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Morphological Identification of Animal Hairs: Myths and Misconceptions, Possibilities and Pitfalls

Silvana R. Tridico*, M.M. Houck, K. Paul Kirkbride, M.E. Smith, B.C. Yates

* Australian Wildlife Forensic Laboratory, Veterinary and Life Sciences, Murdoch University, Perth, Western Australia, 6150, Australia

b Department of Forensic Sciences, Consolidated Forensic Laboratory, 401 E Street SW Washington, D.C. 20024, USA e mail: Max.Houck@DC.gov

c School of Chemical and Physical Sciences, Flinders University, GPO Box 2100, Adelaide, South Australia, 5001, e mail: paul.kirkbride@flinders.edu.au

d Forensic Scientist – Morphology National Fish and Wildlife Forensics Laboratory, 1490 East Main Street, Ashland, Oregon 97520, USA e mails: cookie_smith@fws.gov & bonnie_yates@fws.gov

* Corresponding author. Tel: +61 8 82785731 e mail: silvanatridico@yahoo.com
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HIGHLIGHTS
1. We compare and contrast skill sets required for practitioners conducting human hair comparative analyses with those required attributing animal hairs to a particular taxon.
2. We discuss the consequences of ill trained or inexperienced practitioners attempting to identify animal hairs in the context of myths and misconceptions.
3. We will discuss the future of the microscopical identification of animal hairs in the context of SWGWILD

We propose recommendations that should be adhered to in order to ensure quality practices in relation to the identification of animal hair.

ABSTRACT
The examination of hair collected from crime scenes is an important and highly informative discipline relevant to many forensic investigations. However, the forensic identification of animal (non-human) hairs requires different skill sets and competencies to those required for human hair comparisons. The aim of this paper is not only to highlight the intrinsic differences between forensic human hair comparison and forensic animal hair identification, but also discuss the utility and reliability of the two in the context of possibilities and pitfalls. It also addresses and dispels some of the more popular myths and misconceptions surrounding the microscopical examination of animal hairs. Furthermore, future directions of this discipline are explored through the proposal of recommendations for minimum standards for the morphological identification of animal hairs and the significance of the newly developed guidelines by SWGWILD is discussed.
Keywords: animal hairs; human hairs; microscopy; morphology; SWGWILD; wildlife forensic

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1. Introduction
The morphological identification of animal (non-human) hairs (MIAH) is based on fundamental aspects of microscopy, biology, and zoology. The purpose of MIAH is to categorize the animal source of an unknown hair sample to a particular taxon based on well-defined, genetically-based features that are characteristic to that group. The breadth of knowledge required to identify mammalian hairs from all potential taxa is extensive but may be relatively simple in certain contexts, for example identification of mammal hairs as encountered in biological fieldwork, in museum curation, or in the textile industry. In contrast, the forensic examination of hair involves knowing not only the range of expression of mammalian hairs within taxa, but also being aware of other structures that may resemble hairs, such as man-made wig fibers and faux fur fibers, insect seta, and plant tendrils. The forensic context is thus wider and more complicated than a controlled mammalian orientation.

This complexity is compounded because forensic hair examiners typically are examiners of human hair. Unlike MIAH, the human hair practitioner is dealing with hairs from a single species, Homo sapiens, and answering a quite different series of questions which may include (but not limited to):

1. Is it a human hair?
2. From what area of the body did it originate?

3. Is there damage, disease or treatment evident in the hair?

4. Are the hairs suitable for forensic nuclear DNA profiling?

5. Does the hair contain sufficient information for comparison to a putative human source or sources?

6. Could the hair have originated from one of those sources?

7. What is the broad ethnic origin of the donor of the hairs? (i.e., Caucasian, Mongoloid or African)

Although questions 1-3 may also be relevant to anthropology, questions 4 –7 are purely forensic in nature and address a concept specific to forensic methods, i.e. source attribution. In fact, categorization and source attribution represent the core and enduring questions asked of a forensic investigation: “What is this material?” “Where did it come from?” and “Does it confirm or reject associations between people, places, and things involved in criminal activities”. The first part, categorization or identification, is common enough among sciences; what sets forensic science apart is its core intention of sourcing where the identified item came from (the victim, suspect, their environments or the scene).

