agrestis (Linnaeus, 1761) – Field Vole
Microtus arvalis (Pallas, 1778) – Common Vole
Microtus bavaricus (König, 1962) – Bavarian Vole
Microtus levis Miller, 1908 – East European Vole
Microtus liechtensteini (Wettstein, 1927) – Liechtenstein's Pine Vole
Microtus oeconomus (Pallas, 1776) – Root Vole
Microtus subterraneus (de Sélys-Longchamps, 1836) – Common Pine Vole
Microtus tatricus Kratochvíl, 1952 – Tatra Vole
Ondatra zibethicus (Linnaeus, 1766) – Muskrat

Castoridae

Castor fiber Linnaeus, 1758 – Eurasian Beaver

Myocastoridae

Myocastor coypus (Molina, 1782) – Nutria

Carnivora

Canidae

Canis lupus Linnaeus, 1758 – Grey Wolf
Canis aureus Linnaeus, 1758 – Golden Jackal
Vulpes vulpes (Linnaeus, 1758) – Red Fox

Nyctereutes procyonoides (Gray, 1834) – Raccoon Dog

Ursidae

Ursus arctos Linnaeus, 1758 – Brown Bear

Procyonidae

Procyon lotor (Linnaeus, 1758) – Northern Raccoon

Mustelidae

Mustela erminea Linnaeus, 1758 – Stoat
Mustela nivalis Linnaeus, 1766 – Weasel
Mustela lutreola (Linnaeus, 1761) – European Polecat
Neovison vison (Schreber, 1777) – American Mink
Mustela putorius Linnaeus, 1758 – European Polecat
Mustela eversmanii Lesson, 1827 – Steppe Polecat
Vormela peregusna (Güldenstädt, 1770) – Marbled Polecat
Martes martes (Linnaeus, 1758) – Pine Marten
Martes foina (Erxleben, 1777) – Stone Marten
Lutra lutra (Linnaeus, 1758) – European Otter
Meles meles (Linnaeus, 1758) – European Badger

Felidae

Felis silvestris (Schreber, 1775) – Wild Cat
Lynx lynx (Linnaeus, 1758) – Eurasian Lynx

Artiodactyla

Suidae

Sus scrofa (Linnaeus, 1758) – Wild Boar

Bovidae

Bison bonasus (Linnaeus, 1758) – European Bison
Ovis orientalis Gmelin, 1774 – Mouflon
Capra ibex Linnaeus, 1758 – Alpine Ibex
Rupicapra rupicapra Linnaeus, 1758 – Alpine Chamois

Cervidae

Cervus elaphus Linnaeus, 1758 – Red Deer
Cervus nippon Temminck, 1838 – Sika Deer
Odocoileus virginianus (Zimmermann, 1780) – White-tailed Deer
Dama dama (Linnaeus, 1758) – Fallow Deer
Alces alces (Linnaeus, 1758) – Moose
Capreolus capreolus (Linnaeus, 1758) – European Roe Deer

Perissodactyla

Equidae

Equus ferus ssp. *przewalskii* Poliakov, 1881 – Przewalski's Horse

Hair atlas of the Central European mammals

7

The Hair Atlas describes and illustrates the trichomorphological patterns of the 123 mammal species occurring in the Central European region. The taxonomy and nomenclature of the species is based primarily on the works of Wilson and Reeder (2005), Mitchell *et al*. (2009), Ascher and Helgen (2010), the related newest publications and the official homepage of the IUCN Red List of Threatened Species.

The overwhelming majority of the examined specimens are preserved in the Mammal collections of the Hungarian Natural History Museum (Budapest; HNHM) and the Natural History Museum Vienna (Wien; NHM); additional specimens were studied in the Tiroler Landesmuseum Ferdinandeum (Innsbruck; TLMF) and the Naturhistoriska Riksmuseet (Stockholm; NRM). The characterisation of each species is based on the studies of at least three specimens originating from different areas of their distribution, analysing the sexual and seasonal differences, if they relevant and if they were available within the frame of this work. The complete data set including also the museum codes of the investigated specimens will be available on the homepage of this book as a freely accessible file.

The units of descriptions of the discussed taxa have a standard structure, following the systematic order: firstly the orders, then the families, the genera and, finally, the species. Certain species can be identified at species level while others are not; there are several cases when the species themselves can be hardly distinguished or even inseparable from each other, but two or more taxa (species and/or genera) represent together a well-supported, identifiable group based on their trichomorphological patterns. These ones are called as "twin-taxa" (Tóth 2002) and are characterised in the same unit.

All diagnoses include the description of the guard hairs, among them the diagnostic and, where it is possible, the taxonomic characters of the given taxonomic group.

Diagnostic character refers to those characters which represent the nodes of the dichotomic identification keys; the identification of the given taxon is based on these features.

The sequence of the descriptive paragraphs in the Atlas chapter are as follows:

- fur: morphological features of the fur;
- hair, macroscopic: macroscopic features of the different types of hairs;
- hair, microscopic: diagnosis of the microscopic hair characters of guard hairs;
- size: quantitative values of the guard hairs: the maximum length (l_{max}); the maximum diameter (d_{max}); the average value of the medullar index (m/d_x);
- taxonomic characters: indicates the distinctive, supposedly apomorphic feature(s) which is/are characteristic of the given taxon; these features are important for the definition of the taxonomic status and relationship, too.
- remarks: additional, non-morphological information (e.g. physiology) is provided for certain taxa.

The figures on the microscopic hair patterns are selected with the aim to focus only the diagnostic and taxonomic characters of the cuticula, medulla, section, transparent view, bulb, tip, etc. The figures are positioned from the left to the right, from the base of the hair towards the tip. The magnification of the light microscopic pictures is 200–400× that of the SEM images is 400–3000×. The proper scale and magnification do not shown on the images but serve the best information.

7.1. Erinaceomorpha

The order is characterised by the modified guard hairs, the spines, which cover the main part of the body. In case of Erinaceinae (spiny hedgehogs), these modified hairs are strong spines which cover densely the dorsal side from the front to the rump and down to the middle of the sides; in certain species, there are spines also on the tail.

Erinaceidae

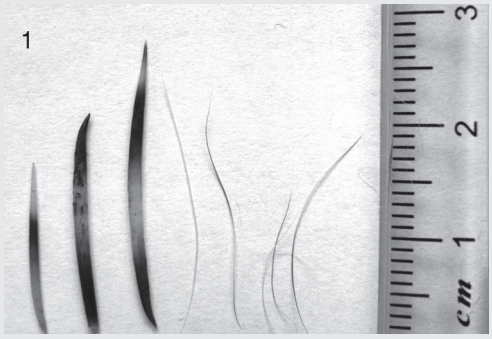
Erinaceus roumanicus & *Erinaceus europaeus*

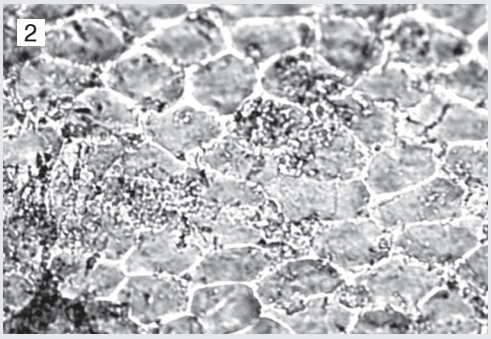
FUR: The two Central European hedgehog species are very similar externally. The number of the spines (GHspine) of an adult hedgehog is on average between 7,000 and 9,000; the hedgehogs have practically no underhairs in the spiny areas of the body. The ground colours of the spines are most often white, brown and yellow, and their different shades; the general colouration of the backside is brownish-greyish. The spines of the albinistic specimens are opaquely white(ish), the skin and the nostrils are pink, while the eyes are bluish-grey or rosy; the leucistic animals are creamy whitish with black eyes; no records of melanistic specimens are known (MORRIS 1994). The spines and the fur may be faded with the ageing of the specimens. The hairy parts of the body are always lighter coloured than the spiny backside; coarse, short greyish hairs cover the face, the chest, the belly, the legs and the short tail. The two hedgehog species can be distinguished by the colouration of the ventral side as *E. roumanicus* has whitish patch on its chest; *E. europaeus* has uniformly light brown chest and belly.

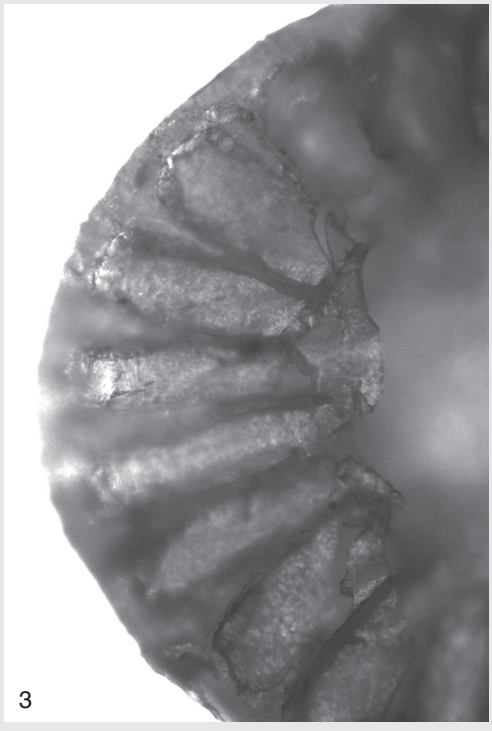
HAIR-MACROSCOPIC: GHspine: The spines are modified hairs, designated here as GHspine. The bulb is large and has a unique mushroom-shape. The base is very narrow but the shaft is abruptly extended: this structure protects the skin and the animal against the physical pressure, caused by predators or falling down. The shaft and the shield of the spine are broadly tubular; the tip is abruptly tapering and acute. A few spines are unicolorate or bicolorate but the majority of them is one- or two-banded. The two-banded spines have dark brown proximal shaft and transit; the distal part of the shaft, the shield and the lower part of the tip are ochreous-white or ochreous-grey; the pointed tip is black, rarely white.

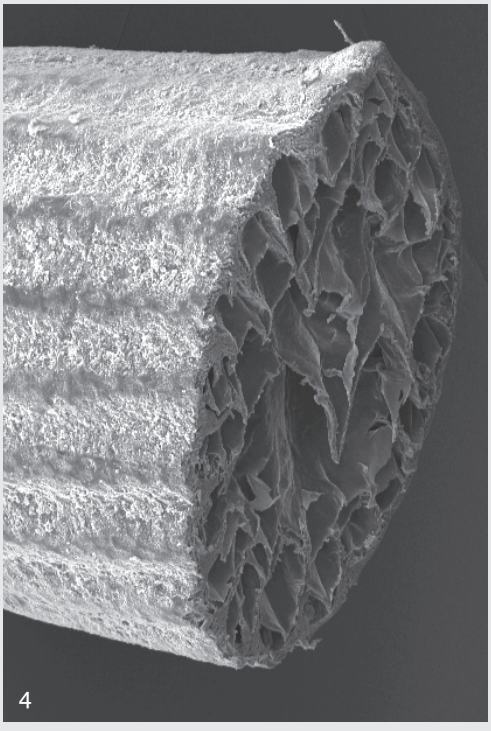
HAIR-MICROSCOPIC: GHspine: There are parallel, deep longitudinal channels around the surface of the spine; the cuticular pattern is unique, meshed mosaic from the shaft to the tip, composed from polygonal, most often regular hexagonal, scales. The medullar cells of the spine are modified into septa. The spacious air-sacs between the septa have a thermal insulation function while the septa increase the flexibility, elasticity and strength of the spines. The cross-section is radial, "rose-window"-like; its contour is circular or oblong.

SIZE: l_{max} GH_{spine} = 28 mm; d_{max} GH_{spine} = 1100 μ; $m/d_{x\ GHspine}$ = 0.95.









***Erinaceus* spp.**: 1 = GH spine and GH ventral types; 2 = spine, cuticula; 3 = spine, cross-section, shield 10×; 4 = idem, SEM

Taxonomic character: the microstructure of the radial pattern of septae ("rose-window") on the spines, which is best recognized on the cross-section.

hair, macroscopic: GHventral: the guard hairs of the ventral side are straight, curved or wavy; white/ish or beige, bicolorate or one-banded. The UHventral is somewhat thinner, regularly wavy, and sometimes longer than the GHventral; white(ish) or greyish-brown. The tip is evenly tapering, more or less transparent.

hair, microscopic: GHventral: the cuticular pattern is smooth margined rhomboidal petal or pine-cone rhomboidal on the shaft; irregular petal on the shield; and figureless, near, sketched scales on the apical section. The medullar pattern is nummiform, or tubular globular on the shaft. The characteristic dark and pale sections on the broadest part of the shield resemble a nummiform pattern, but after expelling the air from the hair by euparal, the colonnade tubular medulla will be clearly visible. The shield is usually flattened section and may have a shallow channel. The cross-section is biconvex, oblong or oval at the broadest section.

size: l_{max} GHv = 20 mm; d_{max} GHv = 160 μ; m/d_x GHv = 0.45.

remarks: "Alderney's blonde hedgehogs": The leucistic, creamy whitish "founder" *Erinaceus europaeus* specimens, inheriting recessively their colouration, were introduced around 1810 in Alderney, an island belonging to the Channel Islands. This resident isolated and inbred population still predominantly preserves its "blonde" colouration. Most probably, the (almost entire) lack of the predators is one of the reasons why these strikingly pale specimens can survive in this island and why this disadvantageous feature has not disappeared from the population (Morris & Tutt 1996).

Biomimicking of natural structures may help to increase the mechanical efficiency of engineering structures (Vincent & Owers 1986, Karam & Gibson 1994). The hedgehog-inspired helmets are designed to absorb rotational hits and to protect against concussions and would be particularly useful for many sportsmen, like the American football players. The physical tests pointed out the efficiency of the honeycomb-like stiffeners, so the helmets are planned to be made of polymer material with structure similar to the hedgehog's spine (Swift *et al*. 2016).

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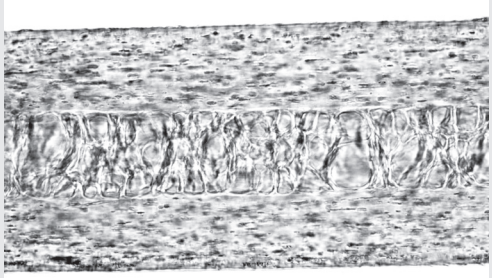

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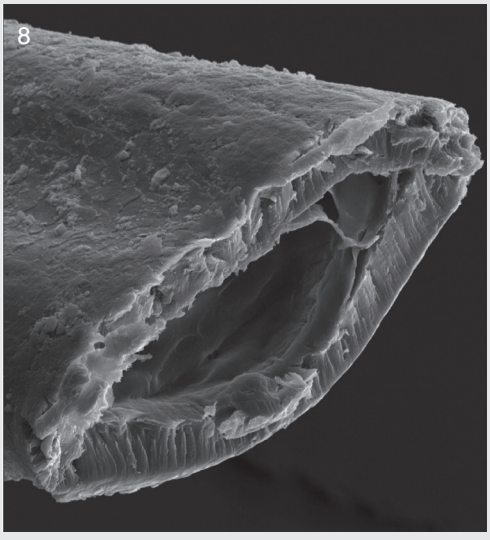

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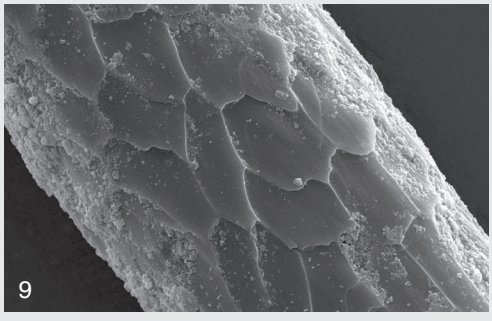

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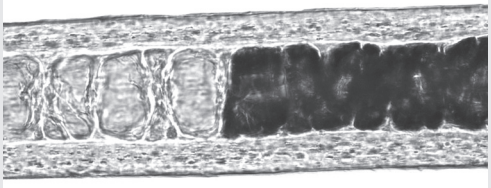

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***Erinaceus* spp.**: 5 = GHv apex; 6 = GHv cuticula, shield; 7 = GHv medulla, shield; 8 = GHv cross-section, shield, SEM; 9 = GHv cuticula, base, SEM; 10 = GHv medulla, shaft

7.2. Soricomorpha

FUR: The fur is fine, velvety and thick, rather homogeneous in structure. It is unicoloured and the main ground colours are brown and grey; the albinistic and melanistic specimens are very rare (CHĘTNICKI *et al.* 2007, NEDYALKOV *et al*. 2014). The dorsal part is always darker. The colours may change seasonally and/or can be variable depending on the environmental conditions of the habitats and the food composition. The arrangement of the bristle hairs along the tails and paws can be a diagnostic generic character (FANG *et al.* 1997).

HAIR, MACROSCOPIC: The hairs are short, thin; the length rarely exceeds 15 mm. The GH0 and GH1 straight guard hairs are sparse; the GH2 and UH hairs are combined zigzag-like or sometimes wavy. Hairs bicolorate or polychrome: the shaft is grey, dark grey or deep brown; the shorter shield is dark brown or reddish brown above the last stricture. Tip transparent, lacking medulla and pigments. The guard hairs of the Soricidae and the Talpidae can be distinguished by the structure of the tip region as the apex is abruptly tapering, long in the shrews while it is long and gradually tapering in the moles.

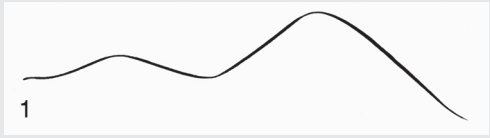
HAIR, MICROSCOPIC: The bulb ball-shaped or knobby. The basal section is tubular or slightly bulbous. The cuticular pattern is corniculate coronal at basal part. The GH1 guard hairs have rhomboid scales on the shaft and the transit; the cross-section is most often circular; a shallow channel may be present on the shield. The cuticular pattern of GH2 is combined petal on the shaft, elongated rhomboid on the strictures, broad petal or rhomboidal pine-cone on the transit. The pattern of the shield is transversal petal at the maximum diameter, often with one or two channels; the apical pattern is figureless waved, apically rippled.

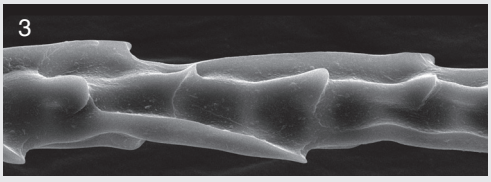
The medulla is nummiform, uniserial regular or chromosomal along the entire hair; tubular amorphous or medullaless at the strictures. The pigments aggregate within the spaces between the medullar cells; on the shield, they can be found densely but diffusely also in the cortex; the tip is usually transparent, lacking the medulla.

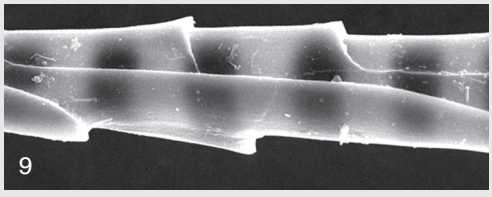
The diagnostic cross section characters are found in the basal part, in the shaft and the maximum diameter of the GH2. The cross sections most often H-shaped or quadri-concave (amoeboid) in the genera *Neomys* and *Sorex*, U-shaped in *Crocidura* and circular or oblong in *Talpa*.

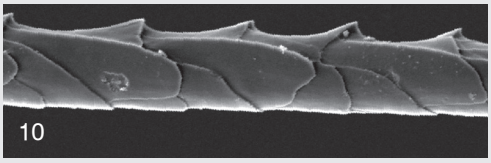
TAXONOMIC CHARACTER of the order: the combined petal cuticular pattern at the shaft.

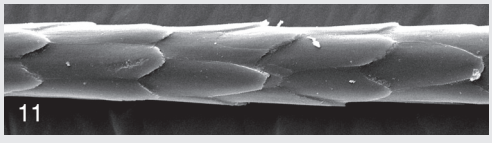
SIZE: $m/d_x = 0.75$











Soricomorpha: 1 = shape of GH2 and UH hairs; 2 = stricture, transparent view; 3 = stricture, SEM; 4 = medulla; 5 = cuticula, channelled transit; 6 = cuticula, transit; 7 = cuticula, distal shaft; 8 = cuticula, proximal shaft; 9 = proximal shaft, SEM; 10 = distal shaft, SEM; 11 = base, SEM; 12 = shapes of basal sections

Soricidae

FUR: The dorsal and ventral side are differently coloured, the ventral side always paler.

HAIR, MACROSCOPIC: The guard hairs usually bicolorate; ground colour of the shaft grey, that of the shield brown; GH0 rather sparse, strikingly long at the rump.

HAIR, MICROSCOPIC: The GH2 guard hairs and the underhairs are characteristically channelled; this channel could be shallow or deep and the inner surface of the channel can be lamellated. The channel originates most frequently in the transit and extends towards the distal part of the shield or even to the tip. The tip is abruptly tapering, long and transparent.

TAXONOMIC CHARACTER of the family: the regular broad petal cuticular pattern on the channelled shield. Generic level taxonomic character: microstructure of the channelled part which can be studied exclusively by SEM. The genera of the subfamily Soricinae, the *Neomys* and *Sorex* species, called sometimes "red-toothed shrews", have H-shaped cross-section (HUTTERER & HUERTER 1981, TEERINK 1991, DOCUMUN *et al.* 1994) and the inner surface of channels are structured, most often lamellate. It is important to note that although this character is apomorphic for this subfamily, it may be absent in some species.

Genus *Neomys*

FUR: The dorsal side is almost black, the ventral side is silvery-greyish; the borderline between them on the flanks is demarcated. A typical feature of the water shrews is that a fringe of bristle hairs runs along the ventral surface of the tail and on the edges of paws; this character is related for their semiaquatic lifestyle. The albinism is rare but small white patches may appear around the eyes and on the tips of the ears.

HAIR, MACROSCOPIC: *Neomys* has bicolorate guard hairs with silvery dark grey shaft and dark brown shield.

HAIR, MICROSCOPIC: The cross-section of the GH2 shield is H-shaped. Within the channel, the central ridge is unexpressed, there are more or less oblique, short, thick lamellae; this feature is a unique diagnostic character of *Neomys* within the Central European Soricidae genera.

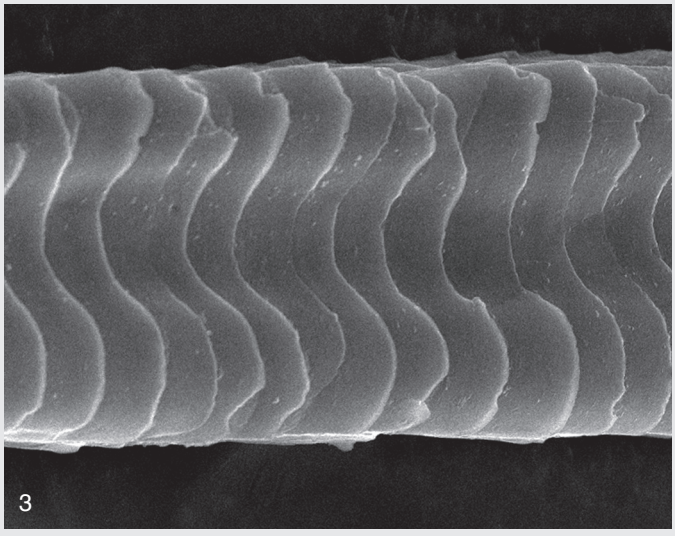
SIZE: l_{max} = 13 mm; d_{max} = 35 µ

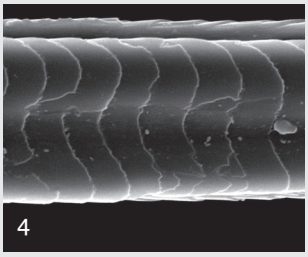
Neomys fodiens

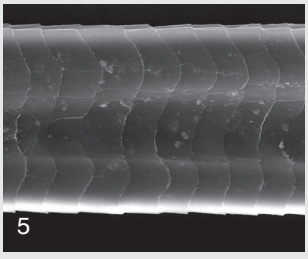
FUR: The dorsum is black(ish), deep chocolate-brown or cinnamon-brown; ventral side much paler, whitish, silvery grey or light greyish-brown. The fringe of bristle hairs runs along the ventral surface of the entire tail.

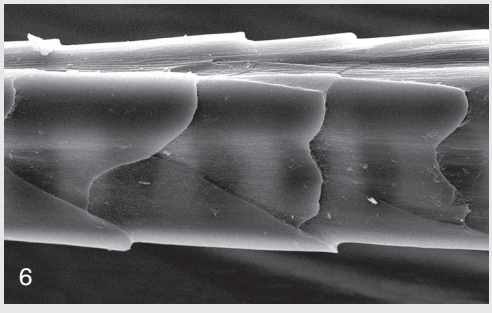
Neomys anomalus

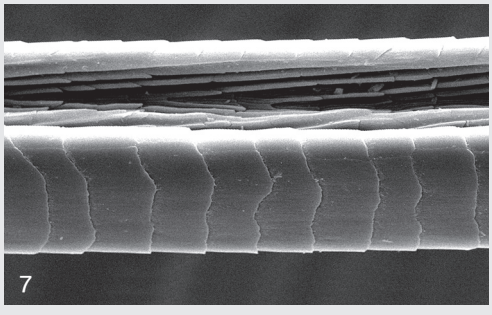
FUR: The fur is dark brown or blackish on the dorsal side while the ventral side is grey or grey-white; the contour line between the colouration of the back and the belly is less distinct than in *N. fodiens*. The fringe of bristle hairs running along the ventral surface of the tail extends towards the proximal third of the tail.

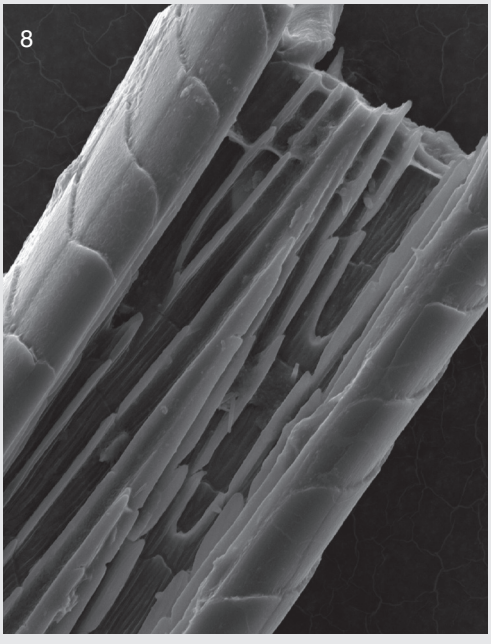












Soricidae: 1 = tip; 2 = tip, SEM; 3 = cuticula, shield, SEM; 4 = deep channel, SEM; 5 = shallow channel, SEM; ***Neomys* spp.**: 6 = cuticula, shaft, SEM; 7 = cuticula, shield, SEM; 8 = deep, lamellated channel, SEM

Genus *Sorex*

FUR: The tail is somewhat flattened and covered with short hairs; its dorsal and ventral sides are differently coloured; the tail ends with a small tuft.

HAIR, MICROSCOPIC: The cross-section of the GH2 shield is H-shaped. Within the channel, the central ridge is expressed, due to the presence of long, deep, thin, V-shaped lamellae; this structure is a diagnostic feature of *Sorex* within the Central European mammal genera.

SIZE: l_{max} = 7.5 mm; d_{max} = 30 μ;

Sorex alpinus

FUR: Ground colour of fur dark grey and its shade varies from silvery grey to blackish; the belly is somewhat lighter, greyish-brown. The dorsal surface of the tail is darker brown or black; the ventral side is lighter.

HAIR, MACROSCOPIC: Shaft silvery grey or pale grey; shield dark grey or dark brown.

Sorex araneus

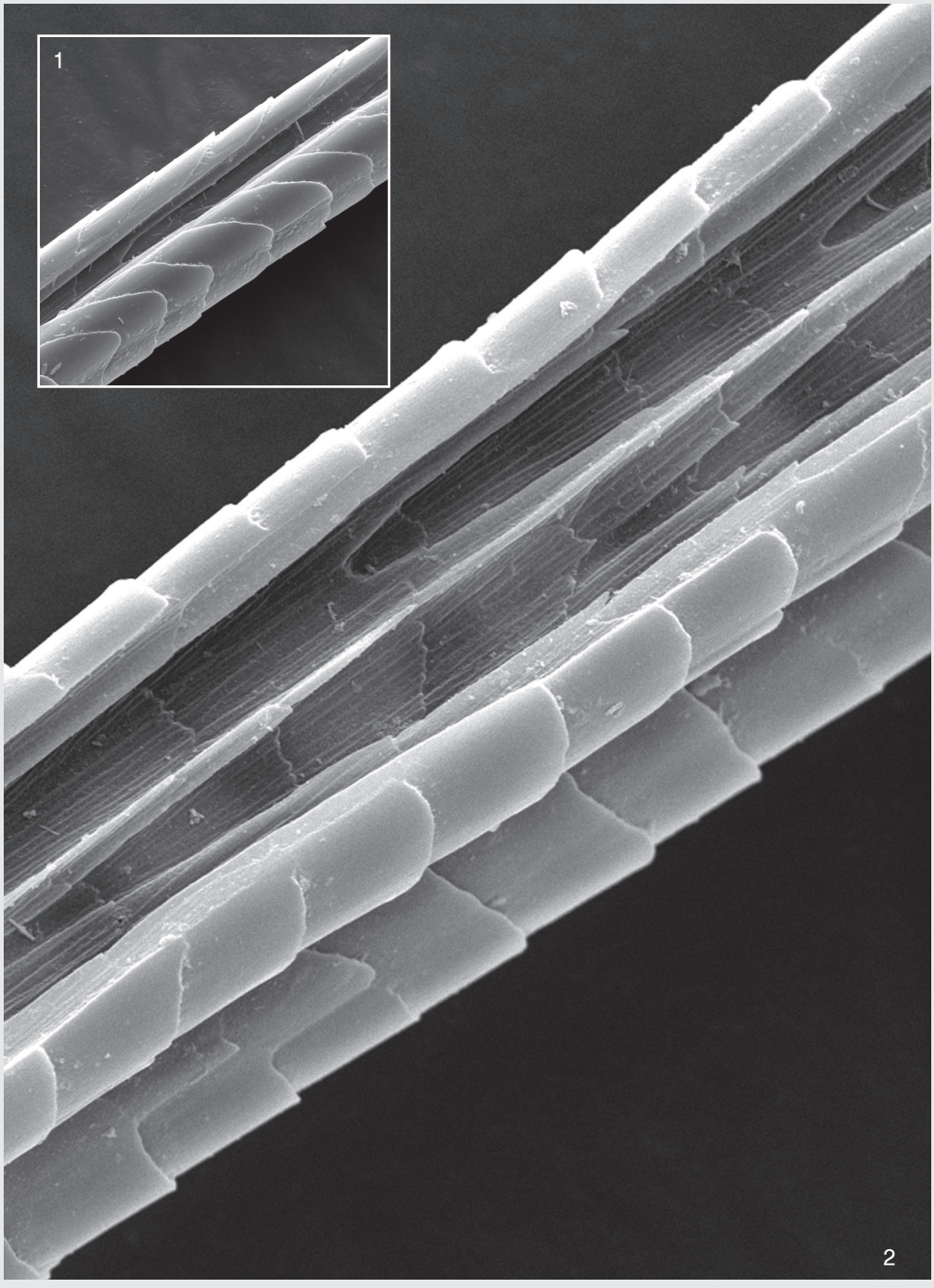
FUR: The fur is tricoloured: the dorsum is dark brown, coffee-brown or slightly reddish-shaded; the ventral side is brownish-grey; the throat and the lateral parts are transitionally coloured, sand-brown, beige, pale clay-coloured or slate-grey.

HAIR, MACROSCOPIC: The shaft is dark brown; the shield is dark grey or rusty-reddish.

Sorex minutus

FUR: The dorsum is brown or dark reddish-brown, usually strikingly separated from the grey or ochreous-whitish belly; the tail is relatively long and hairy.

HAIR, MACROSCOPIC: Shaft dark grey, shield ochreous-brown; the apical section may turn into dark brown.



***Sorex* spp.**: 1 = channel, transit, SEM; 2 = lamellated channel, shield, SEM

Genus *Crocidura*

FUR: The tail is slightly flattened and its ventral side lighter. The lateral edges of the tail are covered by long, whisker-like white hairs; this is a diagnostic feature of *Crocidura* within the Central European mammal genera.

HAIR, MACROSCOPIC: The GH polychrome or bicolorate with grey shaft and ochreous-brown shield.

HAIR, MICROSCOPIC: The channel of the shield is shallow, broad and inarticulate, U-shaped. The apical edges of the broad petals are rippled.

SIZE: l_{max} = 7 mm; d_{max} = 17 µ

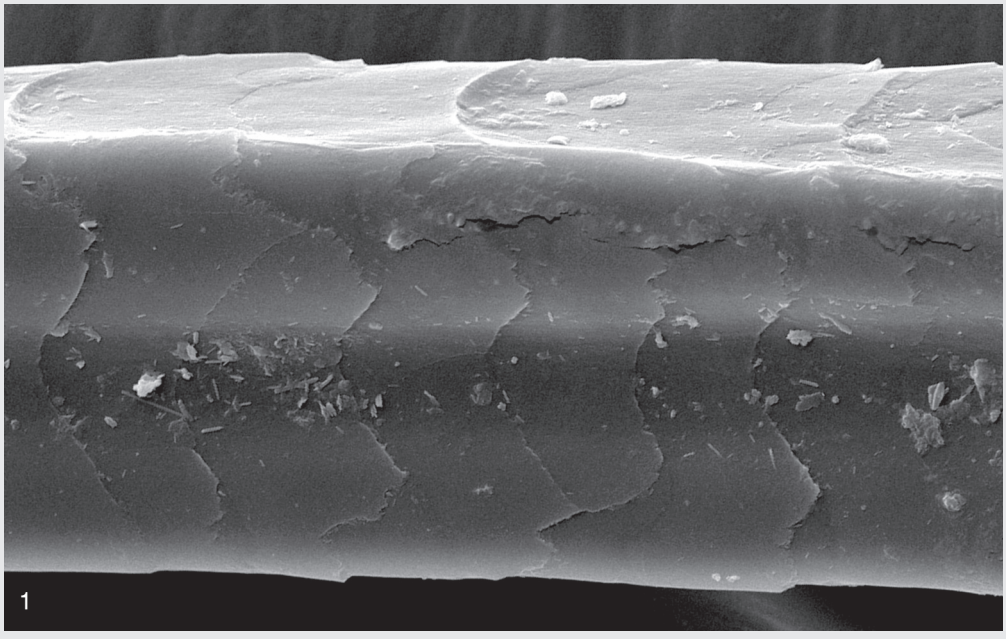
Crocidura leucodon

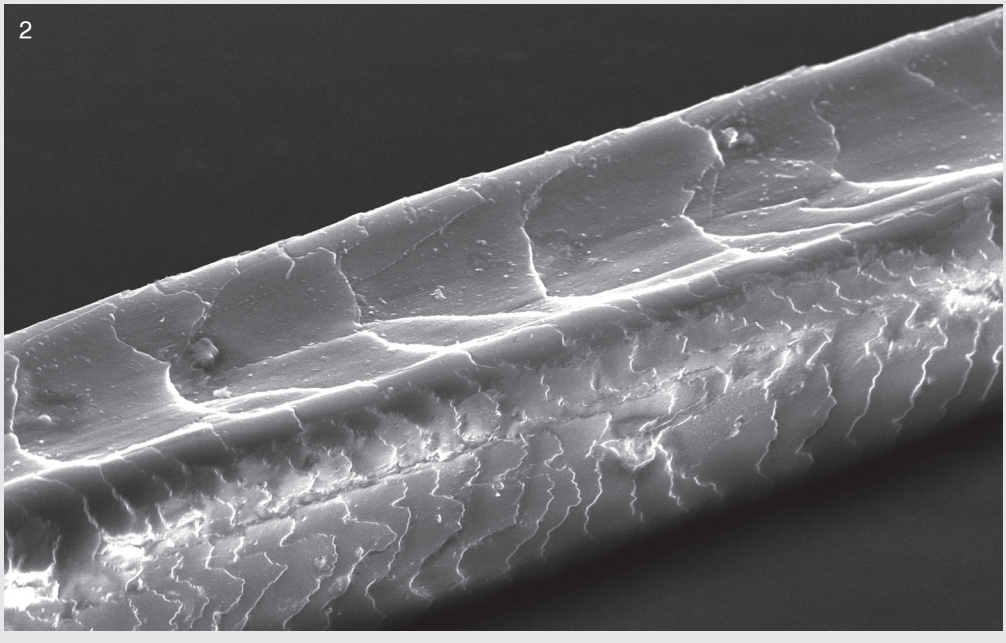
FUR: The back is covered by short, dense, dark brown fur while the underside is white or greyish- brown, with a sharp dividing line among them; there are slightly longer hairs on the tail.

Crocidura suaveolens

FUR: The back is brown, hazel or reddish-brown; the colouration of the underside is varies from pale grey to ochreous-brown; there is no sharp demarcation on the flanks.

REMARKS: "The hairs on the throat often yellow, but this yellow is not due to the colour of the pigments of the hairs but is a natural colouring supposedly attributed to the intake of carotinoids contained in certain invertebrates serving as food; in the case of water-shrews, the Gammaridae shrimps or the *Daphnia* species are the "carotin sources". *Sorex coronatus* may occur at the western edges of Central Europe; it is very similar to *S. araneus*. *Sorex arunchi* is endemic in Udine region (Italy), probably occur in Slovenia (Lapini & Testone 1998); this species is very similar to *S. araneus. Crocidura russula* also may occur at the western borders of Central Europe; it has reddish or brown dorsum and greyish or yellowish grey belly.





***Crocidura* spp.**: 1 = cuticula, shield, SEM; 2 = shallow channel, shield, SEM

Talpidae

FUR: The majority of the taxa of the family have a fossorial life. Albinistic, leucistic and mottled specimens are known.

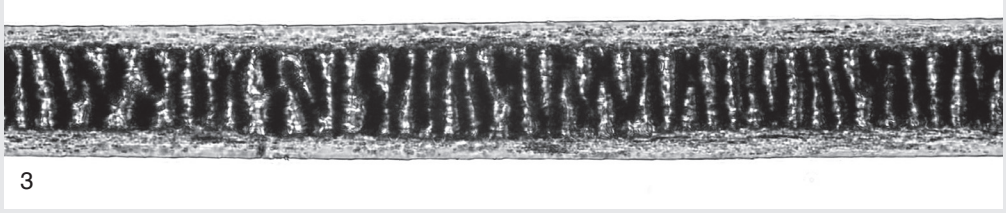
Talpa europaea

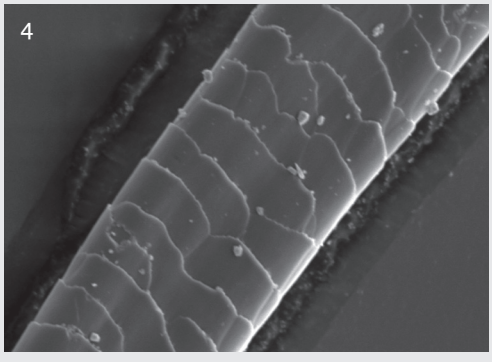
FUR: The fur is velvety and thick. The dorsum is blackish-brown or bluish shaded black; the ventral side is paler. Creamy, silver grey fur, or yellowish, orange-like patches on the ventral side are not rare. The structure of the fur is rather homogeneous. Relatively long hairs cover the short tail; a part of them is supposedly sensory hairs.

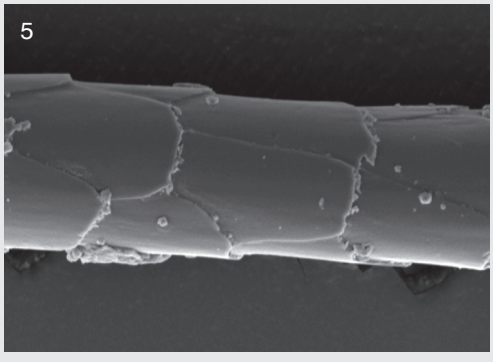
HAIR, MACROSCOPIC: Shaft thin, dark grey; shield tapering, shining dark brown. The GH2 and the underhairs are hardly distinguishable, their shape is combined zigzagged or wavy.

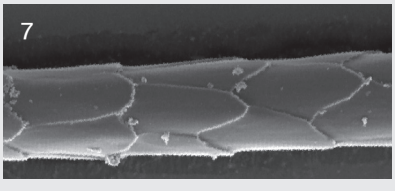
HAIR, MICROSCOPIC: The cuticular pattern of the shield is broad petal consisting of 1–3 scales; the apical section is figureless, wavy, closed. The medulla is chromosomal nummiform at the maximum diameter. The proximal part of the shield may be flattened moderately. The tip is gradually tapering, short and transparent. The cross-section is circular or oblong.

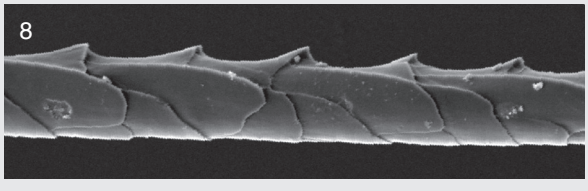
SIZE: l_{max} = 12 mm; d_{max} = 45 μ; m/d_x = 0.75











Talpa europaea: 1 = shape of GH2 and UH; 2 = tip; 3 = medulla, shield; 4 = cuticula, shield, SEM; 5 = cuticula, transit, SEM; 6 = cuticula, shaft, proximal; 7 = shaft, basal, SEM; 8 = cuticula, shaft, distal, SEM

7.3. Chiroptera

The Central European bats belong to four families: Rhinolophidae, Vespertilionidae, Miniopteridae, and Molossidae. The identification of the different taxa usually requires the study of the cuticular prints and the transparent view while the specific configuration of the cuticular scales can be investigated principally by SEM.

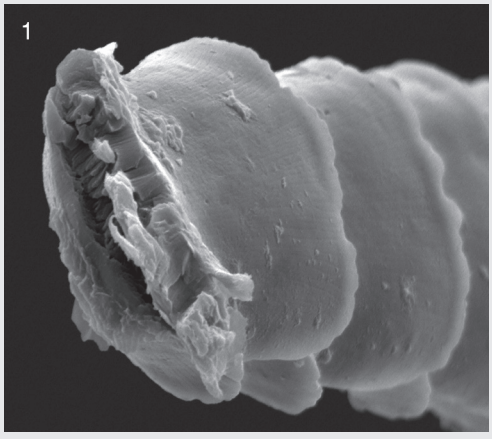
FUR: The fur is velvety and soft to the touch, fluffy and sometimes shaggy. The ground colour is most often brown(ish). The dorsum always darker then the belly, mainly unicoloured, but sometimes grizzled or marbled. SANTANA *et al*. (2011) found strong support that the roosting ecology in bats has driven the evolution of pelage markings, as those bats root in the vegetation have evolved fur markings may function as crypsis, and that the larger colonies and larger size of bats tend do not have fur markings, supposedly because of reduced predation pressures. The presence of chromatic aberrations in bats seems to be a worldwide phenomenon, but rare and sporadic within a given area; there is no proof that these chromatic disorders are detrimental to the bats (LUCATI & BAUCELLS 2016).

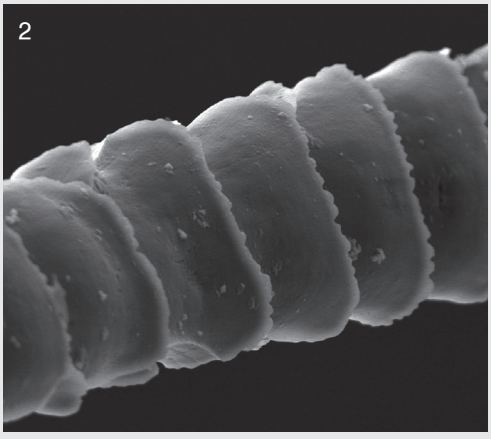
HAIR, MACROSCOPIC: The fur is rather homogeneous; the different types of guard hairs are hardly distinguishable, and the GH and the UH can be also very similar. Hairs short, very thin; GH1 curved, appearing only in low density; GH2 and UH wavy. It is worth to note that the details of the shape and colouration of the hairs (ground colour, colour transitions, bands, etc.) is not or only poorly visible by the naked eye due to the small size of the hairs, especially in case of small samples. The use of white or pale coloured background can help considerably in the recognition of these characters.

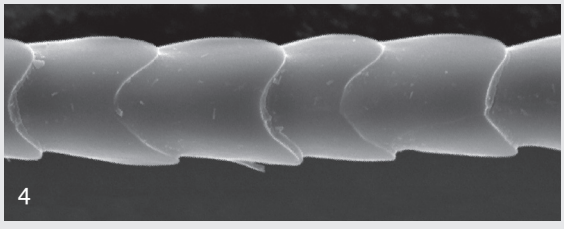
HAIR, MICROSCOPIC: The ball-shaped bulb is small; the basal part is tubular or bulbous. The cuticular scales are coronal, variably shaped; their configuration is the most important feature for the identification. The coronal scales may be variably strongly divergent from the axis of the hair; their apical margins can be partially overlapping which often causes a characteristic "shadow pattern" in the microscopic view. The apical part is gradually tapering; the arrangement of the scales on the tip is branching or telescopic. The margins of the stem are smooth or spiky on the transparent view. The arrangement of the pigments is diffuse or aggregated; the pattern of this aggregation might be a diagnostic character. The cross-section of the hair is most often circular or oblong but convex-concave, quadrangular or triangular cross-sections also appear in Chiroptera.

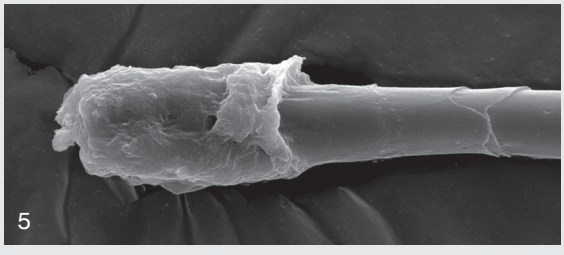
SIZE: l_{max} = 12 mm, d_{max} = 22 µ

TAXONOMIC CHARACTER: The Chiropteran hairs are characterised exclusively by coronal scales along the entire length of the hair; the general shape and the form of the apical margins of coronal scales show high diversity (BENEDICT 1957).









Chiroptera: 1 = cross-section, shield, SEM; cuticula, shield, SEM; 3 = node, transparent view; 4 = cuticula, shaft, SEM; 5 = bulb, SEM; 6 = hairs, transparent view

Rhinolophidae

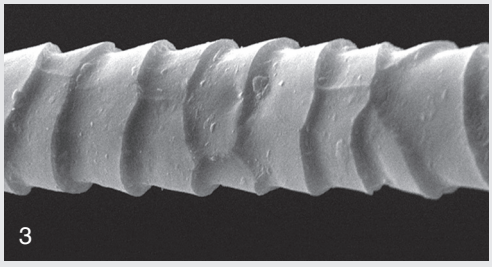
FUR: The Central European *Rhinolophus* species (*R. hipposideros*, *R. ferrumequinum*, *R. blasii*, *R. euryale* and *R. mehelyi*) cannot be distinguished by the characters of the fur. The fur is remarkably loose, with velvety touch; its ground colour is the buff and its shades. The dorsum is dark, brownish, greyish-brown or reddish-brown and the ventral side is paler, white or whitish, ochreous-white or pale greyish; the transition between the dorsal and ventral colouration is gradual, without sharp demarcation.

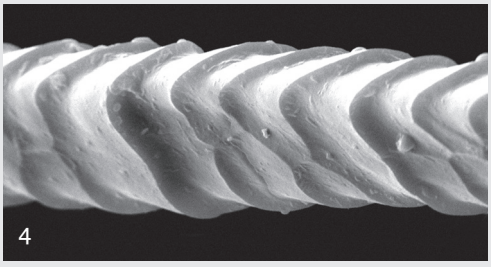
HAIR, MACROSCOPIC: The hairs are polychrome; the shaft is rather transparent and shining, whitish-ochreous or straw-coloured; the shield and the tip dark, brownish, reddish-brown or ochreous-brown. The underhairs are unicolorate, silvery or silvery-whitish, sometimes pale brown. The shape of the hairs is wavy or curved.

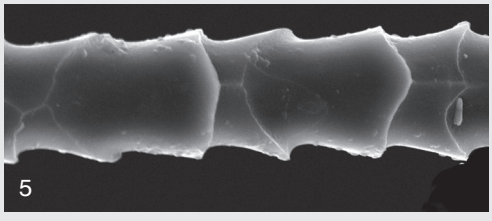
HAIR, MICROSCOPIC: The basal section is tubular or bulbous (PIERALLINI *et al*. 2004); in *Rhinolophus hipposideros, R. ferrumequinum* and *R. blasii* both types of the basal section may be present while in *R. euryale* and *R. mehelyi,* the tubular structure is typical. The cuticular pattern is regular zigzagged coronal on the basal section; on the shaft and shield, all Central European *Rhinolophus* species have uniformly K-shaped coronal pattern. The cuticular scales are tightly closed on the shaft, but gradually dilated and larger towards the distal part of the shield and their apical parts become somewhat divergent from the axis; the scales have smooth apical margins. The arrangement of the pigments is diffuse on the shaft and diffuse or densely linear on the shield. The arrangement of scales on the tip is of telescopic type. The cross-section of the guard hairs is triangular in the shield; this feature is a diagnostic character of *Rhinolophus* in the Central European mammals.

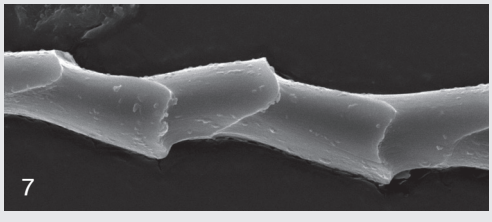
SIZE: l_{max} = 14 mm; d_{max} = 22 μ

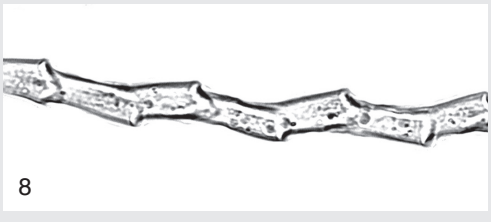
TAXONOMIC CHARACTER: The K-shaped coronal cuticular pattern is typical of the Rhinolophidae only.











***Rhinolophus* spp.**: 1 = tip; 2 = transparent view, shield; 3 = cuticula, shield, SEM; 4 = shape of cross, shield, SEM; 5 = cuticula, shaft, SEM; cuticula, 6 = idem; 7 = cuticula, basal, SEM; 8 = idem

Vespertilionidae

FUR: The fur is variably coloured, most often brown or brownish; the touch of the loose fur is velvety.

HAIR, MACROSCOPIC: The hairs are polychrome or one-banded; usually the shaft is the darkest part of the hair. The tip is mainly brown but white or transparent tips may also exist; the colouration of the tip cannot be used as an identification character.

HAIR, MICROSCOPIC: The cuticular pattern is zigzagged, corniculate or spiked coronal on the shaft; most often mosaic coronal on the shield; the apical margins of the scales may be smooth, rippled or dentate.

Genus *Eptesicus*

FUR: Ground colour of fur shining dark brown; the structure is loose and shaggy.

HAIR, MACROSCOPIC: The hairs are unicolorate brown or reddish; sometimes one-banded.

HAIR, MICROSCOPIC: The basal section is tubular. The cuticular pattern is spiked or corniculate coronal on the shaft; asymmetrical mosaic coronal on the shield, the scales are conical-shaped; the margins of the stem are smooth or spiky on the transparent view. The apical edges of the cuticular scales are rounded and smooth. The pigmentation is denser in the shaft, more diffuse in the shield. The tip is telescopic or slightly branched. Cross-section is oblong or convex-concave.

The species of the genus *Eptesicus* cannot be distinguished by their hair pattern characters.

SIZE: l_{max} = 10 mm; d_{max} = 22 μ;

Eptesicus serotinus

FUR: The fur is homogeneous brown, coffee-brown or hazel on the back and paler shaded, most often greyish-brown on the belly; the throat may be ochreous-brown in certain specimens.

HAIR, MACROSCOPIC: The hairs are reddish-brown.

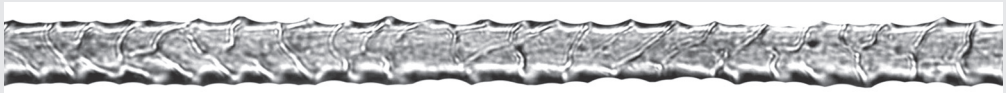
Eptesicus nilssonii

FUR: The fur is dark brown or blackish-brown on the back, marbled with light ochreous-brown.

HAIR, MACROSCOPIC: The majority of the hairs is unicolorate brown, mixed with banded hairs, arranged into randomly located lighter patches. These banded hairs have brown shaft; the band in the shield light yellow; the short apical section and the tip are light brown.

