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1 Introduction

Mammalian hair plays a variably important part in several branches of human society. Since historical time, the hair of mammals has been important not only as fur for clothing but also, in combination with natural or artificial fibres, for the production of cloth. Furthermore, the natural character of the hair of, for example, the marten, badger, and squirrel, is widely used in the manufacture of many different kinds of brushes. Finally – and this brings us to the subject of the present study – scientific research in such fields as animal ecology, wildlife biology, gamekeeping, hunting, and nature management, as well as forensic research, is often supplied with information by the unknown former bearer of hair found in nature or in the stomach, gut, and the faeces of carnivores and the pellets of owls and raptors (Twigg, 1975), where the hair often shows relatively little or no damage. The results of such research often contribute to a more detailed understanding of the distribution of mammals and give the investigator, interested in carnivores, more insight into the quality of the diet of these animals in different areas.

According to Tupinier (1973), early studies on mammalian hair were performed by Brewster in 1837 and Quekett in 1844. In 1920, however, Hausman promoted morphological hair research by undertaking some classification of the great variety of morphological structures occurring in mammalian species, and the terminology he introduced is widely used. Wildman (1954), too, devoted an extensive and thorough study to various kinds of hair, especially in relation to the textile industry. He examined both hair growth and hair morphology, and dealt not only with the manufacture of cross-sections, medulla, and cuticula, but also enlarged the terminology used for the description of cuticular and medullar patterns.

Many other scientists have contributed, each in his own way, to our knowledge of mammalian hair. Lochte (1938) dealt with the hair of a variety of species – up to the leopard, puma, and gorilla – in an extensive atlas. Unfortunately, an appreciable number of European mammals were omitted. Because it was published in the Polish language, the accessibility of Dziurdzik's (1973) key is very limited, but some years later (1978) her study on the Gliridae (six species) appeared in English. In Switzerland, a number of studies dealing with hair were performed. Tupinier (1973) used the scanning electron microscope to examine the cuticle of 29 West-European Chiroptera species belonging to ten genera and concluded that the cuticular scale forms have limited taxonomic value. Keller (1978–1981 *a*, *b*) published keys in a series of four papers providing valuable information concerning hair characters. Although it has no keys and almost no commentary, the atlas produced by Debrot *et al.* (1982) contains drawings of cross-sections and photographs of cuticula and medulla of European mammals that are very useful for comparison. All of these publications have the most relevance for the morphology and structure of the hair of European mammals, but outside Europe, too, a number of scientists contributed to this field: Mathiak, 1938*a*, Williams, 1938, Benedict (1957; Chiroptera), and Brunner & Coman, 1974.

In general, identification of a plant or animal is difficult if only minor parts are available. When there are a few hairs of a mammal, the only clues are provided by the colour, form, and length of the hair and the structure of cuticula, medulla, and cross-sections. Nevertheless, it is often possible to reach correct determination by using combinations of these few data. This makes it absolutely necessary to provide the reader with an identification key in a way allowing him to learn to distinguish the often small differences between hairs. A photo atlas alone is not sufficient for reliable identification. The same holds for the great majority of the published identification keys, because the character information is inadequate and poorly defined. It is especially important that keys intended for hair identification provide both detailed pictures and text to keep the user from going astray. In the present publication he will find detailed keys with many drawings and a comprehensive photo atlas given in Parts II and III, respectively.

2 Hair growth

Several authors have described the development and growth process of hair (Hausman, 1930; Wildman, 1954; Lyne, 1966). The following is a simplified summary of this process.

The skin of an animal has two main layers: a lower layer called the dermis and an upper layer called the epidermis (Fig. 1). The epidermis is composed of layers of dead and living cells. One of the latter is the basal layer whose cells continually divide and maintain the epidermis. The outermost layer of the epidermis forms a thin, horny covering composed of dead cells which peel off continuously. At a given moment, the basal layer starts to show a shallow downward growth locally into the dermis, where, in combination with a dermal papilla, it forms a small solid plug. This is a young hair follicle. Cells of the dermis then form a connective-tissue sheath and small blood capillaries around the growing follicle to supply nutriment to the newly organized tissue

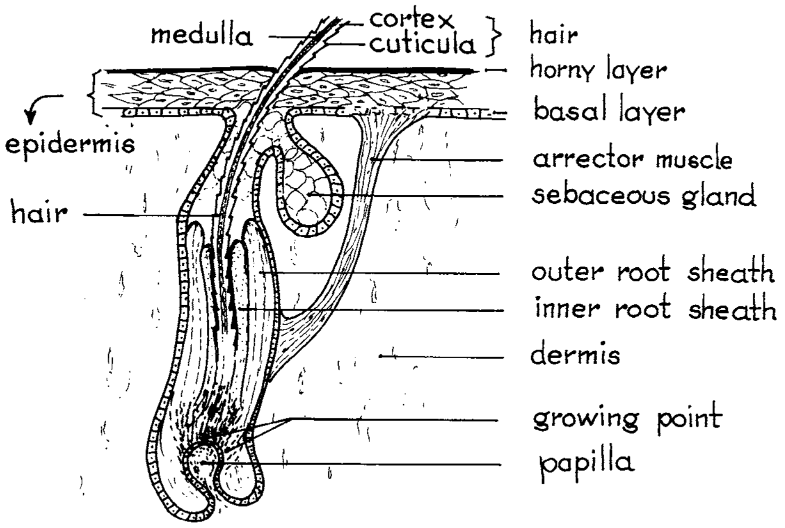

Fig. 1.
Schematic representation of section of a hair follicle.