The composition and origins of materials lend themselves to a greater or lesser specificity of sourcing. Hairs, because of their complex matrix and variable expressivity, are limited by their “intra sample variations (which) can be nearly as large as variations between certain samples from different sources… the results of a hair comparison (are) far less than certain” (1). The process of human hair comparison is widely considered as fundamentally ‘subjective’ in the context that results and conclusions are not quantifiable but based on opinion. This practice is not unique to forensic analyses; it is also relevant in areas of the medical profession such as histology (e.g.
Typically, three conclusions can be drawn from a human hair comparison, given suitable samples:

1. The questioned hair exhibits the same microscopical characteristics as the known sample and therefore could have come from the person from which the known was taken,
2. The questioned hair exhibits different microscopical characteristics as the known sample and therefore could not have come from the person from which the known was taken,
3. The questioned hair exhibits both similarities with, and differences to, the known sample and therefore no conclusion can be drawn as to the source of the questioned sample.

In some instances positive associations deduced from this comparative process have been afforded more probative value than is scientifically warranted resulting in individuals being wrongfully incarcerated (2). As a consequence, criticism has been leveled at forensic human hair comparison, which may tarnish related or similar disciplines, especially MIAH. However, there is a fundamental difference between comparative examinations between human hairs to infer an association to a particular individual (sourcing) and MIAH, which is an exercise in taxonomy to identify an animal hair to a particular taxon and not to a particular animal. Therefore, criticisms leveled at the former are not relevant to the latter.

This paper is primarily aimed at raising awareness levels of what can go wrong for inexperienced, unwary or inadequately trained practitioners attempting to microscopically identify animal hair. The paper also discusses the future of MIAH in the context of accreditation of the discipline and its practitioners.

2. Morphological Identification of Animal Hairs

All mammalian hair is composed of the protein keratin. Mammalian hairs are all similar in their
chemical composition and major structural features but they do differ to a greater or lesser extent in morphology at varying taxonomic levels. Mammalian hair consists of three layers: an outermost cuticle, an inner cortex, and a central core or medulla as illustrated in Figure 1. Mammalian hairs bear morphological features characteristic for a particular taxon that may be phylogenetic in origin or functionally derived, these are:

1. the configuration of cells in the medullae of guard hairs,
2. cuticle scale patterns,
3. transverse cross-sectional shapes.

Additionally, mammals exhibit somatic variation in hair morphology that must be taken into consideration for taxonomic identification. Whilst the examination of animal hairs takes into consideration gross morphological features such as color (banded or uniform), length and general profile, these are not, in general, taxon specific. However, these features may assist in excluding animals from a particular taxon as sources of the hair in question if a number of taxa share similar microscopical morphological characteristics.

3. Myths and Misconceptions

Several popular myths and misconceptions exist regarding MIAH that demonstrate ‘a little knowledge is a dangerous thing’ when exercised without any competence in MIAH.

3.1 Myth: Cat (Felis catus) and Dog (Canis lupus familiaris) hairs can be reliably identified solely on root shapes

Hairs from cats and dogs are undoubtedly the most commonly encountered animal hairs in forensic (crimes against the person) examinations. There are a number of forensic publications that state that the identification of these two species may be effected solely on the basis of their root shapes (3, 4). It is generally accepted in the scientific community that hairs from these two species can be distinguished, and identified, on the basis of the shape of their hair roots, i.e., dog hairs exhibit spade-shaped roots, and cat roots are fibrillated (Figure 2). However, both of these root shapes can
occur in both species (5) and other species. In order to effect an accurate identification, and one that withstands scientific scrutiny, the examiner must consider details of the medulla and scale pattern throughout the length of guard hairs in order to distinguish between each of these species - not solely the root shapes. Furthermore, the examiner must query the aggregate morphological characteristics in order to consider what other animals might exhibit similar features in all aspects, i.e. medulla pattern, cuticle pattern, and in some instances, cross-sectional shapes.

Some early work by Peabody et al (6) indicated that medullary index (i.e. the ratio of the medulla diameter to the hair diameter) could be used as a basis for discriminating domestic cat (*Felis catus*) hairs from dog (*Canis lupus familiaris*) hairs. Although this work was original and important, we believe that it is of limited forensic value. Identifications were effected by comparing data derived from reference hairs of unknown body origin with questioned hairs of unknown body origin. We believe a more scientifically valid approach would have been to produce different data sets derived from hairs from known body areas, for comparison with data derived from the questioned hairs from unknown body areas. This is because morphological characteristics of animal hair varies in relation to somatic origin i.e. body area (7). In addition, Peabody et al (6) attempted to corroborate their quantitative findings with scale pattern analysis. Unfortunately these authors compared scale patterns from what they believed to be domestic cat hairs (*Felis catus*) (based on their medullary index) with the images of cat hairs produced by Appleyard (8). However, the cat hairs Appleyard (8) examined came from an African Wild Cat (*Felis ocreata catus*) and not a domestic cat (*Felis catus*). Each of these felid species exhibit different scale patterns as illustrated in Appleyard (8) and Brunner and Coman (7).