1

2



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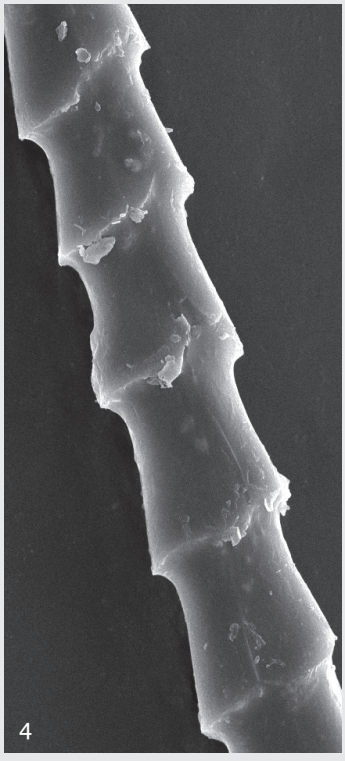

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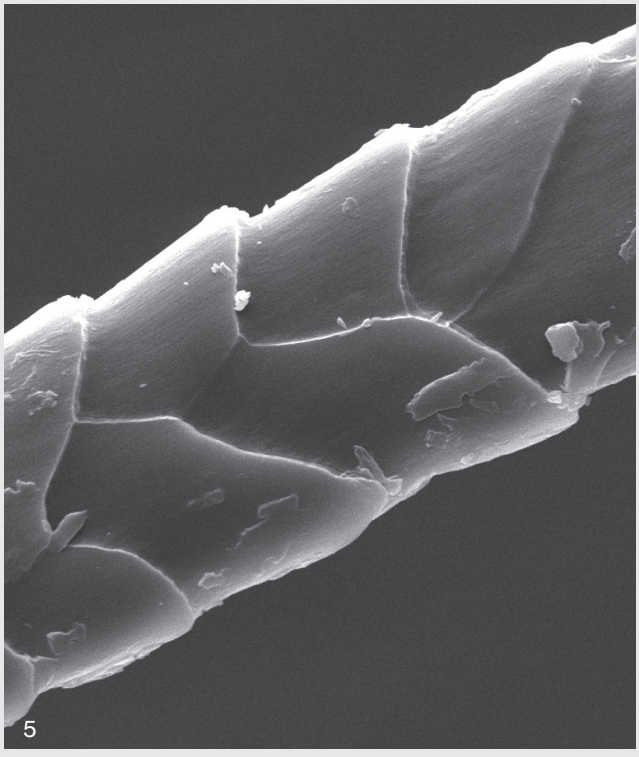


5

6

***Eptesicus* spp.**: 1 = tip; 2 = cuticula, shield; 3 = idem, transparent view; 4 = cuticula, basal, SEM; 5 = cuticula, shaft, SEM; 6 = transparent view, shaft

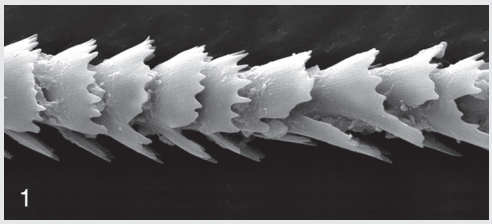
Genus *Pipistrellus*

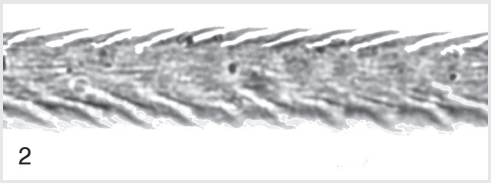
FUR: The fur of the four Central European species, *Pipistrellus kuhlii*, *P. nathusii*, *P. pygmaeus*, and *P. pipistrellus*, is loose, has a velvety touch. The ground colour of the dorsum is reddish-brown and the belly is pale beige, ochreous or greyish.

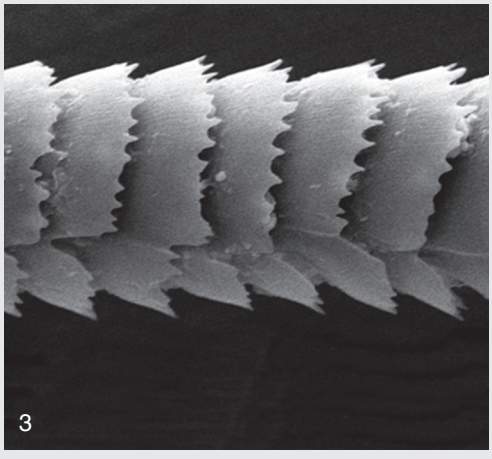
HAIR, MACROSCOPIC: The GH is bicolorate or polychrome; the shaft is dark grey while the shield is paler, ochreous-brown, reddish-brown or brown; the tip is usually transparent.

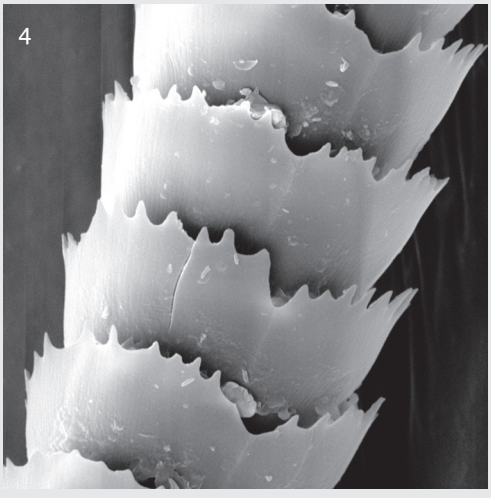
HAIR, MICROSCOPIC: The basal section is tubular. The cuticular pattern asymmetrical corniculate coronal with apically slightly divergent scales on the proximal part of the shaft is; spiked coronal on the distal part of the shaft; symmetrical compressed coronal on the shield; the scales longitudinally elongated in the apical region. The compressed coronal scales are cup-shaped in the *Pipistrellus kuhlii*, and cornet-shaped in the *P. nathusii, P. pygmaeus* and *P. pipistrellus*, as the apical edges of the scales are slightly overlap. The apical margins of the scales are rippled, divergent from the axis along the entire length of the hair; the transparent view of the shield is spiky. The tip is branching. The pigments of the shaft are aggregated apically, those of the shield are diffuse but more densely arranged along the medial line; pigmentless parts may appear along the stem. The cross-section is oblong.

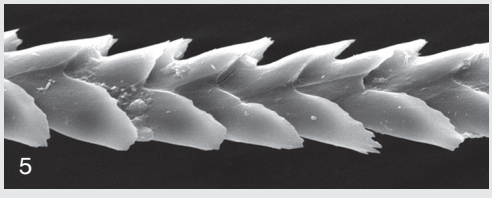
SIZE: l_{max} = 8 mm; d_{max} = 18 μ;

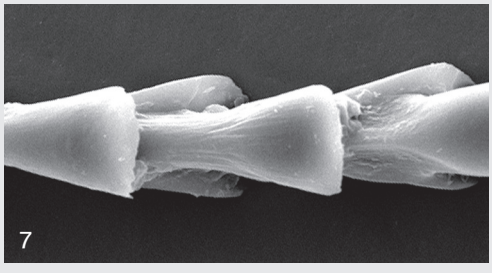


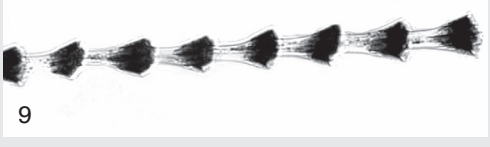








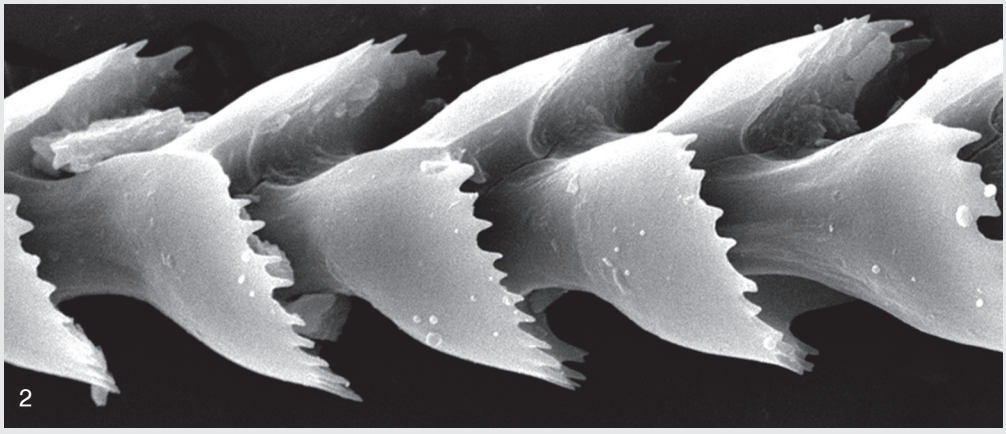


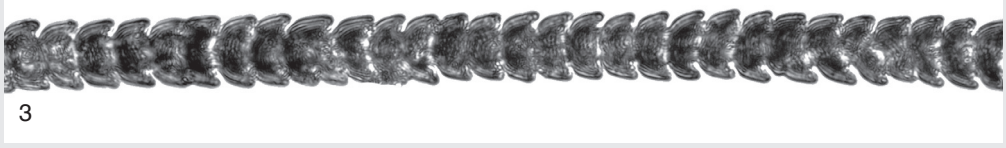


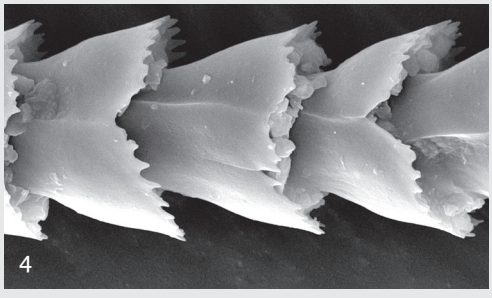
***Pipistrellus* spp.**: 1 = cuticula, apical section, SEM; 2 = idem, transparent view; 3 = cuticula, distal shield, SEM; 4 = cuticula, proximal shield, SEM; 5 = cuticula, shaft, SEM; 6 = idem, transparent view; 7 = cuticula, basal, SEM; 8 = idem; 9 = idem, transparent view

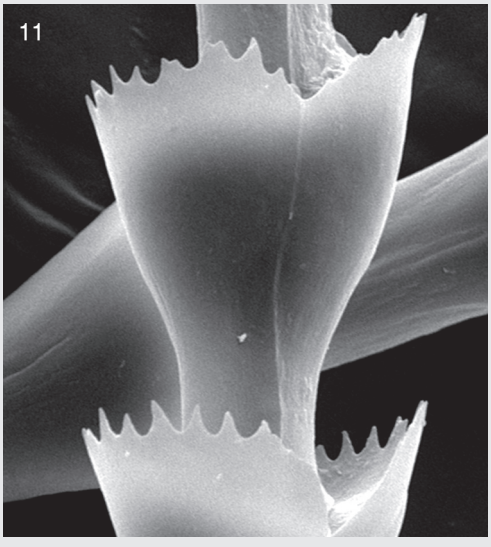
Pipistrellus kuhlii

HAIR, MICROSCOPIC: The compressed coronal scales are cup-shaped, the apical edges of scales do not overlap.









Pipistrellus kuhlii: 1 = tip, transparent view; 2 = cuticula, shield, SEM; 3 = idem, transparent view; 4 = cuticula, distal shaft, SEM; 5 = cuticula, proximal shaft; 6 = idem, SEM

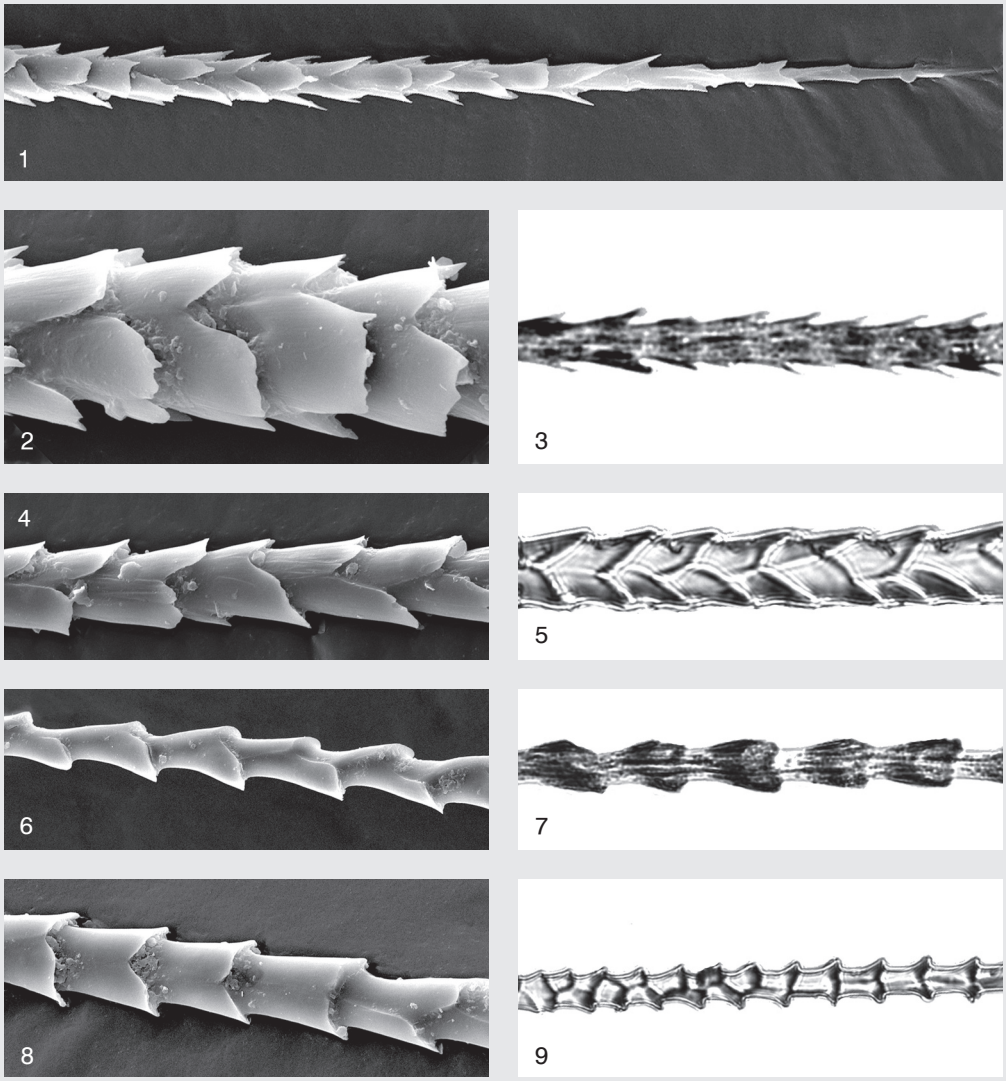
Genus *Nyctalus*

FUR: The fur of the three Central European *Nyctalus* species (*N. noctula*, *N. lasiopterus* and *N. leisleri*) is very similar; the ground colour of both the dorsum and the ventral side is brown or rusty brown. The fur of *N. leisleri* is the most variable in colour; it could be dark brown, chestnut-brown or reddish-brown and the pelage is more extended onto the wings than in the other two *Nyctalus* species.

HAIR, MACROSCOPIC: The hairs can be unicolorate or polychrome; the unicolorate hairs are reddish-brown; in the polychrome hairs the shaft is greyish-brown, while the shield is reddish-brown.

HAIR, MICROSCOPIC: The basal section is tubular. The cuticular pattern is zigzagged coronal pattern, consisting of tight or slightly divergent scales of smooth apical margins on the shaft; the proximal part of the shield has regular spiked coronal pattern; the pattern of the distal shield is mosaic coronal in the print. With SEM, the scales are deeply scalloped, asymmetrical, elongated, and divergent from the axis; their apical margins are cutted, finely rippled but become acute towards the tip. The transparent view is spiky in the shield and the apical section. The pigments arrange apically in the shaft, and diffuse in the shield. The arrangement of apical scales usually branching. The cross-section of the hair is circular or oblong.

SIZE: l_{max} = 8 mm; d_{max} = 22 μ



***Nyctalus* spp.**: 1 = tip, SEM; 2 = cuticula, distal shield, SEM; 3 = idem, transparent view; 4 = cuticula, proximal shield, SEM; 5 = idem; 6 = cuticula, shaft, SEM; 7 = idem, transparent view; 8 = cuticula, basal, SEM; 9 = idem

Genus *Myotis*

The characters of fur and hairs are suitable for the separation of twin-species within the genus but cannot be used for species-level identification.

FUR: The fur is loose, fine, and sometimes shaggy; the dorsum is always darker and homogeneous and sharply distinct from the remarkably lighter, usually greyish ventral side.

HAIR, MACROSCOPIC: The hairs could be unicolorate, bicolorate or banded. The lower part of the stem is usually darker; the tip is pale brownish or reddish.

HAIR, MICROSCOPIC: The basal section is mostly tubular, might be bulbous. The cuticular pattern is simple, monotonous coronal or zigzagged on the basal part and the proximal shaft; spiked coronal on the distal shaft; closed, asymmetrical mosaic coronal on the shield, the scales are conical-shaped. The surface of the scales is finely grooved. The pigmentation of the shaft and apex is rather dense; that of the shield is diffuse or aggregated along the medial axis. The tip of the hair is telescopic. The cross-section is circular or oblong.

SIZE: l_{max} = 12 mm; d_{max} = 22 μ

Myotis capaccinii

FUR: The ground colour rather pale greyish-brown; the dorsum is dark brown or greyish-brown, the ventral side is greyish-white. The hind tibiae and interfemoral membrane covered densely with hairs.

HAIR, MACROSCOPIC: The guard hairs are unicolorate brown or bicolorate; the distal part transparent, whitish, the tip is dark brown.

Myotis myotis

FUR: The dorsum is coffee-brown or grey-brown; ventral side ochreous-grey.

HAIR, MACROSCOPIC: The GH is unicolorate dark brown or banded; in the banded hairs, the shaft is dark brown, the distal section of the shield bears a broad, transparent ochreous-brown band; the width of the band is ca one-third of the entire stem.

Myotis blythii

FUR: The dorsum is brown to greyish-brown or pale rusty-brown; ventral side whitish-grey.

HAIR, MACROSCOPIC: The GH is polychrome or banded; the banded hairs have brown or dark grey shaft; the band on the shield ochreous-yellowish.

Myotis emarginatus

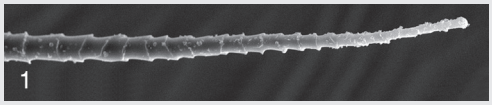
FUR: The dorsum is pale rusty or reddish-brown; ventral side is paler, sometimes pale grey or cream-coloured.

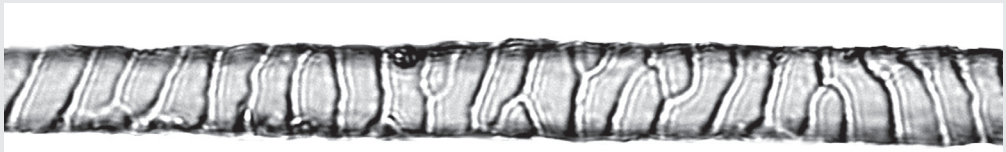
HAIR, MACROSCOPIC: The GH is most often banded; the shaft is dark brown; the pale ochreous-brown band is relatively narrow, its width is ca 1/4 of the entire stem.

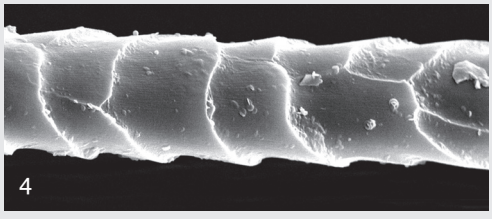
Myotis dasycneme

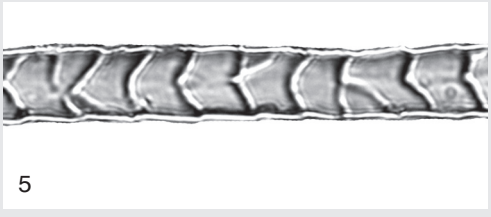
FUR: The dorsum is dark brown; belly whitish-greyish or pale greyish-brown.

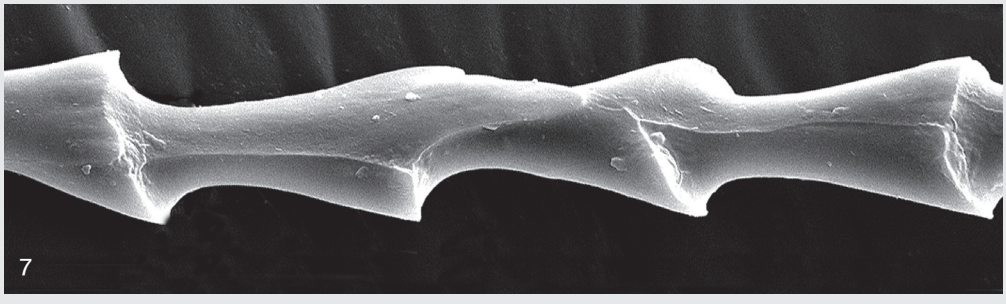
HAIR, MACROSCOPIC: the GH is polychrome; shaft dark grey or dark brown, distally somewhat paler but not banded; the wider shield is brown to ochreous-brown.











***Myotis* spp.**: 1 = tip, SEM; 2 = transparent view, apical section; 3 = transparent view, distal shield; 4 = cuticula, distal shield; 5 = cuticula, transit, SEM; 6 = idem; 7 = cuticula, shaft, SEM

Myotis bechsteinii

FUR: The dorsum is homogeneous brown; belly pale, most often greyish-brown.

HAIR, MACROSCOPIC: The GH is polychrome, the shaft is dark brown, the more distal parts of the stem are gradually getting light towards the tip; no distinct band is visible but the colouration of the apical region turns gradually to dark brown.

Myotis nattereri

FUR: The dorsum is variable in colours, from pale brown to ochreous-brown or greyish-brown; ventral side ochreous-grey or whitish-grey. The specific character of *M. nattereri* is the presence of rigid, curved hairs on the interfemoral membrane between the hind limbs. The sensitive function of these hairs was not proved by the studies on their fine structure (CZECH *et al*. 2008), but this structure may be used for sweeping the insect preys hide in the canopy.

HAIR, MACROSCOPIC: Guard hairs polychrome, with dark brown shaft and ochreous-brown shield; the apical region is also ochreous-brownish.

Myotis alcathoe

FUR: The ground colour is brown; dorsal part dark brown, turning gradually to pale brown or greyish-brown on the belly.

HAIR, MACROSCOPIC: The Gh is unicolorate dark brown or polychrome with somewhat darker shaft and slightly paler, more reddish shield and tip.

Myotis brandtii

FUR: The dorsum is dark brown to grey-brown, ventral part somewhat paler grey-brown, ochreous-grey or even whitish; the dark dorsal colouration is turning gradually into the paler belly.

HAIR, MACROSCOPIC: The GH is unicolorate dark brown or polychrome. The gradual change of the colour along the length of the polychrome hairs is very characteristic: the shaft is dark brown or grey-brown, the tapering transit is pale ochreous-brown while the widening shield and the tip are brown.

Myotis daubentonii

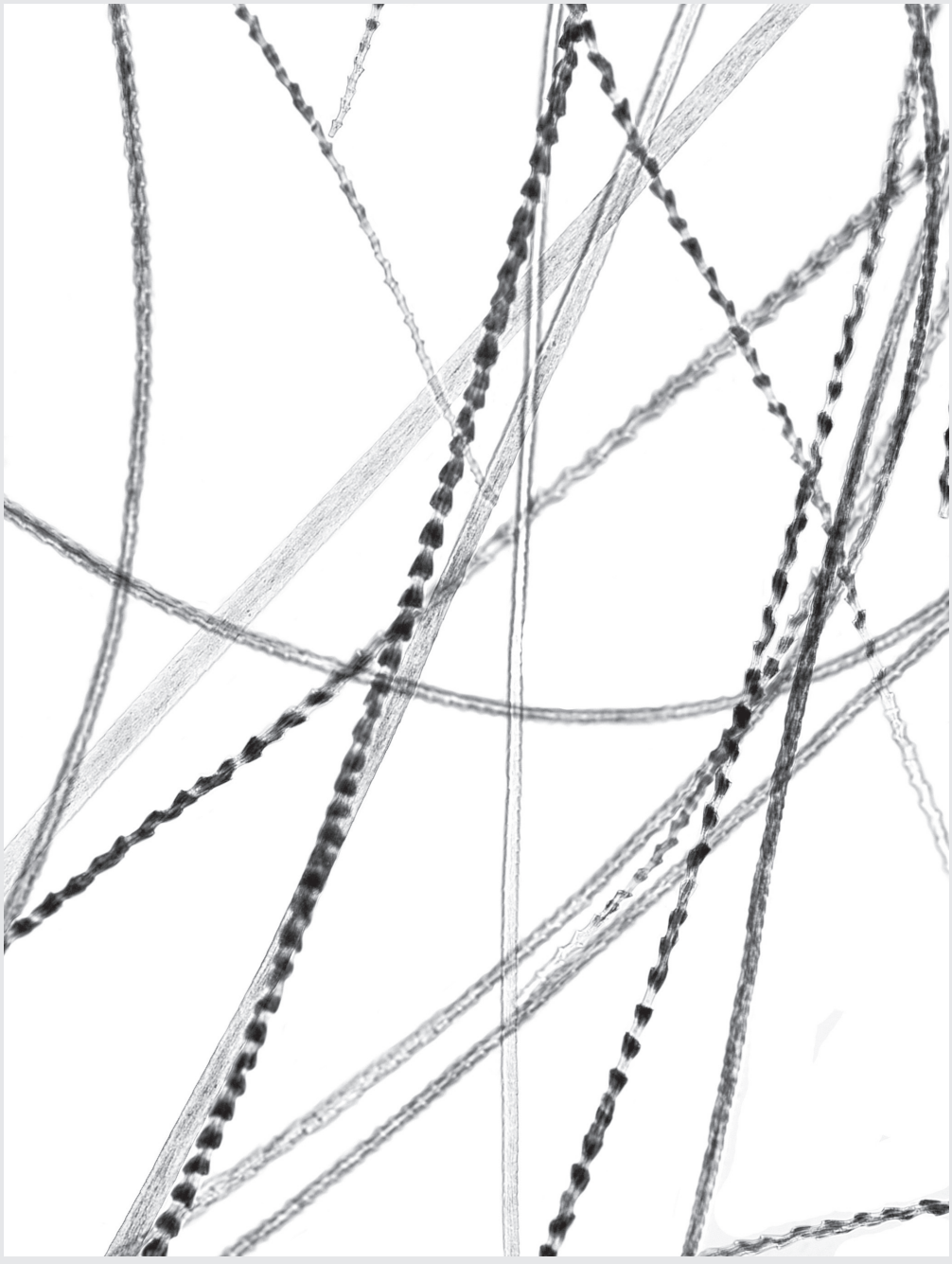
FUR: The dorsum is brown; the ventral side is grey, ochreous- or whitish-grey.

HAIR, MACROSCOPIC: The GH is unicolorate dark brown or polychrome with somewhat darker shaft and paler, more reddish shaded tip.

Myotis mystacinus & *Myotis aurascens*

FUR: The fur of *M. aurascens* and *M. mystacinus* is very similar. The dorsal part can be brown, grey-brown or dark greyish-brown; the ventral part variable shades of grey, sometimes whitish-ochreous.

HAIR, MACROSCOPIC: The GH is unicolorate dark brown or polychrome with dark shaft and paler, reddish-brown or ochreous-brown apical region.



***Myotis* spp.**: transparent view of hairs

Genus *Plecotus*

FUR: The fur is loose and shaggy, in particular the nape and the shoulder blade have longer hairs.

HAIR, MACROSCOPIC: The GH is banded; the pale band is transparent, honey-coloured; the apical region is brown; the shaft is strongly wavy.

HAIR, MICROSCOPIC: The basal section is tubular or slightly bulbous. The cuticular pattern on the basal part and the proximal section of the shaft is spiked coronal; the distal section of the shaft and the proximal part of the shield are characterised by spiked coronal pattern, the distal part of the shield has mosaic coronal pattern, the shape of the scales are conical. The apical edges of scales are smooth. The pigments arrange diffusely along the entire length of the hair. The transparent view is smooth or finely spiky. The tip is most often telescopic. The cross-section is oblong.

SIZE: l_{max} = 12 mm; d_{max} = 22 μ

Plecotus auritus

FUR: The dorsum is brown, pale brown or reddish-brown; the nape may bear a whitish patch; sides of the neck sometimes marked by reddish patches; the ventral side is pale grey with whitish-ochreous shade.

HAIR, MACROSCOPIC: The shaft is pale brown or reddish-brown, with less distinctly marked band.

Plecotus austriacus

FUR: The dorsal part is grey-brown, the ventral part is whitish-grey.

HAIR, MACROSCOPIC: Shaft dark brown; pale band distinctly contoured.

Plecotus macrobullaris

FUR: Dorsal side is grey or greyish, the belly is uniformly white, whitish-grey or pale ochreous-grey.

HAIR, MACROSCOPIC: The band is very broad, ca half as wide as the entire length of the hair. The shaft is brown or whitish, the band is ochreous, the shield and the apical part are brown.

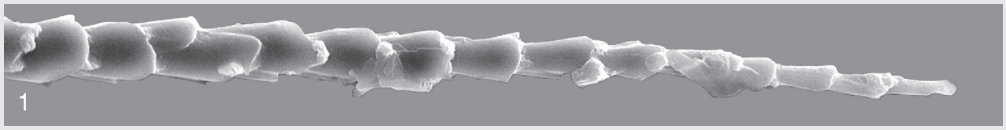
Hypsugo savii

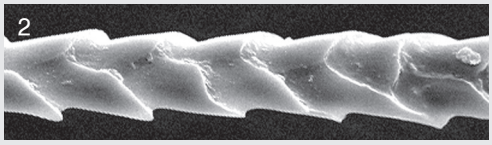
FUR: Dorsal side dark brown or deep brownish-grey; ventral side whitish-grey; the two sides are sharply contoured.

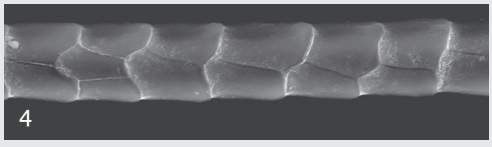
HAIR, MACROSCOPIC: Guard hairs unicolorate brown to dark brown, strongly wavy.

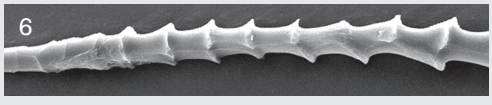
HAIR, MICROSCOPIC: The basal section of hair is long; it is tubular. The cuticular pattern is zigzagged coronal in the proximal part of the shaft, spiked coronal in the distal part of the shaft. The pattern of the shield is mosaic coronal in lower magnification, asymmetrical, slightly divergent conical-shaped scales in larger magnification. The transparent view is smooth or slightly spiky. The distribution of the pigments is generally diffuse along the entire hair but some apical or linear aggregations can be seen on the shaft.

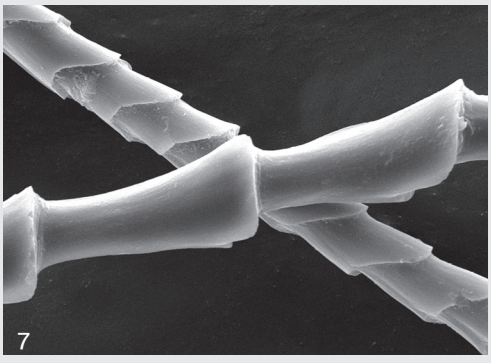
SIZE: l_{max} = 7 mm; d_{max} = 10 μ

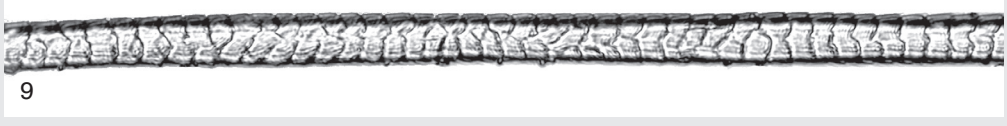


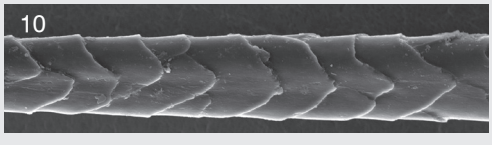












Plecotus* spp.**: 1 = tip, SEM; 2 = cuticula, distal shield, SEM; 3 = idem; 4 = cuticula, transit, SEM; 5 = transparent view, shaft; 6 = cuticula, basal, SEM; 7 = cuticula, proximal shaft, SEM; ***Hypsugo savii: 8 = tip; 9 = cuticula, shield; 10 = cuticula, distal shaft, SEM; 11 = idem; 12 = bulb and base; 13 = cuticula, basal

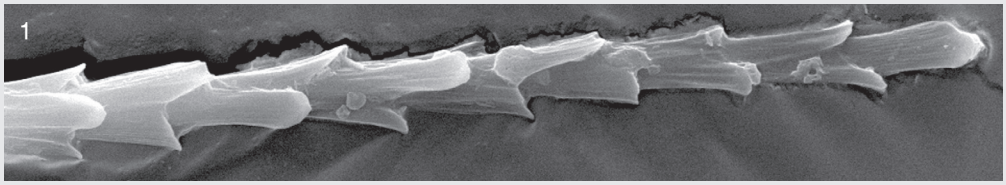
Barbastella barbastellus

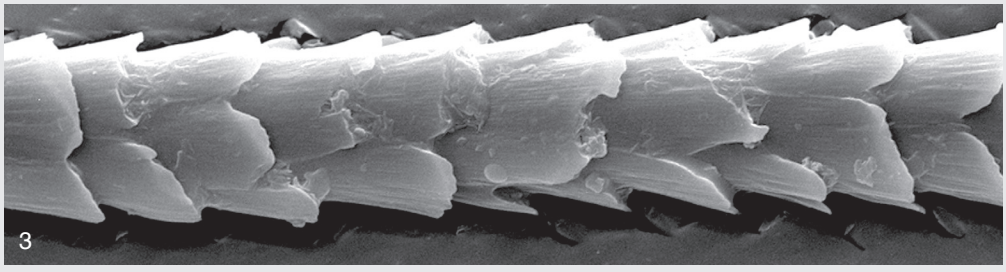
FUR: The structure of the fur is shaggy, stapled. Ground colour of the dorsal side is silky black or dark brownish-grey, spotted randomly with creamy, pale grey and/or ochreous spots and patches.

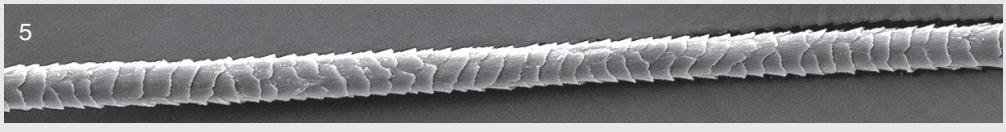
HAIR, MACROSCOPIC: Guard hairs most often uniformly dark brown, sometimes with some reddish shade; in the light patches, polychrome guard hairs can also be found.

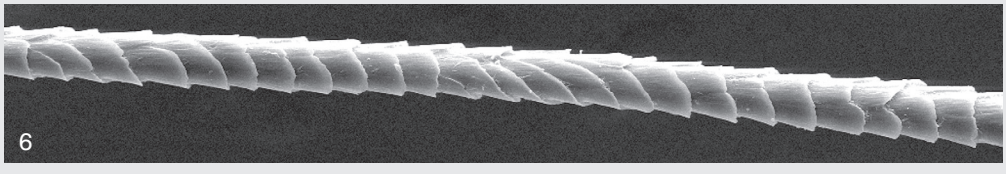
HAIR, MICROSCOPIC: The basal section is tubular, sometimes bulbous. The cuticular pattern is zigzagged coronal of the proximal part of the shaft; spiked coronal on the distal part; irregular, mosaic coronal pattern with apically rippled scales on the proximal section of the shield. On the distal section of the shield and the on the apical section the scales are longitudinally elongate, divergent from the main axis, their apical margins are arcuate. The surface of the scales on the shield is grooved. The margins of the hair are smooth or spiky in the transparent view. The structure of the apex is branching. The shaft is darker then the shield; the arrangement of the pigments is diffuse in the shaft, often linear in the shield. The cross-section is circular.

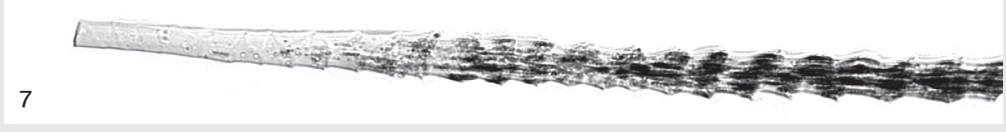
SIZE: l_{max} = 10 mm; d_{max} = 16 µ











Barbastella barbastellus: 1 = tip, SEM; 2 = transparent view, distal shield; 3 = cuticula, distal shield, SEM; 4 = cuticula, proximal shield, SEM; 5 = idem; 6 = cuticula, shaft, SEM; 7 = transparent view, basal

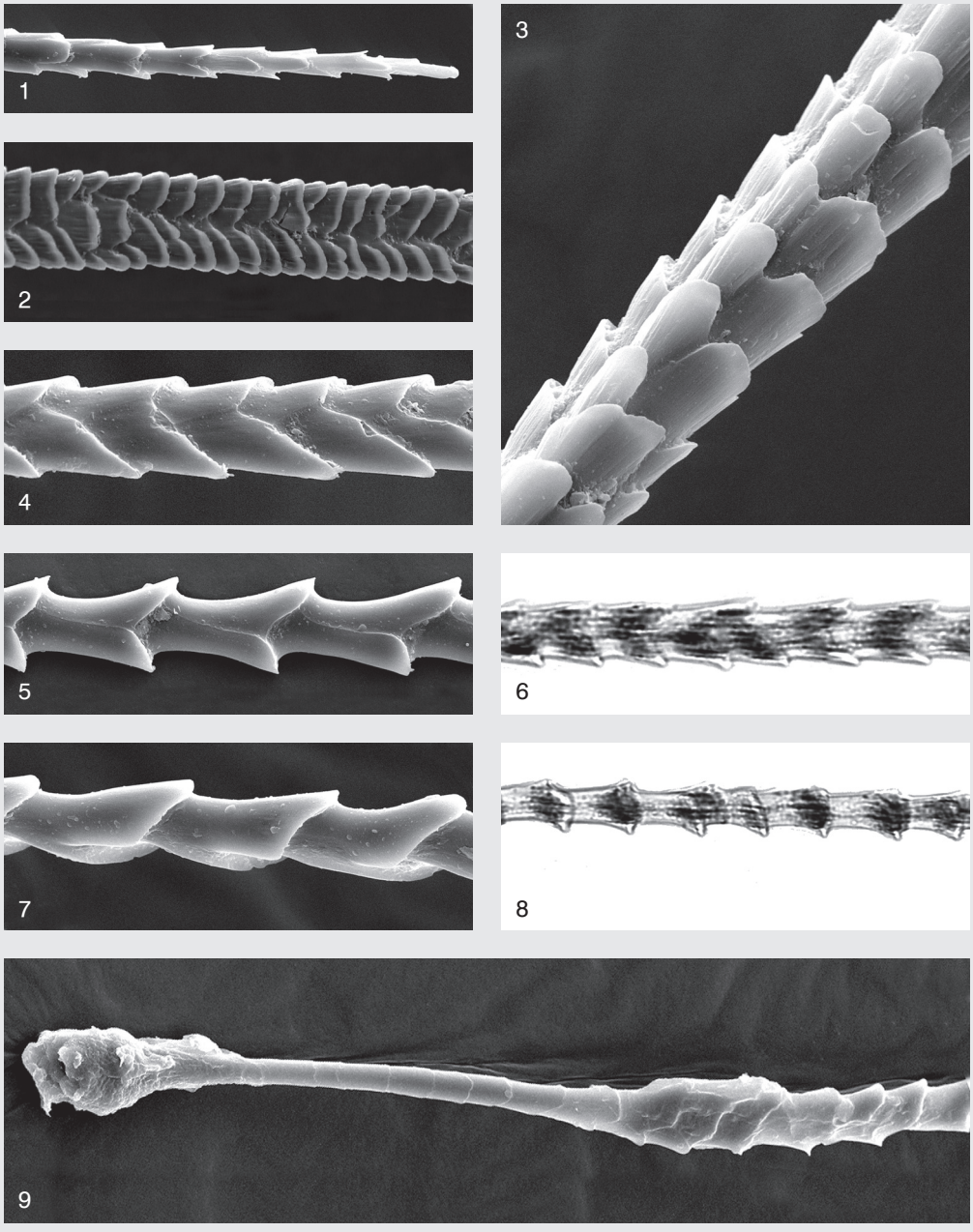
Vespertilio murinus

FUR: Dorsal side is shaggy, dark blackish-grey with lighter staples; ventral fur is more compact and thick, extending far onto the wings. Ventral side is paler grey or whitish-ochreous, the throat is most often whitish. The colouration of the backside and the belly is distinctly separated.

HAIR, MACROSCOPIC: Guard hairs polychrome or bicolorate; the shaft of the bicolorate hairs is brown; the shield is ochreous and the tip is transparent.

HAIR, MICROSCOPIC: The basal section is bulbous. The cuticular pattern on the proximal part of the shaft is asymmetrical, spiked coronal; the proximal part of the shield has irregular mosaic coronal pattern. The apical margins of the scales are smooth. The distal part of the shield is channelled; the scales of this section are longitudinally elongated and divergent from the main axis of the hair, and they are symmetrically and deeply scalloped, with rounded, smooth or finely rippled apical margins. The surface of the scales on the shield is grooved. The transparent view is smooth or spiky. The structure of the apex is branching. The arrangement of the pigments is diffuse or apically aggregated on the shaft, diffuse on the shield. The cross-section is biconcave or oblong.

SIZE: l_{max} = 8 mm; d_{max} = 16 μ



Vespertilio murinus: 1 = tip, SEM; 2 = cuticula, proximal shield, SEM; 3 = cuticula, distal shield, SEM; 4 = cuticula, distal shaft, SEM; 5 = cuticula, proximal shaft, SEM; 6 = idem, transparent view; 7 = cuticula, basal, SEM; 8 = idem, transparent view; 9 = bulb and basal section, SEM

Miniopteridae

Miniopterus schreibersii

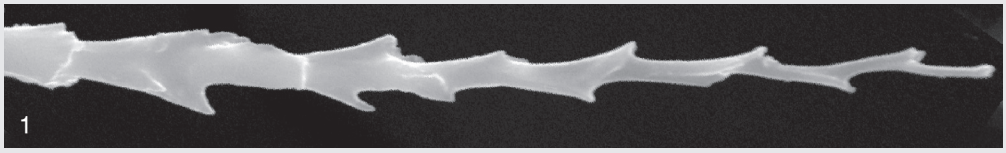
FUR: Dorsal fur pale grey-brown or ochreous-brown, gradually turning into the paler ochreous-grey or brownish-grey belly.

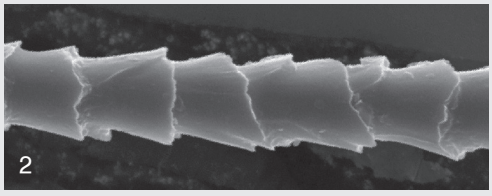
HAIR, MACROSCOPIC: Most hairs unicolorous brown or red-brown; the polychrome hairs have darker shaft and paler shield.

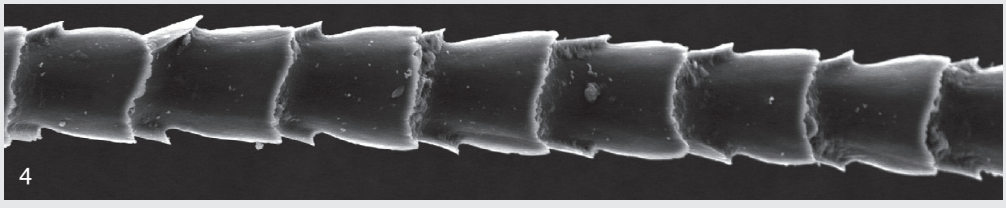
HAIR, MICROSCOPIC: The cuticular pattern is zigzagged coronal on the proximal part of the shaft; hastate coronal on the distal part of the shaft and the proximal section of the shield. The distal section of the shield has broad, mosaic coronal pattern. The apical margins of the scales are finely angular and irregularly wavy. The pigments are aggregated apically in the shaft, and display a diffuse or linear arrangement in the shield. The tip is branching.

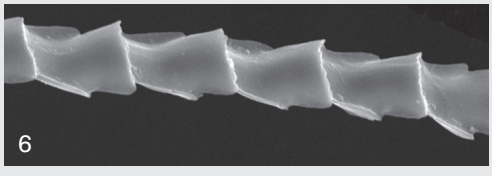
SIZE: l_{max} = 8 mm; d_{max} = 10 μ

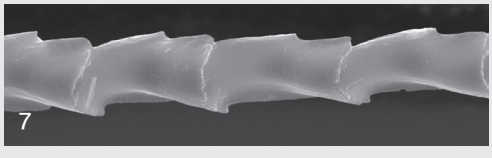
TAXONOMY: The hastate coronal pattern was described by BENEDICT (1957) for *Miniopterus australis* and the Phyllostomidae family; in the Central European bat fauna, only *M. schreibersii* possesses this cuticular pattern.

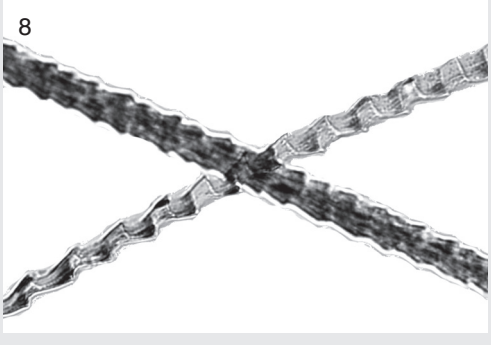












Miniopterus schreibersii: 1 = tip, SEM; 2 = cuticula, distal shield, SEM; 3 = idem, transparent view; 4 = cuticula, distal shield, SEM; 5 = idem; 6 = cuticula, distal shaft, SEM; 7 = cuticula, basal, SEM; 8 = transparent view, hairs

Molossidae

FUR: The fur of the Free-tailed Bats is mostly unicoloured, buff, greyish or brown; the touch is velvety.

HAIR, MACROSCOPIC: Most species of the Molossidae are characterized by the presence of several types of specialized hairs; like the "spoon-like" spatulated hairs on the toes, face, lips, and cheeks; the thorn-like spatulated hairs (or hyperkeratinized hairs) around the nostrils; the osmetrich hairs on the chest; and in some species, there might be erectile crest on the top of the head. There are also "naked" bats within the family. The curved, spatulated hairs on the outer toes are used in the cleaning and grooming of the fur (ALLEN *et al.* 1917, NOWAK & PARADISO 1983, GREGORIN & CIRRANELLO 2015).

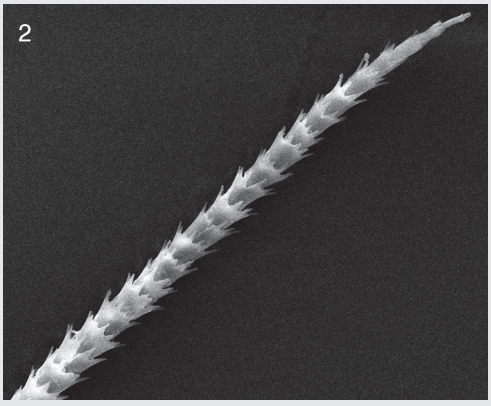
Tadarida teniotis

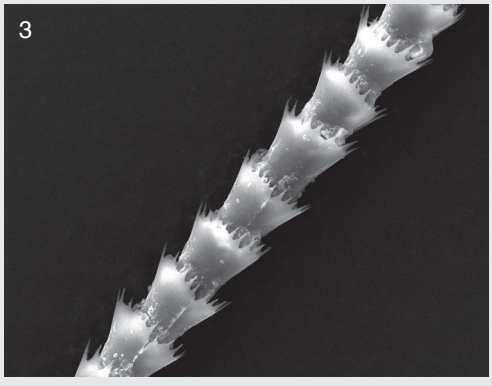
FUR: The fur is thick, short, velvety, unicoloured dark grey or greyish-brown; the ventral side is paler. Hairs extend onto wings.

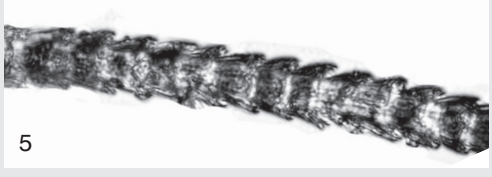
HAIR, MACROSCOPIC: All kinds of hairs are straight. The unicoloured hairs are brown, dark grey, whitish or silver-like; the shaft of the bicoloured hairs is grey or brown; the shield is transparent whitish.

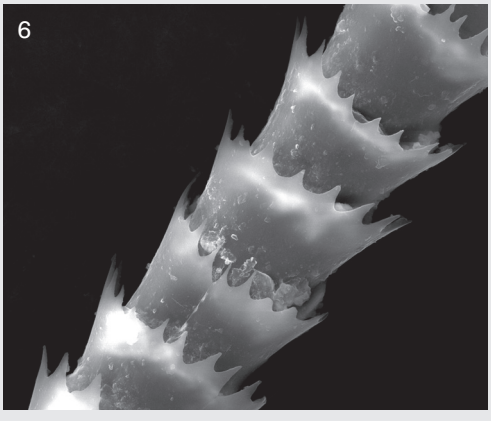
HAIR, MICROSCOPIC: The shape of the shaft is tubular. The cuticular pattern is symmetrical; the scales are remarkably elongated, thin and slender coronal on the basal section; regular, corniculate coronal on the shaft; compressed coronal on the shield. The apical edges of the scales are divergent from the axis, do not overlap along the entire length of the hair and their margins are regular dentate; the dens are characteristically long and thin, and fringe-like on the distal shield, result the crown-shaped appearance of scales. The transparent view is spiky. The pigments are aggregating distally, resulting in a peculiar banded appearance on the transparent view. The tip is telescopic.

SIZE: l_{max} = 9 mm; d_{max} = 12 μ









Tadarida teniotis: 1 = tip; 2 = tip, SEM; 3 = cuticula, distal shield, SEM; 4 = idem, transparent view; 5 = transparent view, proximal shield; 6 = cuticula, proximal shield, SEM; 7 = cuticula, shaft; 8 = transparent view, shaft; 9 = transparent view, basal

7.4. Lagomorpha

The order is easily distinguishable from the closest related Rodentia and the other mammalian orders by its apomorphic macroscopic and microscopic hair and fur characters. On the other hand, these characters are very constant throughout the entire order; therefore, the genera and the species are practically indistinguishable by the features of the hairs. As an adaptive colouration in lagomorphs, there are a few significant relations in their role; like the camouflage by the pale fur in open habitats, the red fur in rocky habitat, the dark fur in humid tropical habitats; the white tail seems to be associated with the sociality of the species, the living on open grasslands and scrubby habitats, and the use of burrows (Stoner *et al*. 2003).

FUR: The fur is thick, long-haired, rather loose and has a velvety touch. The ground colour varies from ochreous-brown to brown and brown-grey, the dorsum always darker then the ventral side; it is grizzled and/or marbled; usually there is sharp demarcation line between the belly and the dorsum and a white ring around the eyes; the paws are covered by fine, short hairs.

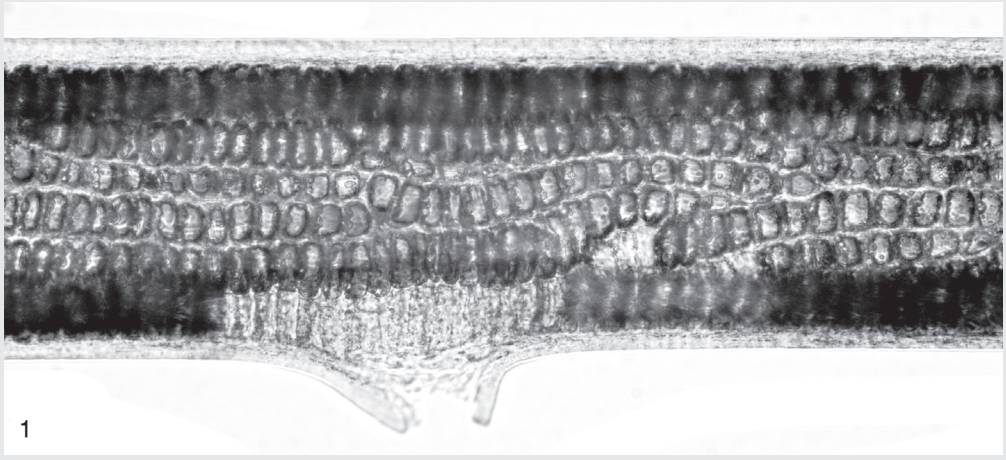
HAIR, MACROSCOPIC: The GH0 guard hairs are unicolorate or bicolorate, they are much longer than the average thickness of the fur. The GH1 and GH2 guard hairs are banded, usually with one, more rarely with two bands: the shaft is long, thin, and pale; the proximal band is light brown and the distal band is ochreous; the apical region is dark brown or black. The shields of the guard hairs are flattened. The hairs are channelled; the channel is long and relatively shallow, at least as long as the half-length of the stem but usually even longer, ca two-thirds of the entire length of the stem. The inner surface of the channel is less articulate. The layer of UH is dense and thick, velvety; the shape of UH wavy; unicolorous or banded on the shield. The tip is long, gradually tapering.

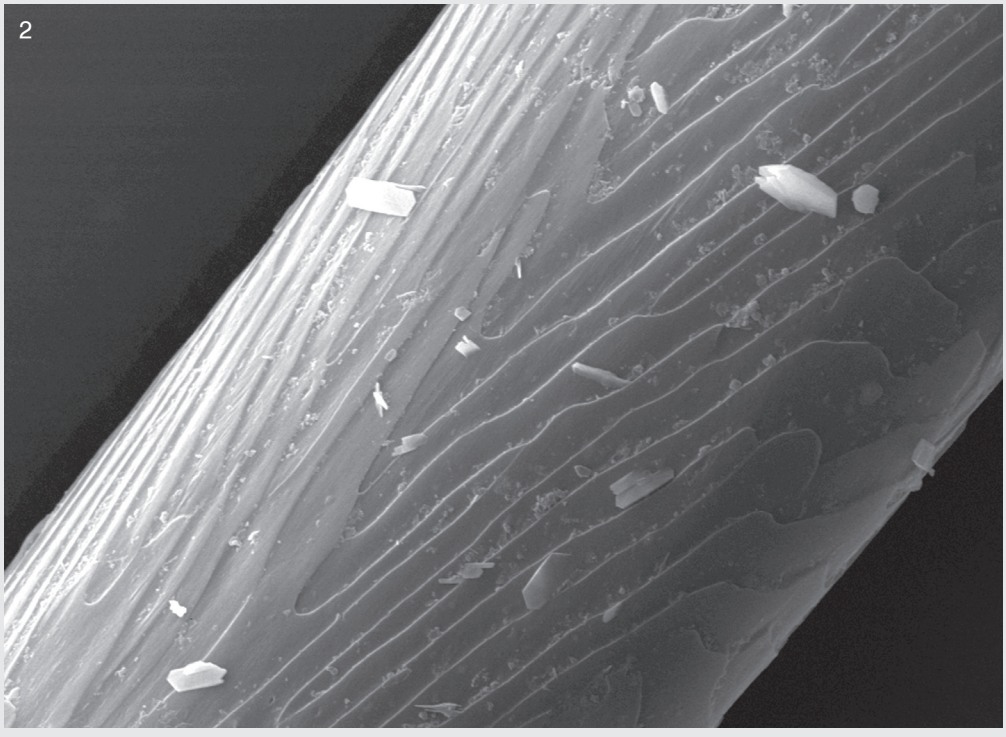
HAIR, MICROSCOPIC: The cuticular pattern of the guard hairs is longitudinally elongated, narrow, rippled or lanceolate chevron on the basal part and the shaft; transversally elongated, near and regular mosaic on the medial and distal sections of the shield. In the apical region, the pattern is waved figureless with crenated scale edges. The medulla is fragmented in the basal part, uniserial nummiform and, more distally, biserial nummiform in the shaft; multiserial, twisted in the shield. The medulla of UH is nummiform, the multiserial twisted medulla is absent. The tip is telescopic. The cross-section is oval in the shaft, convex-concave or plano-concave in the shield.

The micro- and macroscopic hair characters of the two European genera show a considerable overlap, therefore the hairs of the *Lepus* and *Oryctolagus* species cannot be distinguished at species level.

SIZE: $1_{max} = 35$; ($GH0_{max} = 50$ mm); $d_{max} = 150$ μ; $m/d_x = 0.85$

TAXONOMIC CHARACTER: the multiserial, twisted medulla and the lanceolate chevron cuticular pattern are apomorphic features of the order Lagomorpha.





Leporidae: 1 = medulla, shield; 2 = cuticula, shaft

Lepus europaeus

FUR: The dorsum is most often ochreous, or greyish-brown, darker on the head and along the backbone ("black-backed"); the tips of the ears are black. The chin is whitish; a well-defined white ring rounds the eyes; the face is whitish; the breast is reddish-brown or ochreous-brown the belly is generally white. The tail-tuft is white, with black dorsal covering.

HAIR, MACROSCOPIC: The underhairs are ochreous or white(ish).

Lepus timidus

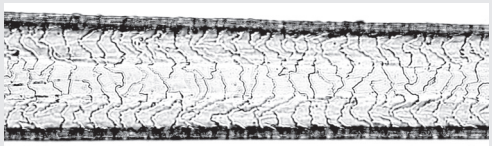
FUR: The summer coat is grizzled, the ground colour is greyish-brown; the winter coat is most often completely white, sometimes pale greyish with darker grey or yellowish-brown patches. The ears are uniformly greyish-brown in summer and whitish in winter, but the tips of the ears are always black; the tail is completely white all year round.

HAIR, MACROSCOPIC: The underhairs are white or pale ochreous-brown.

Oryctolagus cuniculus

FUR: The fur is grizzled, the ground colour is greyish-, yellowish brown. The lateral sides of the body are generally greyish, the ears are unicolorous brown. The chin is white; a narrow white ring rounds the eyes; the face and the breast are brownish; the belly is white or pale greyish-brown; the underside of the tail is white, dorsally dark greyish-brown.

HAIR, MACROSCOPIC: The underhairs are pale grey or pale ochreous-brown.



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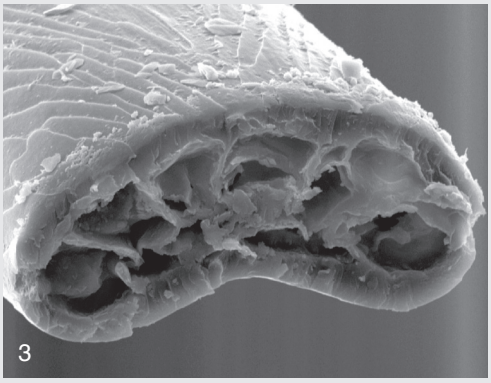

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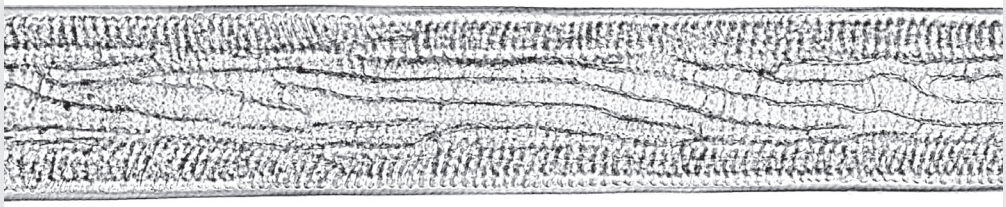

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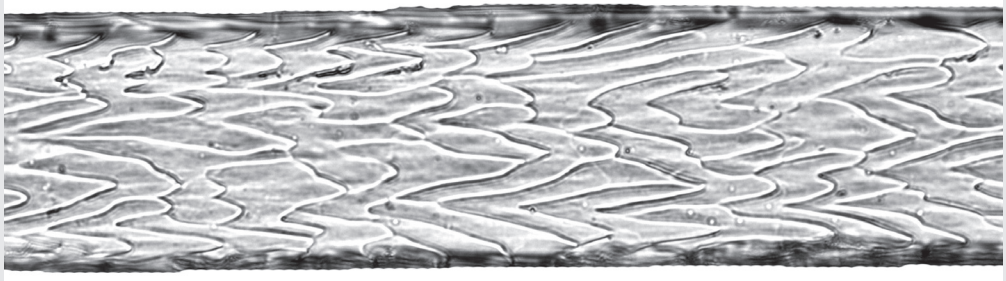

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Leporidae: 1 = cuticula, apical section; 2 = cuticula, shield; 3 = cross-section, transit, SEM; 4 = medulla, shield; 5 = cuticula, shaft; 6 = cuticula, basal; 7 = medulla, shaft

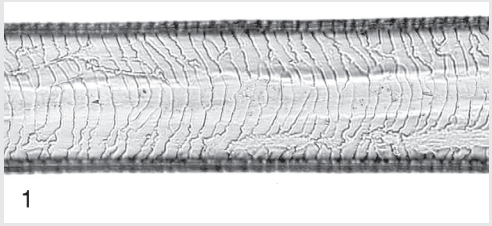
7.5. Rodentia

FUR: The rodents are the most species-rich order of the mammals, displaying a wide range of variation in all morphological characters, including the microstructure of the hairs and fur. The dorsum might be grizzled, marbled, or mottled.

HAIR, MACROSCOPIC: The different types of the guard hairs are clearly distinguishable although there are several macrostructural types and variations within the order. In the Central European taxon, the GH1 is usually unicolorate; the GH2 often banded and usually has two different types: one of them is thicker, curved and combined wavy, the second is thinner and strongly wavy. In the thicker type of GH2, the ochreous-whitish band is a shorter or longer section on the proximal part of the shield, while in the thinner type of GH2; the short band is located on the distal part of the shield. The UH is slightly wavy or zigzag-shaped, unicolorate, polychrome or banded; most often whitish, pale greyish or ochreous shaded.

HAIR, MICROSCOPIC: The microscopic patterns are also remarkably variable but there are certain rodent features, which ones can be recognised in the great majority of the species: these are the chevron or rhomboidal cuticular pattern on the shaft and the multiserial, cob-like medulla at the widest diameter of the shield. The channelled hair and the grooved surface of the cuticula scales appear frequently in the order; the bulb is always knobby; the basal part most often tubular. The variation of the medullary index is considerable in the order: $0.2 \leq m/d \leq 0.8$.

TAXONOMIC CHARACTER: the cob-like multiserial medulla at the maximum diameter of the shield is an apomorphic feature of the order Rodentia. This type of the medulla is variable throughout the rodent groups due to the variable shapes of the cells, the absence or presence and arrangement of septa and the air sacs.



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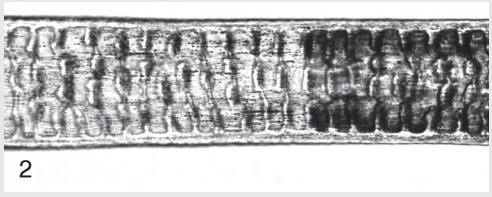

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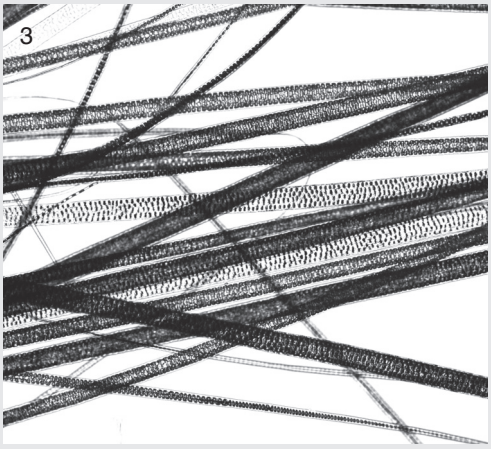

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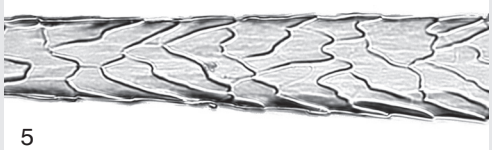

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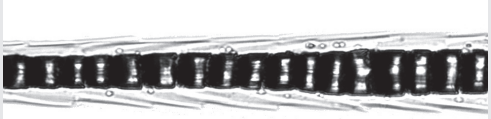

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Rodentia: 1 = cuticula, apical section; 2 = medulla, distal shield; 3 = transparent view, hairs; 4 = medulla, proximal shield; 5 = cuticula, shaft; 6 = cuticula, transit; 7 = bulb; 8 = medulla, shaft

Sciuridae and Gliridae

In case of Sciuromorpha (including the species belong to the families Sciuridae and Gliridae in Europe) the camouflage seems to be the major factor which determines the colours and patterns of fur, meanwhile the social communication (e.g. ear and/or face marking, tail pattern) and regulation of physiological processes play minor roles (Ancillotto & Mori 2017).

Sciuridae

FUR: The fur is variable in structure and colouration; the ground colours are the brown, ochreous-brown and red-brown; albinistic, leucistic and melanistic specimens also exist. The mottled fur, with stripes or speckles, is more common in the Sciuridae than in the other families of rodents (Kryštufek & Vohralík 2012).

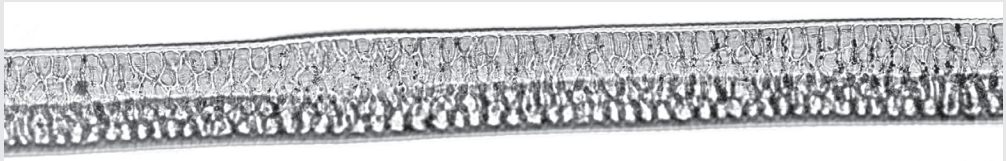
HAIR, MACROSCOPIC: The hairs usually banded and channelled.

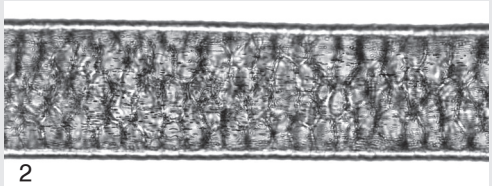
Sciurus vulgaris

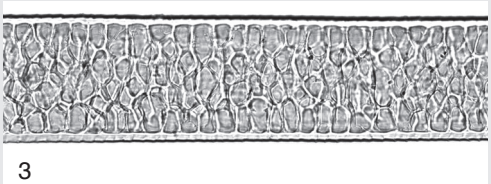
FUR: The fur is dense and soft, its touch generally silky. It has three main ground colours: red, brown and grey-brown. The colouration of the individuals could be strongly variable within the same population. The colouration of the fur has seasonal changes; the winter fur is usually paler and denser, consisting of shorter hairs. The dorsum is grizzled, marbled or unicoloured; the throat and the ventral side are white or creamy. The darker dorsal and the paler ventral sides are sharply demarcated, occasionally bordered by characteristic vivid red or grey stripe. The red squirrel has thick and long, reddish or brown ear tufts in the winter season, while in the summer, these tufts are shorter or absent. The tail is long, bushy, evenly thick, mostly grizzled, greyish or reddish.

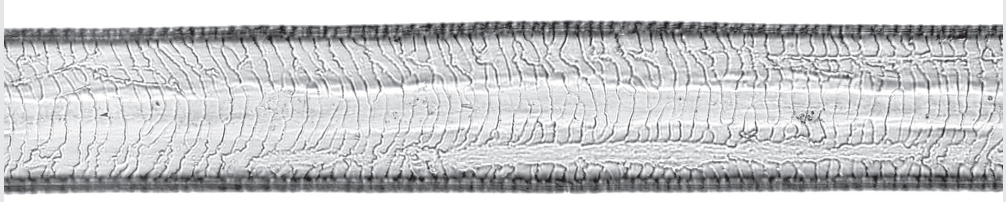
HAIR, MACROSCOPIC: The macroscopic features of the hairs display considerable variation. The dorsal GH of the red coloured specimens is unicolorous red-brown, rarely polychrome. The dorsal GH of grizzled specimens can be unicolorate white, red-brown or black, bicolorate or banded. The number of the bands varies from 1 to 4; these bands can be white, red, brown or black. The location and length of the band are variable in the one-banded hairs; the length of the bands is rather uniform in the hairs having 2–4 bands. The tip is most often reddish-brown but could be also white or brown. The GH hairs of the tail are remarkably longer than that of the hairs of the body, the number of the bands varies between 1 and 5.

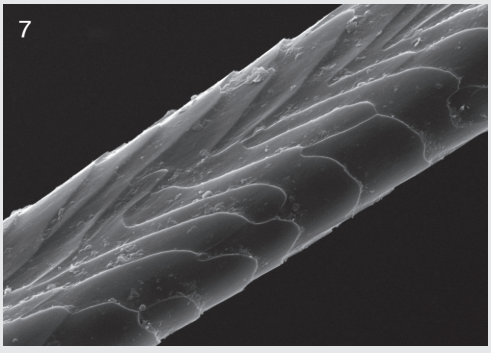
HAIR, MICROSCOPIC: The cuticular pattern is rhomboidal pinecone on the basal part; cuneate chevron on the shaft; transversal, irregular mosaic on the transit, and regular mosaic on the shield. The scales of the apical region are waved, figureless with crenate apical edges. The medulla is uniserial nummiform on the base; biserial nummiform on the shaft; and cob-like multiserial at the shield, where the medullar cells are polygonal or rounded, usually rather equal in size. The pigments are concentrated in the medulla; the cortex is thin. The shield is flattened; its distal section channelled by a wide, shallow channel. The tip is long, gradually tapering. The cross-section of the shield is oblong, biconcave, or convex-concave.







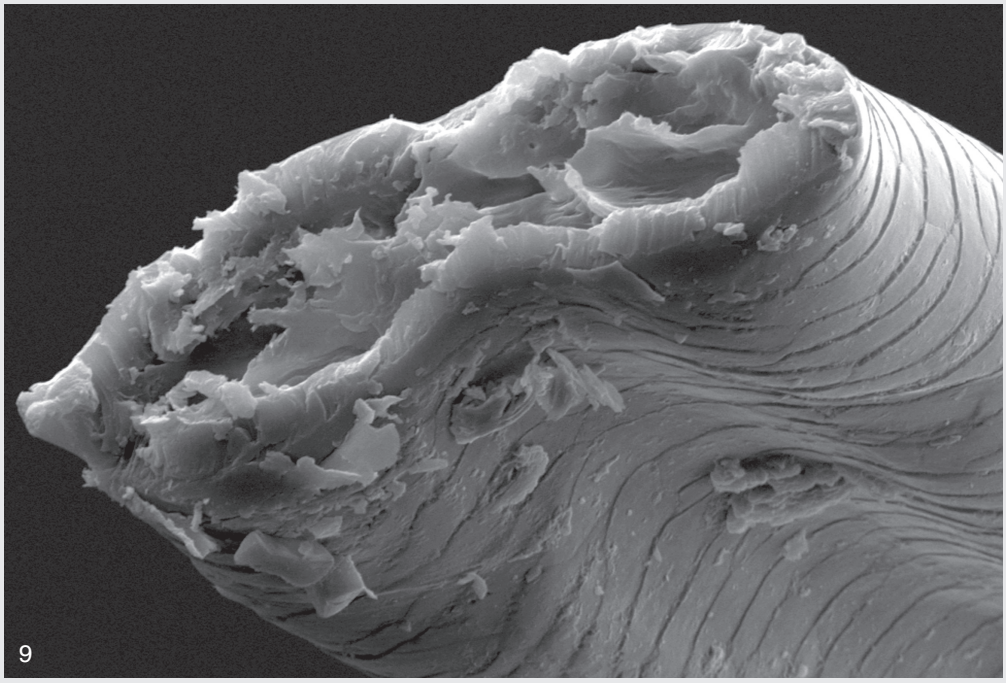


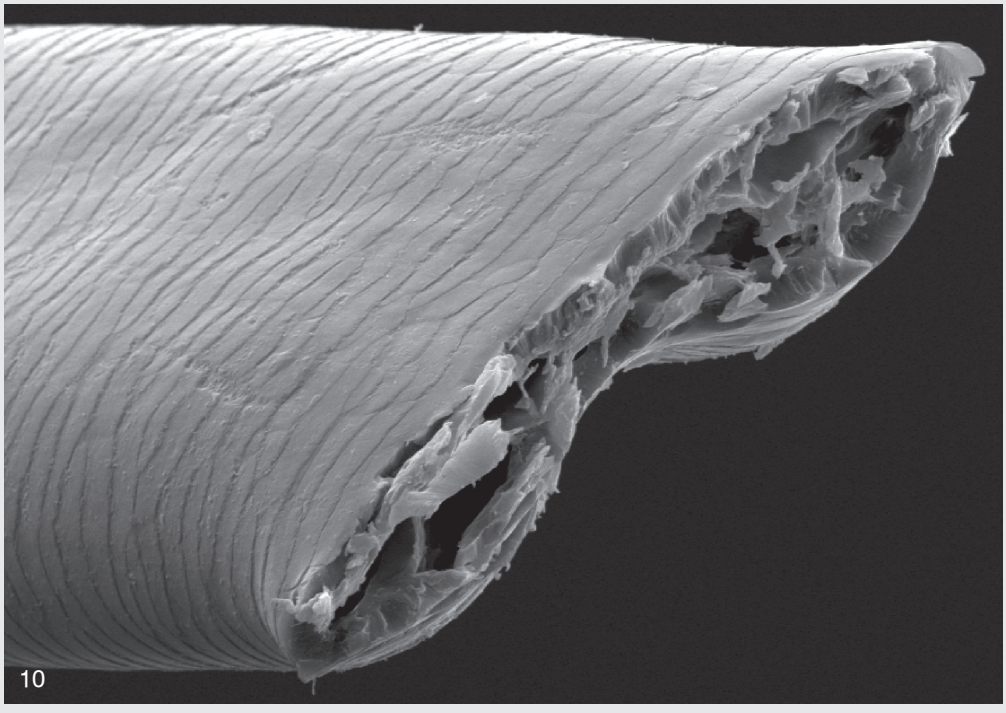


Sciurus vulgaris: 1 = medulla, on channelled shield; 2 = medulla, distal shield; 3 = medulla, proximal shield; 4 = cuticula, on channelled shield; 5 = cuticula, transit; 6 = cuticula, shaft; 7 = cuticula, basal; 8 = cuticula, shaft, SEM

SIZE: l_{max} = 25 mm; d_{max} = 125 μ; m/d_x = 0.85

REMARKS: *Sciurus carolinensis* – Eastern Grey Squirrel is native in North America. It was introduced to Great Britain, Ireland, Italy, and many other parts of World. It has become an invasive alien species; in Europe, the Grey squirrel endangers or even replaces the native Red squirrel as its competitor and disease-vector species (BERTOLINO *et al.* 2014). There are no registrations of Grey squirrel in Central Europe yet, and its further expansion must be impeded. The Eastern Grey Squirrel is similar at first sight to the Red Squirrel but is clearly separable from it by some morphological characteristics. The dorsum is grizzled, the ground colour is greyish, greyish-brown. The ears are tuftless; the belly is white, greyish or cinnamon; the tail faintly flattened with long guard hairs arranged axially symmetrically at the margins. The monitoring of the presence, number and activity of these species using hair tubes might be an important method for conservation biologists (GURNELL *et al.* 2004), but the identification of these species on the basis of microscopic hair character requires practice, as the differences are very small (TEERINK 1991, TÓTH 2015).





Sciurus vulgaris: 9 = cross-section, transit, SEM; 10 = cross-section, shield, SEM

Eutamias sibiricus

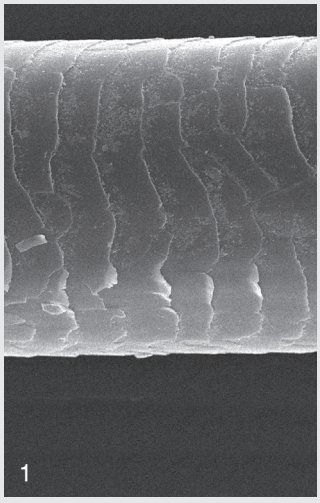
The Siberian chipmunk was introduced from Asia to several countries of Europe where it is breeding in smaller, isolated populations.

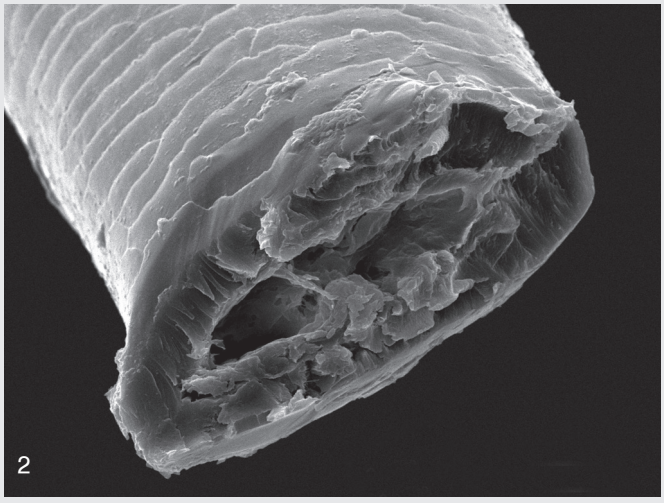
FUR: The fur is silky in touch, consisting of short hairs. The dorsum is mottled; the ground colour is pale yellowish-brown or reddish brown; the chest and the belly are white, yellowish or creamy, with usually stepwise transition from the darker backside to the lighter ventral side. The dorsal side bears 5 longitudinal dark stripes running parallel with the backbone, with 4 lighter stripes in between them; the width of these stripes are equal and subequally spaced, lateral ones are shorter than the median trio (PATTERSON & NORRIS 2016). The colour of the lighter stripes is usually different: the two lateral ones are yellowish, while the two paler stripes bordering the middle dark stripe are whitish. The nape is greyish. The face is masked, with a whitish band running from the tip of the nose to the eyebrows and from behind the eyes to the ears; the chin is ochreous-white, the front is light brown. The tail is flattened dorso-ventrally; the longest whitish and dark brown guard hairs give a rather shaggy appearance to the grizzled, greyish-brown, medially somewhat lighter tail.

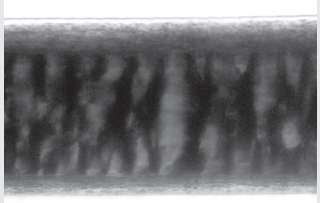
HAIR, MACROSCOPIC: The GH1 is unicoloured, dark brown; the GH2 is bicoloured or one banded, the band is yellowish or reddish. The tip is brown to red-brown.

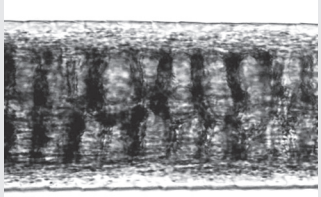
HAIR, MICROSCOPIC: The cuticular pattern is broad petal on the basal section; broad rhomboidal or cuneate chevron on the proximal part of the shaft; near, mosaic on the transit; and close, regular mosaic on the shield; figureless, near, wavy on the apical section, with rippled edges of the scales. The medulla is uniserial nummiform in the basal part, biserial nummiform in the shaft; here the air sacs between the medullar cells may span through the entire width of the medulla; cob-like multiserial on the shield. The pigments arrange diffusely in the medulla and the inner part of the cortex. The tip is long, gradually tapering. The cross-section is circular.

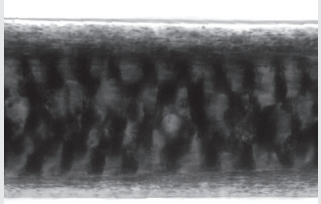
SIZE: l_{max} = 18 mm; d_{max} = 75 μ; m/d_x = 0.8

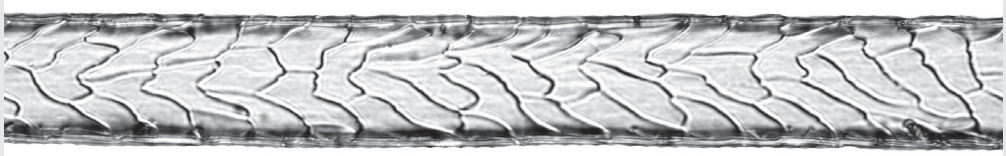


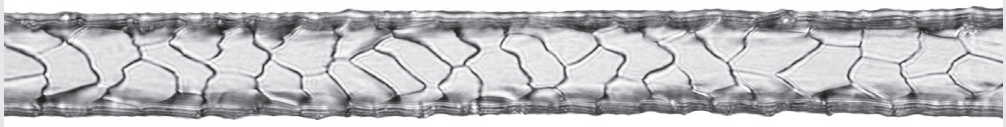












Eutamias sibiricus: 1 = cuticula, shield, SEM; 2 = cross-section, shield, SEM; 3 = medulla, proximal shield; 4 = idem; 5 = medulla, distal shield; 6 = cuticula, shaft; 7 = cuticula, shaft

Marmota marmota

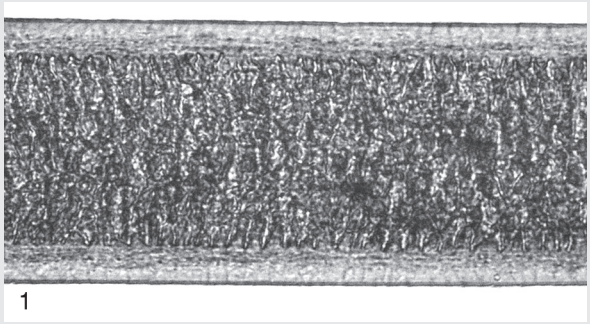
FUR: The fur is thick, slightly coarse. The pattern of the fur is marbled and grizzled, with sporadically arranged yellowish, reddish brown and grey patches. The dorsum is ochreous-brown, reddish-brown or greyish-brown; the chest, the legs and the belly are paler ochreous, yellow or orange, more uniformly coloured; the transition is gradual between them. The head is darker greyish. The base of the tail is darker brown, reddish-brown or chestnut-brown; the tip of the tail is obtuse, ended in black stripe.

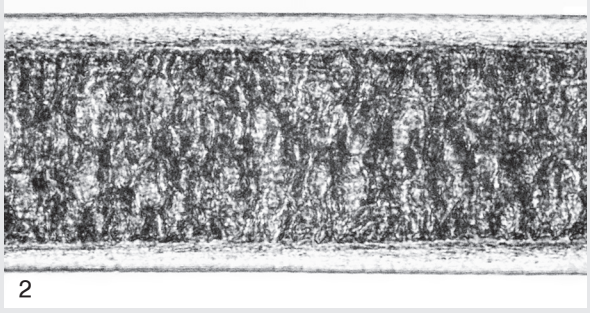
HAIR, MACROSCOPIC: The GH1 is unicolorate or bicolorate; the GH2 may be bicolorate, one-banded or two-banded. The bicolorate hairs have dark brown shaft and reddish-brown shield; the one-banded GH2 has dark brown shaft with reddish band and black shield and tip. The two-banded GH2 has two types: in the first type, the shaft is light brown, the two bands are dark brown and reddish while the apical region and the tip are dark brown; in the second type, the shaft is dark brown, the first band reddish, the second dark brown. The hair is gradually whitened from the shield towards the transparent and light tip.

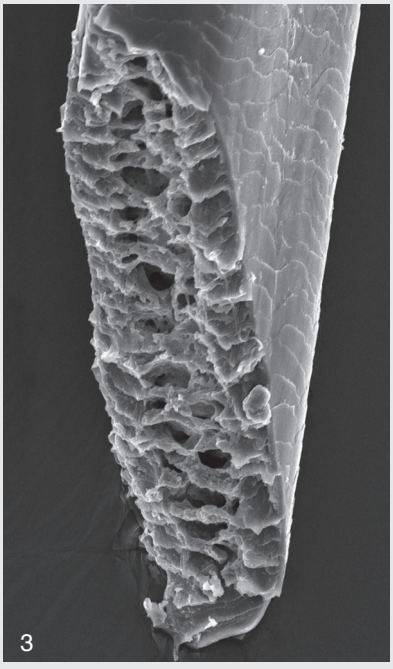
HAIR, MICROSCOPIC: The cuticular pattern of the basal section is broad petal. The scales on GH1 shaft are cuneate chevron; the transit and the shield are transversal mosaic. The cuticular pattern of the GH2 is mostly homogenous, despite its macroscopic variability: the shaft, the transit and the shield have transversal, broad, irregular mosaic pattern; figureless in the apical section; the edges of scales are near and wavy or rippled. The surface of scales might be scratched. The medulla is fragmented at the base; irregular nummiform with wider air sacs in the shaft; and cob-like multiserial in the transit and the shield with polygonal medullar cells. In the widest part of the shield, the cortex becomes thin and the margin of the medulla is crested or fringed. The pigments arrange diffusely, and concentrate in the medulla. The outer layer of the cortex is transparent, being rather broad in the shaft and the transit (m/d = 0.6). There are no channels on the hairs. The stem is flattened on the shield. The tip is long and gradually tapering, transparent. The cross-section is oblong.

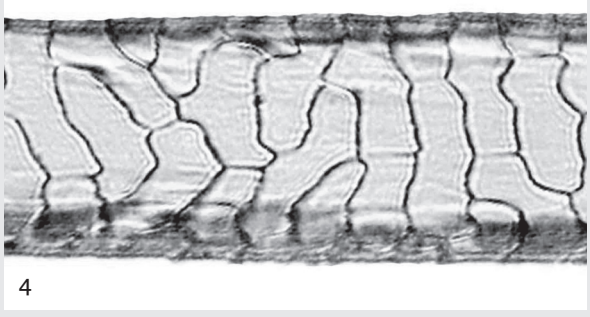
SIZE: l_{max} = 40 mm; d_{max} = 138 μ; m/d_x = 0.8

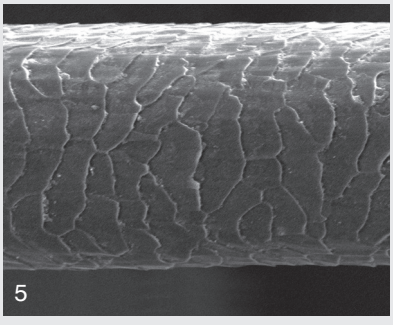
REMARKS: ARMITAGE (2009) reviewed the colour variability of the fur of the genus *Marmota* and discussed its physiological role. Besides the high variability of the furs within the populations of a given species, there are genetically determined colours of fur resulting in white, albinistic, and melanistic forms, while the bluish form is a physical reflection of the bicolorate and the banded hairs; but all of these fur variants are rare. The light colours increase the reflection while the dark colours increase absorption, thus the high variability of colours of the fur may provide advantages for practically all seasons and days within the harsh environment. Armitage stated that the main function of the colours of the fur is the heat transfer.

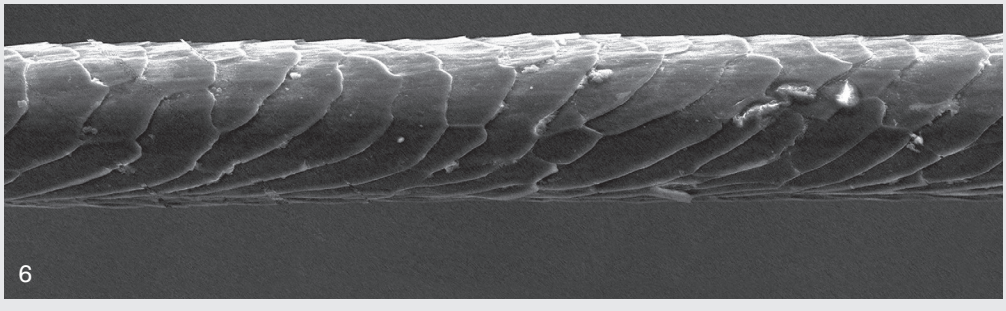












Marmota marmota: 1 = medulla, distal shield; medulla, proximal shield; 3 = cross-section, shield, SEM; 4 = cuticula, transit; 5 = cuticula, shield, SEM; 6 = cuticula, shaft, SEM

Genus *Spermophilus*

FUR: The fur is rough in touch, consisting of short hairs. The pattern of the fur is mostly grizzled, sometimes marbled or mottled; the ground colour is yellowish-brown. The dorsal surface is dark, while the throat, the breast (and often the inner parts of the forelegs), and the belly are uniformly whitish-ochreous. The ventral side is paler; even the melanistic specimens have at least a few light patches. The *Spermophilus* species have whitish rings around the eyes. The short tail grizzled, and the hairs banded.

HAIR, MACROSCOPIC: The GH0 hair is scarce, straight, uniformly dark brown. The GH1, GH2 hairs are straight or curved, and usually banded. The UH is wavy, bicolorate or banded with darker shaft and ochreous shield; the band is whitish.

HAIR, MICROSCOPIC: The cuticular pattern is broad petal at the base; cuneate chevron on the shaft; irregular mosaic on the transit; transversal, regular mosaic on the shield; and figureless, waved on the apical section. The surface of the scales is finely grooved. The medulla is cob-like multiserial at the maximum diameter of the shield. The microscopic features of the two central European species are generally the same, only the shape of medullar cells differs slightly: the *S. citellus* has transversally elongated cells while the *S. suslicus* has mostly rounded cells.

The transit and the proximal section of the shield are channelled; the channel is wide, inarticulate. The tip is long, gradually tapering, brown or transparent. The shield is flattened; the cross-section in this part of the hair is convex-concave or plano-concave.

Spermophilus citellus

FUR: The fur is grizzled and marbled, sometimes with small whitish spots and patches on the dorsum; the ground colours are ochreous-grey and ochreous-brown.

HAIR, MACROSCOPIC: The GH1 is banded; the band is long, covering the entire shaft and the shield. The GH2 is also banded, with 1–3 variably long bands; the whitish-ochreous band of the distal shield is always the broadest.

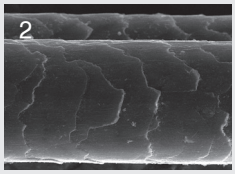
SIZE: l_{max} = 15 mm; d_{max} = 110 μ; m/d_x = 0.85

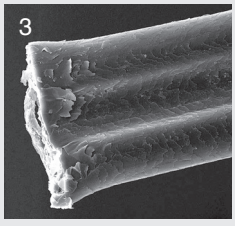
Spermophilus suslicus

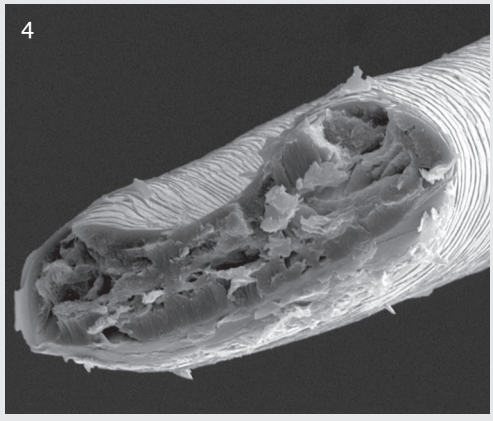
FUR: The fur is grizzled and mottled; the dorsum is darker brownish (or darker greyish) than in *S. citellus*, and the small white patches are larger and more distinctly marked.

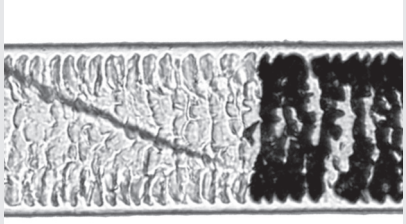
HAIR, MACROSCOPIC: The GH1 hair is unicolorous dark brown; the GH2 is unicolorous brown or one-banded with a long whitish band extending from the transit to the distal section of the shield.

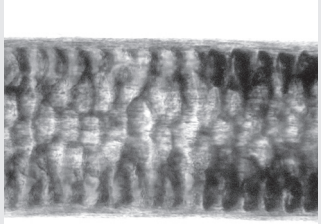
SIZE: l_{max} = 12 mm; d_{max} = 80 μ; m/d_x = 0.85

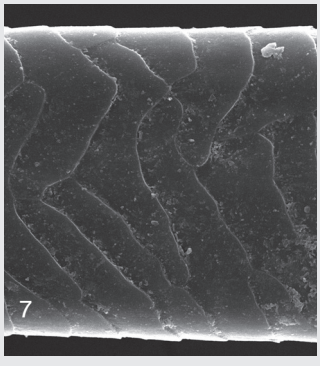


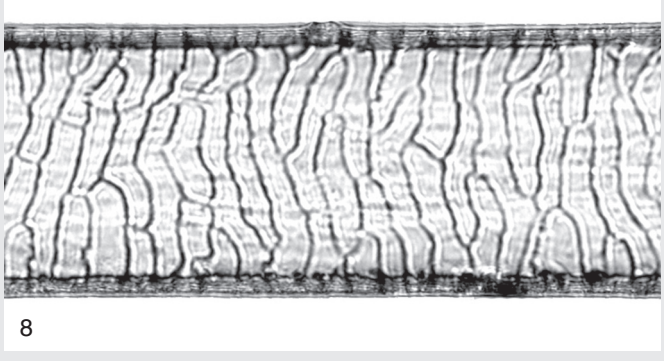


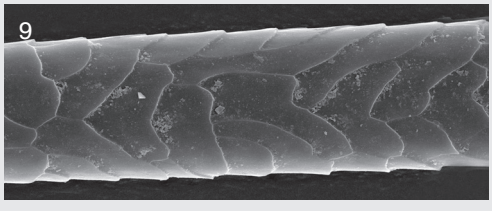


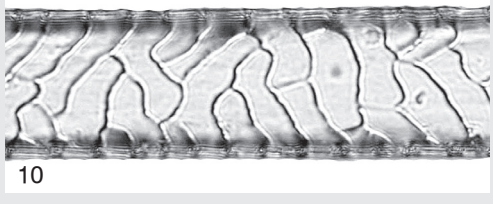












Spermophilus* spp.**: 1 = transparent view, tip section; 2 = cuticula, channelled apical section, SEM; 3 = channelled shield, SEM; 4 = cross-section, shield, SEM; 5 = ***S. citellus, medulla, shield; ***S. suslicus***: 6 = medulla, shield; 7 = cuticula, transit, SEM; cuticula, shield; 9 = cuticula, shaft, SEM; 10 = idem

Gliridae

FUR: The fur is thick, velvety in touch, marbled or unicoloured; the face might be masked. The colour and structure of the more or less bushy tail are usually characteristic of species.

HAIR, MACROSCOPIC: The GH0 and GH1 hairs are polychrome or unicolorous. The shaft of the polychrome hair is greyish, the transit is ochreous-brown, and the shield and the apical region are dark brown or reddish-shaded. The GH2 and UH are banded; the band can be seen in both hair types on the distal section of the shield.

HAIR, MICROSCOPIC: The base of GH1 is most often tubular; the base of GH2 and UH is bulbous. The cuticular pattern is elongated rhomboidal or broad petal on the proximal shaft; cuneate or galeate chevron on the distal shaft and the transit; transversal, regular mosaic on the distal shield, and figureless, waved at the apical section. The medulla might be uniserial or chromosomal nummiform, or fragmented tubular. The apical region is gradually tapering; the tip is always dark brown. The cross-section of GH is circular or oblong.

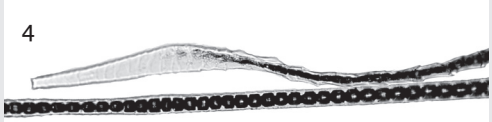
Glis glis

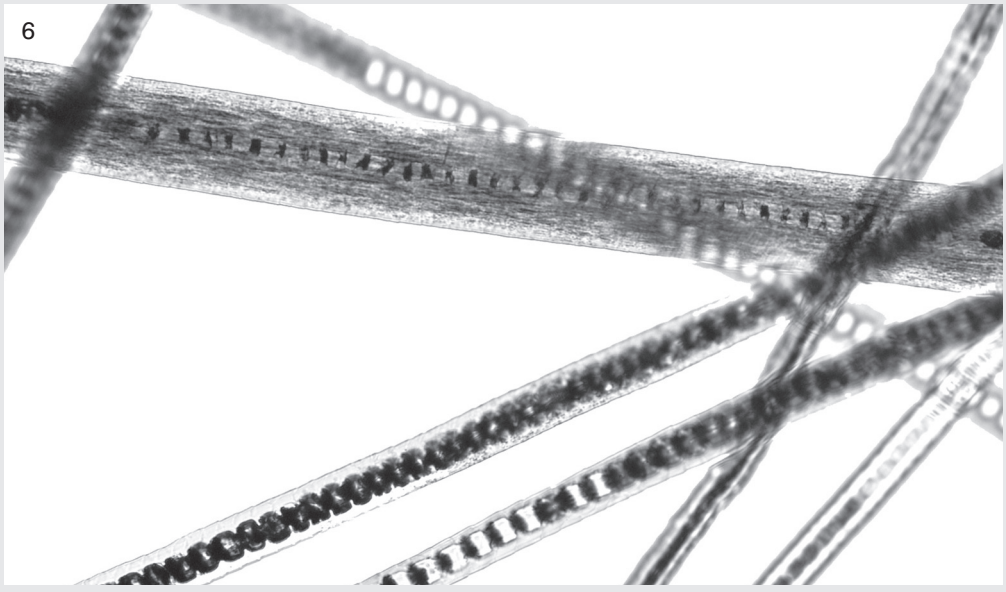
FUR: The fur is thick, marbled, and usually greyish-brown. The face is not masked but there are characteristic dark grey rings around the eyes. The belly is white or creamy, and the line of demarcation between the dark dorsum and the light belly is rather well defined. The dense, bushy tail is uniformly haired, greyish-brown, with whitish medial stripe ventrally.

HAIR, MACROSCOPIC: The GH2 and the UH are banded, having a silvery sheen; the shaft is dark grey, the band is transparent, honey-coloured.

HAIR, MICROSCOPIC: The cuticular pattern is cuneate chevron on the shaft. The thickness of the medulla is randomly variable. The cortex is rather thick in the shield and, therefore, the medullary index is remarkably smaller in this section than in the other parts of the hair.

SIZE: l_{max} = 20 mm; d_{max} = 60 μ; m/d_x = 0.25





Gliridae: 1 = tip section; 2 = medulla, shaft; 3 = medulla, shield; 4 = basal section; 5 = basal section; ***Glis glis***: 6 = transparent view, hairs; 7 = cuticula, shaft; 8 = medulla, shield

Muscardinus avellanarius

FUR: The fur is unicolorous, most often pale reddish-brown, more rarely reddish, hazel or greyish-brown. Longer bristle hairs cover sparsely the distal end of the tail. The chin, the throat, the breast and the belly are always paler, whitish with variably strong ochreous-brownish shade; the transition is gradual from the darker dorsum to the paler ventral side.

HAIR, MACROSCOPIC: The GH2 and UH are unicolorous or banded; the shaft is grey-brown; the band is pale reddish or yellowish.

HAIR, MICROSCOPIC: The cuticular pattern is elongated rhomboidal on the GH2 proximal shaft; broad rhomboidal on the distal shaft and the transit.

SIZE: l_{max} = 13 mm; d_{max} = 40 μ; m/d_x = 0.65

Dryomys nitedula

FUR: The dorsum is marbled, most often grey-brown, and occasionally rusty-reddish. The face is masked, defined by a dark stripe running from the nose to the ears, bypassing the eyes; the ridge of the nose and the frontal stripe greyish-brown. The face, the chin and the throat are ochreous or whitish; the belly is ochreous-grey. The transition between the darker dorsum and the paler belly is usually stepwise. The tail is somewhat flattened, rather shaggy; the dorsal side is grey-brown, the ventral side has a white medial stripe; the terminal part of the tail has long, grey bristle hairs.

HAIR, MACROSCOPIC: The GH2 and the UH are banded; the band is transparent, pale ochreous or yellowish.

HAIR, MICROSCOPIC: The cuticular pattern is galeate chevron on the distal shaft, cuneate chevron on the transit.

SIZE: l_{max} = 10 mm; d_{max} = 40 μ; m/d_x = 0.75

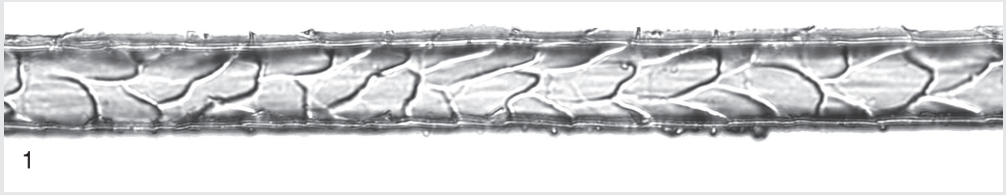
Eliomys quercinus

FUR: The ground colour of the dorsum is greyish-brown or reddish; the fur is marbled. The face is masked, defined by a broad black stripe from the middle of the face bypassing the eyes and continued around the ears; there are tiny white patches around the base of the ear. The ridge of the nose and the frontal stripe ochreous-brown; the cheek, the throat, and the belly are white. The dark dorsum and the light ventral side are sharply demarcated. The outer side of the foreleg is marked by a brown stripe. The tail is slightly widening towards the tip and tricolour: the basal part is brown or reddish, the dorsal side is dark greyish, sometimes black, laterally framed by long white hairs; the ventral side of the tail and the tip are white.

HAIR, MACROSCOPIC: The GH2 and UH are banded; the band is ochreous or yellowish.

HAIR, MICROSCOPIC: The cuticular pattern is galeate chevron on the distal shaft; transversal petal on the shield.

SIZE: l_{max} = 15 mm; d_{max} = 40 μ; m/d_x = 0.7



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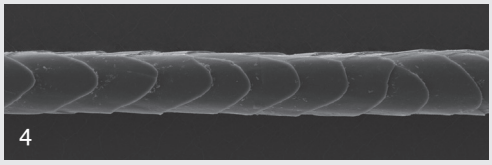

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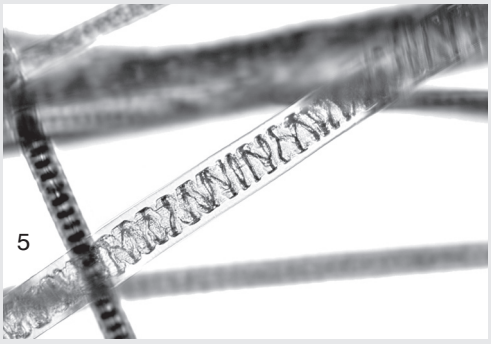

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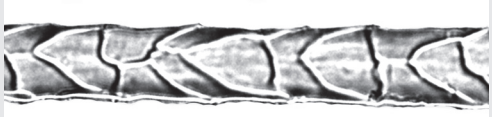

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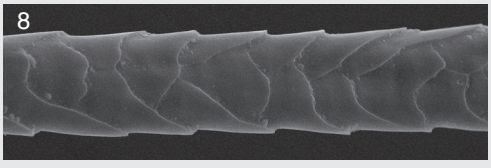


8

Muscardinus avellanarius: 1 = cuticula, distal shaft; 2 = cuticula, proximal shaft; ***Dryomys nitedula***: 3 = cuticula, distal shaft; 4 = cuticula, proximal shaft; 5 = transparent view, hairs; ***Eliomys quercinus***: 6 = cuticula, shield; 7 = cuticula, basal; 8 = cuticula, shaft

Dipodidae

The two Central European species of the family belong to the genus *Sicista*. This genus is characterised by the presence of the dark stripe running along the backbone; the colouration and the width of this stripe shows a remarkable intraspecific and intra-populational variation. The fur is marbled, silky, the ground colour is sandy ochreous or greyish.

Sicista subtilis & Sicista betulina

FUR: The dorsum is grey-brown, sometimes with rusty or reddish shade; the paler lateral sides of the body and the belly are ochreous or greyish-white, occasionally clear white; the colour transition is stepwise from the dorsum towards the belly. The long tail has longer, transparent bristle hairs.

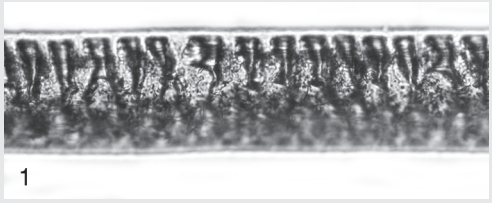
In *S. subtilis*, the dark dorsal stripe is longer, running on the backbone from the frons to the base of the tail; this stripe may be interrupted, sometimes only partial and/or oblique. The dark dorsal stripe can be defined by pale ashy grey stripes on both sides; in the young animals, additional dark lines may border these grey stripes.

In *S. betulina*, the black stripe running along the backbone is shorter and has no paler borderlines from the head to the base of the tail.

HAIR, MACROSCOPIC: The GH1 is unicolorous dark brown or black, flattened at the shield. The GH2 is banded, its shape is combined wavy; the shaft is dark grey, the band is honey-coloured and located on the proximal shaft or transit. The tip is gradually tapering, dark brown or black.

HAIR, MICROSCOPIC: The cuticular pattern is broad petal on the base; cuneate chevron on the shaft; irregular mosaic on the transit and regular, transversal, mosaic on the shield. The medulla is uniserial nummiform in the shaft; chromosomal nummiform in the transit; cob-like multiserial at the maximum width of the shield. The hairs are not channelled; the cross-section is oblong or circular.

SIZE: l_{max} = 10 mm; d_{max} = 53 μ; m/d_x = 0.85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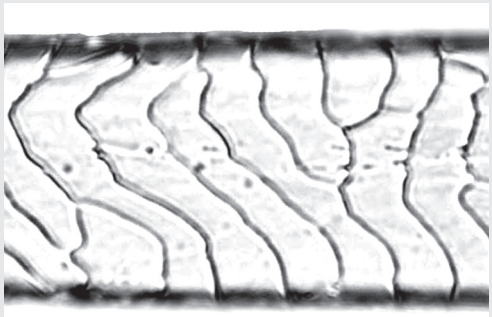
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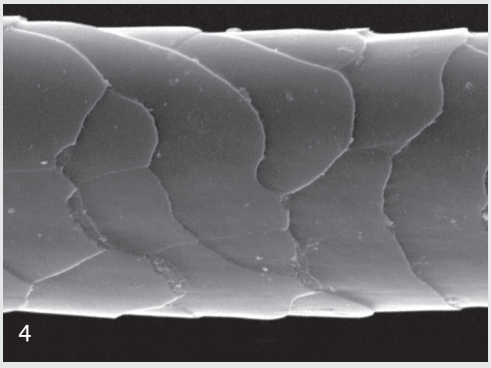
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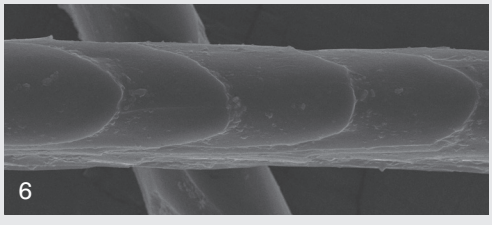
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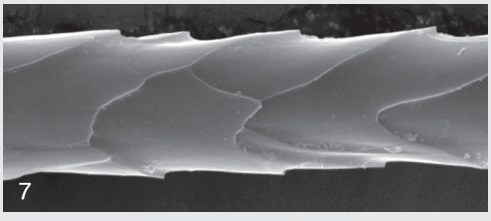
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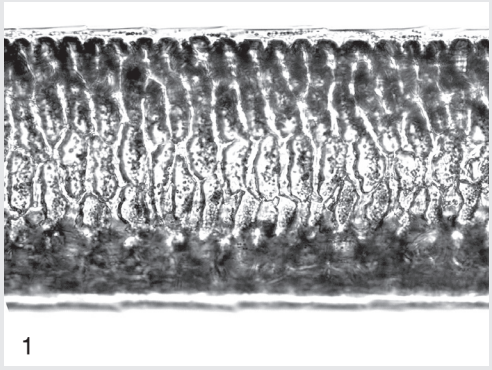
***Sicista* spp.**: 1 = medulla, shield, without air; 2 = medulla, shield, with air; 3 = cuticula, shield; cuticula, transit; 4 = cuticula, distal shaft; 5 = cuticula, distal shaft; 6 = cuticula, basal, SEM; 7 = cuticula, proximal shaft, SEM

Muridae

FUR: The fur of the Muridae species is mostly short-haired and soft to the touch. The ground colour varies from ochreous to greyish-brown ("mouse-grey"); the colouration of the specimens depends on the age of the animals and the season: the summer fur is usually more vividly coloured and the younger specimens have darker fur; they are grizzled and/or marbled. The tail can be moderately hairy, "spiky" or naked.