### 3.2 Misconception: Pig (*Sus scrofa*) hairs may be mistaken for human hairs

Not infrequently forensic scientists need to identify hairs recovered from environments such as forests, beaches, or caves to determine whether the hairs are human or animal in origin. If human, authorities may be looking for an injured or deceased person and law enforcement personnel need
a timely, accurate identification of these hairs in order to determine an appropriate course of action.

Whilst it is accepted that pigskin is commonly used as a surrogate for human skin, and pig corpses are used in taphonomic studies *in lieu* of human cadavers, the hairs of these two species are absolutely distinguishable as demonstrated in Figure 3, which depicts features exhibited in dorsal hairs of adult pigs. An additional feature characteristic of adult porcine hairs is that the tips of pig guard hairs are split (commonly referred to as ‘flagged’) in most instances. This myth highlights the necessity of forensic animal hair examiners to be competent and capable of correctly identifying animal hairs from wild and ‘domesticated’ fauna in their particular geographic location.

3.3 Misconception: Scanning Electron Microscopy (SEM) is more effective than Transmitted Light Microscopy (TLM) in animal hair identification

It is widely espoused (e.g. (9-13)) that by using high magnification and sophisticated digital microscopy more details will be revealed that will provide more power of observation and therefore more exactitude in MIAH - this is unfounded. Although SEM can certainly deliver high magnification and depth of field (much higher than transmitted light microscopy), it is a monochromatic, surface-imaging technique that cannot provide details of color or internal structure. As noted by Rowe (14) ‘…SEM for hair examinations is limited because most the morphological features used to identify species of animal from which the hair originated and used to compare evidentiary and exemplar hairs are within the hair, not on its surface’.

Transmitted light microscopy is the recommended and most widely used method for examining internal features and cuticle scale pattern along the entire length of the hair, as well as hair cross-sectional morphology. This provides the examiner with a comprehensive view of the specimen
and allows study of all available taxonomic features that may be critical to effect an accurate identification.

3.4 Myth: Polar bear (Ursus maritimus) hairs are hollow

The most prevalent and widely cited myth, which appears to be universally accepted on the Internet and in peer-reviewed literature (15, 16), is that polar bear hairs are hollow. Polar bear hairs have been described by Morioka (17) as having a shaft that resembles an ‘end-capped straw,’ implying that the shaft is like a hollow tube. Furthermore, Morioka (17) also states that polar bear hairs lack medullae.

Each of these assertions is demonstrably incorrect as shown in (Figure 4). The medulla or core of the hair shaft is composed of air filled cells and vacuoles, which, under transmitted light appears dark; however, if the hair shaft integrity is compromised, mounting medium may seep into the hair and fill the medulla cells and vacuoles. The result is that the entire hair becomes translucent and apparently devoid of a medulla using transmitted light microscopy.

It is possible that inexperienced researchers, concluding that polar bears as hollow, may have based this observation on hairs with a cleared medullae (Figure 4). However, as Morioka (17) did not provide the images from which he derived his conclusion it is impossible to ascertain what is was that led him to his “hollow hair” conclusion.

4. Possibilities in MIAH

Assuming a competent practitioner conducts the identification process, the taxon level to which the animal hair in question can be attributed is dependent on the following criteria

1. The hair type
2. Condition of the hairs

1 Using Google, a search of the Internet using the string ‘polar bear hair hollow’ returned in excess of 450,000 ‘hits’ that supported this premise.
3. Availability of reference hairs from known, vouchered specimens for comparison with the morphological characteristics from the questioned hair

As discussed in Section 1, guard hairs are recognized as the hair types that contain the most diagnostic features upon which a microscopical identification may be made. If the condition of the hair in question is such that insufficient morphological characteristics are present (e.g. short, broken hair fragments or hairs that have been degraded by environmental processes) identification may only be possible to a higher taxonomic level such as Order, rather than at a lower level such as Family or Genus.

Confirmation of the identification necessitates the comparison of the characteristics exhibited by the questioned hair with relevant hair(s) from a vouchered animal reference specimen. MIAH cannot attribute the source of a questioned hair to an individual animal; however, some studies suggest limited associations may be possible (18, 19).