HAIR, MACROSCOPIC: The fur is dominated by the banded GH1, GH2, and UH hairs, usually only the sparse GH0 guard hairs are non-banded. The band is ochreous; the shaft is greyish. The underhairs are very thin, wavy or zigzagged.

HAIR, MICROSCOPIC: Most species of the family cannot be identified at species level by their microscopic hair characters but the family itself and several genera are clearly separable by their characters. The cuticular pattern is chevron or rhomboidal on the shaft; the medulla is nummiform in the shaft and cob-like multiserial at the maximum diameter of the shield. The cuticula is wavy figureless on the apical section; the tip is long and gradually tapering. The cross-section is variable: circular, oblong, convex-concave, plano-concave or tetra-concave.



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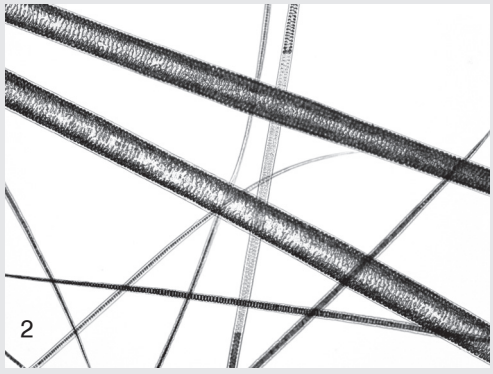

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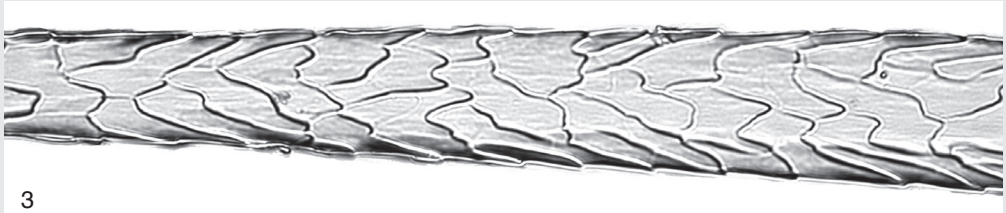

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4

Muridae: 1 = medulla, shield; 2 = transparent view, hairs; 3 = cuticula, shaft; 4 = cuticula, shaft

Genus *Rattus*

The rats are native in Asia but distributed all over the World.

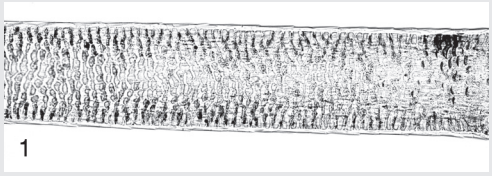
Rattus rattus & Rattus norvegicus

FUR: The fur of the rats is long-haired, soft in touch, slightly shaggy; the ground colour is most often grey-brown; the fur is grizzled, sometimes finely marbled; the range of colour variation is rather wide, therefore the two Central European species cannot be distinguished using only the colour characters. The fur of *Rattus rattus* is usually darker coloured, the dorsal side is dark grey or grey-brown, more rarely blackish or dark ochreous-brown; the belly is ochreous-white, brownish, off-white or grey; the darker dorsum and the paler ventral side have blurring transition. In case of *R. norvegicus*, the fur is usually lighter and the dorsal and ventral sides are more contrastingly coloured.

HAIR, MACROSCOPIC: The GH0 is long, unicolorous, shining dark brown. The structure of the GH1 is characteristic: abruptly widen above the short, tubular basal part; flattened and channelled even from the proximal shaft, it is polychrome with pale grey shaft and dark brown shield. The GH2 is banded; the shaft is dark grey or brown; the ochreous, reddish or brown band is located on the distal section of the shield; the tip is short and black.

HAIR, MICROSCOPIC: The cuticular pattern is broad petal on the basal part; broad rhomboidal on the shaft; irregular, elongated rhomboidal petal on the transit; and transversal, regular mosaic on the shield. The scales have usually deeply grooved surface on the transit and the shield. The medulla is chromosomal nummiform, or globulose tubular on the shaft; cob-like multiserial at the maximum width of the shield, where the number of rows of small, oblong or rounded medullar cells might be 8–10; the medullar margin is crested or straight. The cortex is thick; but thin at the maximum width of the shield section. The pigments are concentrated primarily in the medulla and the inner part of the cortex. The wide channel runs on the transit and the proximal shield. The cross-section is convex-concave or oblong.

SIZE: l_{max} = 25 mm; l_{max} GH0 = 30; d_{max} = 120 μ; m/d_x = 0.9



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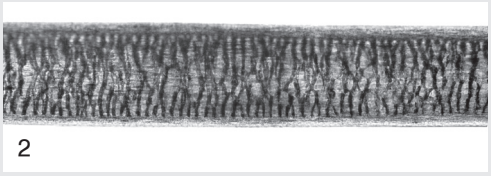

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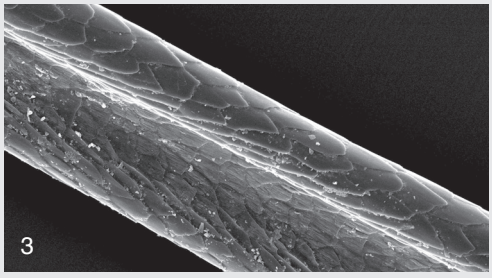

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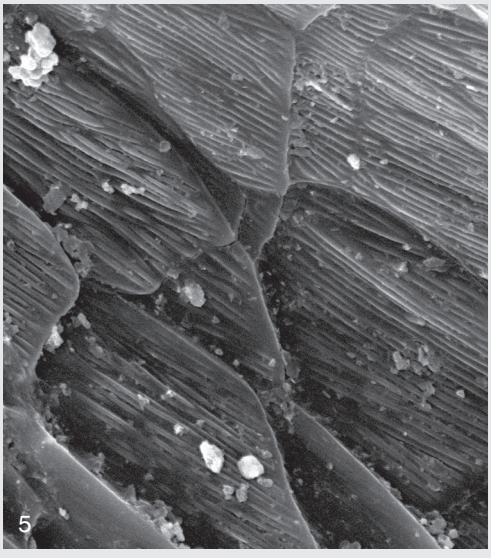

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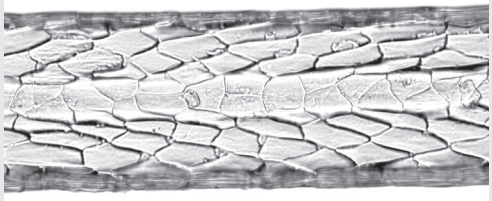

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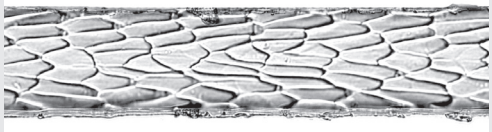

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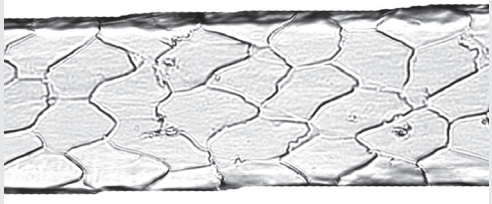

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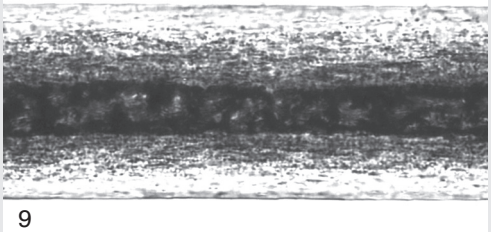

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***Rattus* spp.**: 1 = medulla, shield, without air; 2 = idem, with air; 3 = channelled transit, SEM; 4 = idem; 5 = cuticula, grooved scales, SEM; 6 = cuticula, transit; 7 = medulla, transit; 8 = cuticula, shaft; 9 = medulla, shaft

Genus *Mus*

Mus musculus & Mus spicilegus

FUR: The fur of the two closely related mouse species, *Mus musculus* and *Mus spicilegus*, is short-haired, and soft in touch. The dorsum is always dark grey or brown, and the ventral side is paler, whitish-grey or creamy. In *Mus musculus*, the fur is somewhat more brownish and the transition between the darker dorsum and the paler belly is blurred; the dorsal side of *Mus spicilegus* is slightly darker and more greyish shaded, and the darker backside and the paler belly are more distinctly demarcated than in *M. musculus*. Despite the above-mentioned differences, the two species cannot be separated satisfactorily using the characters of their fur.

HAIR, MACROSCOPIC: The GH1 is unicolorous or polychrome, dark grey or black. The GH2 is banded; the shaft is dark grey; the often transparent, yellowish or ochreous-brown band is located on the distal shield; the tip is very short, dark brown or black.

HAIR, MICROSCOPIC: The cuticular pattern is cuneate chevron on the basal part; the GH1 has broad rhomboidal, the GH2 has cuneate chevron pattern on the shaft and the transit. The medulla is nummiform in the shaft, cob-like multiserial at the maximum width of the shield; the shape of medullar cells is oblong and arranged into 3–5 rows. The shield section might be channelled slightly. The cross-section is convex-concave or oblong.

SIZE: l_{max} = 10 mm; d_{max} = 55 μ; m/d_x = 0.85

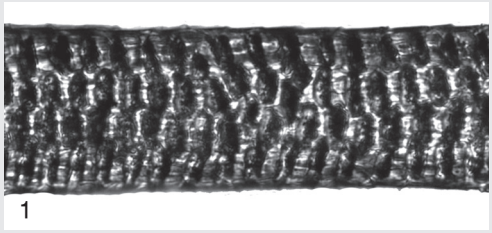
Micromys minutus

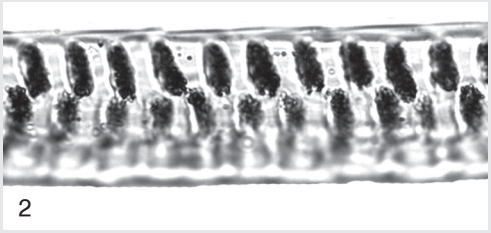
FUR: The fur is soft and short-haired; the dorsum is variably coloured: it might be hazel, reddish-brown, greyish-brown or dark brown; the ventral side is much paler: whitish, ochreous-whitish or pale grey; the dorsal and the ventral sides usually sharply demarcated.

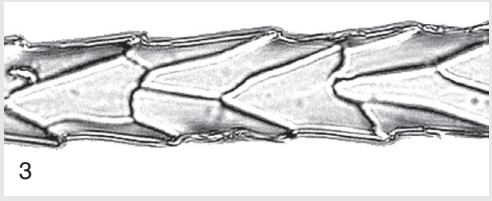
HAIR, MACROSCOPIC: The GH1 is unicolorous or polychrome, dark grey or black. The GH2 is banded; the shaft is grey or greyish and the band of the shield is vivid yellow or reddish. The tip is dark.

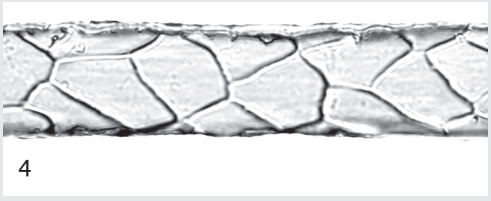
HAIR, MICROSCOPIC: The cuticular pattern is cuneate chevron on the basal section; elongated rhomboid on the shaft with dentate apical edges; broad, rhomboidal petal on the transit and the shield with rippled apical edges of scales. The medulla is uniserial nummiform in the shaft, and biserial or chromosomal nummiform at the shield. The hair might be channelled slightly on the transit and the proximal shield. The cross-section is circular, oblong, or convex-concave.

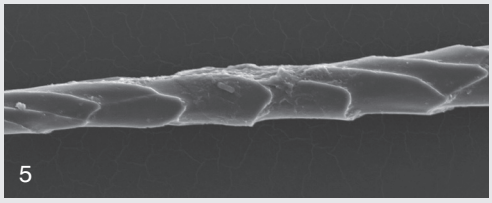
SIZE: l_{max} = 10 mm; d_{max} = 50 μ; m/d_x = 0.85

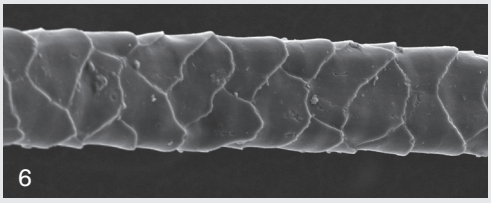


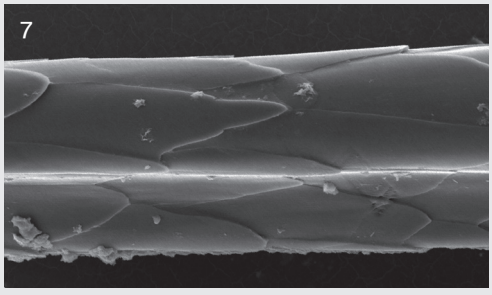


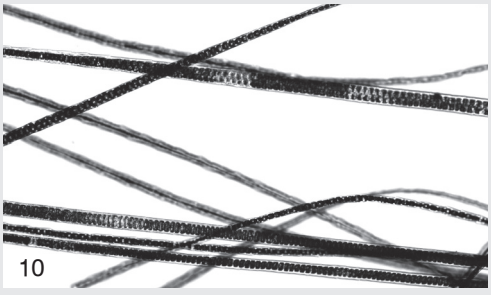


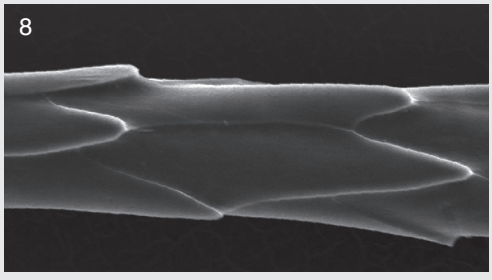


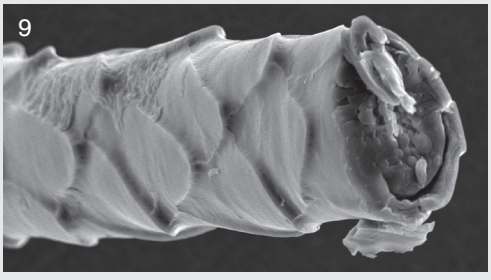












Mus* spp.**: 1 = medulla, shield; 2 = medulla, transit; 3 = GH2 cuticula, shaft; 4 = GH1 cuticula, shaft; 5 = cuticula, basal, SEM; 6 = cuticula, transit, SEM; ***Micromys minutus: 7 = cuticula, proximal shaft, SEM; 8 = cuticula, basal, SEM; 9 = cuticula, transit, SEM; 10 = transparent view, hairs

Genus *Apodemus*

FUR: The fur is short-haired and soft in touch; the dorsum is generally ochreous-brown or reddish-brown, grizzled and marbled; the belly is greyish-white or whitish. The breast of the *Apodemus* species might be contoured; certain species have smaller ochreous patches and stripes of characteristic shape and size but they cannot be used for the separation of the taxa due to the variability of this pattern. The tail is sparsely hairy.

HAIR, MACROSCOPIC: The GH1 is polychrome and shining, with dark grey shaft and dark brown or black(ish) shield. The GH2 is one-banded; the band is pale ochreous or ochreous-brown; the tip is dark brown.

HAIR, MICROSCOPIC: The cuticular pattern is elongated rhomboid on the basal section and on proximal shaft; broad rhomboid on the distal shaft; rhomboidal petal on the transit; regular, distant, transversal mosaic on the shield. The medulla is chromosomal nummiform in the shaft; cob-like multiserial in the maximum width of the shield; the small, transversally slightly elongated medullar cells are arranged into up to 8 rows on the maximal diameter. The pigments arranged diffusely in the medulla and in the cortex on the shield. The hairs are deeply channelled on the transit and shield; there could be 2–3 parallel channels on the shield. The cross-section is tetra-concave, convex-concave or plano-concave; oblong only on the base.

The hair samples of the *Apodemus* species cannot be identified at species level due to their overlapping macro- and microscopic characters.

SIZE: l_{max} = 12 mm; d_{max} = 80 μ; m/d_x = 0.85

Apodemus agrarius

FUR: The reddish-brown dorsum and the greyish-white belly are sharply demarcated; the dorsum is marked by a contrasting, narrow black stripe running along the backbone from the front to the rump.

Apodemus alpicola

FUR: The reddish-brown dorsum and the greyish-white belly are sharply demarcated. The breast may bear a paler, elliptical or triangular, ochreous patch.

Apodemus flavicollis

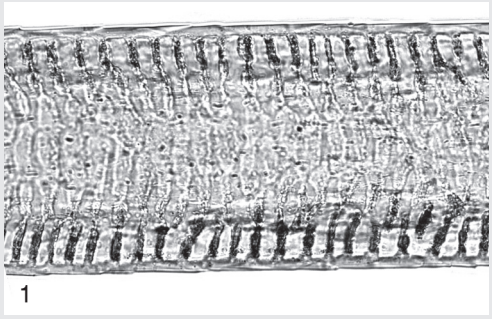
FUR: The reddish-brown dorsum and the greyish-white belly are sharply demarcated; there is an ochreous transversal, complete collar on the breast between the neck and the base of the forelegs.

Apodemus sylvaticus

FUR: The transition of the dark reddish-brown dorsum and the pale greyish-whitish belly is more or less blurred; there is not so distinct demarcation like in *A. flavicollis*. The breast and, rarely, the middle line of the belly may bear short ochreous stripe.

Apodemus uralensis

FUR: The transition of the dark dorsum and the pale belly is most often somewhat blurred; the breast and the belly both may bear a small, rather diffuse, ochreous patch.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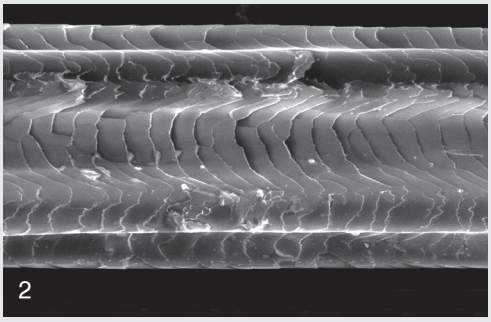
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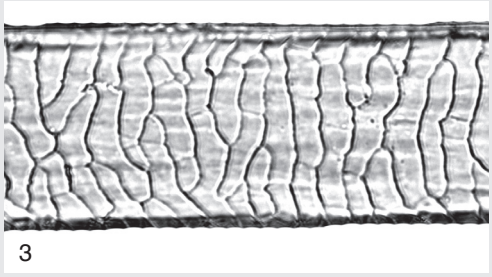
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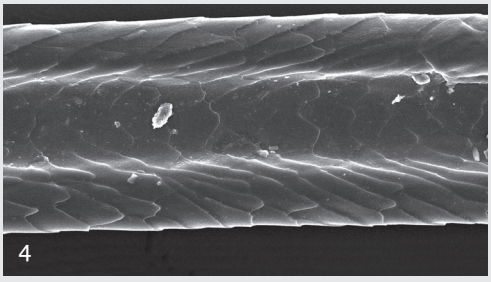
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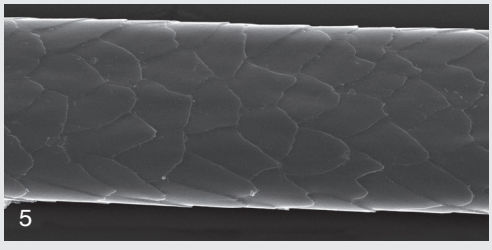
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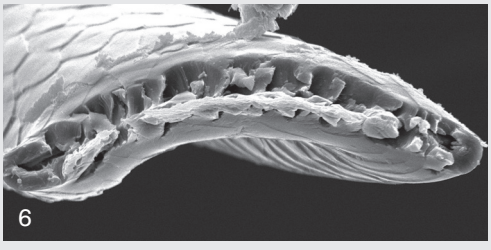
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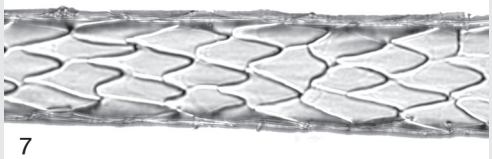
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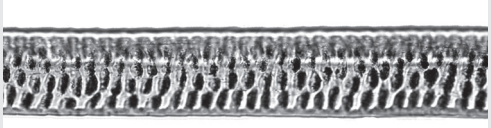
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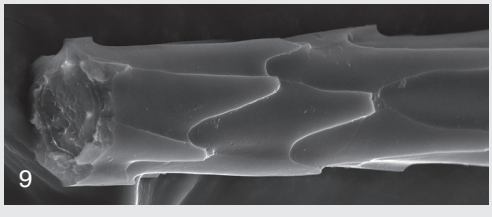
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***Apodemus* spp.**: 1 = medulla, shield; 2 = channel, shield, SEM; 3 = cuticula, proximal shield; 4 = channel, transit, SEM; 5 = cuticula, transit, SEM; 6 = cross-section, transit, SEM; 7 = cuticula, shaft; 8 = medulla, transit; 9 = cuticula, basal, SEM; 10 = medulla, shaft

Spalacidae

All Central European species belong to the subfamily Spalacinae. Taxonomic and phylogenetic studies revealed the remarkable intra-specific and intra-populational genetic variation of the different Spalacinae taxa (Csorba *et al*. 2015, Arslan *et al*. 2016); the morphological features of the fur and the hairs are, however, practically identical in the genera *Spalax* and *Nannospalax* belong to the Spalacinae subfamily. These fossorial small mammals have two peculiar fur characters: the first is the extremely soft touch of the dense and slightly shaggy fur, due to the non-directional growth of the hairs, despite the ordinary head to tail growth of the other rodents. The second diagnostic feature of the family is the presence of the "whiskers", the long, stiff bristle hairs on the sides of the cheeks which can be used for shovel grains of sand or/and pack the sides of tunnels (Feldhamer *et al.* 2015), and may have also sensory function.

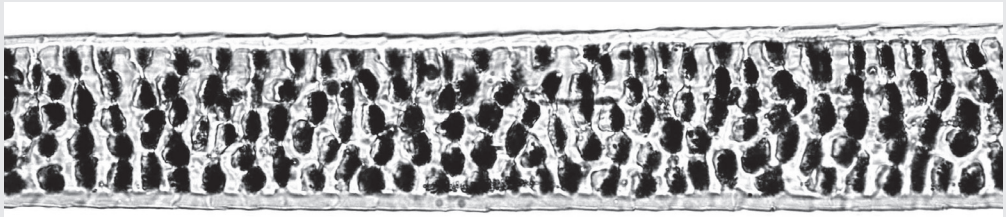
Nannospalax (superspecies) leucodon, Spalax antiquus, S. zemni, S. graecus

fur: The cheek is characterised by the variably strongly developed, often white, ochreous-white or pale greyish-brown coloured whiskers. There are often whitish ochreous or greyish-ochreous patches or stripes around the mouth, on the ridge of the nose, and from the nostrils to the edges of the eyes and on the chin; some pale colouration can be seen between the forelegs and the belly.

hair, macroscopic: The GH1 is straight, unicolorous grey or brown, sometimes polychrome; the GH2 is combined wavy, bicolorate with darker, more greyish shaft and paler, more or less transparent reddish-brown, golden yellow or ochreous shield. The tip is transparent.

hair, microscopic: The cuticular pattern is broad petal on the basal section; longitudinally elongated cuneate chevron on the proximal shaft; broad cuneate chevron with pointed apical edges on the distal shaft and the transit; regular mosaic on the shield; the apical region has figureless wavy pattern with rippled scale edges. The surface of scales might be slightly grooved. The medulla is uniserial nummiform in the shaft and the apical region; regular, cob-like multiserial at the maximum width of the shield where the polygonal medullar cells show a regular arrangement in 4–5 rows. The hair may have a very shallow, wide channel running from the distal shaft to the proximal shield; the transit and the shield are somewhat flattened; the tip is gradually tapering. The basal section, the apex and the entire cortex are pigmentless; the pigments arrange diffusely in the the medulla. The cross-section is circular or oblong.

size: l_{max} = 14 mm; d_{max} = 70 μ; m/d_x = 0.8



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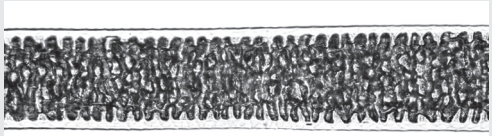

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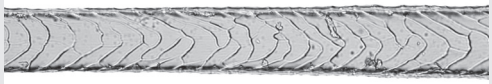

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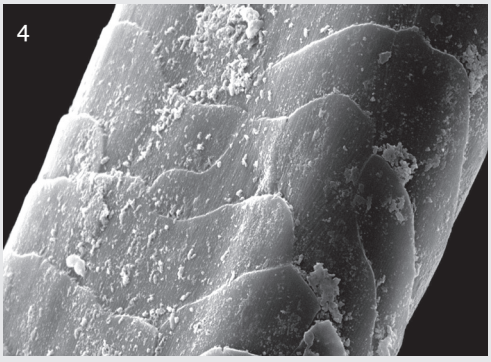

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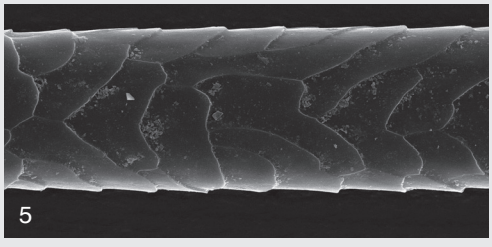

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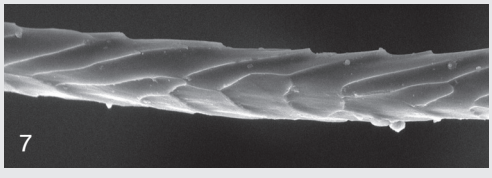

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8

Spalacinae: 1 = medulla, shield; 2 = idem; 3 = cuticula, transit; 4 = idem, SEM; 5 = cuticula, shaft, SEM; 6 = medulla, shaft; 7 = cuticula, basal, SEM; 8 = cuticula, shaft, proximal

Cricetidae

FUR: The great morphological diversity of this species-rich family is reflected also in the diversity of fur and hair patterns. The fur is most often marbled and grizzled but can be unicoloured or mottled; certain species have a facial mask or contoured breast; several species of Cricetidae have specialized hairs like spines, quills, or osmetrich hairs. The ground colour of the fur is principally brown, with a great variety of shades. The ventral side is always paler. The touching of the fur may be fine, silky or coarse. The tail might be tufted, or sparsely hairy or almost fully naked.

HAIR, MACROSCOPIC: The mass of the fur of species belong to this family is dominated by the banded GH2, UH hairs; but the GH0 and GH1 type usually not banded. The colour of the band is variable; the shaft is generally greyish. The shape of guard hairs is straight, curved or combined wavy.

HAIR, MICROSCOPIC: The microscopic hair characters are typical mainly of the family and certain genera; the species-specific characters are rare. The cuticular pattern is longitudinally elongated, narrow petal or rhomboidal on the basal section; most often cuneate chevron or rhomboidal on the shaft; near, transversal, regular mosaic on the transit and the proximal shield; irregular, dense, figureless on the usually flattened distal shield. The margins of the scales are rippled. The medulla is nummiform on the shaft and cob-like multiserial on the shield; the hairs often channelled.

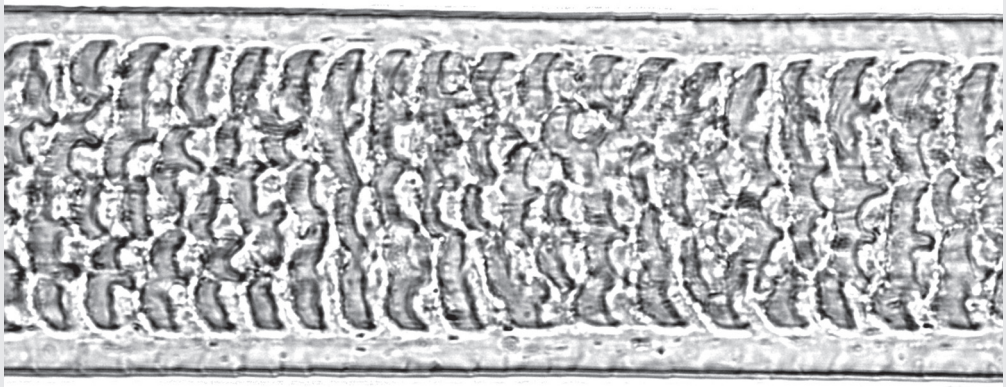
Cricetus cricetus

FUR: The fur is thick, fine in touch; it is characteristically tricoloured and mottled: the ground colours are yellowish-brown-grey, white and black. The face is masked: the vertex greyish-brown; the front, the wings of the nose and the side stripes -crossing the eyes- are rusty-reddish; the cheeks, the chin and lips are white, while a wide white "cape" runs around the face, which never reaches the eyes. There are small white patches at the base of the ears, and sometimes on the base of the femur; large white patches or stripes are on the shoulders and under the hind legs. The dorsum is yellowish-brown, grizzled; the ventral side and the legs are unicolorous black; the feet are white. The short tail is ochreous-brown. The melanistic specimens are not rare; their feet and chin remain white; the tail is fuscous or rusty-brown.

HAIR, MACROSCOPIC: The GH1 is black, dark brown or ochreous-white, depending on the colour of the given part of the body. The GH2 and UH banded: the shaft is dark grey; the long, whitish or ochreous, transparent band takes ca. two-thirds of the shield. The apical section and the gradually tapering tip are dark brown.

HAIR, MICROSCOPIC: The cuticular pattern is cuneate on the base; broad rhomboidal on the shaft; transversal, regular mosaic on the proximal shield; waved figureless on the distal shield and the apical section; the scales have rippled, cracked edges. The surface of the scales is often scratched. The medulla is multiserial, cob-like at the maximum width of the shield; the medullar cells are transversally elongated, characteristically crescent-shaped. The hairs not channelled; the cross-section is oblong.

SIZE: l_{max} = 25 mm; d_{max} = 85 μ; m/d_x = 0.7



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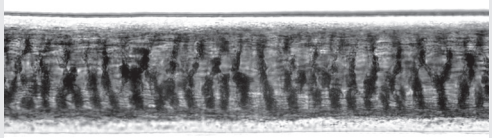

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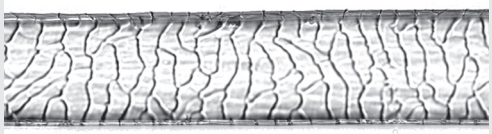

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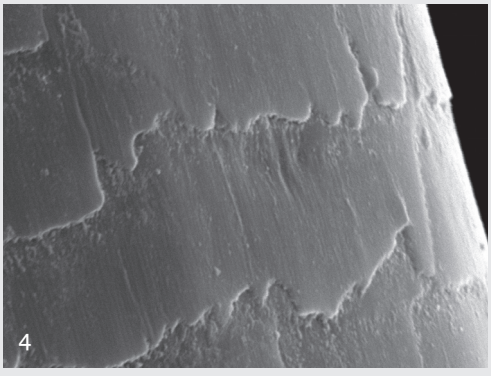

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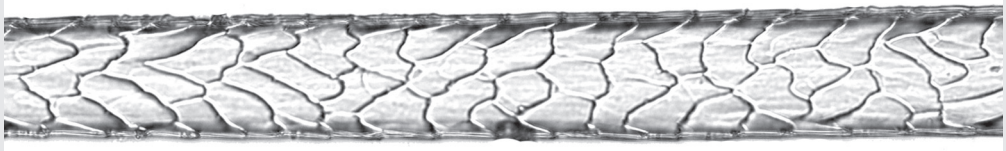

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Cricetus cricetus: 1 = medulla, shield; 2 = medulla, transit; 3 = cuticula, proximal shield; 4 = scratched scales, apical section, SEM; 5 = cuticula, distal shaft; 6 = cuticula, proximal shaft

Arvicola amphibius & Arvicola scherman

The trichomorphological characters are similar and not reflecting the remarkable differences in the habitat preferences and lifestyles of these two *Arvicola* species.

FUR: The fur is shaggy, soft in touch. It is unicoloured or finely grizzled; the ground colour of the dorsal side is most often dark, various shades of brown and grey, sometimes could even be blackish; the belly is paler. The tail is sparsely hairy; the longer bristle hairs at the end of the tail are brown, rarely white.

HAIR, MACROSCOPIC: The GH1 is unicolorous dark brown; the GH2 is banded: the shaft is dark grey; the ochreous-brown or rusty-red band is located on the distal shield. The tip is long, gradually tapering; usually dark brown or black.

HAIR, MICROSCOPIC: The cuticular pattern is cuneate chevron on the shaft and on the transit; regular mosaic on the shield; near, wavy, apically rippled, and figureless on the apical section. The surface of the scales might be finely grooved. The medulla is regular, cob-like multiserial at the maximum width of the shield; the medullar cells are oblong, arranged into 4–5 rows at the maximum diameter. The cortex and the medulla are pigmented densely, diffusely, except in the basal and apical sections. The hair is flattened practically in its entire length, but not channelled. The cross-section is oblong on the shield.

SIZE: l_{max} = 16 mm; d_{max} = 73 μ; m/d_x = 0.85

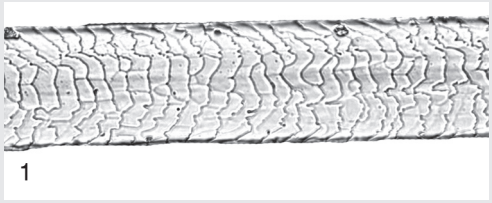
Myodes glareolus

FUR: The dorsal side of the fur is dark reddish-brown from the crown of the head to the rump in a broad zone along the backbone; the colouration becomes stepwise paler towards the greyish, ochreous-grey or whitish belly. The tail is evenly hairy, except at the end where the longer bristle hairs form a small tuft. The dorsal side of the tail is grey or greyish, the ventral side is paler, whitish or greyish-white.

HAIR, MACROSCOPIC: The GH1 hair is unicolorous dark brown. The GH2 and UH hairs are banded and combined wavy: the long, wavy shaft is usually silvery-grey or dark grey; the vivid red-brown or ochreous band of the shield is sharply demarcated; only the short apical region is brown(ish).

HAIR, MICROSCOPIC: The cuticular pattern is cuneate chevron on the shaft; transversal, regular mosaic on the transit. The medulla is regular, cob-like multiserial at the maximum width of the shield; the medullar cells are oblong in shape, and arrange into 3–4 rows at the maximum diameter of the hair. There might be 1–3 parallel, narrow but rather deep, inarticulate channels on the hairs. The cross-section is tetra-concave or plano-concave.

SIZE: l_{max} = 15 mm; d_{max} = 60 μ; m/d_x = 0.85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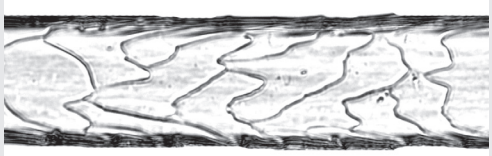
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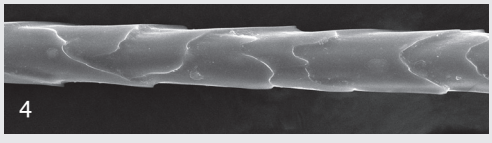
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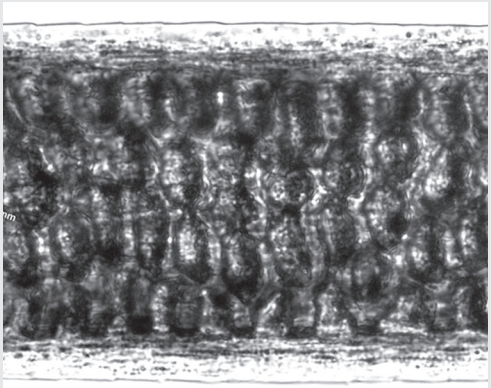
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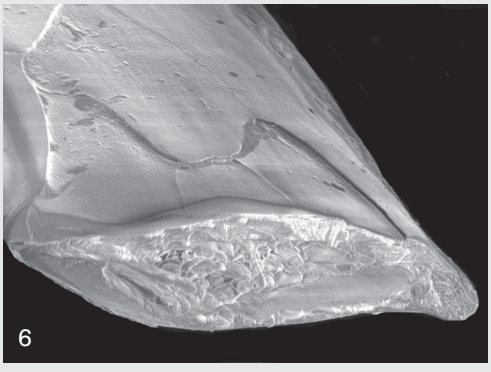
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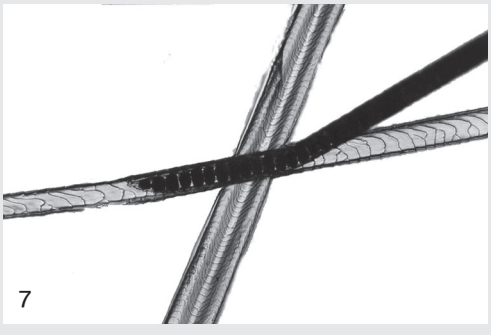
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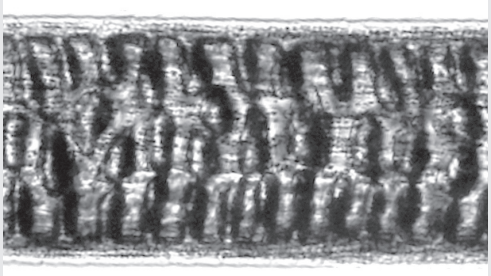

8

Arvicola* spp.**: 1 = cuticula, apical; 2 = cuticula, shield; 3 = cuticula, shaft; 4 = cuticula, basal, SEM; 5 = medulla, shield; 6 = cross-section, shaft, SEM; ***Myodes glareolus: 7 = transparent view, hairs; 8 = medulla, shield

Chionomys nivalis

FUR: The fur is silky, dense and finely grizzled; the ground colour is most often greyish-brown, more rarely dark grey or paler reddish-brown; the ventral side is paler, greyish or whitish. The small ears are covered with fine greyish hairs. The transition of the colour from the dorsum towards the belly is gradual. Short, sparse hairs cover the short tail.

HAIR, MACROSCOPIC: The GH1 is unicolorous, shining dark brown; the GH2 is banded; the transparent ochreous-brown band is located on the distal shield. The UH is unicolorous greyish-brown.

HAIR, MICROSCOPIC: The cuticular pattern is cuneate chevron on the shaft; regular mosaic on the transit and the shield; waved figureless on the apical section. The medulla is regular, cob-like multiserial at the maximum width of the shield; the oblong-shaped medullar cells arrange into 3–4 rows at the maximum diameter. The hair is channelled on the shield; the channel is wide, shallow. The pigmentation is diffuse and dense. The cross-section of the shield is convex-concave or oblong (KELLER 1981).

SIZE: l_{max} = 18 mm; d_{max} = 65 μ; m/d_x = 0.85

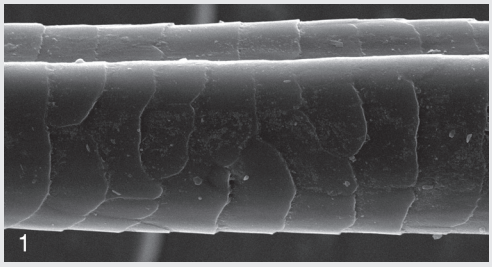
Dinaromys bogdanovi

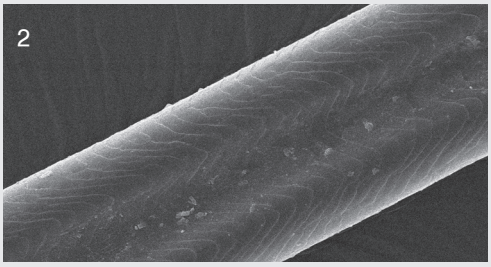
FUR: The grizzled fur is dense, with silky, soft touch. The dorsum is greyish-brown; the belly is much paler greyish or whitish; the transition between them is most often gradual. The large ears are covered densely with short hairs. The long tail is sparsely hairy, dorsally dark brown, while the ventral side and the apical bristle hairs are whitish.

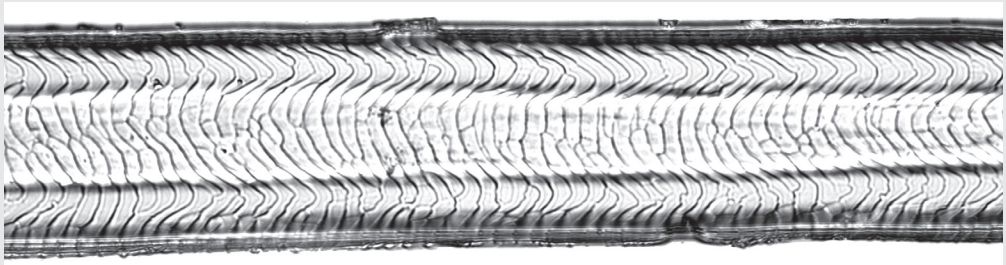
HAIR, MACROSCOPIC: The GH1 is unicolorous, brown or dark grey; the GH2 is unicolorous or banded; the shaft is grey; the band is whitish; the shield and the tip is brown; the UH are transparent silvery-greyish.

HAIR, MICROSCOPIC: The cuticula is cuneate chevron on the shaft; regular mosaic on the transit and the shield; the apical section is waved figureless. The medulla is regular, cob-like multiserial at the maximum width of the shield; the medullar cells are oblong, arranged into 3–4 rows at the maximum diameter. The hair is flattened from the distal shaft towards the shield; it is channelled between the shaft and the apical region, the channel is wide, deep. The cross-section at the shield is plano-concave or concave-convex.

SIZE: l_{max} = 18 mm; d_{max} = 60 μ; m/d_x = 0.85







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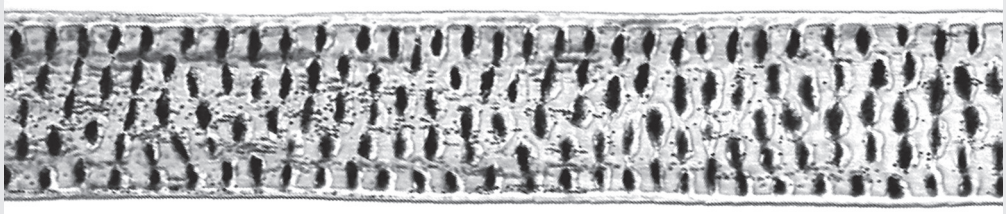

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Chionomys nivalis, ***Dinaromys bogdanovi***, ***Microtus* spp.**: 1 = channel, transit, SEM; 2 = channel, shield, SEM; 3 = cuticula, shield; 4 = medulla, shield; 5 = medulla, transit

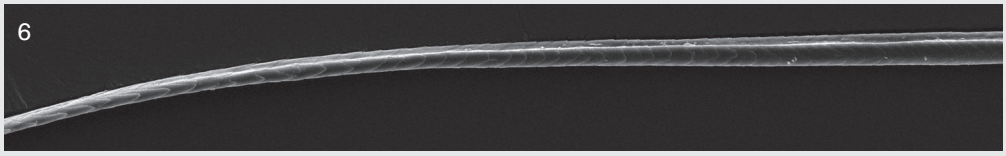
Genus *Microtus*

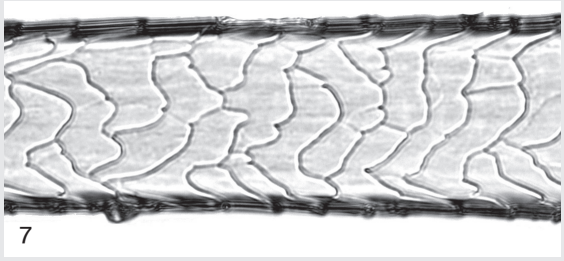
FUR: The fur is shaggy, soft in touch, grizzled; the ground colour is greyish- or somewhat reddish-shaded brown. The dorsal side is always dark, greyish-brown, reddish-brown, sometimes ochreous-brown in *Microtus agrestis* and *M. levis*; more reddish, usually rusty brown in *Microtus arvalis*, *M. bavaricus*, *M. liechtensteini* and *M. tatricus*; dark grey-brown (more rarely red-brown or blackish-brown) in *Microtus oeconomus*; while paler brownish-grey in *Microtus subterraneus*. The transition is gradual from the darker dorsum towards the paler, whitish, ochreous-grey or grey belly. The tail is similarly coloured; its dorsal and ventral sides fit in colour with those of the dorsum and the belly. The tail is evenly hairy; the bristle hairs at the end of tail may form a tiny tuft.

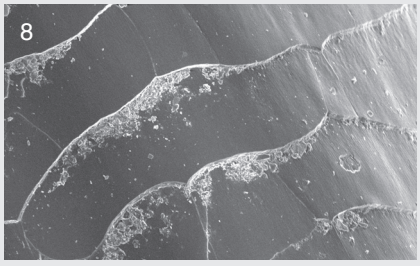
HAIR, MACROSCOPIC: The shape of GH1 and GH2 is combined wavy; rather spatula-like with long and very thin shaft and widening shield; the UH curved or slightly wavy. All these three types of hairs are banded: the shaft is grey, the band is ochreous-brown, straw-coloured or reddish, always transparent; the shield and the tip are brownish-grey, dark brown or even black. The apical region is gradually tapering towards the tip.

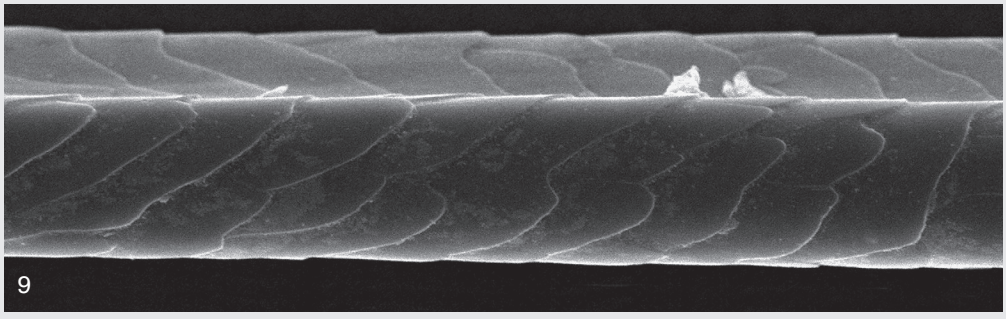
HAIR, MICROSCOPIC: The cuticular pattern is broad petal at the short basal section; cuneate chevron on the shaft; transversal, irregular mosaic on the transit; transversal, near, regular mosaic on the shield. The medullar pattern is chromosomal nummiform on the shaft; regular cob-like multiserial on the shield; the medullar cells are rounded or oblong and arrange usually into 4 rows at the maximum width of the shield. The hairs are channelled. The pigments arrange diffusely and concentrate in the medulla. The cross-section is concave-convex, biconcave or oblong. The hair samples of the *Microtus* species cannot be identified at species level due to their overlapping macro- and microscopic characters.

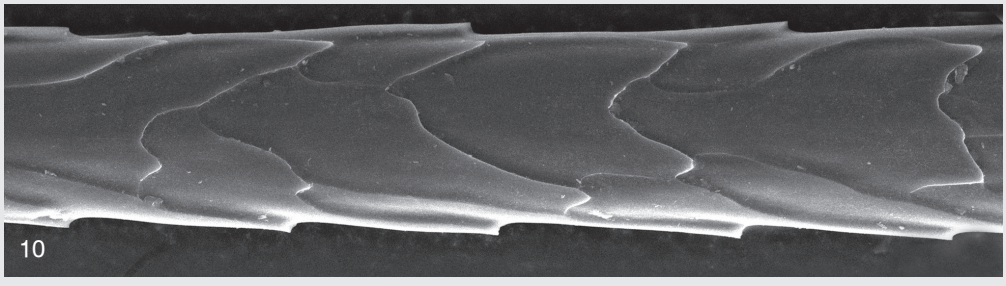
SIZE: l_{max} = 14 mm; d_{max} = 65 μ; m/d_x = 0.85











***Chionomys nivalis, Dinaromys bogdanovi, Microtus* spp.**: 6 = channelled hair, SEM; 7 = cuticula, transit; 8 = idem, SEM; 9 = cuticula, shaft, SEM; 10 = cuticula, basal, SEM

Ondatra zibethicus

The Muskrat was introduced to Europe from North America as fur animal; after the first specimens escaped from fur-farms, the Muskrat spread rapidly, colonized wetlands and has become a significant species in the Central European fauna.

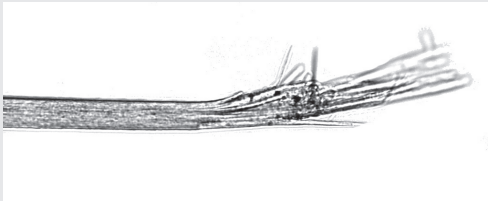
FUR: The fur is thick, shaggy, and water-repellent. The underhairs are remarkably denser and shorter than the guard hairs. The fur is soft and silky in touch, and somewhat greasy. The ground colour is glossy red-brown, grey-brown or ochreous-greyish shaded brown. The fur is marbled; the dorsum is darker, darkest along the backbone from the front to the rump; the transition is gradual towards the whitish, creamy or pale red-brownish belly, throat, cheeks and chin. There are fringes of strong, long bristle hairs functioning as webs on the sparsely hairy edges of the side-by-side compressed tail, on the ankles of forelegs, on the edges of the paws and among the toes of the hind feet. The special modification and appearance of hairs are connected with the aquatic lifestyle of this species.

HAIR, MACROSCOPIC: The GH0 and GH1 are straight, long and shiny; the GH2 is curved. The GH are unicolorous or polychrome; reddish, ochreous-, or grey-brown, sometimes silvery-grey; the apical region is transparent, ochreous-brown. The UH is polychrome with greyish shaft and brownish, ochreous or reddish shield; the tip is gradually tapering, sometimes splitted.

HAIR, MICROSCOPIC: The cuticular pattern is broad petal on the basal section; cuneate chevron on the shaft; transversal, regular mosaic on the transit and the proximal shield; figureless, sketched on the apical section. The medulla is nummiform on the shaft; amorphous tubular on the transit and the apical section; regular, cob-like multiserial in the shield, with small, characteristically rounded medullar cells arranged into 5–6 rows. The pigments arrange diffusely and concentrate in the medulla and the inner part of the cortex. The cortex is thick. There is no channel on the hair; the cross-section is oblong.

SIZE: l_{max} = 30 mm; GH0 l_{max} = 45 mm; d_{max} = 110 μ; m/d_x = 0.45

1



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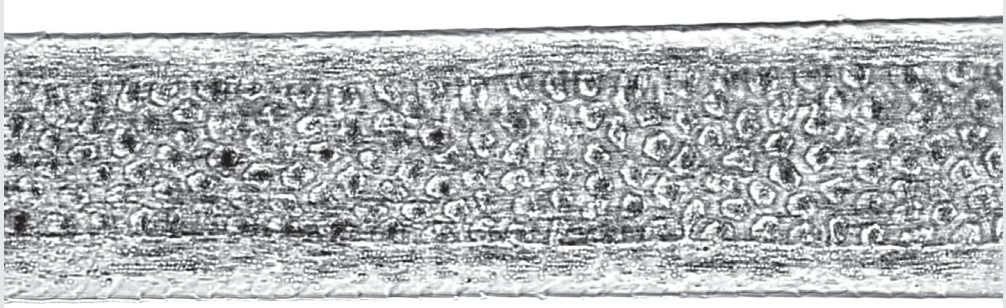

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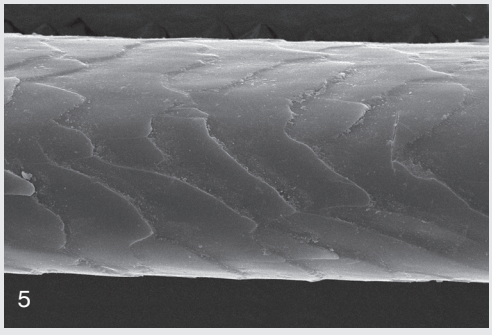

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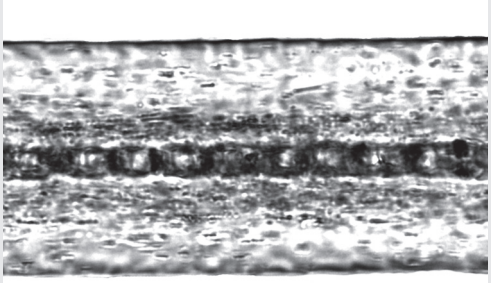


6

Ondatra zibethicus: 1 = cuticula, shield; 2 = tip; 3 = medulla, apical section; 4 = medulla, shield; 5 = cuticula, shaft, SEM; 6 = medulla, shaft

Castoridae

There are only two recent species of the family, which are indistinguishable by their trichomorphological characters. The presence of *Castor canadensis*, introduced to Europe from North America, is insignificant in Central Europe.

Castor fiber

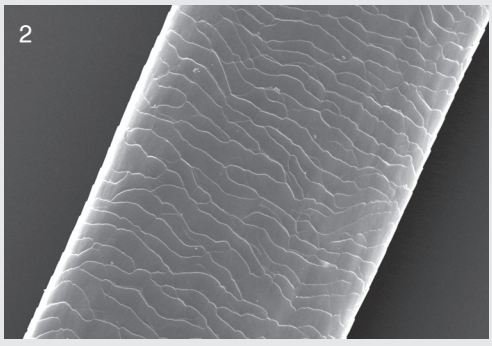
FUR: The fur is water-repellent, shaggy, dense and thick, especially the layer of fine underhairs; its touching is silky and slightly greasy. The ground colour is glossy dark brown; the dorsum is reddish-brown or chestnut-brown; its pattern is marbled or unicoloured; the sides of the body are uniformly dark brown. The belly is only slightly paler, brown, reddish-brown or beige; the cheeks, the nose, the chin and the throat are often reddish, ochreous-brown or even whitish. The flat tail is hairless.

HAIR, MACROSCOPIC: The GH types are unicolorous, polychrome or banded; the banded hairs very rare, and grow only within small patches of the dorsum. The ground colour is red-brown; in the banded hairs, the long shaft is brown, the shield is red and the tip is dark brown. The shield is wide and flattened. The UH is slightly wavy, greyish-brown.

HAIR, MICROSCOPIC: The bulb is knobby. The cuticular pattern is irregular petal on the base; transversally elongated, irregular mosaic on the shaft and the transit; dense, figureless on the shield with rippled margins of the scales; sketched figureless on the apical section. The medulla is colonnade tubular on the shaft and on the distal shield; thin, fragmented or amorphous tubular on the proximal shield. The cortex is thick all along the entire hair. The pigmentation is dense and diffuse in both the cortex and the medulla. The tip is abruptly tapering, short and pigmented. The hairs are not channelled. The cross-section is oblong at the shield.

SIZE: l_{max} = 65 mm; d_{max} = 90 μ; m/d_x = 0.25–0.45

1



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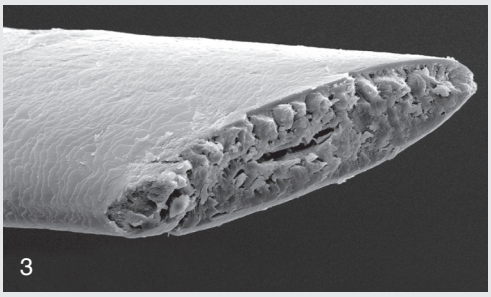

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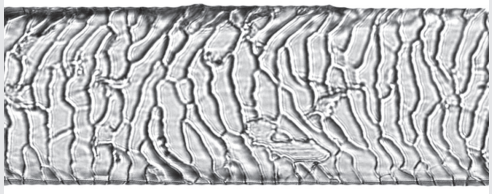

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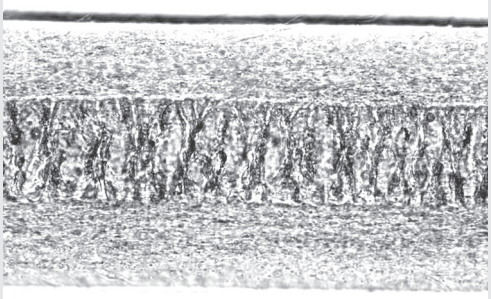

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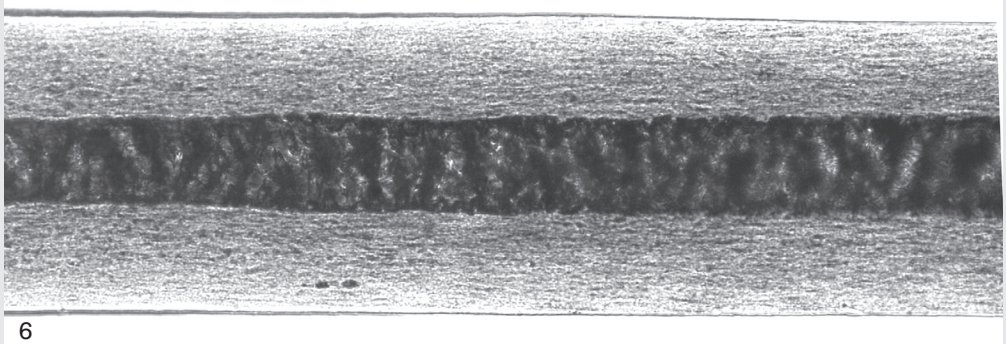

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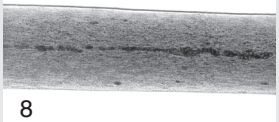

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Castor fiber: 1 = tip; 2 = cuticula, distal shield, SEM; 3 = cross-section, shield, SEM; 4 = cuticula, proximal shield; 5 = medulla, shield; 6 = medulla, shaft; 7 = bulb; 8 = medulla, basal

Myocastoridae

Myocastor coypus

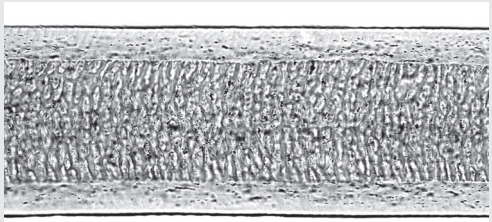
The Nutria was introduced to Europe from South America as fur animal; it is spreading, colonizing the wetlands and may become a significant species in Central Europe.

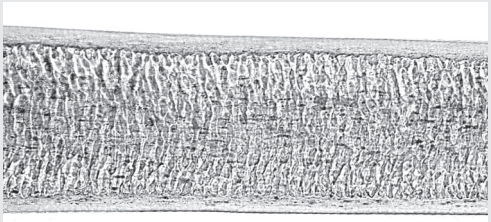
FUR: The fur is water-repellent, thick and dense; its touching is fine, silky, and slightly greasy; the shorter, greyish underhairs are especially dense. The colouration is marbled, finely grizzled; the ground colour varies from reddish-brown to greyish-brown. The darkest part of the fur is the middorsal section along the backbone; the transition is gradual towards the paler ventral side. The chins and the nostril are whitish, which is sometimes the case also for the throat and the cheek. The belly is pale rusty brown. The rounded (in cross) tail is sparsely hairy.

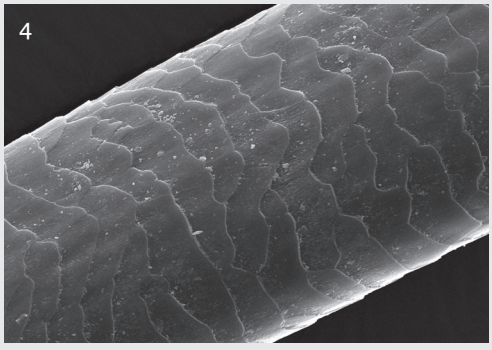
HAIR, MACROSCOPIC: The GH0 is long, glossy, brown; the GH1 and GH2 are unicolorous or banded, with grey shaft, whitish band and red-brown tip; the UH is wavy, grey.

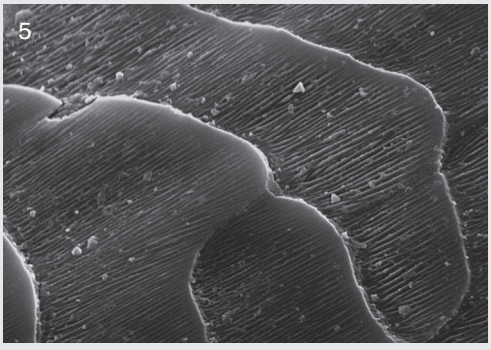
HAIR, MICROSCOPIC: The cuticular pattern is broad petal on the base; cuneate chevron or irregular petal on the shaft; transversal, regular mosaic on the proximal shield with rippled apical edges; regular, waved figureless on the distal shield, and sketched figureless on the apical region. The surface of the scales is deeply grooved. The cob-like multiserial medulla is thin on the shaft, the transit and the apical section, with variably sized and shaped medullar cells; at the same, the medulla is thick, the medullar cells are typically small, transversally elongated on the shield; the number of toughly closed rows of medullar cells can be up to 10. The cortex and the medulla are pigmented densely, diffusely. The margin of the medulla is straight or crested. The hair is considerably flattened and widening on the shield; the tip is long and abruptly tapering. The cross-section at the shield is narrow, oblong.

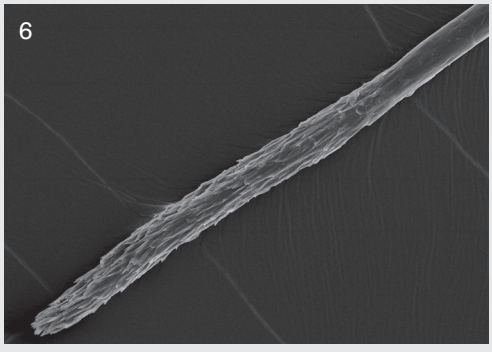
SIZE: l_{max} = 55 mm; d_{max} = 200 μ; m/d_x = 0.85

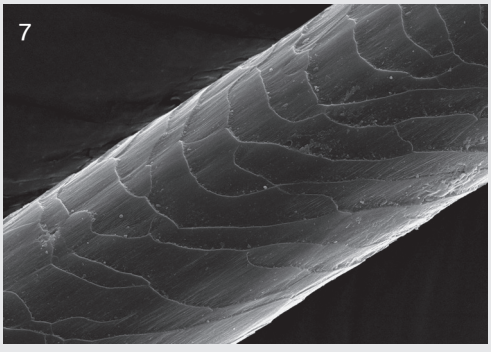












Myocastor coypus: 1 = tip; 2 = medulla, proximal shield; 3 = medulla, distal, shield; 4 = cuticula, shield, SEM; 5 = grooved scales, SEM; 6 = bulb, SEM; 7 = cuticula, shaft, SEM

7.6. Carnivora

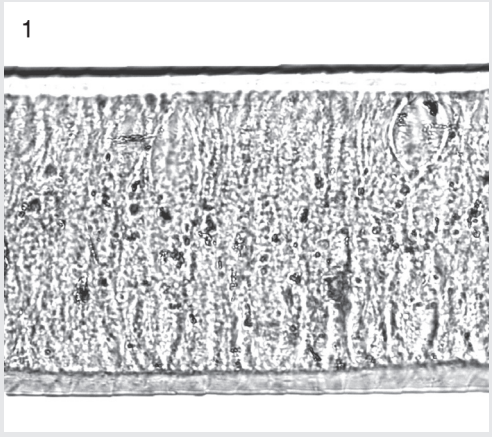
FUR: The Central European representatives of the family, as well as the entire order, display a great variety in their morphological features, including the characters of the hairs and the fur. The fur is dense; its touching is mostly fine and silky. The ground colour is brown with various shades; the other colours – grey, white, ochreous or reddish – provide usually the pattern of the fur. The dorsum might be unicolorous, marbled, grizzled or mottled; certain species have contrasting colourations, like characteristically masked face, contoured breast, black-backed pattern, and specific tail structure and patterns. These signals can advertise the possession of noxious anal gland secretions, the physical strength, and/or the great ferocity. Generally, the white dorsum is characteristic in sprayers that are primarily nocturnal; the horizontal stripes on the body is characteristic in species that have the ability to spray anal secretions accurately; the masked face is characteristic in burrowing species that keep their heads exposed to attack. These patterns are evolutionary, and ecologically controlled signals. The phylogenetic reconstructions suggest that these aposematic colourations have evolved more than once in the evolution of the terrestrial carnivores and their main function is a warning signal to deter predation from larger carnivores (NEWMAN *et al.* 2005, STANKOWICH *et al.* 2011).

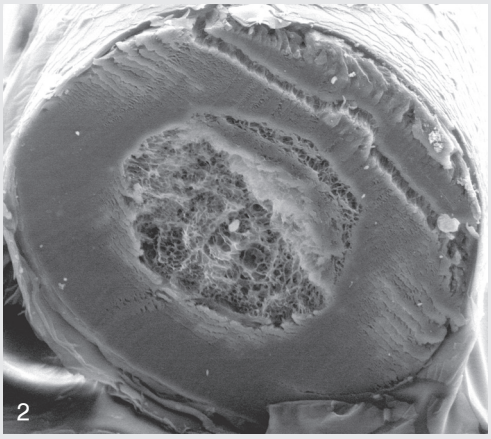
HAIR, MACROSCOPIC: The different types of hair are clearly distinct. The GH0 is unicolorate and glossy; GH1 and GH2 might be unicolorate, bicolorate, polychrome or banded; the length and position of bands might be characteristic; shape of GH2 is straight or curved. The UH layer is markedly dense and silky, fine in touch; UH is curved or wavy, more rarely crispy.

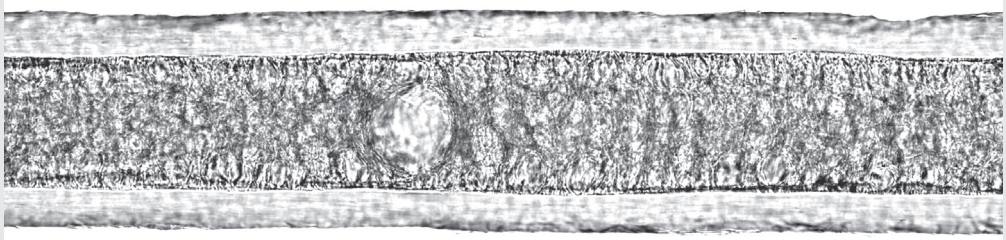
HAIR, MICROSCOPIC: The bulb is knobby and the basal section is tubular. The cuticular pattern is broad or transversal petal on the basal part; mostly rhomboidal on the shaft; transversal mosaic on the transit; waved figureless on the shield, and often sketched figureless on the apical region. The medullar structure is most often chambered multiserial on the shield, but might be foamy multiserial on the distal shield; colonnade tubular or fragmented on the apical section. The shape of the GH is often spatula-like. The tip is gradually tapering and might be splitted.

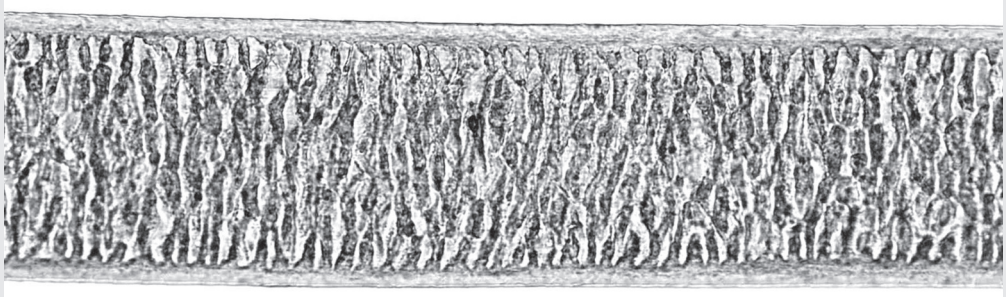
SIZE: $m/d_x \approx 0.7$

TAXONOMIC CHARACTER: The chambered and foamy multiserial types of the medulla at the maximum diameter of the shield are diagnostic features of the order Carnivora.









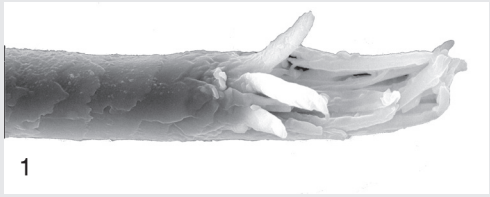
Carnivora: 1 = medulla, distal shield; 2 = cross-section, shield, SEM; 3 = medulla, proximal shield; 4 = medulla, shield; 5 = cuticula, shaft

Canidae

FUR: The fur is dense, with long and strong guard hairs and plentiful underhairs of silky touch. The colour and patterns of the fur is variable; the ground colour is brown and/or grey of variable shade; the pattern is most often marbled or/and grizzled. Distinct patterns are characteristic for many species, like the "mane" on the shoulders and the neck or/and the whitish ruff framing the muzzle, the black-backed pattern, and the contoured breast. The melanistic forms frequently occur in this family while the albinism is rather rare, although white or whitish specimens are known is several species. The tail is generally long, flag-like, and shaggy, often with specific pattern.

HAIR, MACROSCOPIC: The GH is usually strong and flexible, long, with coarse touching, bicolorate or banded with 1–2 bands. The tip is gradually tapering, often splitted. The UH is dense and silky in touch, unicolorous or polychrome.

HAIR, MICROSCOPIC: The cuticular pattern of the GH2 is transversal mosaic or broad rhomboidal on the shaft. The medulla is foamy or chambered multiserial at the maximum diameter of the shield; the margin of the medulla is straight or crested. The cross-section is circular or oblong.



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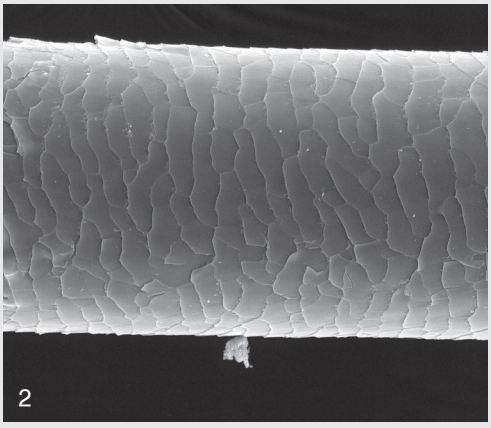

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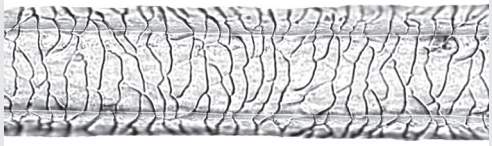

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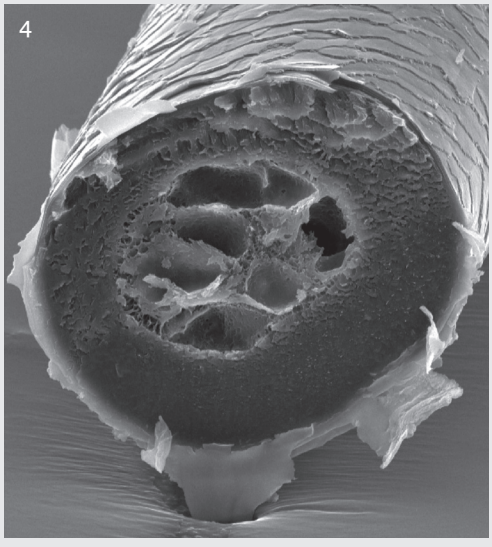

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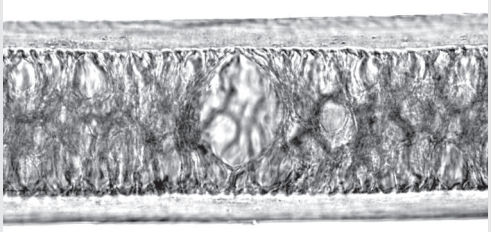

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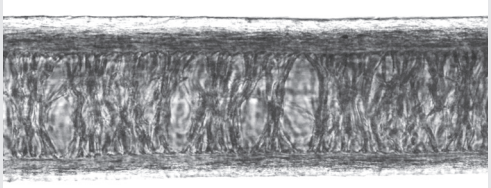

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Canidae: 1 = apex, SEM; 2 = cuticula, shield, SEM; 3 = cuticula, transit; 4 = cross-section, transit, SEM; 5 = medulla, shield; 6 = medulla, shield; 7 = cuticula, shaft; 8 = cuticula transit

Genus *Canis*

FUR: The fur of the Grey wolf and of the Golden jackal is similar, especially those of the old animals and for winter fur. The fur is shaggy, dense and fine; the most typical colours are grey, grey-brown and ochreous-brown. The dorsum is grizzled and marbled. A transition between the dorsum and the ventral side is usually gradual; the sides of the body are generally marbled, rufous, ochreous-brown or light brown. The belly and the inner sides of the legs are unicolorous, cream-coloured or whitish; the front and the ridge of the nose are grey, reddish, or yellowish-brown; the chin and the throat are white. The long hairs of the ruff are white, grey or ochreous-brown. The basal parts and the outer sides of the ears are rufous, brown or grey. A diagnostic character of the genus *Canis* is the white "middle-collar", a band on the chest, running in a semi-circle between the white throat and the white joint-line of the forelegs. The tail is shaggy, long-haired, grizzled; the tip of the tail is black. The winter fur is thicker and denser, more greyish shaded; the summer fur is more reddish-rufous, with more contoured markings.

HAIR, MACROSCOPIC: The GH1 is most often two-banded, more rarely one-banded or unicolorous. The two-banded GH1 is "tetra-coloured" as the two bands and the intermediate sections are usually differently coloured: black, white, brown and red-brown. The GH2 is one-, or two-banded. The tip of the hair is always dark. The UH is wavy or crispy; unicolorous or polychrome, greyish, whitish or ochreous.

HAIR, MICROSCOPIC: The medulla is foamy multiserial in the distal shield. The medullar cells are polygonal in the transit and the proximal shield; they become characteristically tiny and tightly closed in the distal shield, and their shape is most often fusiform. The larger, usually globular or fusiform intercellular air sacs between the medullar cells may span the entire width of the medulla. The pigmentation is diffuse and dense in both the cortex and the medulla.

Canis lupus

FUR: The ground colour of the fur is grey-brown; the dorsum is greyish-brown of various shades, marbled and grizzled; there is a characteristic, blurred, dark brown or blackish marking ("black-backed pattern") along the backbone. The cheeks and the surroundings of the lips are white or whitish; the middle-collar is less distinctly marked than in Golden Jackal. The mane of the adults is well developed.

HAIR, MACROSCOPIC: The bands of the two-banded hairs are most often different in length.

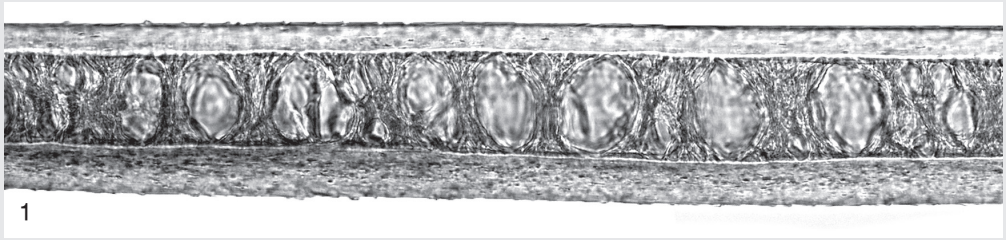
SIZE: l_{max} = 115 mm; d_{max} = 150 μ; m/d_x = 0.65

Canis aureus

FUR: The ground colour of the fur is pale ochreous-brown, often with weaker or stronger orange-brown shade in certain parts of the body; the dorsum is marbled and/or grizzled. The dark brown or blackish black-backed pattern along the backbone is usually contoured. The lips are white; the cheeks are greyish-brown. The middle-collar is well developed; the mane is absent or weakly developed.

HAIR, MACROSCOPIC: The bands of the two-banded hairs are most often equal in length.

SIZE: l_{max} = 110 mm; d_{max} = 140 μ; m/d_x = 0.65



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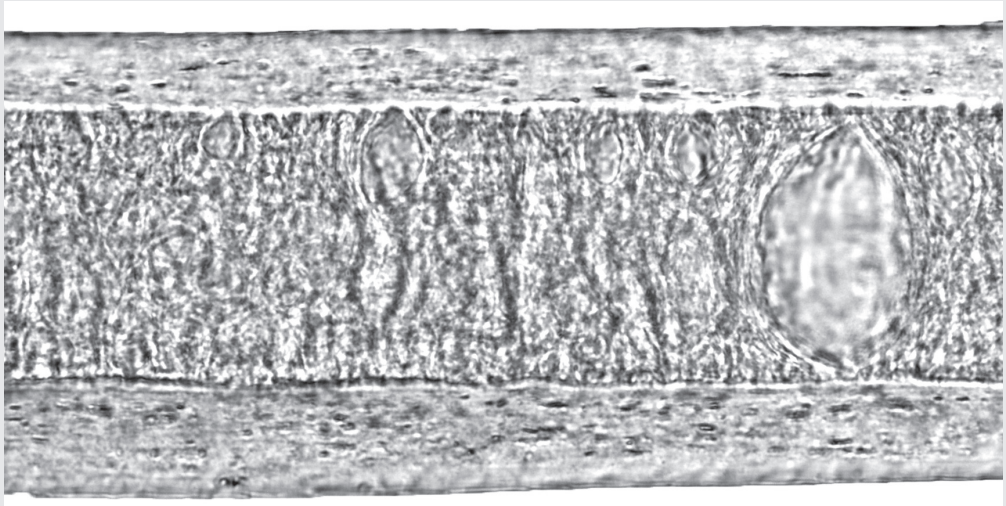

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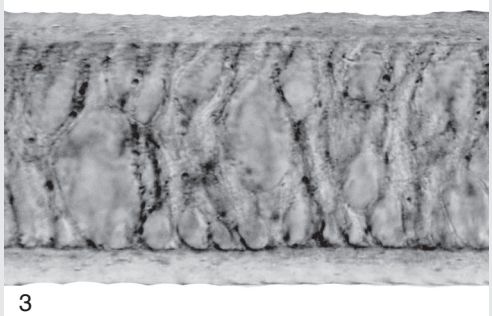

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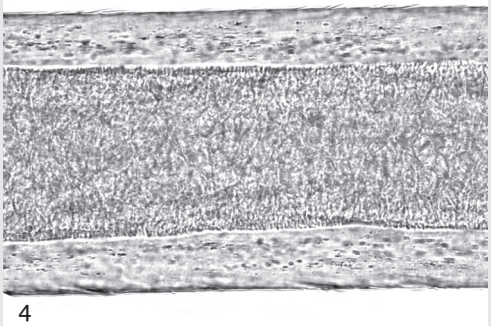

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Canis* spp.**: 1 = medulla, apical section; 2 = medulla, distal shield; ***Canis aureus: 3 = medulla, proximal shield; ***Canis lupus***: 4 = medulla, proximal shield

Nyctereutes procyonoides

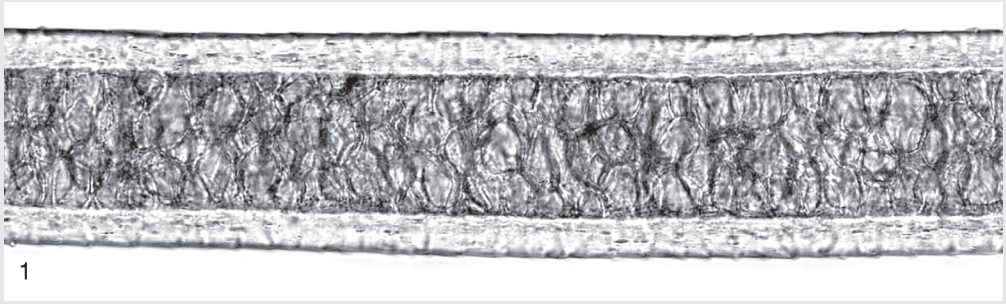
The Raccoon Dog is native in South-East Asia. As a relevant fur animal, it is breaded in several Eurasian countries. The specimens escaped from the fur-farms are spreading over large areas and reproducing successfully. Both the human introduction and the natural dispersion of this species resulted in the stable populations and intensive spreading in Central Europe, too.

FUR: The fur is prominently thick and dense, shaggy and long, with soft, silky touch; the pattern is grizzled and marbled. The winter fur is variably dark grey, the summer fur is usually ochreous-reddish brown, sometimes brown-grey or even blackish. The face is black-masked. The shape of the head is "hooded": there is a large, conspicuous, dense, laterally broader greyish-whitish mane consisting of very long bristle hairs, growing forward from the nape towards the forehead, the base of ears and the nose. The nose is white-ringed; the ridge of the nose, the front and the inner surfaces of the ears are white or pale greyish-brown. A black stripe may be present along the backbone running towards the base of the tail; additional shorter dark bands may also present running perpendicularly to the dorsal stripe. The throat, the breast and the legs are dark brown or black(ish); the belly is much paler, usually light brown with some ochreous-cinnamon red shade, more rarely whitish. The tail is shaggy, thick, with obtuse tip; its dorsal part is dark grey or grey-brown; the ventral side is somewhat paler; the tip of the tail is always black.

HAIR, MACROSCOPIC: The GH1 is unicolorous; the GH2 is one-, or two-banded; the length of white bands mostly different. The tip of the hair might be black or dark brown, occasionally white or transparent.

HAIR, MICROSCOPIC: The medulla of the shield is chambered multiserial; the shape of the medullar cells at the maximum width of the shield is globular or hexahedral; the volume of air sacs does not reach the entire medulla. The pigmentation is similarly dense and diffuse in the cortex and the medulla. The cross-section at the shield is circular or oblong.

SIZE: l_{max} = 110 mm; d_{max} = 135 μ; m/d_x = 0.65



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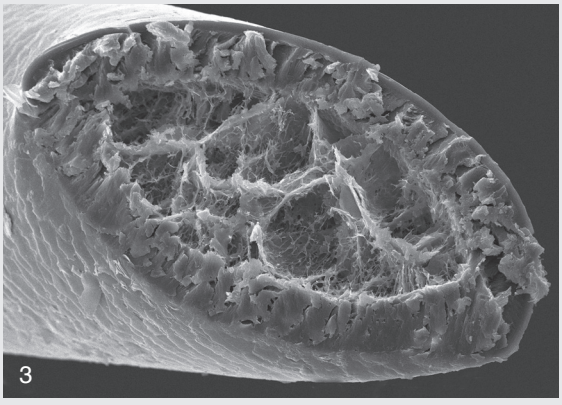

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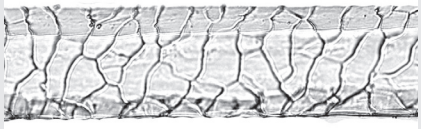

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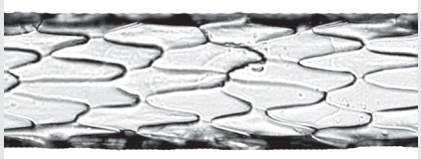

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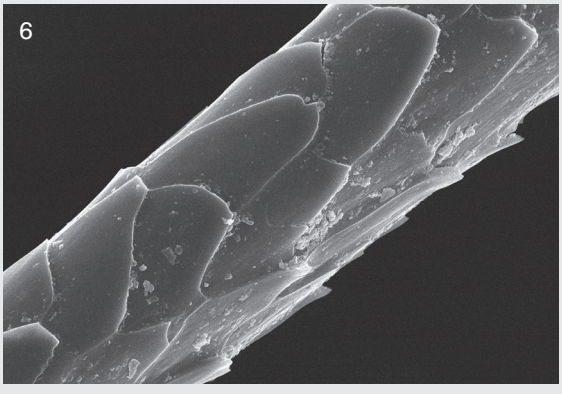

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Nyctereutes procyonoides: 1 = medulla, shield; 2 = cuticula, shield; 3 = cross-section, shield, SEM; 4 = cuticula, transit; 5 = cuticula, shaft; 6 = idem, SEM

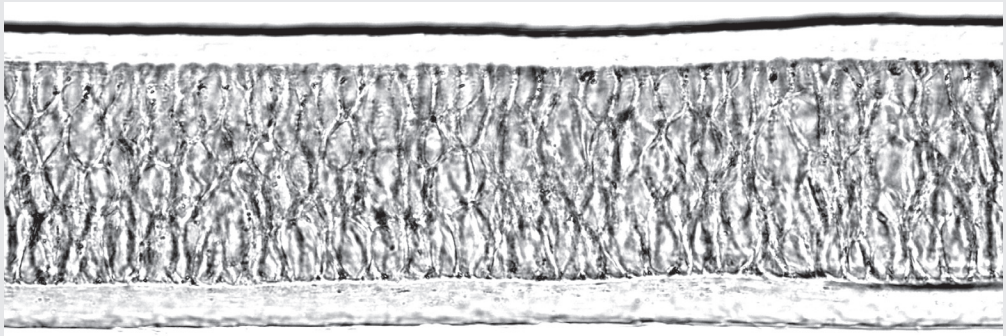
Vulpes vulpes

FUR: The fur is thick and rather loose, silky in touch; the main ground colour is intense reddish-brown. The dorsum is rufous or greyish-brown, unicolorous, or marbled around the neck; the mid-dorsal part of the rump is grizzled usually; the rump is often greyish or silvery shaded, especially in the older animals. The lips, the cheeks, the throat, the belly and the inner sides of the legs are white or whitish, distinctly separated from the darker parts. The inner side of the ear is cream-coloured; the outer side is black or blackish. The shanks and often the feet are dark brown or blackish. The paws are hairy. The tail is conspicuously long and longhaired, shaggy, marbled and/or grizzled. The tip of the tail is variably coloured, most often distinctly and broadly white.

HAIR, MACROSCOPIC: The GH1 are unicolorous, or bicolorate with black shaft and reddish-rufous shield. The GH2 is most often one-banded; the GH2 growing on the back have pale rufous band and dark brown or black shaft and tip while the GH2 from the sides of the body and the rump are shorter and tricolored, with brown shaft, milk-white band and vivid reddish shield.

HAIR, MICROSCOPIC: The medulla in the distal shield is chambered or foamy multiserial; the shape of the medullar cells is fusiform or globular; the medullar cells are elongated at the maximum width of the shield, but not closing tightly; the rather thick, fusiform intercellular air sacs may span the entire width of the medulla. The cross-section at the shield is circular or oblong.

SIZE: l_{max} = 60 mm; d_{max} = 120 μ; m/d_x = 0.7



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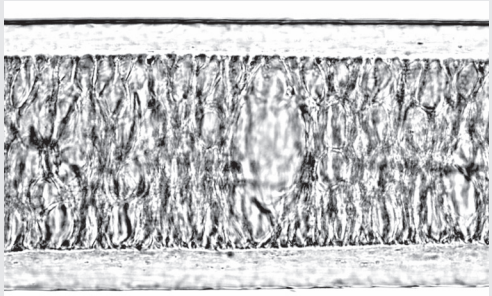

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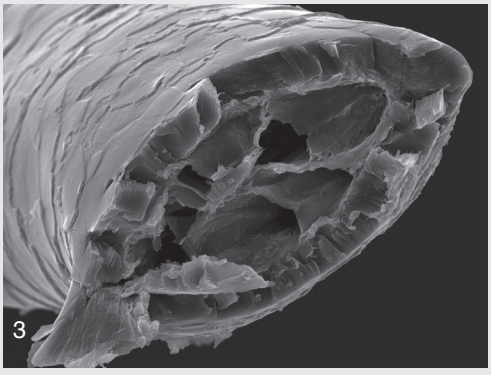

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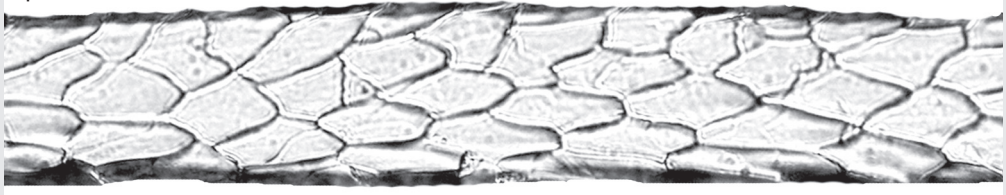

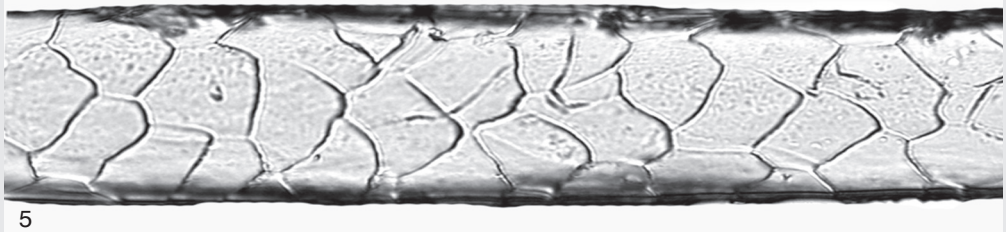

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Vulpes vulpes: 1 = medulla, distal shield; 2 = medulla, proximal shield; 3 = cross-section, transit, SEM; 4 = cuticula, proximal shaft; 5 = cuticula, distal shaft

Ursidae

The fur is compact, coarse in touch, with dull sheen. The ground colour is brown with a great variety of shades. The fur is usually unicolorous but might be strongly marbled and/or grizzled. The melanistic specimens are much more frequent than the rarely occurring albinistic and leucistic ones. The tail is short and shortly hairy, regularly unicolorous.

Ursus arctos

FUR: The fur is most often unicolorous dark brown or reddish-brown but can be also cinnamon-brown, yellowish brown or blackish, sometimes even nearly black. The fur is long on the back from the nape to the rump and on the sides of the body; the pattern is often marbled in these parts of the body where the apical section of hairs is greyish, silvery, whitish or pale rufous. The appearance of "mane" on the forehead and the nape is typical of the old animals; the fading of the muzzle and the backside is connected also with the age of specimens. The belly has shorter and looser, paler fur; sometimes with lighter greyish or ochreous patches.

HAIR, MACROSCOPIC: The shape of the GH is most often curved or wavy; the hairs are unicolorous or polychrome with paler shaft; the shield is dark brown, reddish, or rarely black. The UH is crispy and polychrome with transparent shaft and pale reddish or brownish shield.

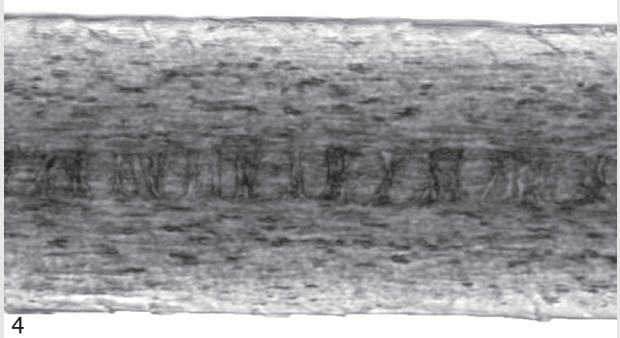
HAIR, MICROSCOPIC: The bulb is elongated and knobby. The cuticular pattern is broad rhomboidal on the shaft; transversally elongated regular mosaic on the transit and the proximal shield; figureless sketched with rippled margins of the cells. The medulla is amorphous or fragmented tubular in the shaft and the apical region; the width of the medulla in the distal shaft and the shield is more or less the same, the medullar pattern is colonnade tubular. The cortex is thick. The pigments are arranged diffusely and sparsely in the medulla, and arranged into lines along the fibres of the cortex. The tip is gradually tapering and often splitted. The cross-section is circular or oblong.

SIZE: l_{max} = 100 mm; d_{max} = 170 μ; m/d_x = 0.3

1

2

3



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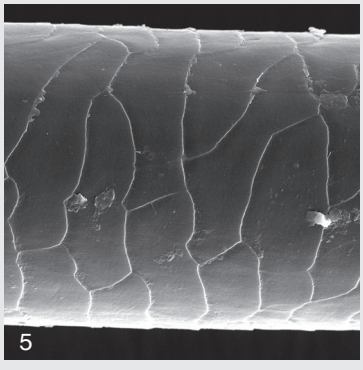

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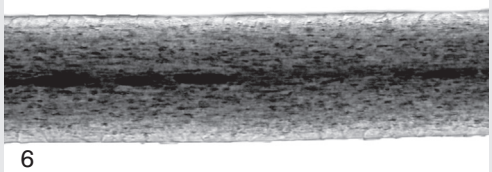

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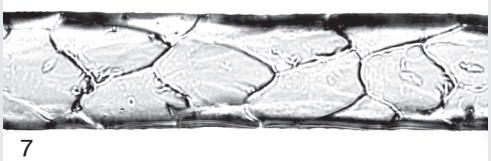


7

Ursus arctos: 1 = cuticula, apical section; 2 = tip; 3 = medulla, shield; 4 = medulla, transit; 5 = cuticula, transit, SEM; 6 = medulla, shaft; 7 = cuticula, shaft

Procyonidae

The family is native in America. The members of the family have a rather diverse appearance and life strategy; their fur is variably coloured, the masked face is typical of several species; leucistic and albinistic animals are found relatively frequently. The Northern Raccoon was introduced to Europe from North America by fur-trade. It is spreading, breeding wild in several countries of Central Europe.

Procyon lotor

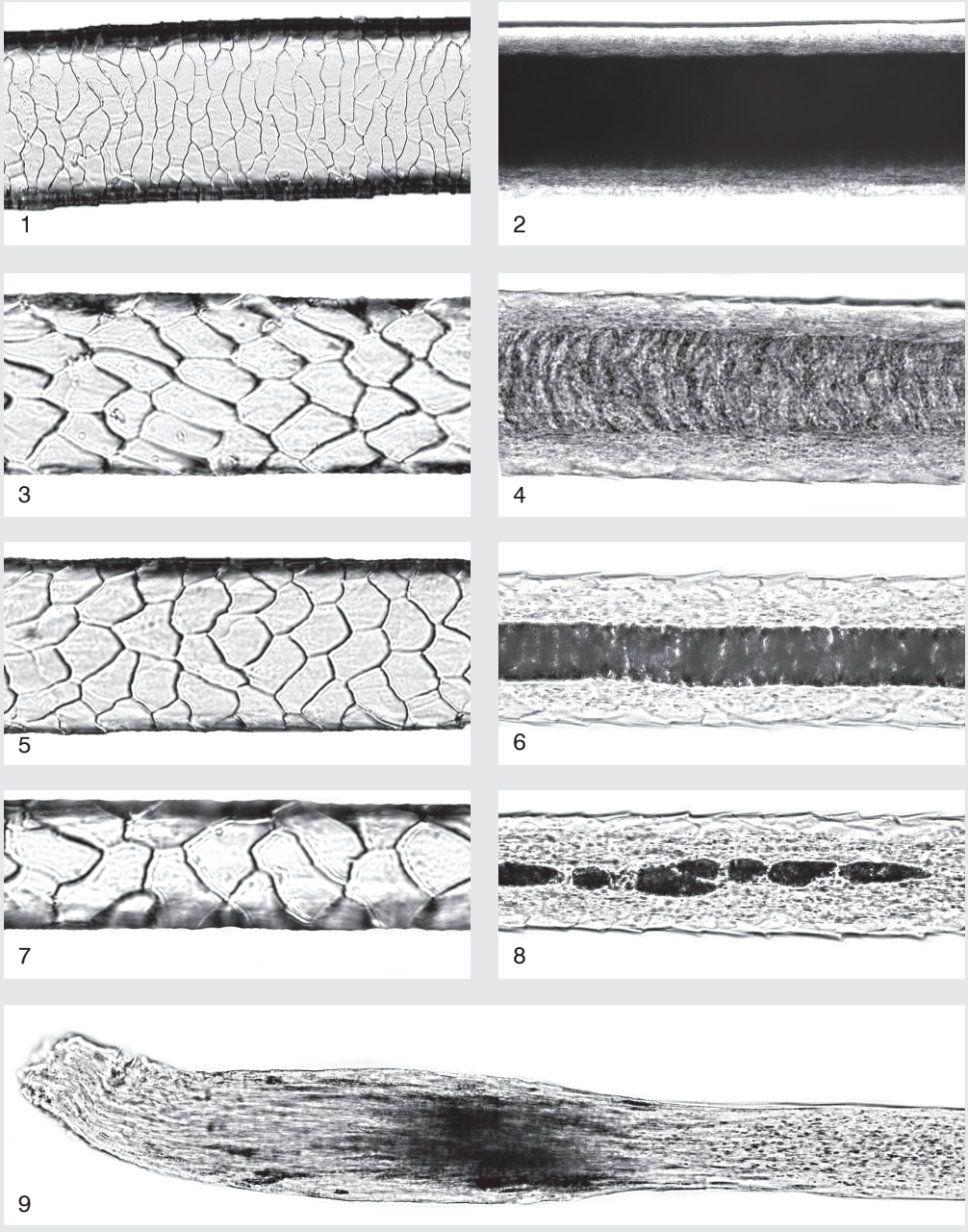
FUR: The fur is compact and thick, longhaired; the touch is fine, silky. The layer of underhairs is very dense and fine. The ground colour is dark grey or brown. The dorsum is marbled and grizzled; the backside may bear a dark stripe along the backbone. The fur is longer on the sides of the body and on the belly; it is unicolorous grey-brown or whitish. The diagnostic features of the Raccoon are the masked face and the ringed tail. The mask is distinctly marked and contoured, somewhat similar to that of the Raccoon dog, composed from the white ring around the tip of the nose and the black band on the muzzle, the ridge of the nose and around the eyes. The mask is surrounded by the long and broad, white "whisker" running downwards from the eyebrows to the breast. The forehead is grey; the throat is black or dark grey; the breast is grey(ish). The tail is long and shaggy; the rings on it equal in length, their colours are whitish, ochreous-brown, dark grey or black; the tip of the tail is black.

HAIR, MACROSCOPIC: The GH1 may be uni- or bicolorate white, brown or black; or banded. The one-banded GH1 has brown shaft with white or cream-coloured band in its mid section; the shield and the tip are black. The two-banded GH1 has a whitish shaft, dark brown band on the transit, pale ochreous brown band on the proximal shield while the section between the two bands and the tip of the hair are black. The GH2 bicolorate. The UH is unicolorous brown or grey.

HAIR, MICROSCOPIC: The bulb is knobby. The basal part of the hair is tubular, often rather long. The cuticular pattern is broad petal on the basal part; broad rhomboidal on the shaft; rhomboidal petal on the transit with isometric scales; irregular rhomboidal petal on the proximal shield; irregular figureless sketched or rippled on the distal shield. The medulla is chambered multiserial at the maximum width of the hair but is not or less transparent due to the strong pigmentation. The medullar cells are transversally elongated and slender in the transit; polygonal on the shield, with a few, variably shaped air sacs between them. The margin of the medulla is straight. The pigmentation is stronger in the shield; the pigments are arranged diffusely in the inner layer of the cortex and in the medulla. The tip is gradually tapering. The cross-section is oblong.

SIZE: l_{max} = 65 mm; d_{max} = 130 μ; m/d_x = 0.65

REMARKS: The fur of the Raccoon was used as Beaver and Sea otter fur imitations (Éhik 1931). As a matter of curiosity, modified furs of certain lagomorphs and Opossums were used to falsify the fur of the Raccoon (Lochte 1938).



Procyon lotor: 1 = cuticula, shield; 2 = medulla, shield; 3 = cuticula, transit; 4 = medulla, without air, shield; 5 = cuticula, distal shaft; 6 = medulla, transit; 7 = cuticula, proximal shaft; 8 = medulla, shaft; 9 = bulb

Mustelidae

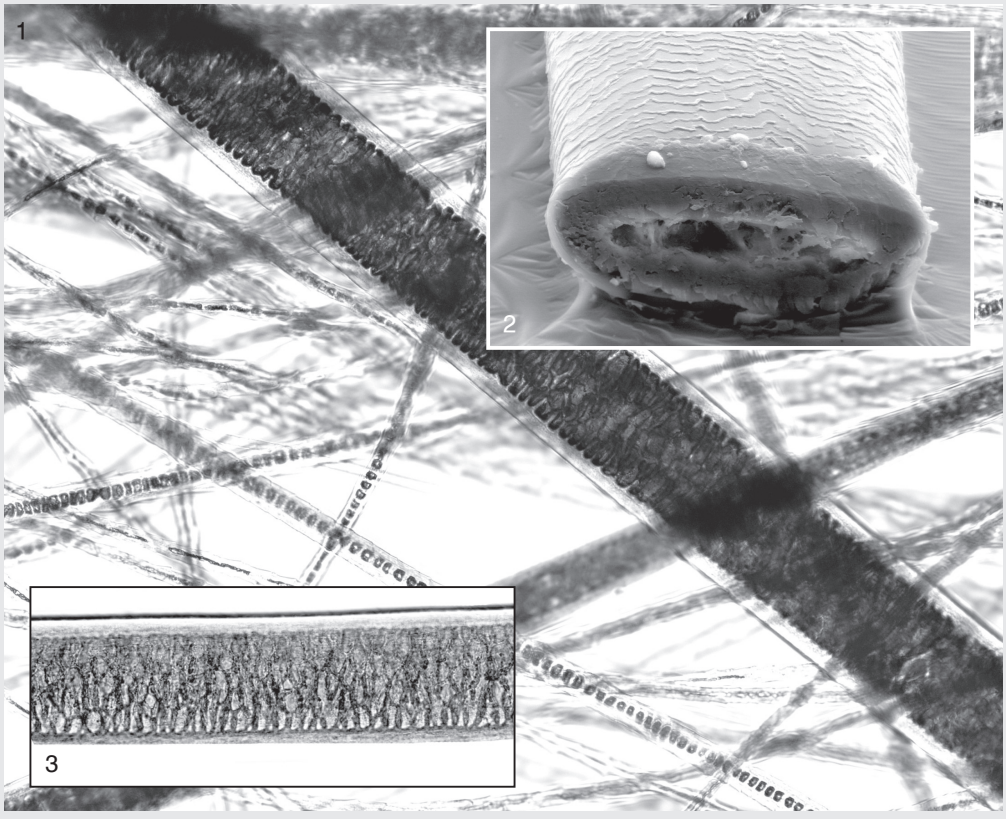
The family Mustelidae is the largest Carnivora group in terms of species richness, morphological diversity, lifestyle and ecological features.

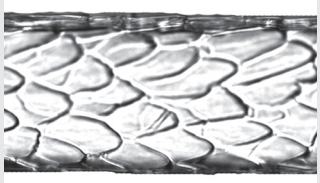
FUR: The fur is most often dense and fine in touch. The main ground colours are reddish or greyish-brown, blackish and white; the dorsum is usually unicolorous or marbled, less frequently grizzled or mottled. The ventral side is always paler and unicolorous, whitish, ochreous-brown or greyish. The masked face and/or the contoured breast occur in several species. The seasonal changes of the colouration of the fur are connected with the seasonal moulting. This change in the fur colour is less conspicuous in the temperate regions (with a few exceptions, like the Stoat) but the winter fur is regularly denser and typically paler than the summer fur. The albinistic, melanistic, erythristic and leucistic animals are very rare. The closely related species occasionally may produce interspecific hybrids that are difficult to identify; the detailed trichomorphological study of the hybrids is still missing.

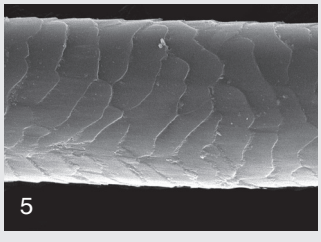
HAIR, MACROSCOPIC: The GH1 and GH2 are usually straight or curved; they might be unicolorous, polychrome or, more rarely, banded. The UH is usually wavy, always paler coloured and polychrome.

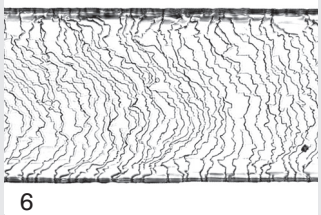
HAIR, MICROSCOPIC: The overwhelming majority of the Mustelidae species can be characterised by the combination of the rhomboidal cuticular pattern on the shaft and the chambered multiserial medulla in the shield. This combination may occur in the other Carnivora families, meanwhile a few Mustelidae taxa lack one or both of these features; therefore most often the combination of macro- and microscopic characters and the qualitative or quantitative differences may help the identification of the species or the similar and/or relative "twin-taxa".

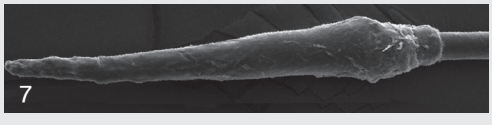
The GH bulb is elongated and knobby; the basal section is tubular. The cuticular pattern is broad, irregular petal on the basal section; elongated or rhomboidal pine-cone on the shaft; elongated, rhomboidal or rhomboidal petal on the transit; transversal mosaic on the shield; and irregular figureless in the apical region, with rippled or sketched margins. The medulla is regular, uniserial nummiform in the basal section, chromosomal nummiform on the shaft, and chambered multiserial in the shield. The medullar cells at the maximum diameter are polygonal and transversally slightly elongated. The medullar margins are mostly crested. The pigments arrange diffusely and concentrate primarily in the medulla. The shape of the hair is usually spatula-like. The tip is long, gradually tapering. The cross-section is circular or oblong. The UH is curved or wavy, and often lacks the medulla.











Mustelidae: 1 = transparent view, hairs; 2 = cross-section, shield, SEM; 3 = medulla, shield; 4 = cuticula, transit; 5 = cuticula, shield, SEM; 6 = cuticula, apical section; 7 = bulb, SEM; 8 = cuticula, shaft

Mustela nivalis & Mustela erminea

FUR: The fur is fine, short, fitting close to the body surface. The dorsum is unicolorous, reddish-brown in various shades.

HAIR, MACROSCOPIC: The GH is glossy and polychrome; the shaft is transparent, light brown; the shield is darker reddish or dark brown.

HAIR, MICROSCOPIC: The cuticular pattern on the shaft is pine-cone rhomboidal. The medullar cells in the shield are transversally elongated and variably sized, more or less globular or polygonal. The cross-section is oblong.