5. Pitfalls

This section discusses common pitfalls witnessed by the authors, either through reviewing literature or reviewing work conducted by inexperienced or inadequately trained animal hair examiners.

5.1 Training

MIAH, like any other scientific discipline, is only as good as its practitioners, the equipment, and the reference materials they use. Pertaining to practitioners, Bisbing and Houck state: “Training and qualification of forensic hair examiners is crucial to the quality and reliability of forensic hair examinations. Many of the weaknesses in forensic hair examinations…are a result of inadequate training of forensic hair examiners and a lack of understanding about the fundamental nature of the examination of hairs”(20). Although this was written in relation to human hair examinations, the
tenet is equally applicable to MIAH. A practitioner seeking to identify an animal hair needs to have knowledge of key morphological features from many different species as opposed to knowledge of only one species, as is the case of human hair examination, or a target species. For MIAH, there needs to be awareness of somatic, inter- and intra-species morphological variations, as stated by Lobert et al (21) ‘We emphasise the need for practitioners to gain considerable personal experience of the technique, the diagnostic characteristics used to identify hair of different species and intra-specific, in order to maximize the reliability of identification results’. 

5.2 Forensic Human and Animal Hair Competencies

A significant pitfall in relation to morphological animal hair identification is the assumption that a practitioner competent in morphological human hair comparison is equally, and automatically, competent in MIAH. However, both examinations have different goals and as such necessitate different competencies in order to accurately conduct each type of analysis. Ogden (22) expresses these sentiments thus: “. . . it is generally easier to teach a wildlife geneticist to do forensic (human based DNA) casework than it is to convert a human forensic DNA specialist into a wildlife DNA forensic scientist. A human (sic) forensic scientist attempting to learn the range of scientific techniques and underlying biological assumptions involved in different wildlife identification enquiries is faced with a very large, diverse body of knowledge to attain”. 

Morphological identification of animal hairs is an exercise in classification that relies on the recognition and interpretation of defined, genetically determined features present in all hairs from animals belonging to a particular taxon. In contrast, human hair examinations rely on the comparison of subjective, albeit genetic, characteristics (e.g. color, pigment type, and distribution) and acquired characteristics (e.g. damage, artifacts, chemical treatments) in order to exclude, or not exclude, an individual(s) as the possible source of the questioned hair. Therefore, forensic practitioners solely trained and experienced in human hair comparisons do not automatically
achieve competency in morphological identification of animal hairs; the same logic applies to those solely trained in MIAH, who would not be competent in human hair comparison.

5.3 Atlases and Literature

Whilst standard reference works (7, 8, 23, 24) serve as excellent examples to illustrate morphological features useful for MIAH, it is crucial that the practitioner, experienced or otherwise, is aware that these are not definitive or exhaustive works, either in regards to the range of animals covered or in regards to all of the morphological features present in each hair type. As Brunner and Coman (7) state in the preface to their animal hair atlas, “It is important to realize that the photographs…represent only some of the multitude of structures observed in the hair of any one species”.

Atlases are of considerable use in training hair examiners as they illustrate the diversity of morphological characteristics present in animal hairs. However, as a sole basis for identification, atlases are of limited utility as they offer ‘snapshot’ images of only one part of the hair; furthermore, it is not uncommon to find that morphological features of hairs, from the same species, differ in different atlases. Therefore, the use of these pictorial references should not be used as substitutes for knowledge and information derived from the examination of vouchered hairs, from a well-stocked reference collection. As Wildman (24) observed ‘…although books and photographs are useful as guides, there is not reliable short-cut method for identifying animal hair fibres by simply ‘matching up’ the microscopical appearance of an unknown fibre with a photomicrograph’.

In relation to keys or other classification schemes that attempt to assist in the identification process, Kirk noted: “Such schemes have a certain value when used with the reservations imposed by experience and study, but their value even in this sense is limited. Experience in examining hair and study of its characteristics will supply far more information than can be obtained by study of
any stereotyped classification scheme”(25). Although this was in relation to classification of human hair types, this tenet is equally, if not more, applicable to MIAH for reasons outlined above.

5.4 Taxonomy and Binomial Nomenclature

Binomial nomenclature is universally understood. It not only crosses linguistic and cultural boundaries, but it also ensures that there is no doubt as to the identity of the animal in question. In a wildlife forensic context, an indictment is predicated on determination of the taxon represented by the evidence and its legal listing as endangered or threatened.