Mustela nivalis

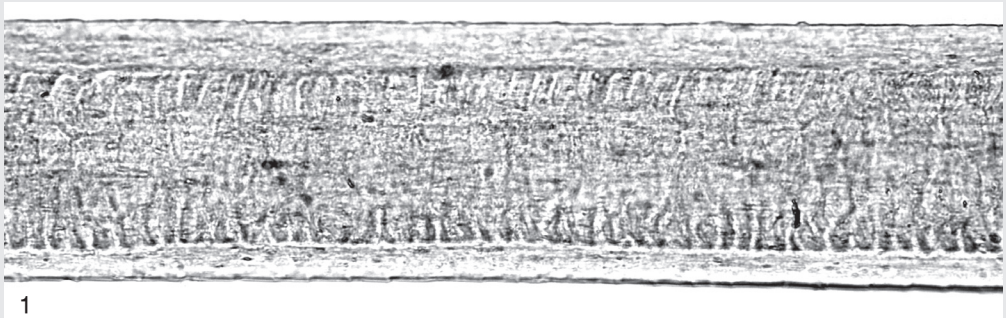
FUR: The head, the outer sides of the legs and the dorsal part of the body are most often glossy red-brown, sometimes dull greyish-brown or dark brown. The lower lips, the chin, the throat and the belly are white, more rarely ochreous-white. The dark dorsum and the light ventral side are separated along a sharp but irregularly sinuous lateral line. The tail is short, brush-like. In the Central European populations, the winter fur becomes paler coloured and denser, while in the more northern populations the entire fur becomes white, including the tail.

SIZE: l_{max} = 10 mm; d_{max} = 110 μ; m/d_x = 0.75

Mustela erminea

FUR: The head and the dorsal part of the body are usually glossy reddish-brown, less frequently dull dark brown or dark grey-brown; sometimes with a darker band along the backbone. The dark dorsum and the white(ish) ventral side are separated along a sharp and almost straight lateral line. In the summer fur, the lower lips, the chin, the throat, the inner sides of the legs and the belly are white or cream-coloured. In Central Europe, the fur of the stoat after the autumnal moulting turns into clear white, ochreous-white or pale greyish-ochreous until the next spring. This white(ish) colour is, however, usually incomplete, and the fur is mottled with brown and white patches. The distal part of the tail is shaggy (max. the half of the length of the tail), it is always black, covered by long hairs.

SIZE: l_{max} = 17 mm; d_{max} = 115 μ; m/d_x = 0.7



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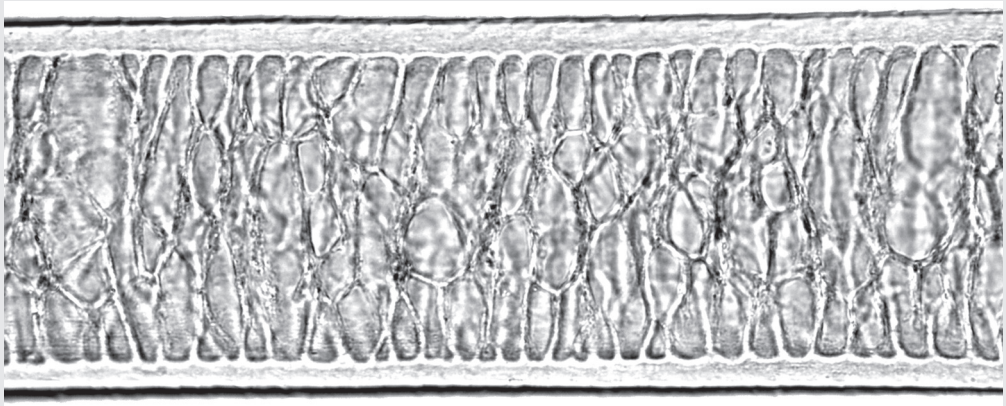

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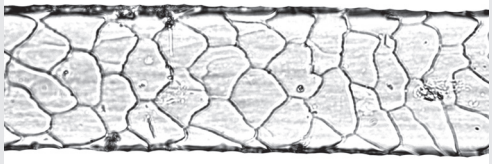

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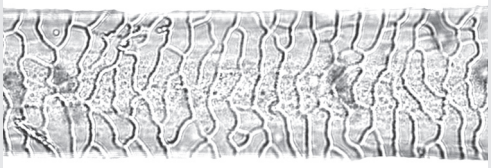

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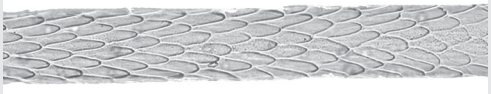

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Mustela erminea & ***Mustela nivalis***: 1 = medulla, distal shield; 2 = medulla, proximal shield; 3 = cuticula, transit; 4 = cuticula, shield; 5 = cuticula, basal; 6 = cuticula, shaft

Mustela putorius & M. eversmanii

FUR: The fur is very fine and soft in touch, long and glossy; the ground colour is brown of various shades. The dorsum is marbled. The face is masked, consisting of a black stripe around and between the eyes (orbicular stripe), contoured by a paler, most often brownish-ochreous muzzle-band between the ears and the eyebrows and by the white(ish) lips and chin. The outer sides and the inner margins of the ears are white or cream-coloured. The legs and the throat are darker brown or black(ish). The belly is much paler, whitish-ochreous, sometimes pale brownish. The tail is long-haired, shaggy, dorsally black or dark brown, ventrally ochreous.

HAIR, MACROSCOPIC: The GH1 and GH2 hairs are displaying a characteristic tricolorate, but not banded, "polecat-type" colour transition: the long shaft is transparent white or ochreous-white, the short transit is vivid yellowish or rufous, which turns gradually into shining dark brown or black on the shield.

HAIR, MICROSCOPIC: The cuticular pattern on the shaft is elongated rhomboidal. The medullar cells in the shield are irregularly polygonal, cask-shaped or globular; the large cells may span the entire diameter. The cross-section is oblong.

SIZE: l_{max} = 65 mm; d_{max} = 145 μ; m/d_x = 0.75

Mustela putorius

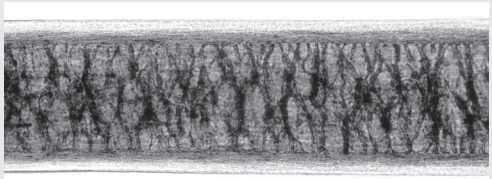
FUR: The fur is dark brown, sometimes even black, but prominently light-coloured, sandy ochreous or sand-brown specimens also occur. The white(ish) bands of the face do not reach the front while the black orbicular stripe extends onto the ridge of the nose and the frons; the white ring around the nose usually does not extend onto the ridge of the nose. The dorsum and the tail are similarly coloured, dark brown, chocolate-brown or blackish-brown.

HAIR, MICROSCOPIC: The medullar cells of the shield are polygonal or cask-shaped, usually slender.

Mustela eversmanii

FUR: The fur is distinctly light coloured; the ground colour varies from pale ochreous to light ochreous-brown. The white(ish) stripe around the lips and the chin and the white muzzle band are broad, expanding onto the frons and sometimes also to the forehead; the white ring around the nose is usually complete, covering also the ridge of the nose. The proximal (basal) part of the tail is matching with the pale sandy brown or ochreous-brown colour of the dorsum but the tip of the tail is always dark brown.

HAIR, MICROSCOPIC: The medullar cells of the shield are smaller, transversally, slightly elongated or globular.



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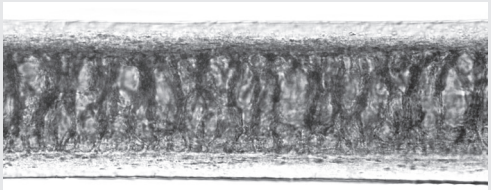

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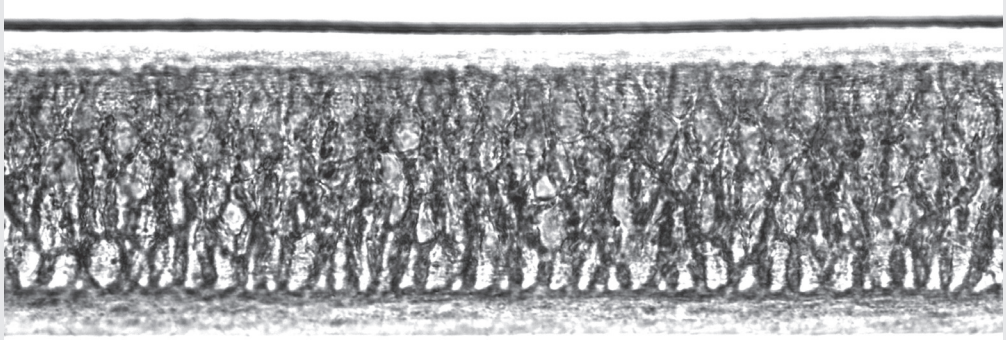

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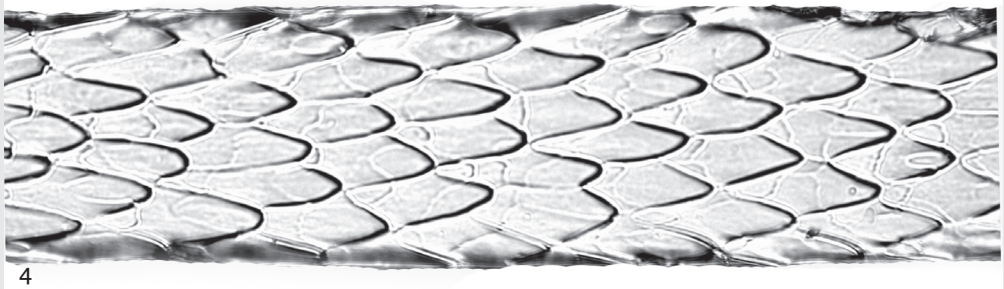

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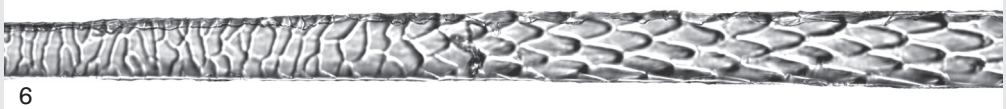

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Mustela putorius & ***Mustela eversmanii***: 1 = medulla, distal shield; 2 = idem; 3 = medulla, proximal shield; 4 = cuticula, shaft; 5 = medulla, transit; 6 = transit section

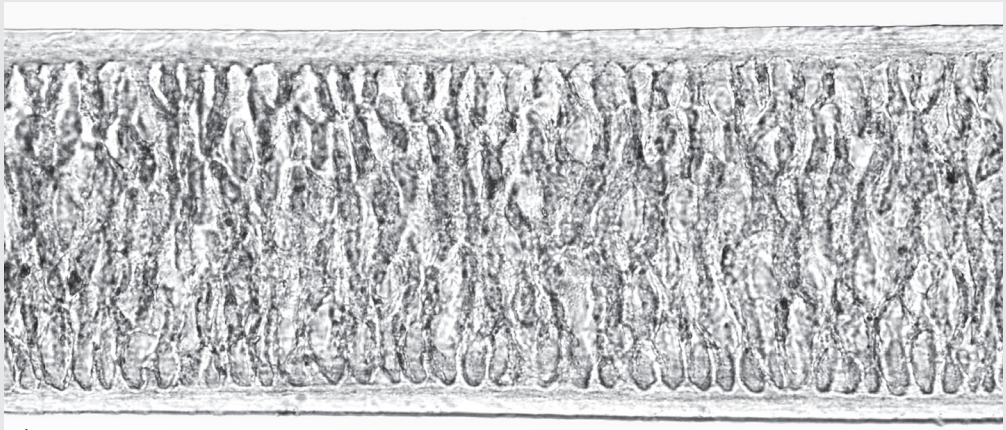
Vormela peregusna

FUR: The fur is very soft, silky in touch; dense and loose. The fur has a characteristic colouration and pattern, showing large individual and geographical variability. The mask on the face is 4-"banded": the forehead is dark between the ears; a white band runs below it around the face crossing the front and brows but never reaches the throat; a dark band is crossing the eyes and frames it; a white ring is running around the nose, limbs and chin. The edges of the rounded ears are covered with white bristle hairs. The breast, the belly, and the legs are always blackish. The nape, the neck, the dorsum, and the lateral sides are mottled. The ground colour of the dorsum is mostly yellowish; the irregular, smaller spots and stripes are brown to reddish-brown; the "negative" dorsum pattern, with blackish ground colour and yellowish spots and lateral bands, is rare. The body hairs are generally shorter, but the long, bushy tail is long-haired. The base of the tail has a yellowish cross-stripe; the tip is mostly dark; in between them, the tail is grizzled, light greyish-brown.

HAIR, MACROSCOPIC: The GH1 and GH2 can be unicolorous white or ochreous or bicolorate with "polecat-type" colour transition: the long shaft is transparent white or ochreous-white; the short transit is vivid yellow or rufous; this colour is turning gradually into shining dark brown or black.

HAIR, MICROSCOPIC: The cuticular pattern is elongated, rhomboidal on the shaft; rhomboidal petal on the transit and the proximal shield, the edges of scales often crenate; and close, figureless on the distal shield. The medulla is narrow, amorphous or fragmented tubular in the basal section; chambered multiserial with small, transversally elongated or isodiametric cells on the shield. The intercellular air sacs are small, never span the width of the medulla. The shaft is transparent, while the shield and the apical part pigmented densely and diffusely. The shield is flattened; the cross-section is narrow, oblong.

SIZE: l_{max} = 16 mm; d_{max} = 105 μ; m/d_x = 0.85



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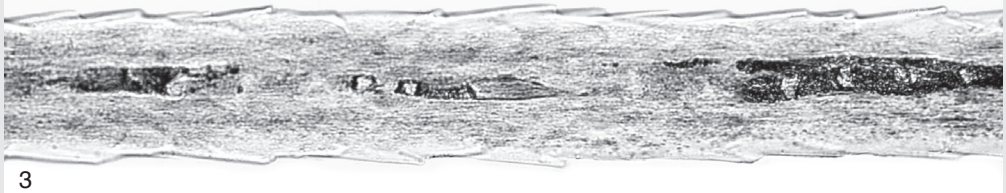

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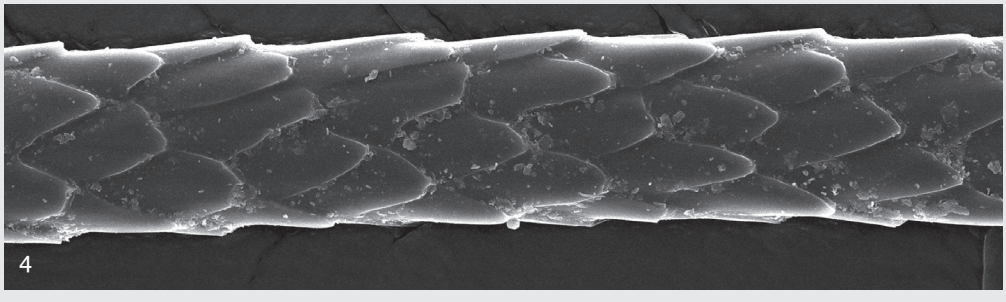


4

Vormela peregusna: 1 = medulla, shield; 2 = cuticula, transit; 3 = medulla, shaft; 4 = cuticula, shaft, SEM

Mustela lutreola & Neovison vison

FUR: The structure of the fur of the two semi-aquatic Mesocarnivora species is very similar; it is dense but not long-haired, and fine, silky in touch. The ground colour of the fur is most often glossy dark brown, less frequently black, chocolate-brown or reddish-brown; the albinos are rare. The fur is unicolorous on the entire body, the ventral side is only slightly paler; smaller white(ish) patches may be present on the throat and the breast; the tail is not or only slightly darker than the dorsum.

HAIR, MACROSCOPIC: The GH is glossy and polychrome, with pale grey-brown or rufous shaft and dark red-brown shield.

HAIR, MICROSCOPIC: The cuticular pattern on the proximal part of the shaft is pine-cone rhomboidal, with pointed apical edges. The medullar cells are variably shaped at the maximum diameter of the shield (GONZÁLEZ-ESTEBAN *et al*. 2006). The cortex is pigmented diffusely; the pigmentation is markedly dense in the inner part of the shield surrounding the medulla. The cross-section is narrow oblong.

SIZE: lmax = 25 mm; dmax = 135 μ; m/dx = 0.75

Mustela lutreola

FUR: The lips and the chin are white.

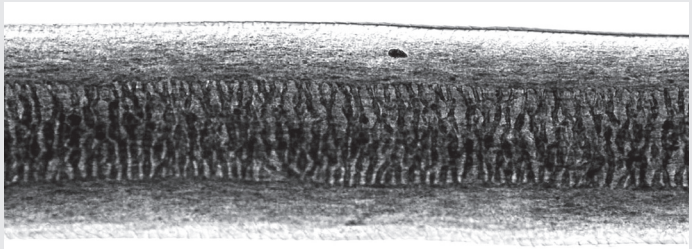
HAIR, MICROSCOPIC: The medullar cells in the shield are transversally elongated, polygonal or cask-shaped; the larger air sacs may span the entire width of the medulla.

Neovison vison

The American mink is native in North America. It was introduced to Europe as fur animal, but specimens escaped from the fur-farms, spreading over large areas, colonizing successfully and establishing feral populations. The mink has become a wild-living alien species in several Central European countries, too (HEGYELI & KECSKÉS 2014).

FUR: The lower lip and the chin are white.

HAIR, MICROSCOPIC: The medullar cells in the shield are smaller, tightly closed, polygonal or rounded; the intercellular air sacs do not span the entire width of the medulla.



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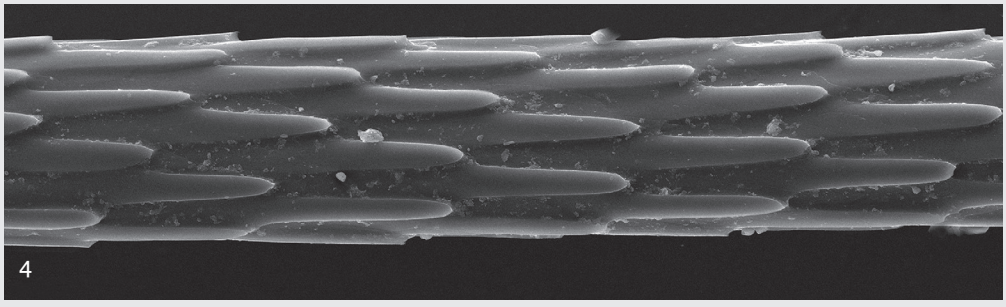

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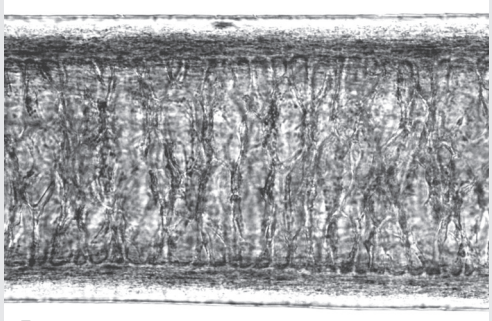

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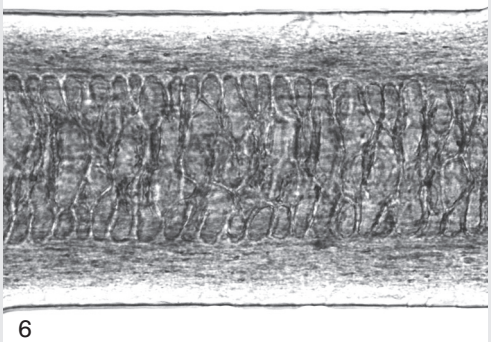

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Mustela lutreola & ***Neovison vison***: 1 = medulla, distal shield; 2 = cross-section, shield, SEM; 3 = medulla, transit; 4 = cuticula, shaft, SEM; ***Mustela lutreola***: 5 = medulla, proximal shield; ***Neovison vison***: 6 = medulla, proximal shield

Martes foina & Martes martes

FUR: The fur is long-haired and finely shaggy, with soft, silky touching; the ground colour is brown of various shades; the dorsum is marbled or unicolorous. The breast is contoured; the whitish or yellowish patch might extend towards the throat and the face. The legs are somewhat darker in shade; the tail is distinctly shaggier, dorsally dark brown, ventrally a bit lighter brown; the belly is somewhat paler coloured.

HAIR, MACROSCOPIC: The GH is polychrome, shining; its colour varies from brown and greyish-brown to rufous-reddish.

HAIR, MICROSCOPIC: The cuticular pattern is elongated rhomboidal on the proximal shaft. The medullar cells in the shield are transversally elongated, arranged regularly on the distal shield. The shield is flattened; the cross-section is narrow, oblong.

SIZE: l_{max} = 60 mm; d_{max} = 145 μ; m/d_x = 0.75

Martes foina

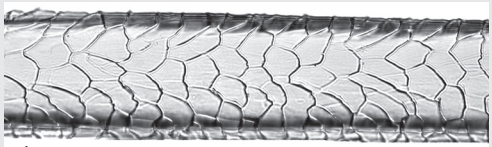
FUR: The fur is most often rather pale greyish-brown or buff but rufous-shaded or dark brown specimens also occur. The large white or ochreous patch of the throat and the breast usually extends towards the forelegs.

HAIR, MICROSCOPIC: The medullar cells of the proximal shield are rounded or polygonal; they are more or less equal in size and closely tighten; the longer axis of the cells is usually not perpendicular to the axis of the stem but closing with it a different angle.

Martes martes

FUR: The fur is dark brown or chestnut-brown, being regularly darker than in the stone marten; the edges of the ears are whitish or ochreous. The large light patch of the throat and the breast is ochreous-yellowish, sometimes even orange-ochreous, and irregularly shaped. There are rather dense and short, soft hairs between the footpads.

HAIR, MICROSCOPIC: The medullar cells of the proximal shield are various in sizes; they are transversally somewhat elongated and polygonal, the longer axis of the cells is usually perpendicular to the axis of the stem.



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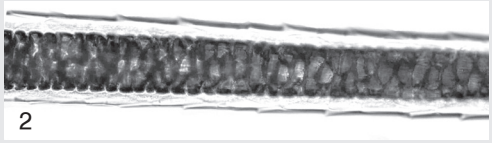

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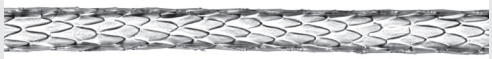

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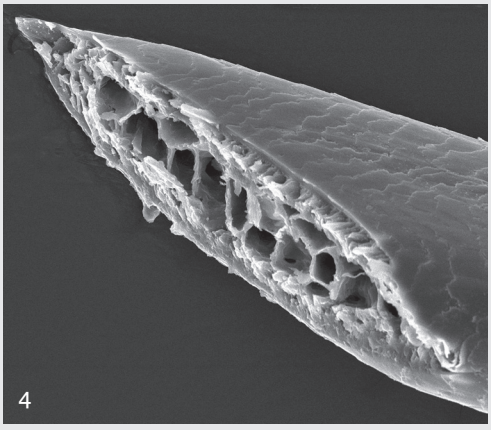

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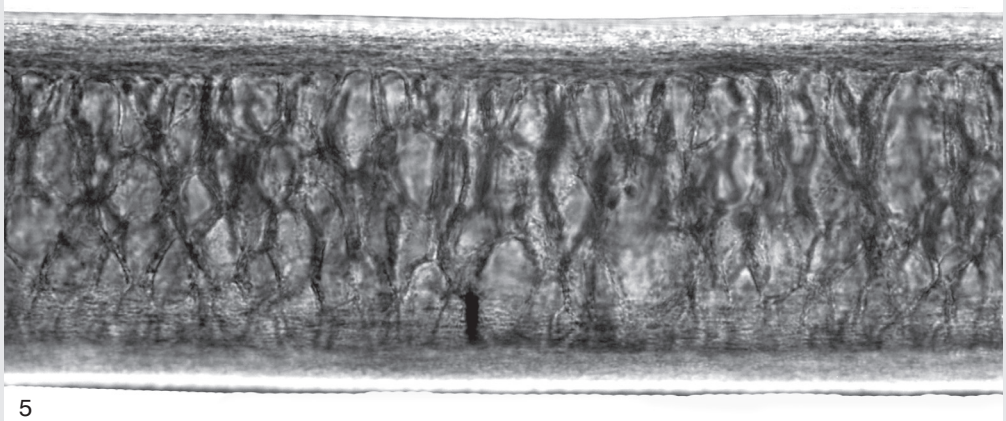

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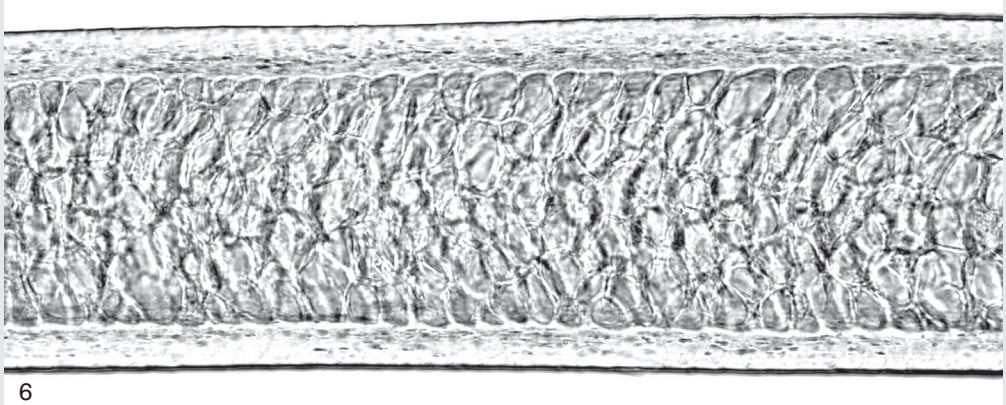

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Martes* spp.**: 1 = cuticula, transit; 2 = medulla, transit; 3 = cuticula, shaft; 4 = cross-section, shield, SEM; ***Martes martes: 5 = medulla, shield; ***Martes foina***: 6 = medulla, shield

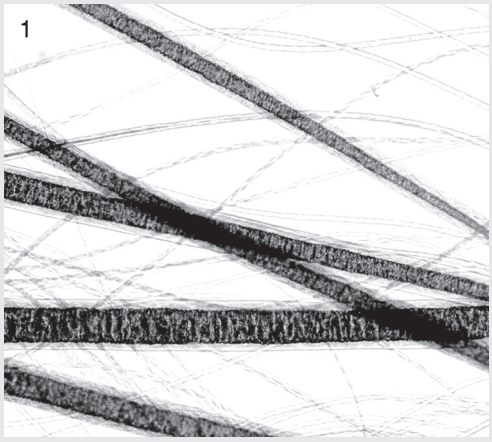
Lutra lutra

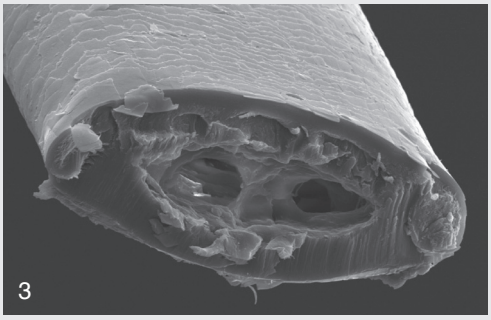
FUR: The fur is dense and short-haired; silky and greasy in touch. The dorsum and the tail are glossy brown or greyish-brown; the ventral side has a large and concolorous white(ish) or grey-white, sometimes pale greyish-brownish patch; this patch may extend from the tiny ears and the lower lips throughout the throat to the belly to the inner sides of the legs.

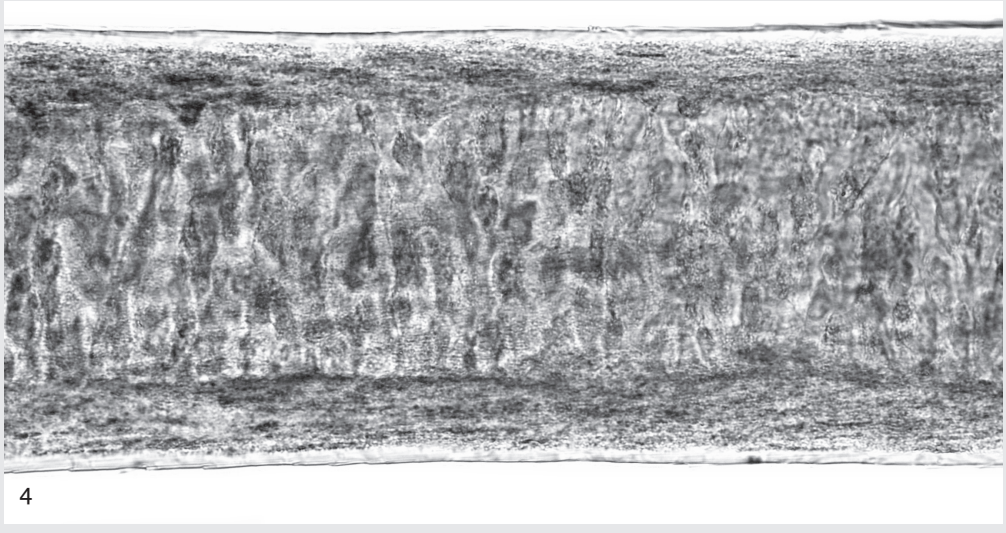
HAIR, MACROSCOPIC: The GH is bicolorate and shining, the shaft is whitish or greyish-brown, and the shield is rufous-brown or dark brown.

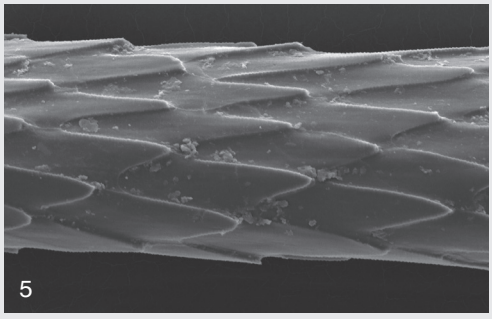
HAIR, MICROSCOPIC: The cuticular pattern is pine-cone rhomboidal on the proximal shaft; broad rhomboidal on the distal shaft; irregular mosaic on the transit. The medulla on the shield looks as an amorphous, obscure structure in the not treated hairs but after elimination of the air bubbles, the chambered multiserial structure will be clearly visible; the medullar cells are transversally elongated or polygonal. The medulla and the cortex are pigmented densely; the pigments of the medulla arrange diffusely, while they are usually aggregated along the fibres in the cortex. The shaft is distinctly short, its length is ca 1/4 of the entire length of the hair or even shorter. The hair is flattened from the transit towards the apical region. The tip is short, abruptly tapering and transparent. The cross-section is narrow, oblong.

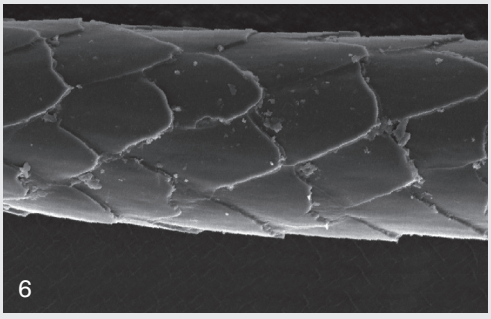
SIZE: l_{max} = 25 mm; d_{max} = 150 μ; m/d_x = 0.6











Lutra lutra: 1 = transparent view, hairs; 2 = tip; 3 = cross-section, shield, SEM; 4 = medulla, shield; 5 = cuticula, shaft, SEM; 6 = cuticula, transit, SEM

Meles meles

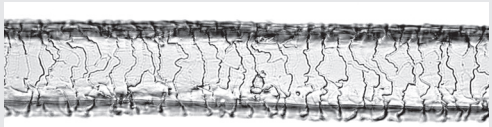
FUR: The fur is rather coarse in touch; the underhairs are relatively sparse. The ground colour is grey in various shades, sometimes dark grey or whitish and the winter fur is regularly paler; the fur is marbled and grizzled. The face is masked; the mask consists of two broad black stripes running from the nose through the eyes towards and behind the ears and the white stripe between them from the nose until the forehead; the tips of the ears, the cheeks and the lateral sides of the necks are white. The white stripes of the forehead and the muzzles are often expanding to the forehead and the proximal part of the dorsum. The throat, the lateral sides and the legs are black(ish) or dark brown. The ventral side is short-haired, pale brownish or ochreous-whitish; the short tail and the backside are greyish-brown or grey-white.

HAIR, MACROSCOPIC: The GH1 is one-banded; the dark band is on the distal shield; the tip of the hair is white or ochreous-white. The GH2 is variable, it can be polychrome brown, bicolorate with darker apical section, or rarely one-banded, with dark band, white tip. The shape of the hair is flattened from the distal shield towards the tip; the tip is often splitted. The UH is slightly wavy, regularly whitish in colour.

HAIR, MICROSCOPIC: The cuticular pattern of the GH is irregular, broad petal on the shaft; the pine-cone rhomboidal pattern, being typical of the other Mustelidae, is rare in the badger and substituted by an irregular, broad rhomboidal pattern on the distal shaft and the transit. The pattern of the proximal shield is closed, irregular, transversal mosaic with smooth edges; the distal shield and the apical region are characterised by a dense figureless pattern with rippled margins. The surface of the scales is often scratched. The medulla is fragmented in the basal part; amorphous, tubular in the shaft and the transit; chambered multiserial in the proximal shield with rounded, small medullar cells; porous tubular in the distal shield; colonnade tubular with large air sacs on the apical section. The arrangement of pigments is dense and diffuse in the medulla and the cortex. The cross-section is circular or oblong.

SIZE: l_{max} = 90 mm; d_{max} = 250 μ; m/d_x = 0.5

1



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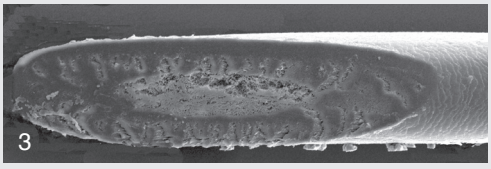

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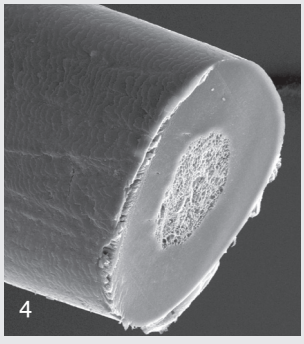

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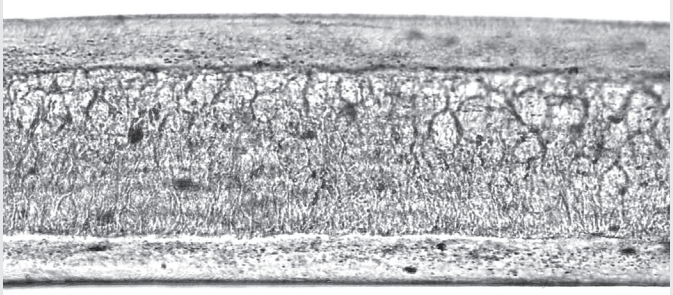

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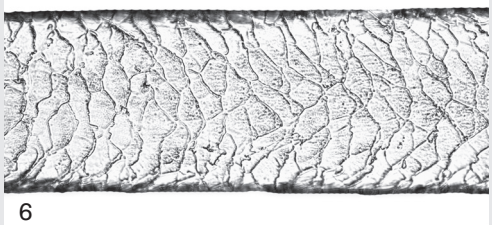

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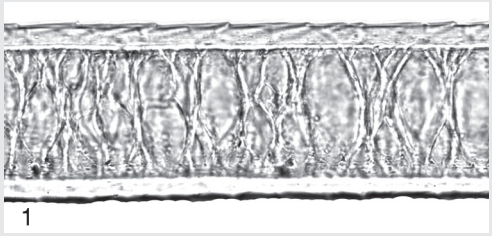
Meles meles: 1 = tip; 2 = cuticula, apical section; 3 = cross-section, apical section, SEM; 4 = cross-section, shield, SEM; 5 = medulla, shield; 6 = cuticula, transit; 7 = cuticula, shield; 8 = cuticula, shaft; 9 = medulla, transit

Felidae

FUR: The fur is dense, mostly rather loose and has a markedly silky, fine touching; the colouration and the pattern of the fur is strongly variable in the entire family; the dorsum could be mottled, marbled, grizzled and unicolorous. The melanistic, leucistic and albino specimens are relatively frequent.

HAIR, MACROSCOPIC: The GH can be banded, bicolorate or polychrome. The thickness of the dense underhairs may exceed the 2/3 of the length of the guard hairs. The UH is wavy, unicolorous or polychrome; the shaft is whitish or greyish, the shield is brownish, cinnamon or smoky grey.

HAIR, MICROSCOPIC: The bulb is knobby. The cuticular pattern is broad petal on the basal section; irregular petal, elongated or broad rhomboidal on the shaft but the rhomboidal pattern appears only in short parts of the GH2 and UH. The transit and the proximal shield have narrow, regular mosaic pattern with crenate edges; the distal shield is characterised by dense figureless pattern with rippled edges. The medulla is uniserial and chromosomal nummiform in the basal part and the shaft, here the cortex is thin; chambered multiserial in the transit and the proximal shield, where the medullar cells are transversally slightly elongated; the air sacs are globular or cask-shaped and may fill the entire width of the medulla. The medulla of the distal shield is foamy multiserial, with finely fringed medullar edges. The pigments arrange evenly and diffusely in both the medulla and the cortex. The tip is gradually tapering and pigmented. The cross-section is circular or oblong.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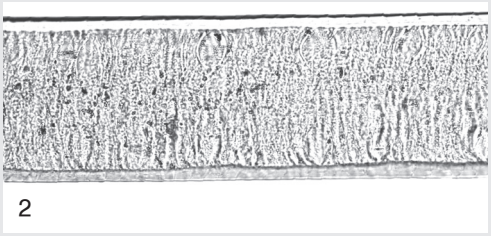
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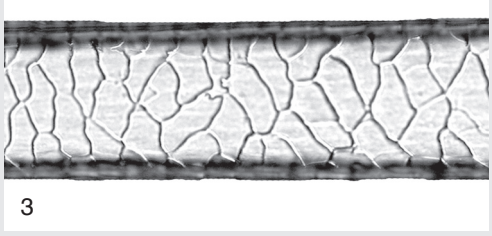
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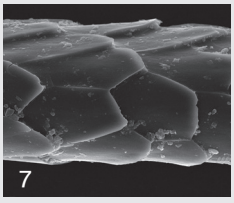
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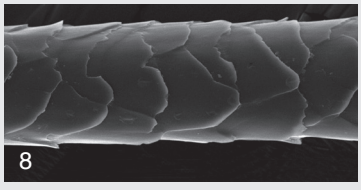
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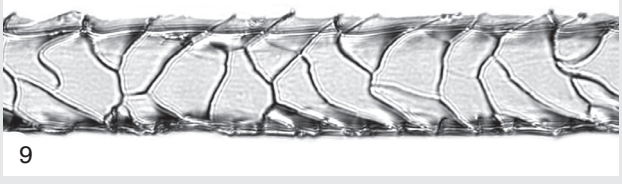
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Felidae: 1 = medulla, proximal shield; 2 = medulla, distal shield; 3 = cuticula, transit; 4 = cuticula, shield; 5 = medulla, shaft; 6 = cuticula, shaft; 7 = idem, SEM; 8 = cuticula, basal, SEM; 9 = idem

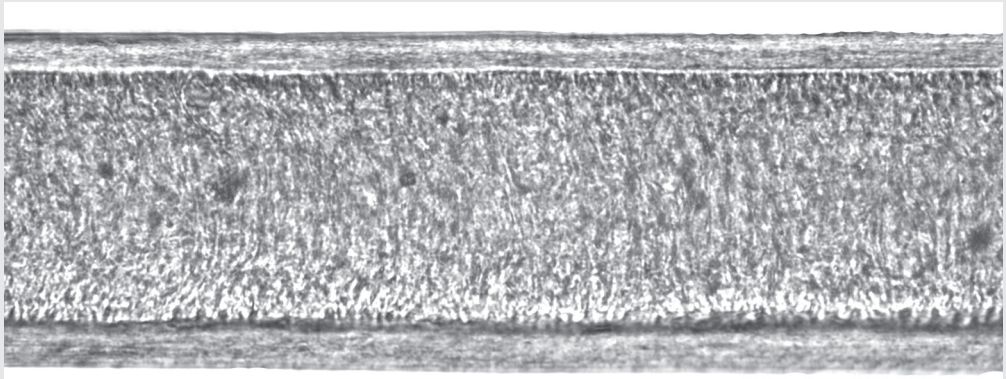
Lynx lynx

FUR: The fur is dense and silky in touch. The ground colour is light greyish-brown or ochreous-grey; the pattern is often variable in the different parts of the body, it can be marbled, mottled or grizzled. There are distinct and/or more or less dark, brownish-greyish spots and stripes on the body, the shape and size of these patterns are strongly variable: the spots appear rather on the backside, the inner and lateral sides of the legs and on the belly, while the stripes occur mainly on the breast and the shanks. The arrangement of the dark patches is even and symmetrical on the backside, the lateral parts of the body, the outer sides of the legs and the belly. The lateral sides are most often rufous-brown or pale reddish-brown. The belly is whitish, greyish-ochreous or rufous; it might be finely spotted by tiny, blurred dark spots, or unicolorous. The generic features of the species are the long ear tufts consisting of long, dark bristle hairs, and the long, prominent side-whiskers on the cheeks. A prominent, rather black(ish) black stripe runs from the edge of the eye downwards to the neck. The usually sandy ochreous or buff forehead is marked by a few (most often four) zigzagged black stripes. The base of the ear is dorsally white or pale grey, while the margins and the tips of the ears are black; whitish or light ochreous-brownish rings surround the eyes; the lips, the lateral edges of the muzzles and the throat are white. The dorsum is marked by a darker brownish band, which includes 2–3 distinctly contoured, parallel rows of spots. Certain specimens have reddish or hazel-coloured, marbled and grizzled fur lacking the darker spots and stripes. The winter fur is remarkably longer and denser with paler colouration and more blurred spots and stripes. The short tail of the Eurasian lynx has 3–4 brown, basal rings; the tip of the tail is always black, this black part may take up the entire distal half of the tail. There are denser, short, soft hairs between the footpads.

HAIR, MACROSCOPIC: The GH1 can be unicolorous white or dark brown, or bicolorate with paler shaft and darker shield; the shaft is greyish-brown, ochreous-brown or pale reddish, the shield is dark brown or black. The GH2 is one- or two-banded; the one-banded GH2 has whitish shaft and reddish band on the transit and the proximal shield, while the distal shield and the apical region are dark brown or red; the two-banded GH2 is shorter and thinner, having white shaft, brown proximal band and white distal band, and dark brown tip.

HAIR, MICROSCOPIC: The air sacs of the proximal shield are usually oblong and/or cask-shaped, only a few air sacs span the entire diameter of the medulla.

SIZE: l_{max} = 60 mm; d_{max} = 100 μ; m/d_x = 0.75



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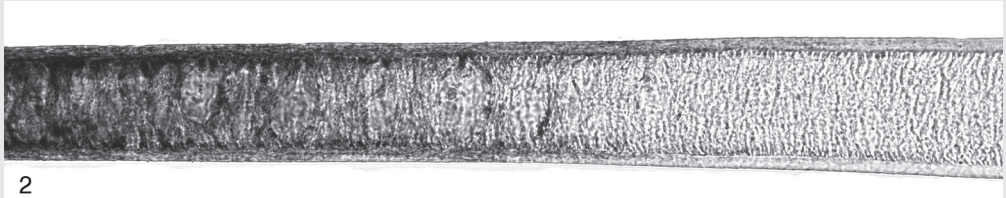

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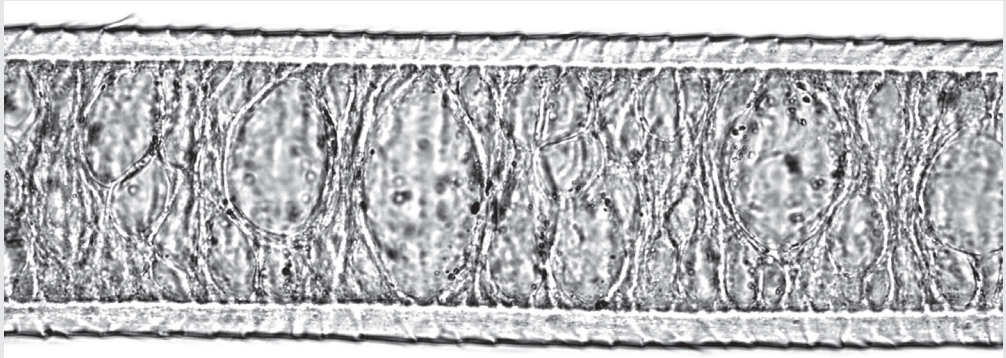


3

Lynx lynx: 1 = medulla, distal shield; 2 = medulla, transit section; 3 = medulla, proximal shield

Felis silvestris

FUR: The fur is dense and silky in touching; its pattern is marbled, grizzled and mottled. Stripes and tiny spots mark the fur of the Wild Cat; their intensity and arrangement is variable, changing by season, habitat and altitude. The ground colours are the grey, grey-brown or ochreous-brown with greyish shade. The dark markings of the head are the 2–2 dark stripes running evenly tapering from the eyes and the mid of the muzzles towards the neck, and the 4 wavy or zigzagged dark stripes of the forehead, of which the two lateral ones may extend stepwise broadened towards the shoulder-blades. The chin and the surroundings of the lips are whitish; there might be a small, irregularly shaped white patch on the throat. The dorsum has a long, dark stripe running from the shoulder blade to the rump along the backbone, often with cross-stripes directing towards the ventral side; these stripes may be partly or fully obsolete in the longer and denser winter fur. This dark dorsal stripe most often does not extend onto the tail; when it does, only a thin line represents it. The rump has no spots; it is marked only by cross-stripes. The breast and the ventral side are pale, usually light ochreous-brownish, sometimes with reddish shade; it is marbled or weakly spotted. The inner sides of the legs are also pale, while the outer sides are dark greyish, sometimes with obsolescent darker stripes. The tail is ringed; the basal dark rings are rather indistinct and incomplete while there are two strong and fully closed dark rings nearby the tip of the tail; the tip is always obtusely rounded and black(ish).

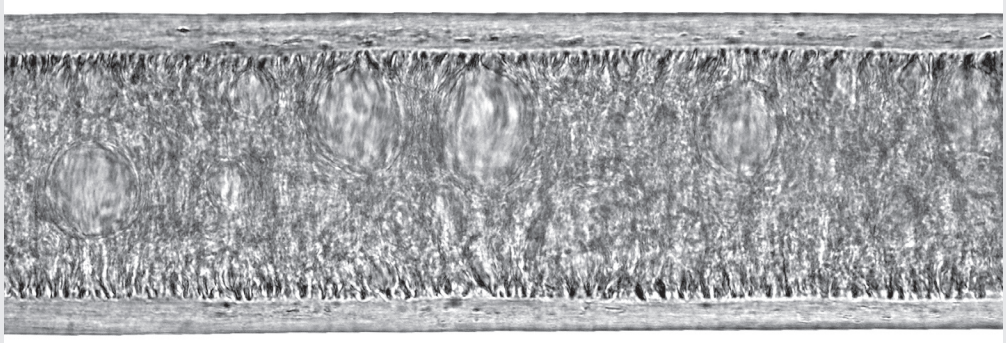
HAIR, MACROSCOPIC: The GH may be unicolorous, bicolorate, and one- or two-banded. The one-banded GH has a variably long ochreous or reddish band in the mid-section of the stem; the length of the band can be very short or, just oppositely, ca. one-third of the entire length of the hair. The two-banded GH1 represents the most typical specific feature of the Wild cat. The GH1 has long white shaft takes ca. 1/3 of the full length of the stem; the band of the proximal shield is dark brown, while the band of the distal shield is white, sometimes with reddish shade; the demarcation is clear between the bands. The tip is long and slightly curved, black or dark brown.

HAIR, MICROSCOPIC: The medullar air sacs of the proximal shield are usually rounded; the larger ones often span the entire width of the medulla.

SIZE: l_{max} = 50 mm; d_{max} = 120 μ; m/d_x = 0.75

REMARKS: The hybridisation of the Wild Cat with the Domestic Cat (*Felis catus*) is a long process showing an unfortunately increasing tendency. This process is associated with the reduction of the natural habitats of the Wild cat and the rapidly growing overlap between the original "wild" biotopes and the built environment. The external morphological character set of the Wild Cat was summarised by RAGNI and POSSENTI (1996) and BALLESTEROS-DUPERÓN *et al.* (2014); the proper identification often requires cranial morphometric and genetic studies, due to the great phenotypical variation of the two cat species and their hybridisation.

1



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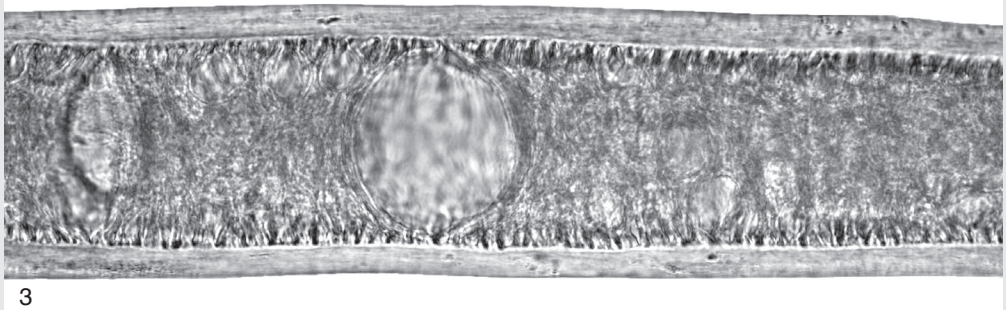


3

Felis silvestris: 1 = cross-section, shield, SEM; 2 = medulla, distal shield; 3 = medulla, proximal shield

7.7. Ungulata: Artiodactyla & Perissodactyla

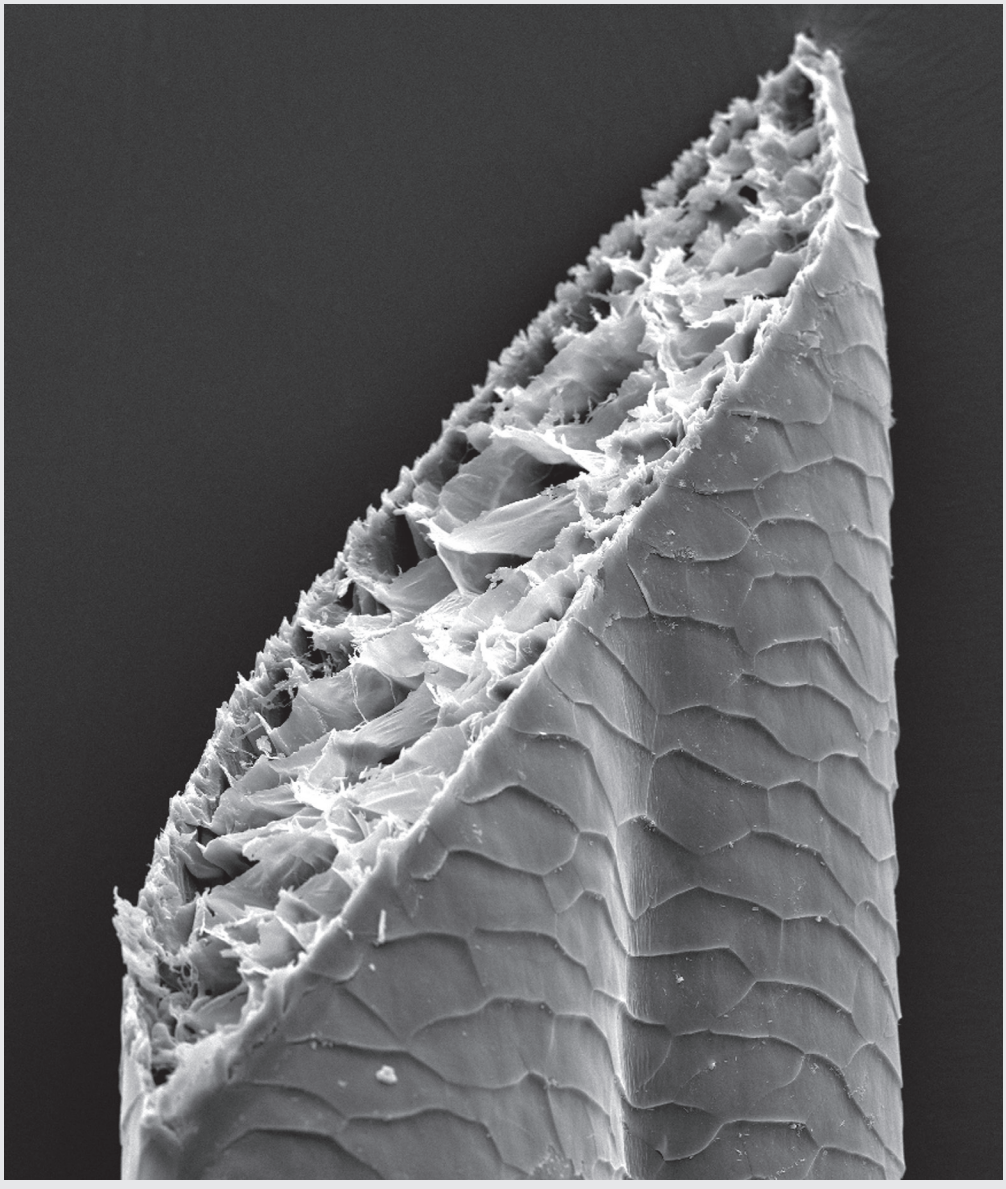
FUR: The ungulates cannot be characterised by universal fur characters, and only certain large groups have easily recognisable diagnostic features. The ground colour of the fur is usually brown, grey or reddish, with a wide range of shades. The dorsum is most often unicolorous, grizzled, marbled or, rarely, mottled. There are species having only sparse and coarse fur, while others possess dense, fine fur; the males might have mane.

HAIR, MACROSCOPIC: The different types of guard hairs are often similar; the size, the air content, and the thickness usually change seasonally. In the Central European taxa, the GH1 is usually unicolorous; the GH2 might be unicolorous, bicolorate or banded. The shape of the hairs is mostly undulating, but rarely, might be straight, or wavy. The shape of UH is variable: wavy, undulating or crispy.

HAIR, MICROSCOPIC: The most common and, at the same time, taxonomic, characters are certain microscopic features of the hair: the meshed mosaic cuticula; the spongoid multiserial medulla; the bottle-neck-shaped base; and the undulating shape.

SIZE: The variation of the medullary index is considerable within the Ungulata: $0.45 \leq m/d \leq 1$.

TAXONOMIC CHARACTERS: the meshed mosaic cuticula; the spongoid multiserial medulla; the bottle-neck-shaped base; and the undulating shape. There are few exceptions (like the Suidae family, or the *Bison* genus).



Ungulata: cross-section, cuticula, shaft, SEM

7.7.1. Artiodactyla
Suidae

The fur is mostly coarse, strong; the ground colours are dark brown, grey-brown and red-brown. The dorsum is mostly grizzled, unicolorous or/and marbled. The macro- and microstructure of hairs of Suidae show certain features being exceptional among the Ungulates.

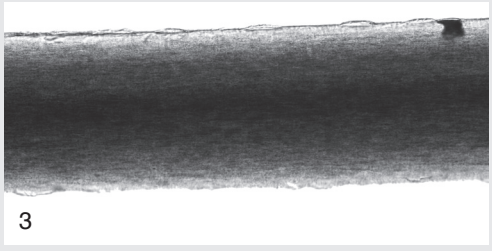
Sus scrofa

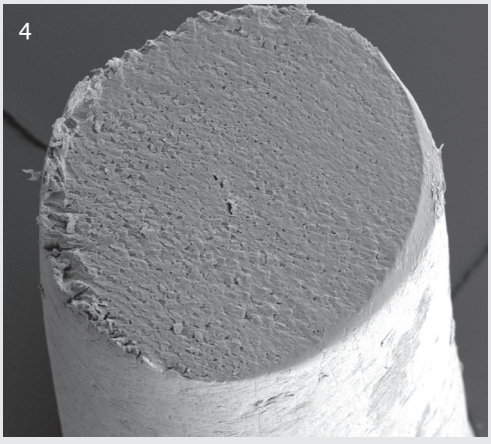
FUR: The fur is long-haired and rather coarse; the inner surfaces of the ears and the parotid region have finer fur covering. The fur of the breast and the belly is remarkably shorter than the dorsal fur but is still long and similarly coarse. Dark, long bristle hairs cover the edge of ears. There is a denser and longer, erectable "mane"-like crest of GH0 hairs on the shoulder blades, the nape and along the backbone, which has a protecting and frightening function. The elder specimens turn into grey, especially the muzzle, the front, the throat and the shoulder blades become ochreous-greyish grizzled. The legs, the lips and the chin are often black(ish). The short tail ends in a loose tuft.

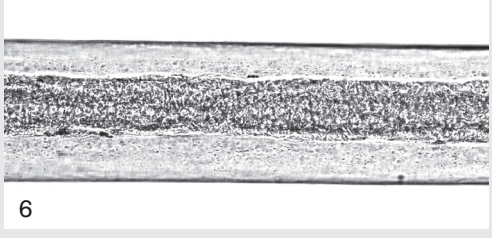
HAIR, MACROSCOPIC: All types of hairs are rigid. The GH0 is straight and might be extremely long. The guard hairs are dark brown, reddish-brown or black, unicolorous or polychrome, and sometimes become stepwise faded towards the tip. The tip of the hair is splitted; this feature is easily recognisable by the naked eye. The UH is crispy, reddish or dark brown; the underhairs are denser in certain parts of the body like the belly or the nape, while they occur sparsely along the middle of the dorsum and in the mane.

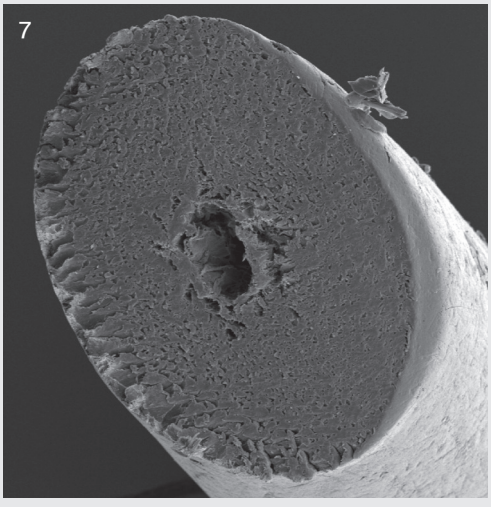
HAIR, MICROSCOPIC: The basal part of the GH is short and thick, tubular. The cuticular pattern on the basal part and the shaft can be irregular, transversal, narrow petal or figureless with crenated edges; it is close, figureless waved or sketched, with rippled edges from the distal shaft to the distal shield. The cuticular scales are usually absent or demolished on the apical section and the cortical fibres may be disrupted. The medulla is amorphous or fragmented tubular along the full length of the hair; it is very thin at the maximum width of the shield and there might be larger air sacs between the fragments. In certain sections of the hair, the medulla may be fully reduced, and inserted by cortical fibres. The structure of the medulla is often hardly visible due to the dense and dark, black to dark brown, pigmentation. The cross-section is oblong or circular.

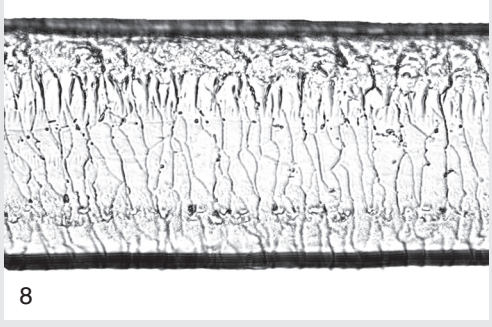
SIZE: l_{max} = 110 mm; l_{max_mane} = 180 mm; d_{max} = 400 µ; m/d_x = 0.5

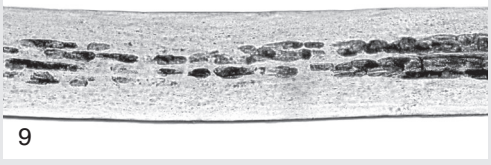












Sus scrofa: 1 = cuticula, apical section; 2 = cortex ont he apical section; 3 = medulla, shield; 4 = cross-section, distal shield, SEM; 5 = cuticula, shield; 6 = medulla, transit and proximal shield; 7 = cross-section, proximal shield, SEM; 8 = cuticula, shaft; 9 = medulla, shaft

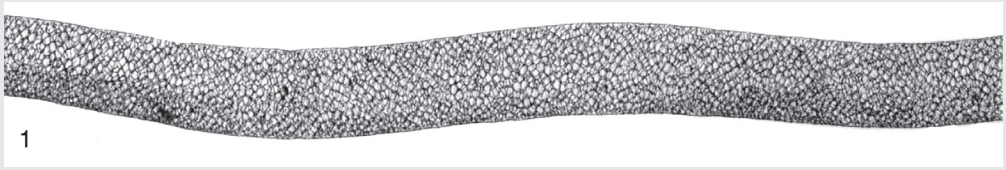
Cervidae & Bovidae

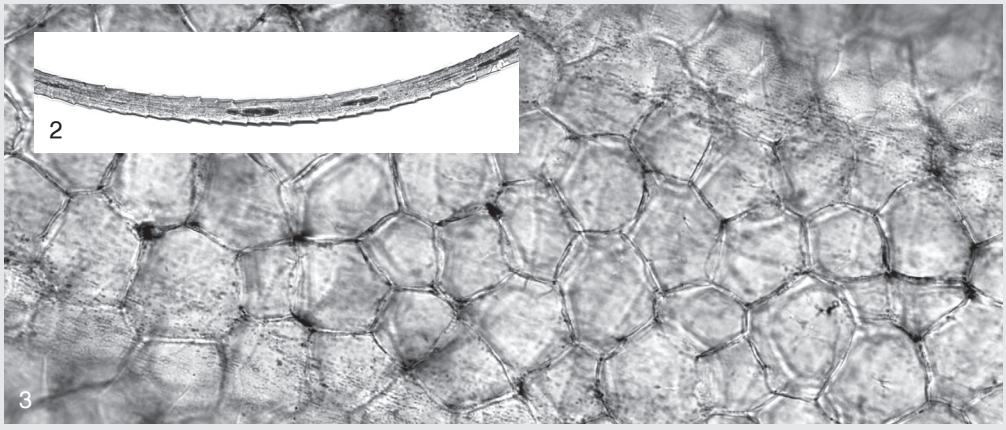
FUR: The fur is coarse and slightly greasy in touch; the ground colour is brown with variable shades. The dorsum is unicolorous, grizzled, mottled or slightly marbled; there are species with masked face and/or contoured rump. The identification of the ruminants is always difficult due to their partially overlapping quantitative and qualitative features, the considerable sexual and seasonal variation, and the different characters of the hairs originating from the different parts of the body. Thus, the species-level separation of the different taxa is often dubious; sometimes, even the generic-level identification is problematic. Melanistic and leucistic animals occur relatively frequently but the albinistic ones are very rare.

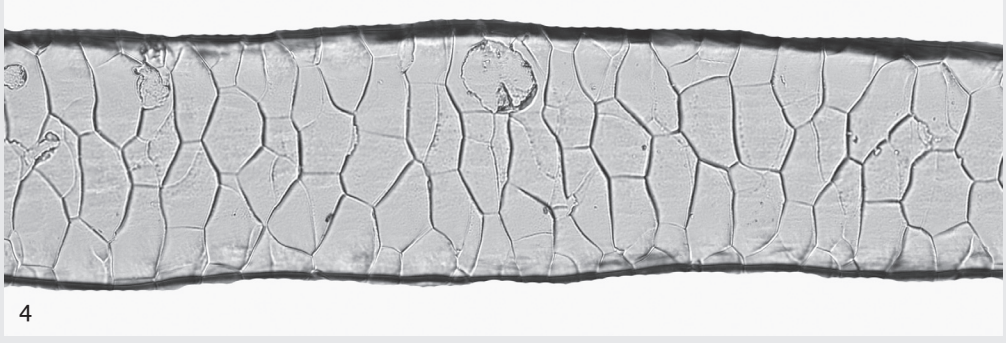
HAIR, MACROSCOPIC: The hairs are usually fragile; their shape is most often undulating, except the tapering basal and apical sections. The hair is thinner and less undulate in summer than in winter. The GH1 is thicker, more undulating than the GH2. The GH on the ventral and lateral sides of the body is unicolorous. The GH most often banded; the band is very short. The tip is most often abruptly tapering, long. The UH is crispy or undulate.

HAIR, MICROSCOPIC: The GH of the Cervidae and Bovidae shows similar macro- and microstructure. The bulb is knobby. The basal part is most often bottleneck-shaped but the GH2 type hairs might have tubular type. The cuticular pattern of GH is meshed mosaic on the shaft and sometimes on the shield; figureless, irregularly waved or sketched on the apical part. The surface of the scales is often scratched. The medulla is spongoid multiserial on shaft, the transit and the proximal shield; porous tubular or foamy multiserial on the distal shield; porous, colonnade or fragmented tubular on the apical section. The shape and size of the medullar cells and the ultrastructures of the septums within and between the cells are strongly variable. The medullar cells are usually larger on the shaft, the transit and proximal shield, their shape is rounded or isodiametric; smaller, polygonal, transversally elongated on the distal shield. The medullar cells arrange in more or less regular rows; the number of the rows and the size of the cells may vary seasonally and may exceed 10 in the shield. The cortex is most often rather thin on the transit and proximal shield. The pigments arrange usually diffusely and concentrate in the medulla. The tip is mostly gradually tapering, but can be abruptly one and long. The medulla of the UH hair is fragmented or absent; the cuticular pattern of UH is rhomboidal or mosaic. The cross-section is variable along the stem due to the constrictions and flat sections of the undulate hair; it is most often circular and oblong, but the distal shield of GH2 may be slightly biconcave, biconvex or concave-convex.

SIZE: The medullary index shows high variability, which depends on the species and changes often seasonally: $m/d_x = 0.45–0.95$.







Cervidae & **Bovidae**: 1 = shape of hair and medulla; 2 = UH: medulla, shape; 3 = medulla, shaft and shield; 4 = cuticula, shaft; 5 = basal section; 6 = basal section

Cervidae

HAIR, MICROSCOPIC: The cuticular pattern is meshed, most often transversal polygonal mosaic on the proximal shaft.

REMARKS: Silky, shiny, short hairs, named the velvet, which protects the ossifying surface of the antler, cover the annually developed, young antlers. The stags fray the antlers against branches and tree trunks to remove the velvet from their matured antlers before the mating season. The macro- and microstructure of these hairs differs from those of the other hairs of the body. Their shape do not undulate but wavy or straight; the mosaic scales are arranged into 4–5 layers and wear off during the scratching; the cortex is thicker; the medulla is not foamy or spongoid but chambered multiserial (WOODS *et al*. 2011).

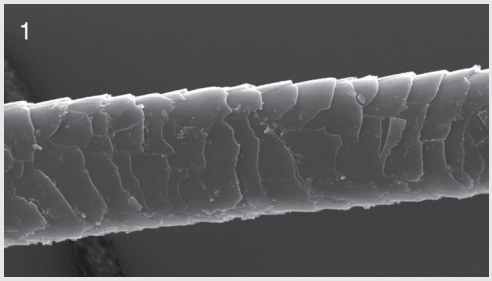
Capreolus capreolus

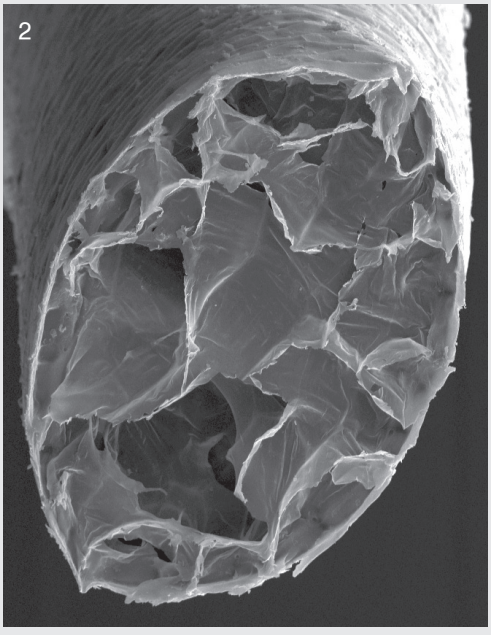
FUR: The dorsum is unicolorous, fawn in summer while grizzled, silver greyish or greyish-brown in winter. The upper limb and the nose are black, the lower limb and the chin are white or paler grey. The front is usually paler greyish-brown. The belly and the rump are white(ish); the shape of the white undertail is narrow, oval-shaped in the buck, while it is heart-shaped in the doe. The inner sides of the legs are white or pale ochreous-whitish in all seasons. The short tail tuft is pale rufous or ochreous-brown.

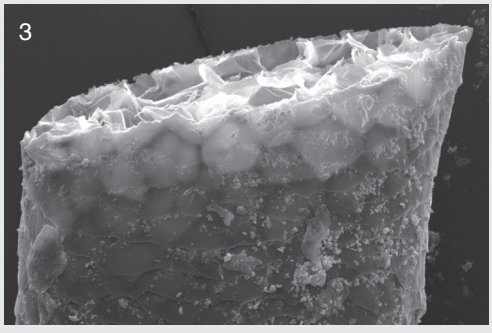
HAIR, MACROSCOPIC: The GH hairs are banded, the winter hair is one- or two-banded, the long shaft is greyish or grey-brown; in the two-banded hairs, the longer black band is located on the proximal shield while the short rufous or ochreous band can be seen on the distal shield. The tip is always black; it is shorter in the summer, and longer and abruptly tapering in the winter.

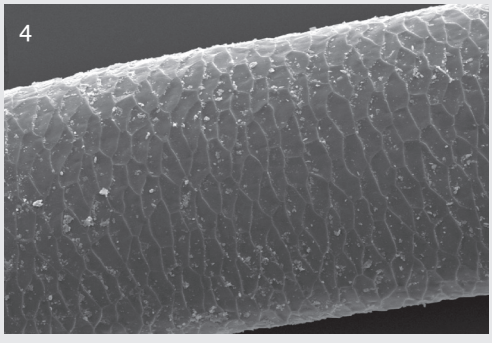
HAIR, MICROSCOPIC: The cuticular pattern is meshed, transversal polygonal mosaic on the shaft. The number of the rows of medullar cells may exceed 10 at the maximum width of the shield and/or winter.

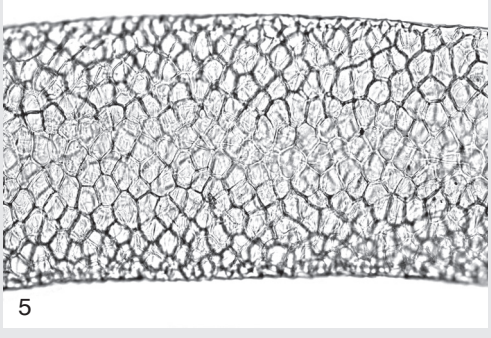
SIZE: l_{max_summer} = 35 mm, l_{max_winter} = 40 mm; d_{max_summer} = 140 μ; d_{max_winter} = 380 μ; m/d_x = 0.85

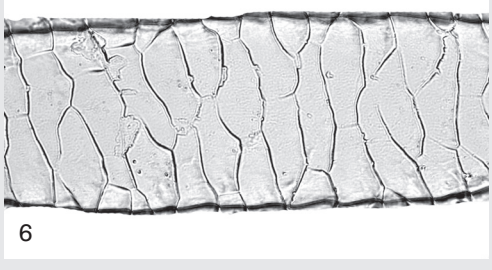


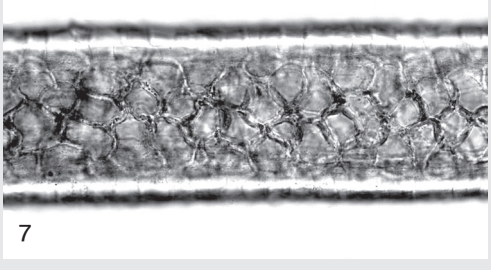












Capreolus capreolus: 1 = cuticula, apical section, SEM; 2 = cross-section, shield, SEM; 3 = idem; 4 = cuticula, shield, SEM; 5 = medulla, shield; 6 = cuticula, shaft; 7 = medulla, proximal shaft

Cervus elaphus

FUR: The summer fur is most often red-brown; the winter fur is more dense and greyish-brown shaded. The muzzles and the neck are pale greyish. The stags have a shaggy mane running from the nape around the neck down to the chest. The ventral side is paler, cream-coloured, with stepwise transition between the darker dorsum towards the paler belly. The rump is creamy or white; the colouration of the undertail and the short tail is somewhat more vivid than that of the dorsum, usually brown, ochreous-brown or rufous-brown.

HAIR, MACROSCOPIC: The GH1 is unicolorous or polychrome, greyish-brown; one narrow band may appear on the shield. The winter GH hair is considerably longer (plus 1.5–2 cm on average). GH 2 is banded: the lower section of the shaft is pale grey, which turns gradually to dark grey or brown towards the rufous or ochreous-brown band of the shield. The tip is always black or dark brown.

HAIR, MICROSCOPIC: The cuticular pattern is meshed, isodiametric mosaic on the shaft. The number of the rows of medullar cells may reach 15 at the maximum width of the shield.

SIZE: l_{max_summer} = 60 mm; l_{max_winter} = 80 mm; d_{max_summer} = 160–280μ; d_{max_winter} = 450 μ; m/d_x = 0.95

Cervus nippon

The Sika deer is native in East Asia, and it was introduced as game animal to several countries of the World. There are small, isolated populations in Central Europe.

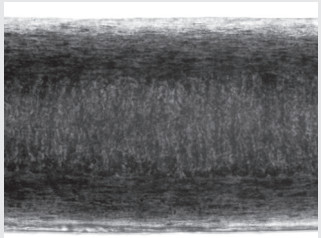
FUR: The ground colour of the fur is dark brown; the muzzle is grey or brown. The inner side of the ear is whitish-haired, that of the outer side is grey. The throat, the belly and the inner sides of the legs are pale, whitish-greyish. The stags have a short but dense mane around the neck. The dorsum of the summer fur varies from rufous to chestnut-brown, with mottled pattern: there are several medium-sized white spots on the dorsal side. The dorsum of the winter fur is dark grey-brown with blurred and faded light spots. The black dorsal stripe is running along the backbone from the shoulder blades to the rump. The flattened, terminally pointed tail is white, with a fine black mid-dorsal stripe; the rump and the undertail are white.

HAIR, MACROSCOPIC: The GH hairs are unicolorous or banded; the band is narrow (1–2 mm wide), white or whitish and located on the apical section, close to the tip.

HAIR, MICROSCOPIC: The cuticular pattern is meshed, isodiametric mosaic on the shaft. The number of row of medullar cells usually does not exceed 10 at the widest part of the shield.

SIZE: l_{max} = 75 mm; d_{max} = 240 μ; m/d_x = 0.9

1



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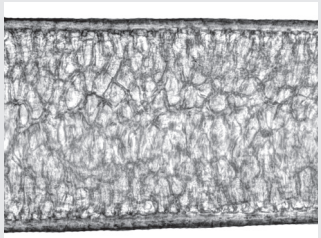

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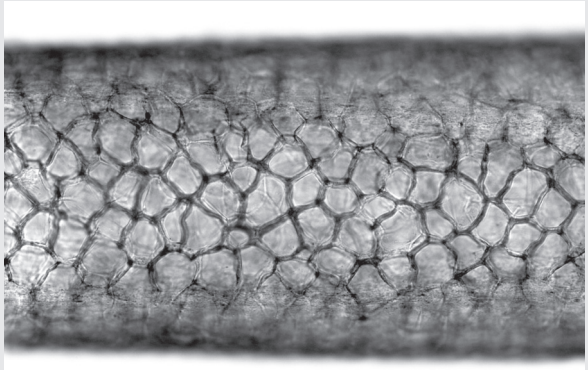

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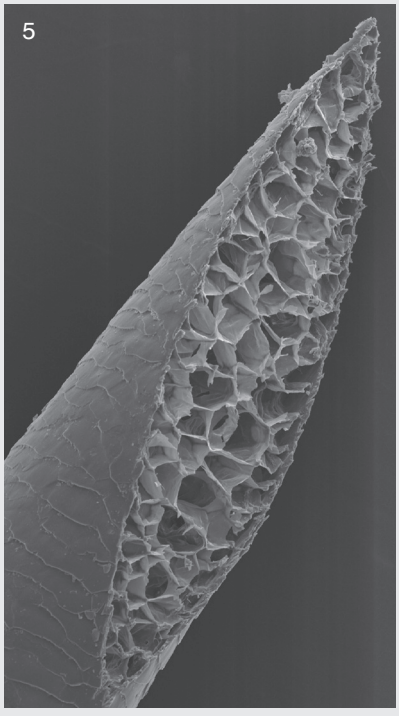

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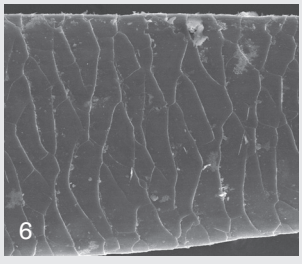

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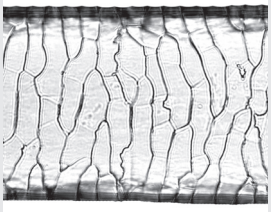

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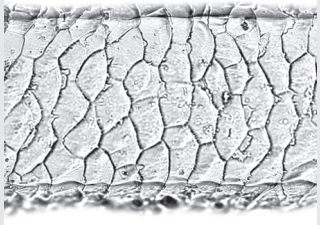

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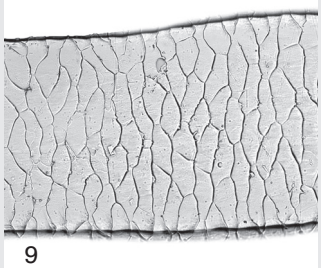

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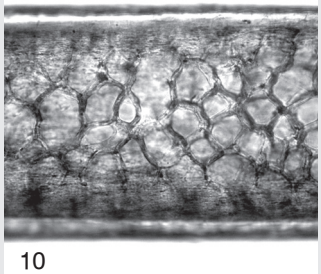


10

***Cervus* spp.**: 1 = cuticula, apical section; 2 = medulla, distal shield; medulla, proximal shield; 4 = medulla, transit; 5 = longitudinal-section, shield, SEM; 6 = cuticula, shield, SEM; 7 = idem; 8 = cuticula, proximal shaft; 9 = cuticula, distal shaft; 10 = medulla, shaft

Dama dama

The Fallow deer is native in the West Palearctic; it was introduced as game animal to several countries of the World.

FUR: The ground colour of the fur is dark brown; the front is dark grey or brown, the muzzle is reddish-brown or greyish-brown. The inner side of the ear is whitish-haired, that of the outer side is grey. The throat, the belly and the inner sides of the legs are white or whitish. The crown of the head and the shoulder blades, often the cranial part of the backside, are brown of variable shades and unicolorous or spotted with pale light spots. The dorsum of the summer fur is rather rufous shaded and mottled by several small white spots on the back and dorso-laterally; a variably strongly developed white lateral stripe is visible. The dorsum of the winter fur is dark grey-brown, the lateral sides are more coffee-brown shaded; the white spots being characteristic of the summer fur are missing or strongly blurred. The white contoured black dorsal stripe running along the backbone extends from the shoulder blade to the rump. The dorsal side of the flattened and terminally pointed tail is black with white margins; the tip of the tail is brush-like due to the long guard hairs; the rump is black, the undertail is white. The white and the melanistic specimens are very rare.

HAIR, MACROSCOPIC: The GH are heterogeneous in colouration, they can be unicolorous (brown, white or dark grey), polychrome or banded; the band is ochreous-brown, the tip of the hair is dark brown or black, the shaft is rufous-reddish.

HAIR, MICROSCOPIC: The cuticular pattern is meshed, transversal polygonal mosaic on the shaft. The number of the rows of medullar cells may be up to 15 at the maximum width.

SIZE: l_{max} = 56 mm; d_{max} = 355 μ; m/d_x = 0.9

Odocoileus virginianus

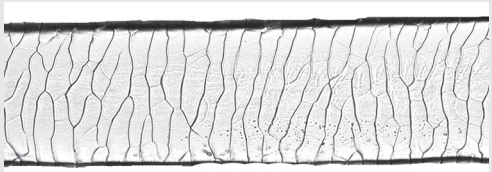
The White-tailed deer is native in America; it was introduced to a few European countries as game animal.

FUR: The ground colour of the fur is unicolorous chestnut-brown. The summer fur is more reddish or yellowish-brown shaded; the mid-dorsum is somewhat darker. The winter coat is greyish or pale-brown. White bands surround the nose and the eyes; the cheek is white, the throat usually has white, quadrangular patch. The dorsum of the long tail is dark brown with white edges; the undertail and the ventral side of the tail are white; the inner sides of the legs and the belly are also white.

HAIR, MACROSCOPIC: GH1 is banded; the colour of the band is reddish and is on the distal shield; the shaft and the transit are reddish-brown, paler greyish on the base and darker on the shield. The GH2 is bicoloured; the shaft is pale greyish, the tip is black.

HAIR, MICROSCOPIC: The cuticular pattern is meshed, isodiametric mosaic on the shaft. The number of the rows of medullar cells can exceeds 10 at the maximum width of the shield. The thick medulla and the thin cortex are pigmented densely and evenly.

SIZE: l_{max} = 50 mm; d_{max_summer} = 160 μ; m/d_{x_summer} = 0.75 ; d_{max_winter} = 350 μ; m/d_x = 0.9



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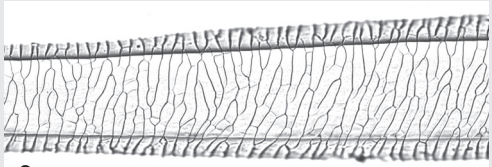

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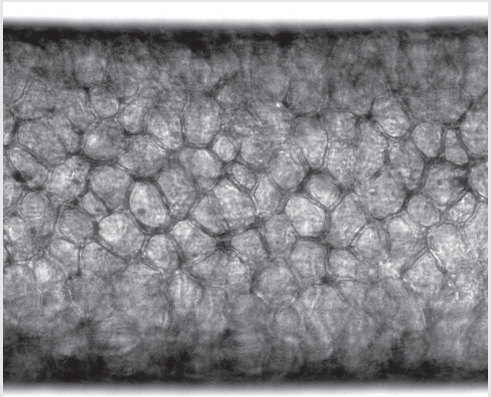

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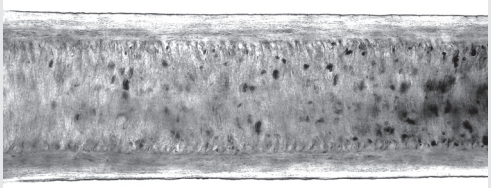

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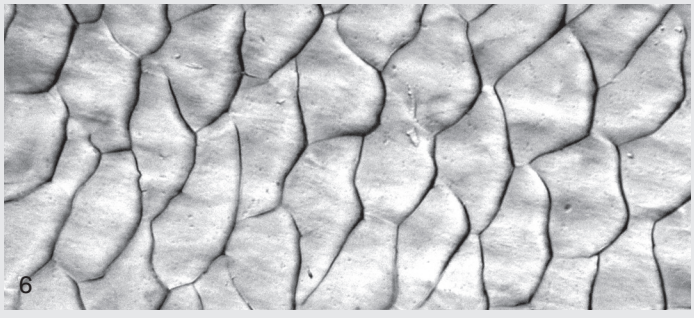

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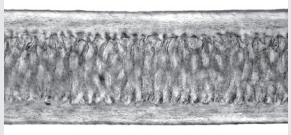

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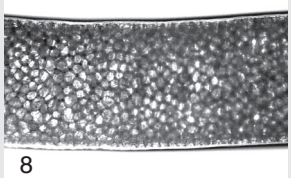

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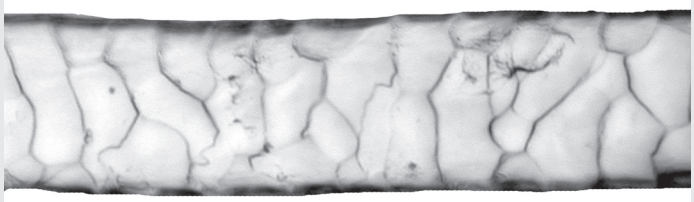

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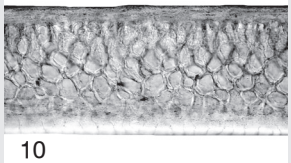


10

Dama dama: 1 = cuticula, shield; 2 = medulla, shield; 3 = cuticula, shaft; ***Odocoileus virginianus***: 4 = cuticula, shield; 5 = medulla, distal shield; 6 = cuticula, distal shaft and transit; 7 = medulla, proximal shield; 8 = medulla, shaft; 9 = cuticula, basal and proximal shaft; 10 = medulla, proximal shaft

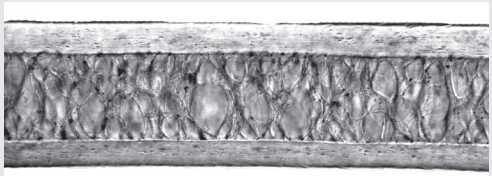
Alces alces

FUR: The fur is unicolorous; its ground colour is dark chocolate-brown, deep red-brown or even black; the legs, sometimes only the shanks, are paler coloured, whitish, greyish or pale brown. A characteristic feature of the moose is the bell (or throat beard), a skin lobe covered by hairs. The dorsum has an irregularly shaped, reddish-brown or ochreous-brown, marbled patch extending from the crown of head to the shoulder blades, sometimes even to the rump. The breast and the belly are paler coloured, greyish or grey-brown. There is no distinct whitish undertail but the hinds may have a thin white ring around the vulva.

HAIR, MACROSCOPIC: The ground colour of the hairs is grey, brown, cream-coloured, and more rarely whitish. The dark hairs are usually banded, the position, length and colour of the band are variable; it can be black in the winter fur, and pale ochreous-brownish in the summer hairs. The tip is black.

HAIR, MICROSCOPIC: The cuticular pattern is meshed, isodiametric mosaic on the shaft. There might be large, rounded or cask-shaped air sacs, which fill up the entire diameter of the hair on the distal shield and apical section. The number of the rows of medullar cells often usually 15 at the maximum width of the shield.

SIZE: l_{max} = 110 mm; l_{max_mane} = 250 mm; d_{max} = 500 μ; m/d_x = 0.95



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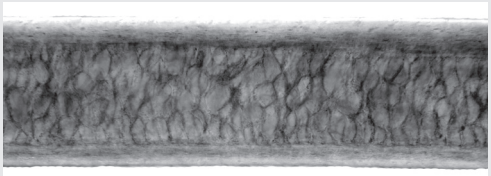

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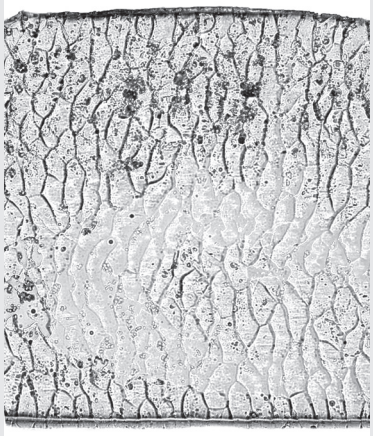

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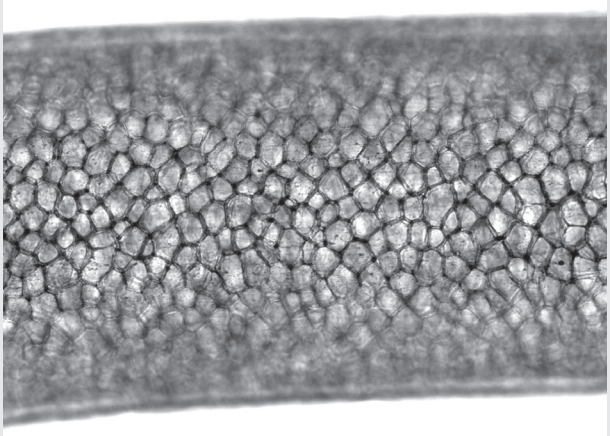

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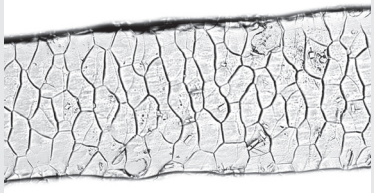

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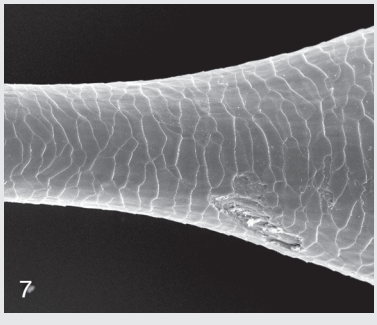

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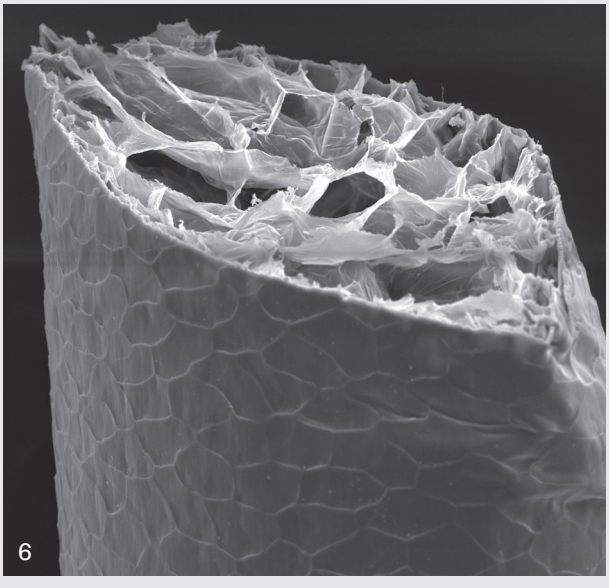


6

Alces alces: 1 = medulla, apical section; 2 = medulla, distal shield; 3 = cuticula, shield; 4 = medulla, proximal shield and transit; 5 = cuticula, shaft; 6 = cross-section, shaft, SEM; 7 = basal section, SEM

Bovidae

HAIR, MICROSCOPIC: The cuticular pattern is meshed, most often isodiametric mosaic on the proximal shaft.

Bison bonasus

FUR: The fur is dense and coarse, woolly and shaggy; unicolorous or partly marbled; the ground colour is dark brown; the head, chest, belly and flanks are darker shaded; the head and the mane might be reddish; the winter coat turns to tan. The forepart of the body is much more robust which is emphasized also by the characteristic "bison mane": bundles of long hairs grow on the forefeet, breast, throat, and chin. A thick patch of shorter, very dense hairs on the bull's forehead helps to protect the head against the hard attack of the competitor bulls. There are dense, long hairs covering the hump between the shoulders; the hairs are remarkably shorter on the back, rump and flanks. The bushy tail has long unicolorous, dark brown hairs.

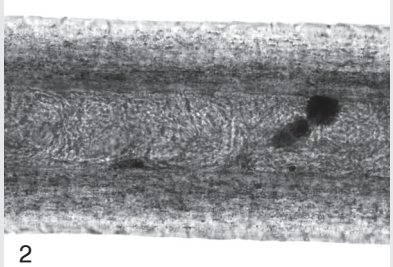
HAIR, MACROSCOPIC: The GH hairs are straight or wavy, unicolorate brownish or reddish.

HAIR, MICROSCOPIC: The cuticular pattern is meshed, isodiametric mosaic on the shaft. The position of the medulla is asymmetrical in most parts of the hair. The medulla is fragmented or globulose tubular on the shaft and the apical sections; porous tubular on the proximal, colonnade tubular on the distal shield and apical section, where, there large, rounded or cask-shaped air sacs which fill up the entire diameter of the distal part of the hair. The margin of the medulla is generally straight. The pigments arrange densely, diffusely in the medulla, and arrange into longitudinal rows in the cortex.

SIZE: l_{max} = 55 mm; l_{max_mane} = 280 mm; d_{max} = 115 μ; m/d_x = 0.45

TAXONOMIC CHARACTER: the porous and colonnade tubular medulla on the shield is an autapomorphy of the genus *Bison*.

1



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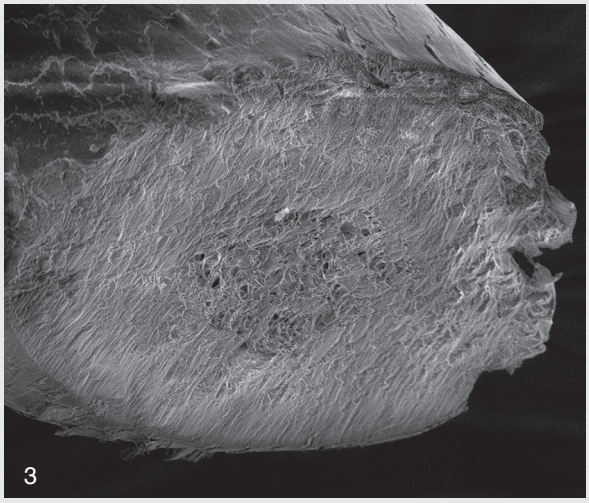

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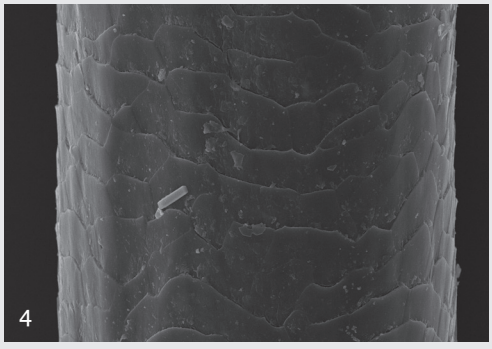

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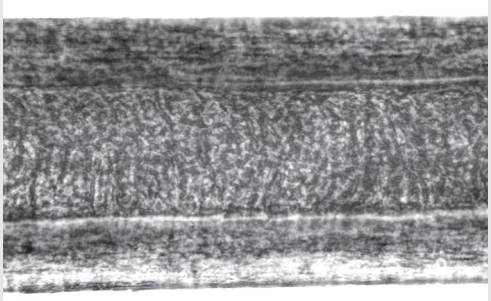

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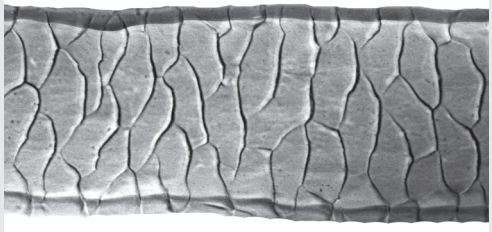

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Bison bonasus: 1 = medulla, apical section; 2 = medulla, distal shield; 3 = cross-section, distal shield, SEM; 4 = cuticula, shield, SEM; 5 = medulla, proximal shield; 6 = cuticula, shaft; 7 = cuticula, transit

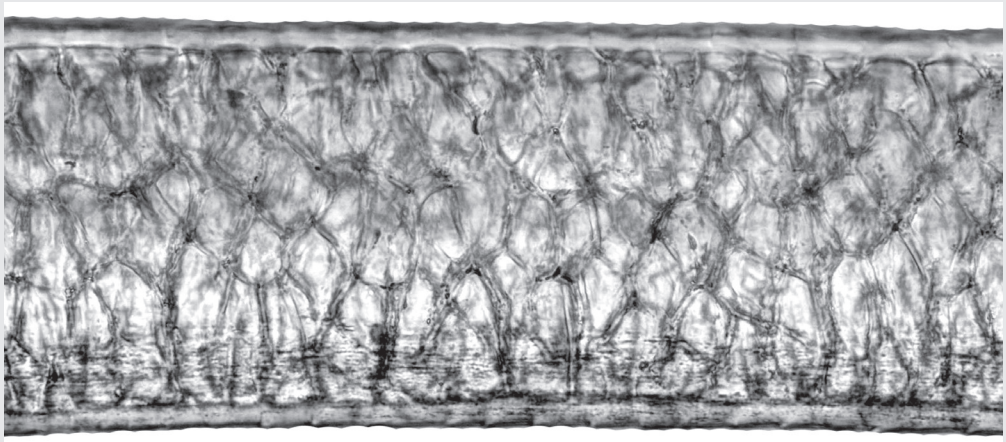
Capra ibex

FUR: The fur is coarse and dense; the dorsum is greyish-brown or hazel and marbled in the summer fur; it is darker and more homogeneous in the winter fur, marbled or unicolorous coffee-brown or chestnut-brown. The lateral side of the body has a blurred ochreous-brown stripe (darker, often black in the young animals), separating the darker dorsal and the paler, usually whitish ventral side. The muzzle, the throat and the neck are similarly coloured but slightly lighter in shade while they are dark grey-brown in the old bucks; the ear is white-haired inside and rufous or brownish on the outer surface. The sexual characteristics of the bucks are the short-haired mane on the neck, the short and loose beard on the chin and the dark stripe along the backbone. The shanks are dark brown outside and white inside. The dorsal side of the short tail is dark, with loose and long-haired terminal tuft; the ventral side of the tail and the undertail are white.

HAIR, MACROSCOPIC: The GH1 is unicolorous brown, less undulating; the GH2 is bicolorate, appearing in two different forms: one has a white shaft and brown or red-brown shield, the other is almost fully white, with a short dark brown apical section only.

HAIR, MICROSCOPIC: The cuticular pattern is meshed, transversal polygonal mosaic on the shaft. The number of row of medullar cells usually does not exceed 10 at the widest part of the shield.

SIZE: l_{max} = 45 mm; l_{max_mane} = 75 mm; d_{max} = 140 μ; m/d_x = 0.85



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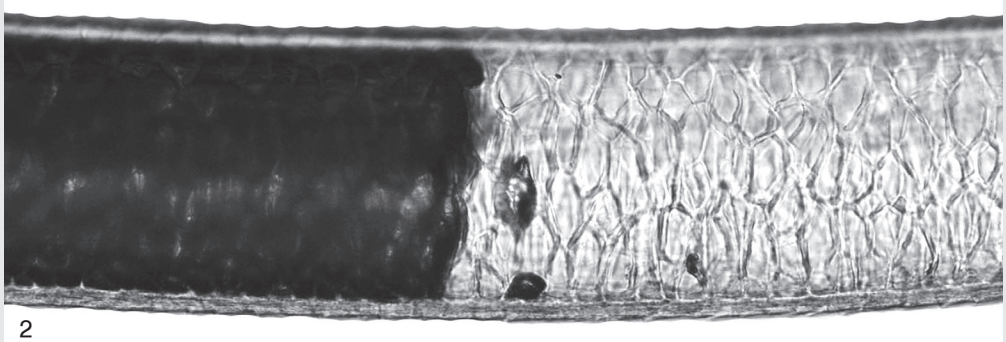

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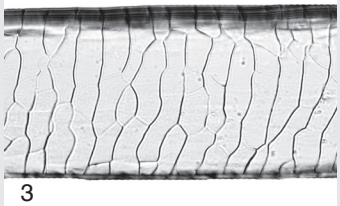

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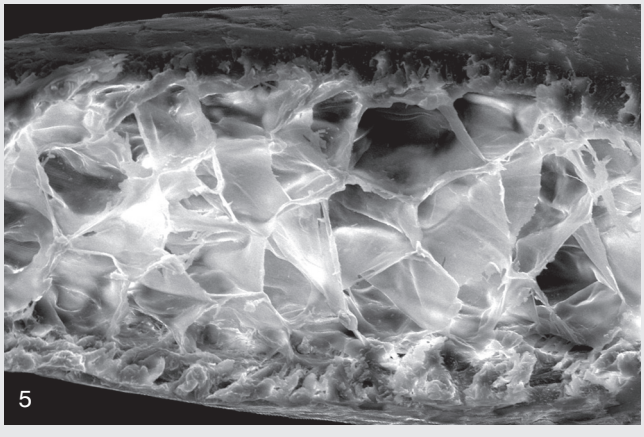

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Capra ibex: 1 = medulla, shield; 2 = medulla, transit; 3 = cuticula, shield; 4 = cuticula, shaft; 5 = cross-section, septae, shield, SEM

Rupicapra rupicapra

FUR: The fur is unicolorous or slightly grizzled, marbled; the summer fur is short-haired, reddish-brown, while the winter fur is denser and long-haired, dark chocolate-brown. The face of the chamois is masked by a broad dark-brown to black stripe running from the nose and the angle of the mouth through the eyes to the parotid area, which is contoured by the pale (white or ochreous-greyish) front and the ridge or the nose; the eyebrows are cream-coloured. The lips, the chin, the lower parts of the muzzle and the throat are white; the inner surfaces of the ears are white-haired. The legs are dark brown or black(ish). The belly is always paler, ochreous or pale rufous in the summer and almost clear white in the winter. The short tail is flattened and black. The undertail is whitish or creamy, oval-shaped.

HAIR, MACROSCOPIC: The GH1 is unicolorous or polychrome, dark brown, greyish or black with dark brown or white tip. The GH2 might be polychrome or one-banded; the shaft is always grey-brown, grey or dirty whitish while the shield is rufous in the summer and dark brown or black in the winter; the band is dark brown or ochreous-brown. The tip is short, white, ochreous-white or dark brown.

HAIR, MICROSCOPIC: The cuticular pattern is meshed, isodiametric mosaic on the shaft. The number of row of medullar cells usually does not exceed 10 at the widest part of the shield.

SIZE: l_{max_summer} = 90 mm; $l_{max\_mane\ \&\ winter}$ = 200 mm; d_{max} = 200 μ; m/d_x = 0.9

REMARKS: The mane of the chamois, which is called by the hunters as "gamsbart", "chamois beard" or "goatee", is long-haired, black or blackish and runs from the neck and/or the shoulder blades to the rump. This is well-known trophy of the chamois hunters, which is used for the decoration of the hunters' hats.

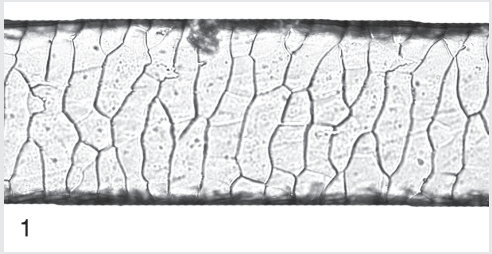
Ovis orientalis

FUR: The fur is greasy and rather elastic in touch; its ground colour is shining dark brown. The dorsum is unicolorous red-brown in the summer fur, more vivid coloured and marbled, mottled in winter, usually chestnut-brown with rufous or coffee-brown shade. The muzzles, the lips and the throat are light coloured, whitish, greyish or cream-coloured; the inner hairs of the ears and the surrounding of the nose and the eyes are most often white. The short but often rather broad, black dorsal stripe is running from the nape to the middle of the back, followed by a larger whitish-greyish dorso-lateral back-patch on the waist, which is typical of the mature animals. The beard (or brisket ruff) on the chest of the ram is blackish. The dorsal side of the tail is brown or black; the rump and the undertail are white. The belly is always lighter, usually whitish and is separated along a sharp line from the dark dorsal side.

HAIR, MACROSCOPIC: The GH hairs are polychrome or banded. The shaft is grey-white, which turns gradually into dark brown or black towards the tip; the distal band is white or ochreous-brown. The tip is long, and most often black.

HAIR, MICROSCOPIC: The cuticular pattern is meshed, isodiametric mosaic on the shaft. The number of row of medullar cells usually does not exceed 10 at the widest part of the shield.

SIZE: l_{max} = 60 mm; d_{max} = 260 μ; m/d = 0.95



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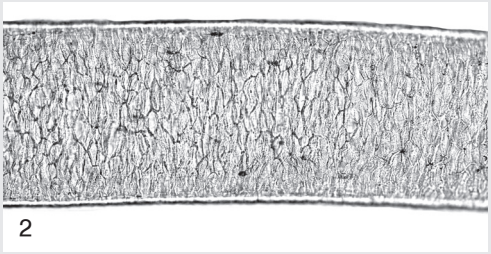

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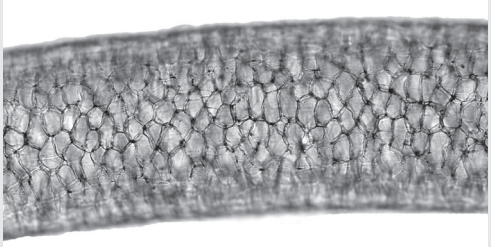

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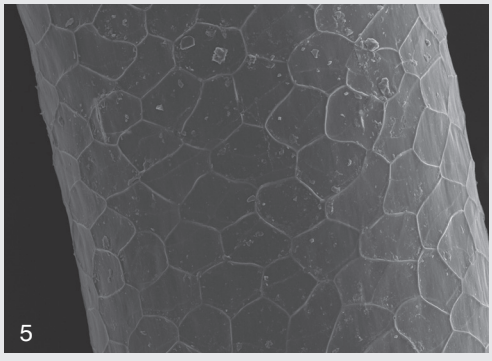

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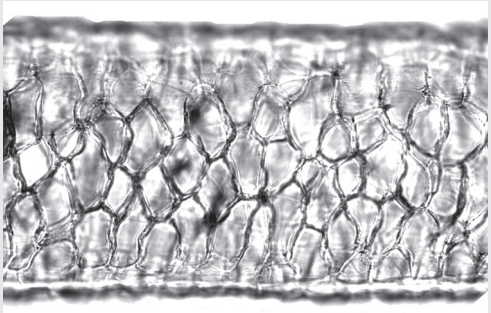

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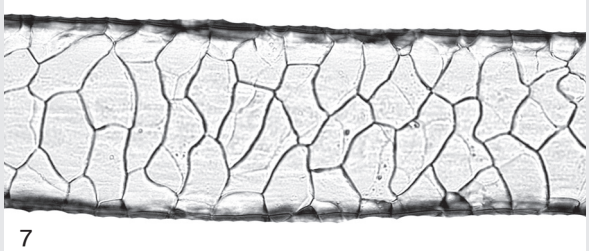

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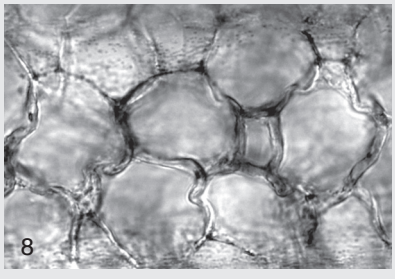


8

Rupicapra rupicapra & ***Ovis orientalis***: 1 = cuticula, shield; 2 = medulla, distal shield; 3 = cuticula, transit; 4 = medulla, proximal shield and transit; 5 = cuticula, shaft, SEM; 6 = medulla, shaft; 7 = cuticula, proximal shaft; 8 = medulla, septae, proximal shaft

7.7.2. Perissodactyla

Equus ferus ssp. *przewalskii*

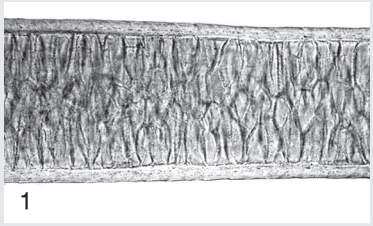
A captive, semi-feral population of this endangered subspecies lives in large grasslands of the Hortobágy National Park, Hungary.