The pitfall of referring to the animal in question solely by its common, or vernacular, name is likely to result in misunderstandings or confusion in relation to the real identity of the animal being discussed. Reference hair collections, or questioned hairs, identified with vernacular names are likely to result in mis-identifications. For example, a sample labeled as dog may be hairs from domestic dog (Canis familiaris) or raccoon dog (Nyctereutes procyanoides), which is a wild species used in the fur industry. Fur apparel labeled as ‘dog’ may be mistaken as originating from a domestic dog instead of a farmed raccoon dog, which may lead to accusations that furriers are using domestic dogs in fur coats. In presenting testimony, we recommend the use of the common name and binomial scientific name when the animal in question is first mentioned and thereafter refer to the animal or taxon in question by its common name (a good example of the confusion that can arise is exemplified by the work of Peabody et al (6) where Felis catus (domestic cat) was confused with Felis ocreata catus (African wild cat)). Unfamiliarity with taxonomy and/or binomial nomenclature of animals cannot justify the sole use of common or vernacular names; in a forensic context the onus of unambiguously identifying the animal of origin of the questioned hair(s) solely relies on the scientist presenting the evidence, not the jury, legal counsel or the judiciary. In the provision of investigative leads, we would advocate the use of common names as
law enforcement personnel are likely to be non-specialists in relation to animal taxonomy, except
if there is a risk of misleading the investigators.

6. Future Directions in MIAH

6.1 Promoting Best Practice

A significant recent direction in MIAH, and other forensic wildlife disciplines, is in the formation
of the Scientific Working Group for Wildlife Forensics (SWGWILD). Founded in 2011 with
affiliation to the Society for Wildlife Forensic Science (SWFS)\(^2\), SWGWILD brings together
world wildlife forensic experts to promulgate best practice across diverse species and evidentiary
material unique to this field through the provision of standards, education, and certification starting
with the disciplines of DNA and Morphology. The production of these guidelines and
recommendations for wildlife forensic practices is the first of its kind. As such, it is a significant
milestone in formalizing practices and standards for this discipline to ensure practitioners and
laboratories are appropriately qualified, accredited and competent to be regarded as experts in the
MIAH.

6.2 DNA analyses and Microscopy

Over the years the molecular analysis of animal DNA has steadily increased in the investigation of
poaching and trafficking in CITES listed mammals (26), animal cruelty cases and crimes against
the person in which animal hairs are submitted for examination (5). However, whilst these
analyses are routine in specialized forensic wildlife laboratories, this is not the case for many
forensic laboratories, which usually deal with crimes against the person. In cases in which animal
hairs are critical to investigations, species identification is commonly outsourced to specialist
laboratories. However, the costs are prohibitive for regular or routine use of these services.
Therefore, it makes good economic and efficiency sense to subject unknown animal hair
specimens to morphological analysis first in order to establish whether molecular techniques are

\(^2\)http://www.wildlifeforensicscience.org/swgwild/
even required. Based on a global benchmarking process for forensic laboratories, FORESIGHT (27) the average cost per case for a human DNA analysis is $2,255 in 2012; if one or more items can be excluded from analysis by a simple microscopical examination, the cost savings to the laboratory can be significant. For example, it can be quickly decided whether the hair in question is human, animal, plant, or textile fiber in origin. If it is assumed that DNA analysis of animal hairs involves a similar cost then MIAH as the first step also makes economic sense for the same reasons. This is likely to remain the case until such time as NGS is routine, simple, validated for forensic purposes and more cost effective.

Research has shown the value of combining DNA analyses with the morphological examination of human hairs (28, 29) and there is no reason to doubt that the two techniques will be also be complementary in regards to animal hair identification as illustrated in the work conducted by Shajpal et al (30) in relation to wildlife forensic cases. Whilst DNA sequencing can identify the origin of an unknown animal hair and in time might even allow individualization within a species, MIAH in addition to providing a highly reliable screen can provide additional value in relation to mode of removal, effects of taphonomy, and identification of artifacts and treatments. For example, in a hypothetical case, a large clump of ‘big cat’ hairs is found in the back of a suspected poacher’s vehicle but further microscopical examination shows the presence of post mortem banding. This means that the hairs could only have originated from a decomposing body, which opens up the possibility that the suspect may have merely picked up a dead body rather than poached it.