FUR: The fur is fine, velvety; unicolorous and shining. The ground colour is pale ochreous-brown; the head and the dorsum are darker while the belly is cream-coloured or whitish, with stepwise transition between them. A narrow black dorsal stripe may run along the backbone from the neck to the base of the tail. The legs are black; several dark stripes can be present on the stifle and the pastern. The white ring around the nose usually extends to the chin and the lips. The hairs of the mane and the tail are coarse and unicolorous, black or dark brown. The erected mane is running from the forehead towards the nape; it is short-haired in the summer, longer in the winter and shaded in every spring. The base of the tail, the "dock", is short-haired and longer than in the domestic relatives (GROVES 1994); the tail is long-haired and loose.

HAIR, MACROSCOPIC: The GH and UH hairs are straight or wavy; unicolorous or polychrome, in the latter case the shaft is white and turns into red-brown towards the apical region.

HAIR, MICROSCOPIC: The bulb is knobby, the basal section is bottleneck-shaped. The cuticular pattern is meshed, transversal polygonal mosaic on the shaft; transversal, regular mosaic on the shield. The medulla is spongoid multiserial; the medullar cells are rounded, smaller, with fine internal-septae on the proximal shield, and polygonal, transversally elongated on the distal shield. The number of row of medullar cells usually does not exceed 10 at the widest part of the shield. The tip is gradually tapering, pigmented and lacks the medulla. The pigments arrange diffusely and concentrate in the medulla. The cross-section is rounded or oblong.

SIZE: l_{max} = 60 mm; l_{max_tail} = 400 mm; d_{max} = 145 μ; m/d_x = 0.75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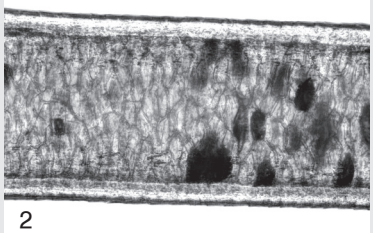
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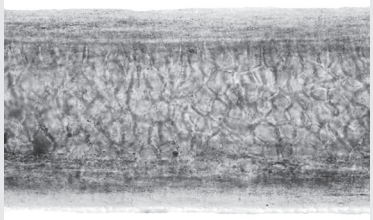
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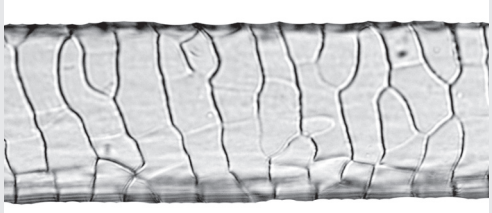
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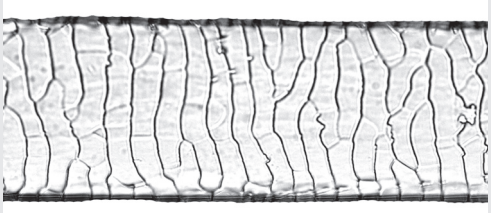
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7

Equus ferus* ssp. *przewalskii: 1 = medulla, distal shield; 2 = medulla, proximal shield; 3 = medulla, shaft; 4 = cross-section, transit, SEM; 5 = cuticula, shaft; 6 = cuticula, shield; 7 = basal section

8 Identification key for the guard hairs of the Central European mammal species

The use of the Identification key require practice in doing good preparations on hairs, the knowledge of the nomenclature of micro- and macroscopic patterns included in the book. The end points of the dichotomic key are the reliable taxonomic level.

Diagnostic characters

1 The stem is thin, flexible; tube-, cornet- or spatula-shaped: it is a hair. 2

– The stem is thick, rigid, the apex acute; spine-shaped: it is a modified hair, the spine. The cross section is circular, inside the "rose-window" pattern of septae. *Erinaceus* sp.

2 The shape of the hair is zigzag-like. It is short, fine and very thin. 3

– The shape of the hair is not zigzagged. 4

3 The cuticular pattern on the shaft is combined petal. 22 *Soricomorpha*

– The cuticular pattern on the shaft is rhomboidal or broad petal. Muridae UH

4 The shape of the GH is most often undulated. 28 Cervidae, Bovidae

– The shape of the GH is not undulated. 5

5 The shape of the hair is straight or wavy. The medullar pattern is spongoid multiserial. The basal section is bottleneck-shaped. The cuticular pattern is transversal mosaic. l_{max} = 60 mm; l_{max_tail} = 400 mm; d_{max} = 145 μ; m/d_x = 0.75 *Equus ferus* ssp. *przewalskii*

– The medulla not spongoid or absent. The basal section not bottleneck shaped. 6

6 The medulla is absent. The cuticula is coronal. The shape of the hair is straight, wavy or combined wavy. The bulb is ball-shaped. 10 Chiroptera

– The medulla is present. 7

7 The micropatterns are homomorph along the hair, usually only one or two kinds of pattern evolve. The cuticular patterns can be petal or mosaic on the shaft, the medullar pattern mostly nummiform, tubular or absent. $m/d_x \leq 0.5$ 8

– The micropatterns are heteromorph along the hair. $m/d_x \geq 0.5$ 20

8 The shape of the hair mostly wavy; it is silky, thin. The cuticular pattern can be petal, rhomboidal or mosaic. The pigmentation is sparse. The medulla is uniserial nummiform or absent. UH

– The hair is straight or curved; unicolorate or polychrome; rigid. The cuticular pattern is irregular mosaic or petal on the shaft. 9

9 The shape of the hair is tubular; it is glossy and smooth in touch. The ground colour is brown, black and white. The pigmentation is sparse. The medulla is uniserial nummiform. *Vibrissae*

– The shape of the hair is cornet-like; it is coarse in touch. The ground colour is dark brown, reddish or black. The medulla is amorphous or fragmented. l_{max} = 110 mm; (GH0 l_{max} = 180 mm); d_{max} = 400 µ *Sus scrofa*

10 The cuticular pattern is K-shaped coronal on the shaft and the shield. Rhinolophidae

– The cuticular pattern is not K-shaped coronal. 11

11 The cuticular pattern is hastate coronal on the distal part of the shaft and the proximal section of the shield. l_{max} = 8 mm; d_{max} = 10 µ *Miniopterus schreibersii*

– The cuticular pattern is not hastate coronal. 12

12 The cuticular pattern is compressed coronal on the shield. 13

– The cuticular pattern is not compressed coronal. 15

13 The apical edges of the scales are dentate; the compressed coronal scales are crown-shaped on the distal shield. l_{max} = 9 mm; d_{max} = 12 µ *Tadarida teniotis*

– The apical edges of scales are rippled. l_{max} = 8 mm; d_{max} = 18 µ 14 *Pipistrellus* spp.

14 The compressed coronal sacles are cup-shaped on the shield. *Pipistrellus kuhlii*

– The compressed coronal scales are cornet-shaped on the distal shield. *P. nathusii*, *P. pygmaeus*, *P. pipistrellus*

15 The cuticular pattern is mosaic coronal on the shield; the scales are divergent, scalloped. 16

– The cuticular pattern is mosaic coronal on the shield; the scales are closed, conical. l_{max} = 12 mm; d_{max} = 22 µ 18

16 The distal part of the shield is channelled. The apical margins of scales are rounded, smooth or rippled. The hair is bicolorate. l_{max} = 8 mm; d_{max} = 16 µ *Vespertilio murinus*

– The distal part of the shield is not channelled. The apical margins of scales are cutted, rippled. The hair is unicolorate. 17

17 The apical margins of scales elongated, acute towards the tip. lmax = 8 mm; d_{max} = 22 µ *Nyctalus* spp.

– The apical margins of scales elongated, arcuate towards the tip. l_{max} = 10 mm; d_{max} = 16 µ *Barbastella barbastellus*

18 The hair is banded. l_{max} = 8–12 mm; d_{max} = 22 µ *Myotis myotis*, *M. blythii*, *M. emarginatus*, *Plecotus auritus*, *P. austriacus*, *Eptesicus nilssonii*

– The hair is unicolorate or polychrome. 19

19 The hair is combined wavy. l_{max} = 8–12 mm; d_{max} = 22 µ *Myotis alcathoe*, *M. aurascens*, *M. bechsteinii*, *M. brandtii*, *M. capaccinii*, *M. dasycneme*, *M. daubentonii*, *M. mystacinus*, *M. nattereri*, *Eptesicus serotinus*, *E. nilssonii*

– The hair is wavy and very thin. l_{max} = 7 mm; d_{max} = 10 µ *Hypsugo savii*

20 The medullar pattern is exclusively uniserial nummiform on the entire hair. 21

– The medullar pattern is changing along the lenght of hair. 27

21 Shape of GH2 is combined zigzag. The cuticular pattern is combined petal on the shaft. Most of the hairs are bicolorate. 22 Soricomorpha

– Shape of GH2 is curved or wavy. The distal part banded, the colour of band is pale, or transparent reddish or yellowish. The cuticular pattern is not combined petal on the shaft. 25 Gliridae

22 No channel on the hairs. The cuticular pattern on the shield is broad petal. The shape of the tip is gradually tapering. The cross-section is circular or oblong. l_{max} = 12 mm; d_{max} = 45 µ; m/d_x = 0.75 *Talpa europaea*

– GH2 and UH are channelled. The cuticular pattern on the shield is transveral petal. The shape of the tip often abruptly tapering, flagelliform. The genus specific characters require SEM study. 23 Soricidae

23 The channel on GH2 is shallow, wide, with smooth inner surface. The cross-section is U-shaped or oblong. l_{max} = 7 mm; d_{max} = 17 µ *Crocidura* spp.

– The channel on GH2 is narrow, deep, with structured inner surface. The cross-section is H-shaped or quadri-concave. 24

24 Within the channel, the central ridge is expressed; there are V-shaped, long, thin lamellae. l_{max} = 7.5 mm; d_{max} = 30 µ *Sorex* spp.

– Within the channel, the central ridge is unexpressed; there are oblique, short, thick lamellae. l_{max} = 13 mm; d_{max} = 35 µ *Neomys* spp.

25 The cuticular pattern is rhomboidal on the shaft. l_{max} = 13 mm; d_{max} = 40 µ; m/d_x = 0.65 *Muscardinus avellanarius*

– The cuticular pattern is galeate or cuneate chevron on the shaft. 26

26 The cortex is pigmented and thick on the shield. l_{max} = 20 mm; d_{max} = 60 µ; m/d_x = 0.25 *Glis glis*

– The cortex is transparent and thin on the shield. l_{max} = 10 mm; d_{max} = 40 µ; m/d_x = 0.75 *Dryomys nitedula*, *Eliomys quercinus*

27 The medullar pattern is twisted multiserial on the shield. The cuticular pattern is lanceolate chevron on the shaft. 1_{max}=30; (l $GH0_{max}$ = 50) mm; d_{max} = 150 µ; m/d_x = 0.85 Lagomorpha

– The medullar and cuticular patterns are different. 28

28 The medullar pattern is spongoid multiserial on the proximal shield. The cuticular pattern is meshed mosaic on the shaft. The basal section is bottleneck-shaped. 29 Cervidae, Bovidae

– The medullar and cuticular pattern are different. The GH is straight or wavy. 33

29 The cuticular pattern is meshed, most often isodiametric mosaic on the proximal shaft. 30 Bovidae

– The cuticular pattern is meshed, most often transversal polygonal mosaic on the proximal shaft. 31 Cervidae

30 The GH banded, unicolorate or polychrome. $l_{max} \geq 50$ mm; $d_{max} \geq 200$ µ *Rupicapra rupicapra*, *Ovis orientalis*

– The GH not banded, but unicolorate. l_{max} = 45 mm; l_{max_mane} = 75 mm; d_{max} =140 µ; m/d_x = 0.85 *Capra ibex*

31 $l_{max} \leq 40$ mm; d_{max}=140–380 µ; m/d_x = 0.8 *Capreolus capreolus*

– $l_{max} < 40$ mm; m/d_x = 0.9 32

32 40 mm < $l_{max} \geq 90$ mm; 160 µ ≤ $d_{max} \geq 450$ µ. The number of rows of medullar cells do not exceed 15. *Cervus* sp., *Dama dama*, *Odocoileus virginianus*

– l_{max} = 110 mm; l_{max_mane} = 250 mm; d_{max} = 500 µ. The number of rows of medullar cells may reach 20. *Alces alces*

33 The medulla is tubular on the shield. 34

– The medulla is different, not tubular on the shield. 37

34 The hair is coarse in touch. 35

– The hair is fine in touch, unicolorate, rarely one banded. The cuticula is transversal, irregular mosaic on the shaft. l_{max} = 65 mm; d_{max} = 90 µ; m/d_x = 0.25–0.45 *Castor fiber*

35 The cuticula is rhomboidal petal or pine-cone rhomboidal on the shaft. The hair is bicolorate or one-banded. l_{max} GHv = 20 mm; d_{max} GHv = 160 μ; m/d_x GHv = 0.45 *Erinaceus* sp., GHv

– The cuticula is not rhomboidal on the shaft. The GH unicolorate or polychrome. $l_{max} > 20$ mm 36

36 The cuticula is broad rhomboidal on the shaft. The medulla is colonnade tubular on the shield. l_{max} = 100 mm; d_{max} = 170 μ; m/d_x = 0.3 *Ursus arctos*

– The cuticula is meshed, isodiametric mosaic on the shaft. The medulla is porous tubular on the shield. l_{max} = 55 mm; l_{max_mane} = 280 mm; d_{max} =115 μ; m/d_x = 0.45 *Bison bison*

37 The medullar pattern is cob-like multiserial on the shield, the cuticular pattern is most often chevron or rhomboidal on the shaft. 38 Rodentia

– The medullar and cuticular pattern is different. The medulla is most often chambered multiserial on the shield; the cuticula is most often rhomboid on the shaft. 53 Carnivora

38 The hairs are channelled. 39

– The hairs are not channelled. 48

39 The channel is only a slight depression on the surface of the hair; observable by SEM. 40

– The channel is deeper, observable on the print, embedding, sectioning of the hair, and by SEM. 42

40 The hairs are not banded, uni- or bicolorate. l_{max} = 14 mm; d_{max} = 45 μ; m/d_x = 0.85 Spalacinae

– The GH2 and UH hairs are banded. l_{max} = 10 mm; d_{max} = 55 μ; m/d_x = 0.85 41

41 The cuticular pattern is cuneate chevron on the shaft of GH2, but rhomboid on the GH1. The medullar pattern is cob-like multiserial; the shape of medullar cells is oblong on the shield. *Mus* spp.

– The cuticular pattern is rhomboid on the shaft. The medullar pattern is biserial on the shield. *Micromys minutus*

42 The cuticular pattern is cunetae chevron on the shaft. 43

– The cuticular pattern is rhomboid on the shaft. 47

43 The cuticular pattern is rhomboid on the basal section. The hairs might have 1–4 bands. l_{max} = 25 mm; d_{max} = 125 μ; m/d_x = 0.85 *Sciurus vulgaris*

– The cuticular pattern is broad petal on the basal section. The hairs have 1 band. 44

44 The hairs have 1 band. d_{max} = 65 μ; m/d_x = 0.85 45

– The hairs have 1–2–3 bands. l_{max} = 15 mm; d_{max} = 110 μ; m/d_x = 0.85 *Spermophilus* spp.

45 There might be 3 deep channels on the shield, observable by SEM. The cross-section is tetra-, or plano-concave. The ground colour of hairs is brownish, the band is reddish. l_{max} = 15 mm *Myodes glareolus*

– There is only 1 wide channel on the shield, observable on the print, embedding, sectioning of the hair, and by SEM. The cross-section is concave-convex, biconcave or oblong. 46

46 The ground colour of hairs is dark grey; the band is ochreous or whitish. l_{max} = 18 mm *Dinaromys bogdanovi*, *Chionomys nivalis*

– The ground colour of hairs is brownish; the band is ochreous or reddish. l_{max} = 14 mm *Microtus* spp.

47 There is only 1 channel on the shield. The cross-section is convex-concave or oblong. The number of rows of oblong or rounded medullar cells might exceed 8. l_{max} = 25 mm; (l_{max} GH0 = 30); d_{max} = 120 μ; m/d_x = 0.9 *Rattus* spp.

– There might be 2–3 channels on the shield. The cross-section is tetra-concave, convex-concave or plano-concave. The number of rows of transversally elongated medullar cells does not exceed 8. l_{max} = 12 mm; d_{max} = 80 μ; m/d_x = 0.85 *Apodemus* spp.

48 There are no banded hairs in the fur. The medullar cells are characteristically uniform, rounded. The cortex is thick. l_{max} = 30 mm; GH0 l_{max} = 45 mm; d_{max} = 110 μ; m/d_x = 0.45 *Ondatra zibethicus*

– The hairs are uni-, bicolorate or banded. 49

49 The length of GH exceed 30 mm. 50

– The length of GH do not exceed 30 mm. 51

50 The medullar cells are polygonal on the shield. l_{max} = 40 mm; d_{max} = 138 μ; m/d_x = 0.8 *Marmota marmota*

– The medullar cells are transversal, elongated on the shield. l_{max} = 55 mm; d_{max} = 200 μ; m/d_x = 0.85 *Myocastor coypus*

51 The medullar cells are crescent-shaped. l_{max} = 25 mm; d_{max} = 85 μ; m/d_x = 0.7
Cricetus cricetus

– The medullar cells are oblong. $l_{max} \leq 20$ mm. 52

52 The number of rows of medullar cells do not exceed 3. l_{max} = 10 mm; d_{max} = 53 μ; m/d_x = 0.85 *Sicista* spp.

– The number of rows of medullar cells can be up to 5. l_{max} = 18 mm; d_{max} = 75 μ; m/d_x = 0.85 *Eutamias sibiricus, Arvicola* spp.

53 The medulla is foamy on the distal shield. The medullar cells are transversal, oval or oblong; the globular or fusiform air sacs between the medullar cells may span the entire width of the medulla. The edge of the medulla is fringed or straight. The cross section is most often circular. 54 Canidae, Felidae

– The medulla is chambered multiserial or tubular on the distal shield. The medullar cells are polygonal, rounded or cask-shaped; the air sacs never span the entire width of the medulla. The edge of the medulla is crested or straight. The cross section is most often oblong. 58 Mustelidae, Procyonidae

54 The hair is fine in touch, silky and thin. The length of the hair do not exceed 65 mm. The two-banded hairs are always GH2 type; the bands are most often short, and do not reach the one-fourth of the hair. l_{max} = 60 mm; d_{max} = 100–120 μ; m/d_x = 0.75 55

– The hair is fine in touch, but strong, thick. The length of the hair exceeds 65 mm. The two-banded hairs are GH1 and GH2 type; the bands are most often long, the length of the one-fourth of the hair. l_{max} = 110–130 mm; d_{max} = 135–150 μ; m/d_x = 0.65 57

55 The palest section of the hairs is always on the shaft. The two-banded GH is having white shaft, brown proximal band and white distal band, and dark brown tip. The medullar cells are transversally slightly elongated; the air sacs are globular or cask-shaped. 56 Felidae

– The palest section of the hairs is never on the shaft. The shape of the medullar cells and air sacs is fusiform or globular. Characteristic hair type is the one-banded GH2, it has two forms. GH2 might have pale rufous band and dark brown or black shaft and tip; or might be "tricolored", with brown shaft, milk-white band and vivid reddish shield. *Vulpes vulpes*

56 Characteristic hair type is the GH2, it has two forms. GH2 might be bicolorate with reddish shaft, and dark brown shield; the one-banded, "tricolour" GH2: has whitish shaft; reddish band on the transit and the proximal shield; and dark brown or red distal shield and apical region. The colour of the tuft is reddish. *Lynx lynx*

– Characteristic hair type is the two-banded GH1: it has long, white shaft; the band of the transit and the proximal shield is dark; the band of the distal shield is white, may have reddish shade; the apical section is dark. The colour of the tuft is greyish.
Felis silvestris

57 The medullar cells are polygonal in the transit and the proximal shield; tiny and tightly closed in the distal shield, and their shape is most often fusiform. The air sacs may span the entire width of the medulla. The tip is always dark brown or black. *Canis* spp.

– The medullar cells are globular or hexahedral at the maximum width of the shield; the volume of air sacs does not fill the entire width of the medulla. The tip of the hair might be black or dark brown, occasionally white or transparent.
Nyctereutes procyonoides

58 The GH1 is banded, GH2 is most often bicolorate. $l_{max} \geq 65$ mm 59

– The GH1, GH2 are uni-, bicolorate or polychrome. $l_{max} \leq 65$ mm 60

59 The hair is fine in touch. The colour of the tip is always dark. The cuticula is broad rhomboidal on the shaft. The medulla is chambered multiserial on the shield.
$l_{max} = 65$ mm; $d_{max} = 130$ µ; $m/d_x = 0.65$ *Procyon lotor*

– The hair is coarse in touch. The colour of the tip is most often whitish. The cuticula is irregular, broad rhomboidal, or rarely pine cone on the shaft. The medulla is chambered multiserial on the proximal shield; porous tubular on the distal shield.
$l_{max} = 90$ mm; $d_{max} = 250$ µ; $m/d_x = 0.5$ *Meles meles*

60 The hairs are unicolorate or polychrome. 61

– The hairs are bicolorate or "tricolorate". 63

61 The cuticula is elongated rhomboid on the shaft. $l_{max} = 60$ mm; $d_{max} = 125$ µ; $m/d_x = 0.75$ *Martes* spp.

61 The cuticula is pine-cone rhomboid on the shaft. $l_{max} \leq 25$ mm 62

62 $l_{max} = 17$ mm; $d_{max} = 115$ µ; $m/d_x = 0.7$ *Mustela nivalis*, *M. erminea*

– $l_{max} = 25$ mm; $d_{max} = 135$ µ; $m/d_x = 0.75$ *Mustela lutreola*, *Neovison vison*

63 The hairs are "tricolorate". The cuticula is elongated rhomboid on the shaft. 64

– The hairs are bicolorate. The cuticula is pine-cone rhomboid on the shaft.
$l_{max} = 30$ mm; $d_{max} = 150$ µ; $m/d_x = 0.6$ *Lutra lutra*

64 $l_{max} = 65$ mm; $d_{max} = 140$ µ; $m/d_x = 0.75$ *Mustela putorius*, *M. eversmanii*

– $l_{max} = 16$ mm; $d_{max} = 105$ µ; $m/d_x = 0.85$ *Vormela peregusna*

Colour atlas of furs of Central European mammals 12

Erinaceomorpha

Erinaceus roumanicus

Erinaceus europaeus

Erinaceus sp.

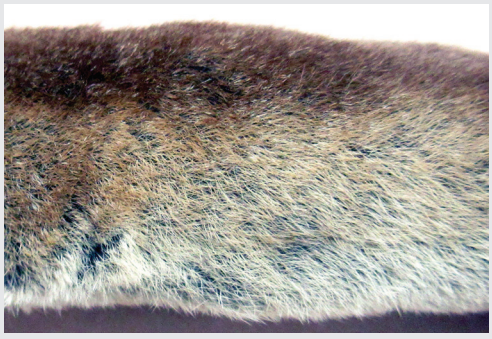
Neomys anomalus

Neomys fodiens

Sorex alpinus

Sorex araneus

Sorex araneus (HNHM)



Sorex coronatus

Sorex minutus

Crocidura leucodon

Crocidura russula

Crocidura suaveolens

Talpidae

Talpa europaea

Rhinolophidae

Rhinolophus blasii

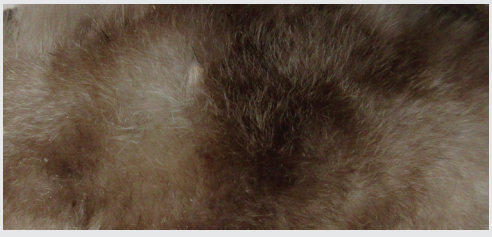
Rhinolophus euryale

Rhinolophus ferrumequinum

Rhinolophus hipposideros

Rhinolophus mehelyi

Rhinolophus mehelyi



Rhinolophus blasii

Vespertilionidae

Eptesicus nilssonii

Eptesicus serotinus

Pipistrellus kuhlii

Pipistrellus nathusii

Pipistrellus pipistrellus

Nyctalus lasiopterus

Nyctalus leisleri

Nyctalus noctula

Myotis alcathoe

Myotis aurascens

Myotis bechsteinii

Myotis brandtii

Myotis dasycneme

Myotis daubentonii

Myotis emarginatus

Myotis myotis

Myotis mystacinus

Myotis nattereri

Plecotus auritus

Plecotus austriacus

Plecotus macrobullaris

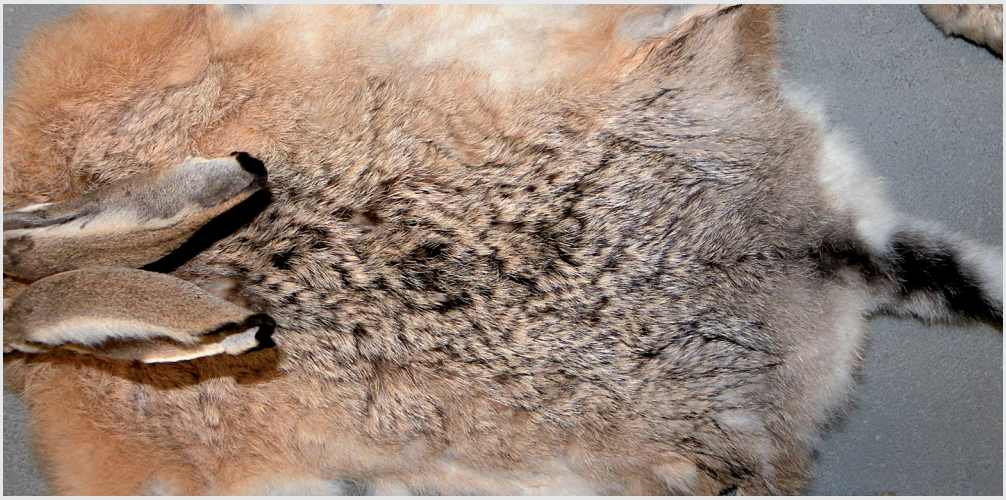
Hypsugo savii

Miniopterus schreibersii

Barbastella barbastellus

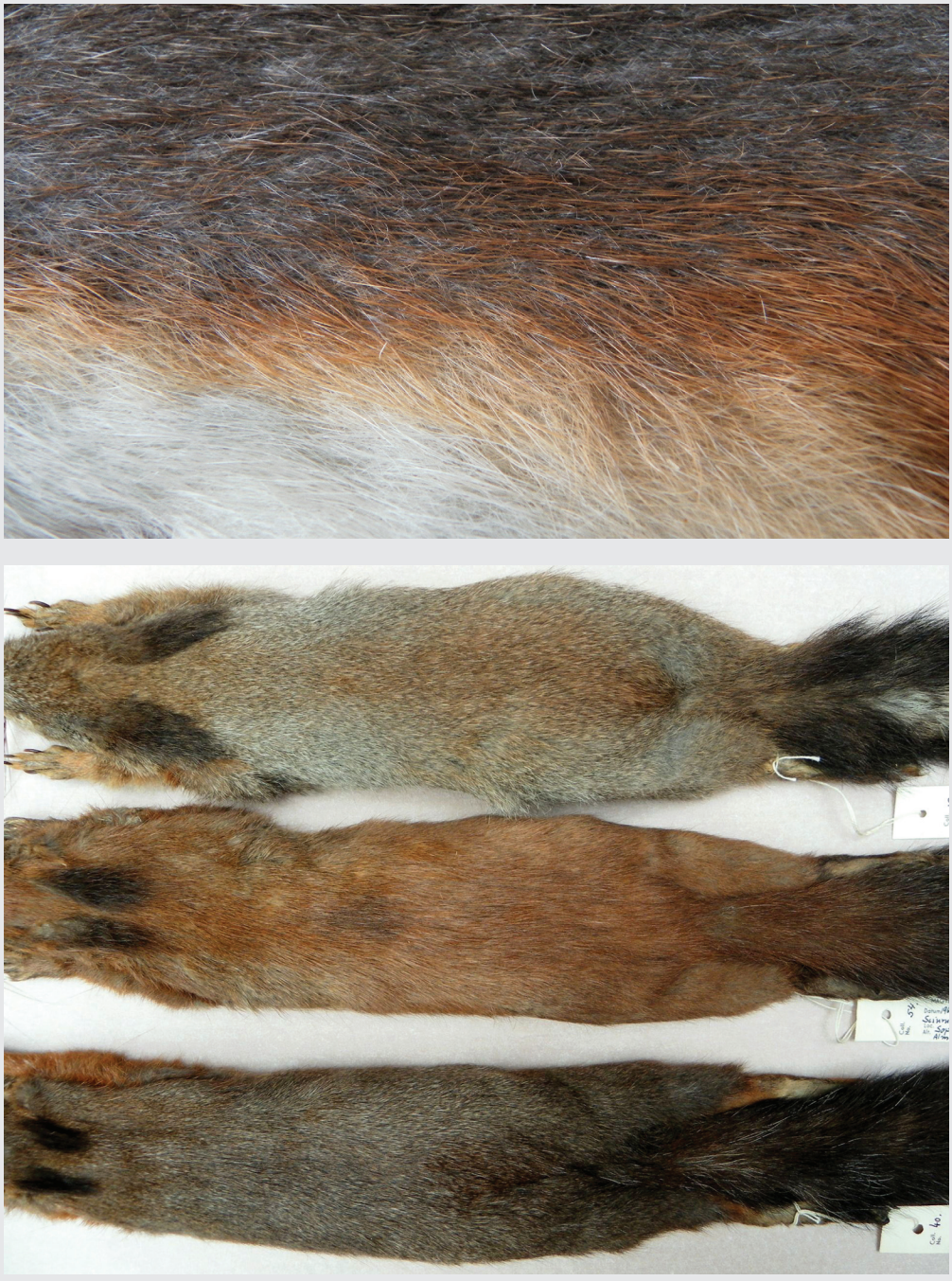
Vespertilio murinus

Lagomorpha



Lepus europaeus

Oryctolagus cuniculus



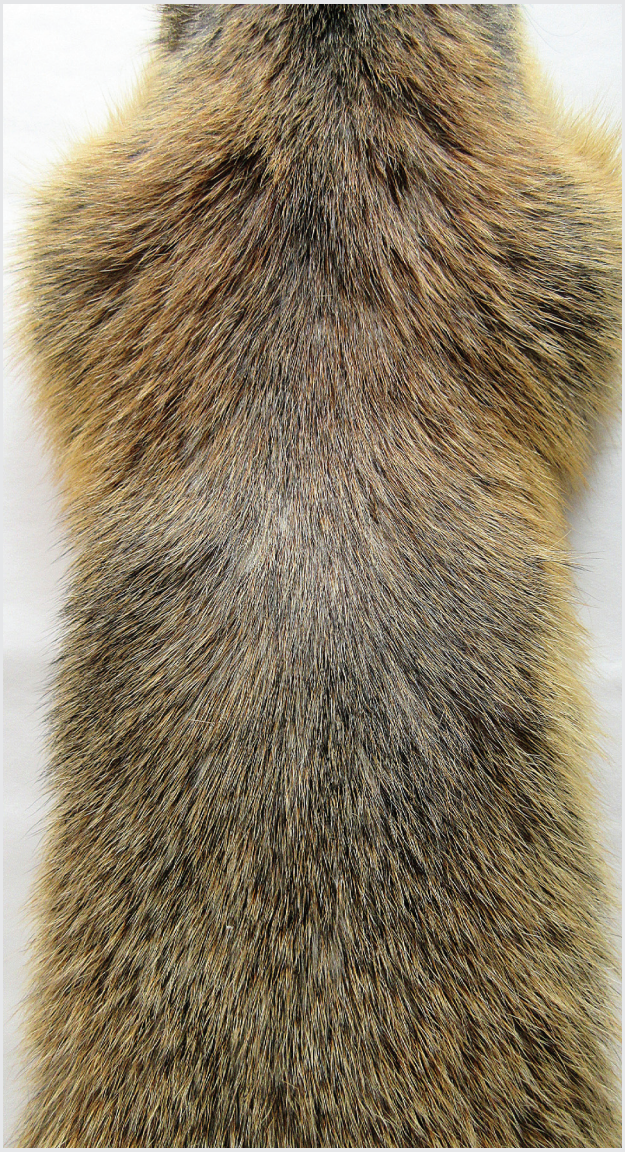
Sciurus vulgaris

Eutamias sibiricus

Eutamias sibiricus

Spermophilus suslicus

Spermophilus citellus



Marmota marmota

Eliomys quercinus

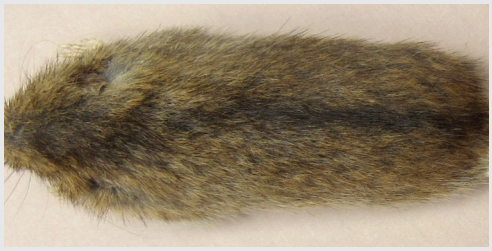
Dryomys nitedula

Eliomys quercinus

Dryomys nitedula

Muscardinus avellanarius

Glis glis



Sicista betulina

Sicista subtilis

Apodemus agrarius

Apodemus alpicola

Apodemus flavicollis

Apodemus flavicollis (ventral)

Apodemus sylvaticus

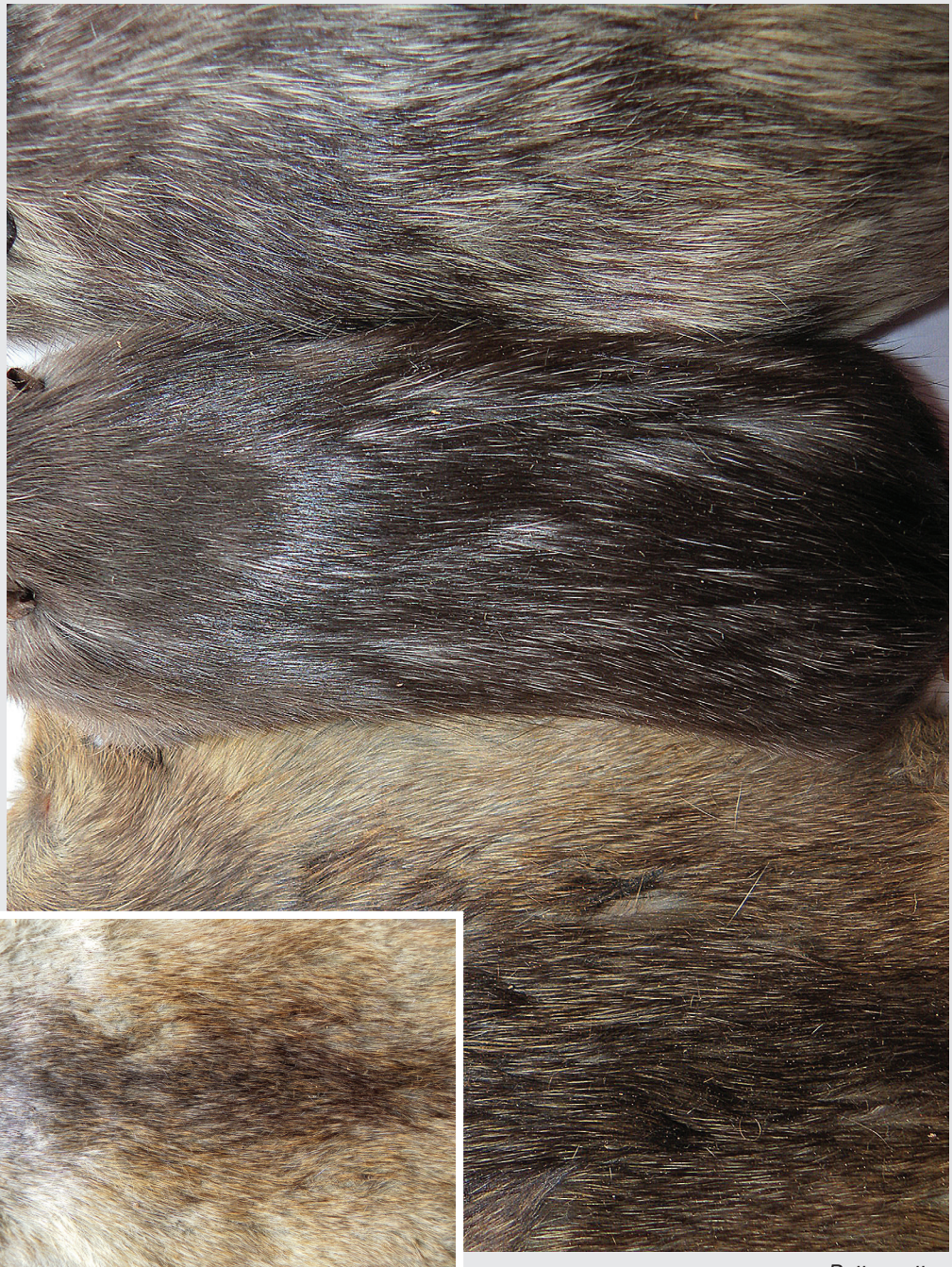
Apodemus sylvaticus (ventral)

Apodemus uralensis

Micromys minutus

Mus musculus

Mus spicilegus

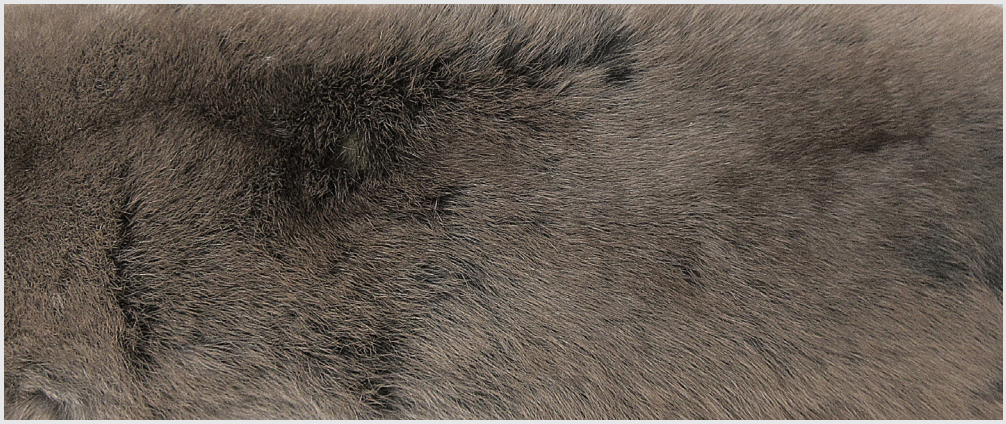


Rattus rattus

Rattus norvegicus

Nannospalax (superspecies) *leucodon*

Spalax zemni (head)



Spalax antiquus

Spalax graecus

Spalax zemni

Cricetus cricetus

Arvicola amphibius

Arvicola scherman

Myodes glareolus

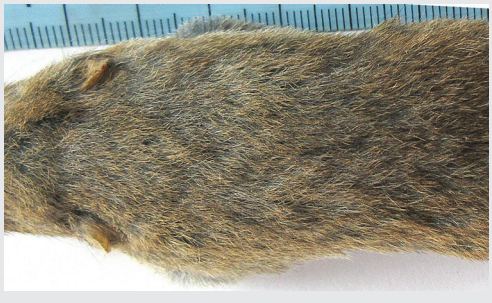
Chionomys nivalis

Dinaromys bogdanovi

Microtus agrestis

Microtus arvalis

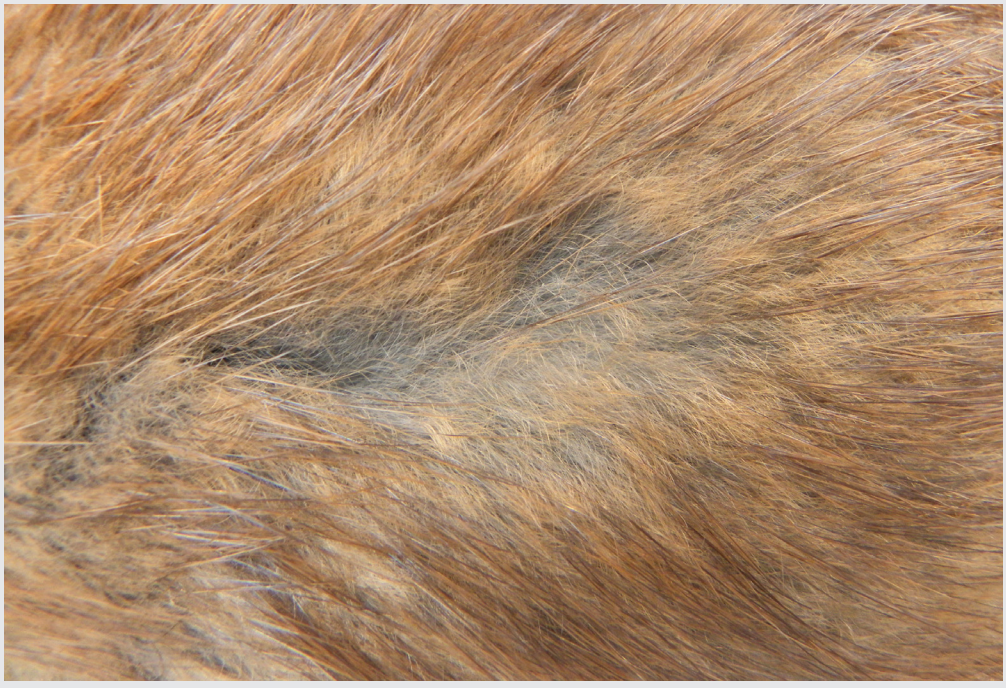
Microtus bavaricus



Microtus liechtensteini

Microtus oeconomus

Microtus tatricus



Ondatra zibethicus

Myocastor coypus

Castor fiber

Castor fiber

Canis lupus (fur and tuft)

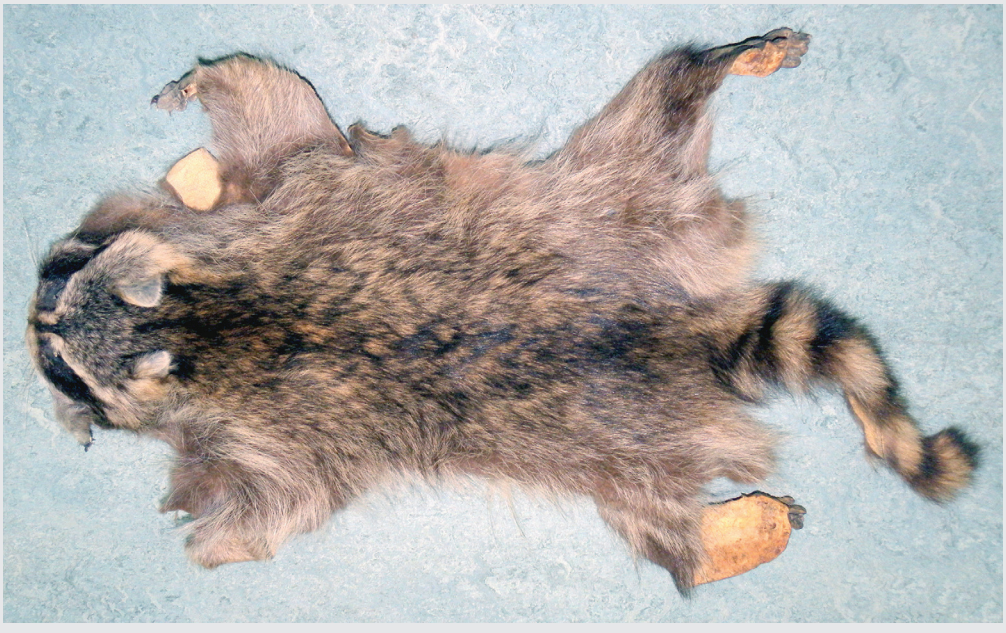
Canis aureus (fur and tuft)

Vulpes vulpes

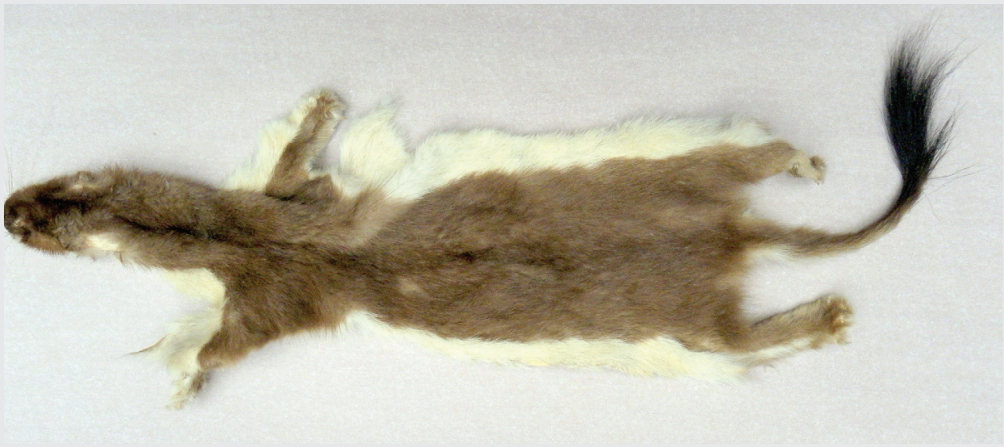
Nyctereutes procyonoides (fur and tuft)

Ursus arctos

Procyon lotor



Procyon lotor



Mustela erminea

Mustela erminea

Mustela nivalis

Mustela nivalis

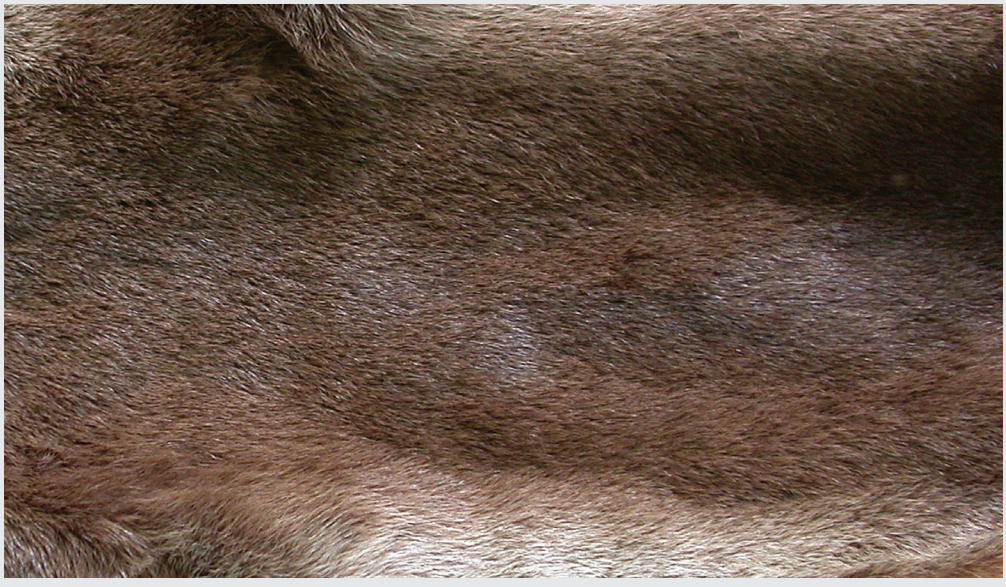
Mustela lutreola

Neovison vison

Mustela putorius (fur and tuft)

Mustela eversmanii ssp. *hungaricus* (HNHM)

Vormela peregusna

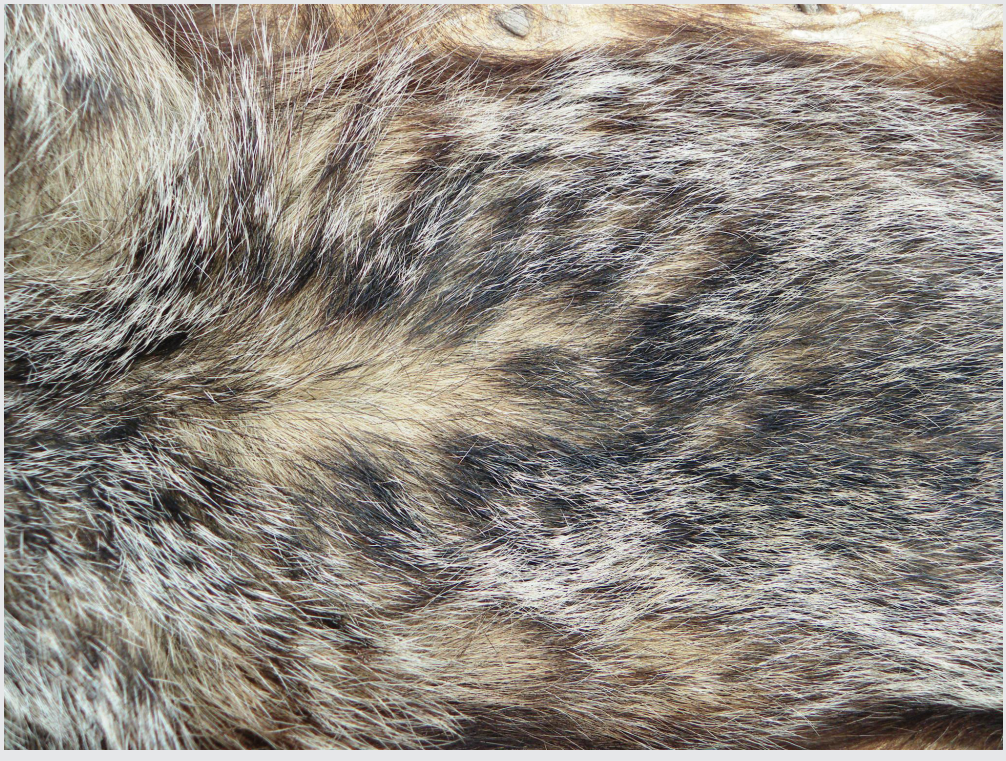


Lutra lutra (fur and tuft)

Martes foina

Martes martes

Martes foina

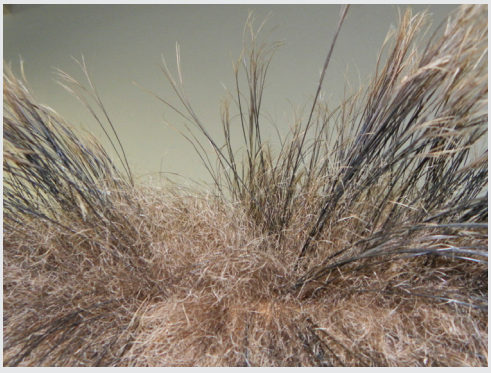


Meles meles (fur and tuft)

Felis silvestris (fur and tuft)

Lynx lynx (fur and tuft)

Artiodactyla

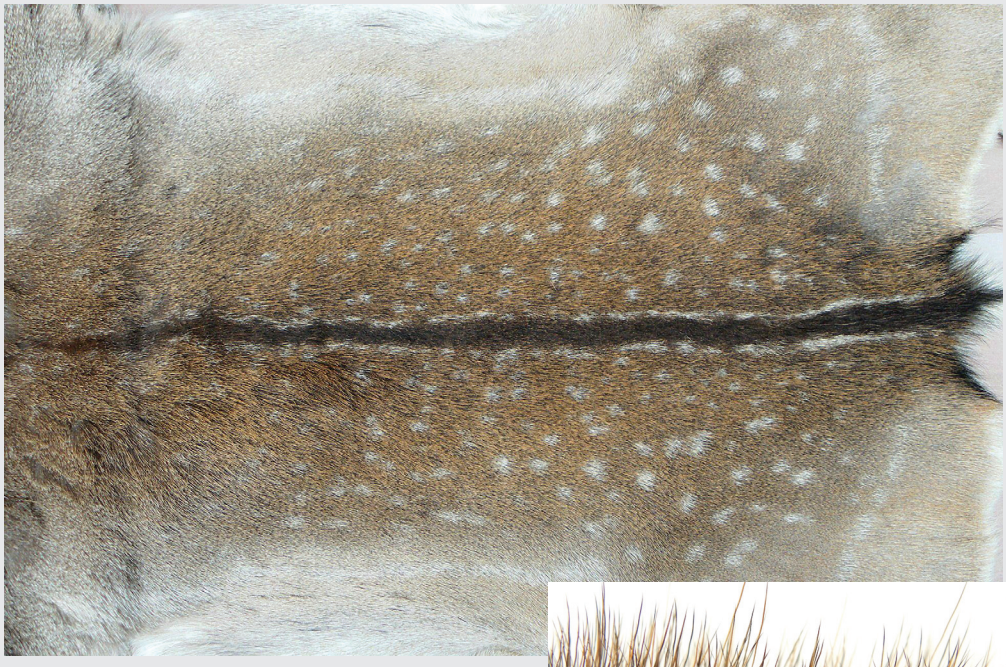


Sus scrofa (fur and tuft)

Capreolus capreolus

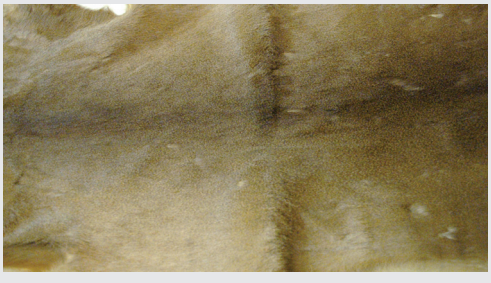
Cervus elaphus

Cervus nippon



Dama dama (fur and tuft)

Alces alces



Odocoileus virginianus

Capra ibex

Capra ibex

Ovis orientalis

Rupicapra rupicapra

Bison bonasus

Sciurus vulgaris (TLMF)

Capreolus capreolus (TLMF)

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