7. Conclusion

Morphological identification of animal hairs is a robust and valid forensic technique; however, the integrity of the results is wholly dependent on the availability of type/or vouchered reference specimens and on the proven ability of the practitioner to accurately identify the animal of origin.
of unknown animal hair based on morphological characteristics and to present appropriate

Budowle et al (31) in their recommendations for animal DNA forensic and identity testing state “It is important to operate under a set of minimum guidelines that assures that all service providers have a template to follow for quality practices that can withstand legal scrutiny”. In this vein, from our experience in the field of MIAH (which amounts to over 60 years total just for two authors), we propose the following recommendations for legal practitioners, investigators, journal editors, and forensic scientists to consider when producing or reviewing MIAH statements, publications or reports.

- Microscopy. Scale patterns, medullae configurations, and root shapes (if present) must be recorded and appraised using representative samples of each hair type present in the sample. Scale patterns and medullae configurations should be determined along the length of the hair shafts.

- Images. Images used to record MIAH must contain scale bars that are clearly visible, the exception being scale cast patterns where it is inappropriate to include scale (since the entire diameter of the shaft may not be in contact with the medium). Image legends must include information on hair type, where on the hair the image was taken, and the somatic origin of the hair (if known). All images should clearly and unambiguously demonstrate the feature of interest.

- Descriptors. Nomenclature describing medullae and scale pattern configurations should include the reference from which the descriptors are taken.

- Comparative analyses. Confirmation of identification must result from a comparative analysis between the characteristics shown by the questioned hair and relevant hairs taken from a vouchered specimen and the points of comparison recorded.
• Taxonomic identification. Common names must be accompanied by binomial nomenclature i.e. scientific (Latin) names (at least at first mention)

References


Figure 1. Generic diagram of a mammalian hair shaft (Centre) which consists of three major components the central core or medulla (A), cuticle (B) and cortex with pigment granules (C) (For illustrative purposes only)
Figure 2. (A) Cat (*Felis catus*) guard hair with fibrillar root (bar 50μm); (B) overhair with spade shape root (bar 200μm).
(C) Dog (*Canis familiaris*) finer guard hair with fibrillar root (bar 100μm); (D) coarse guard hair with spade shape root (bar 200μm)
Figure 3. Images demonstrating that Pig (Sus scrofa) may be easily distinguished from human scalp hairs on at least two morphological characteristics. (A) Pig guard hair scale pattern showing close rippled margins of cuticle (guard hair along shaft length), compared with (B) human scalp hair which shows wider separation of scales. (C) Medullae exhibited by pig body guard hairs (mid shaft areas) compared with (D) finer, amorphous medulla in human scalp hair (along shaft length) (scale bars: C) 100 μm; D) 50 μm)
Figure 4. Transverse cross-sections of (A) polar bear (Ursus maritimus) dorsal overhairs and guard hairs (distal shafts) and (B) human beard hair, each showing a dark, central air filled medulla in unpigmented corte: Polar bear guard hairs showing (C) air filled medulla and (D) translucent or ‘cleared’ medulla filled with mounting medium. (Scale bars in C and D = 100μm)
Fig. 1. Generic diagram of a mammalian hair shaft (Centre) which consists of three major components the central core or medulla (A), cuticle (B) and cortex with pigment granules (C)  
(No scale bar, illustrative purposes only)

Fig. 2. Images of root morphologies that may occur on cats (*Felis catus*) and dog (*Canis familiaris*) hairs. Top panel cat guard hair with fibrillar root (bar 50μm), (B) overhair with spade shape root (bar 200μm). Lower panel: dog guard hair with fibrillar root (bar 100μm), (D) coarse guard hair with spade shape root (bar 200μm)

Fig. 3. Images demonstrating Pig (*Sus scrofa*) hairs may be readily distinguished from human scalp hairs, based on at least two morphological characteristics. Top Panel shows a close ripple scale pattern, with close margins on a pig guard hair (far left) and medullae exhibited by pig body guard hairs compared with human scalp hair which shows wider, smoother and regular wave cuticle scales and an amorphous central medulla.  
(Scale bars: (C) 100 μm; (D) 50 μm)

Fig 4. Transverse cross-sections of (A) polar bear (*Ursus maritimus*) dorsal overhairs and guard hairs (distal shafts) and (B) human beard hair, each showing a dark, central air filled medulla in unpigmented cortex.  
Polar bear guard hairs showing (C) air filled medulla and (D) translucent or ‘cleared’ medulla filled with mounting medium.  
(Scale bars (C) and (D) = 100μm)