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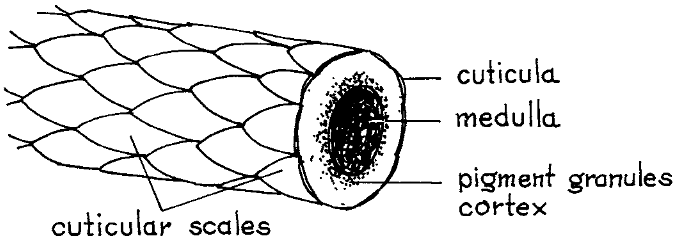
(Wildman, 1954). Next, outgrowths appear on the neck of the follicle and form a wax gland. In some animal species, an arrector muscle develops as well, which permits hairs to be set up. The cells at, and around, the base of the follicle (i.e. the growing point) then divide rapidly. Those situated beside the growing point form the layers of the inner and outer root sheaths, the hair itself being formed of the more centrally placed cells.

When the cells are pushed further from the growing point, their nuclear bodies gradually become smaller and the formation of horn or keratin starts in the cell. Particularly in the cells forming the inner root sheath, this process of cornification proceeds faster and starts lower down, than it does in the more central layers that form the final hair. Two factors, i.e. the presence of the comparatively rigid inner root sheath round the soft, flexible young fibre cells and the direction of the growing point, play an important role in determining the shape of the hair when it eventually emerges from the skin (Wildman, 1954). The wax gland (called the sebaceous gland) introduces into the young follicle wax cells through which the tip of the growing hair can easily push its way. This, in turn, produces a bulge in the rather tough horny layer of the epidermis still lying over the tip. When the pressure becomes too strong, the bulge in the horny layer ruptures, which allows the tip of the new hair to emerge above the skin surface (Wildman, 1954) (Fig. 1).

A hair consists of three layers, all of which are very important for identification, i.e. the cuticula, the cortex, and the medulla (Fig. 2). In many species the hair follicles are grouped together, the size and arrangement of the groups varying widely. Some time after the onset of follicle formation, two more follicles appear, one on each side of the primordial follicle, forming what is called a trio group. After that, other hair follicles may develop. In various groups of animals, secondary follicles emerge via bulges on the inner side of a hair follicle after passing through roughly the same developmental stages as the original follicle and then using the same opening to emerge. In adult Merinos, for example, as many as nine follicles can occur in one bundle with a common orifice (Lyne, 1966).

The continuation of the physiological processes in the animal's skin finally leads to moulting. Many hair physiologists have discussed this phenomenon. Apparently, the moulting process differs between species. Becker (1952) reported that, in the brown rat, *Rattus norvegicus*, moulting is independent of season, both in the laboratory and in the wild. In *Microtus* and *Apodemus*, moulting takes place throughout the year with peaks in the autumn and spring, especially in *Apodemus* (Stein, 1960). In the bank vole, *Clethrionomys glareolus*, less than 2% of the animals moult in the winter as against 37% in the summer. Moulting is somewhat more dependent on the season in this species (Stein, 1960). In the striped field mouse, *Apodemus agrarius*, the hair is shorter and thicker in the summer than in the winter (Haitlinger, 1968 *a*). In Soricinae, the H-profile is always the same whatever the season (Keller, 1978; Vogel & Köpchen, 1978).

Fig. 2.
Schematic representation of a cross-section of a hair.



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Thus, it is clear that moulting does not simplify identification. However, the morphology of cuticula, medulla, and cross-section is not so variable as to make identification impossible.

Note
During the development of a hair, the proportion outside the skin increases steadily. The structure of the cuticula, cortex, and medulla of the exposed part no longer changes, because the cells have died and become keratinized.
The fur of a moulting animal shows many hairs in different stages of development, which means that such hairs lack basal parts to some extent. It is of great importance that these parts be distinguished, which can be done on the basis of the cuticular pattern and the medulla. In a full-grown hair the last cuticular cells to be formed always have a simple structure at its extreme base and the medulla is absent in that area (Fig. 3).

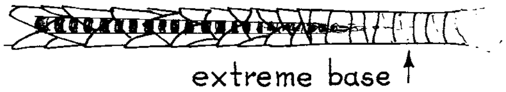


Fig. 3.
Basal part of a hair.

There are various types of hair, e.g. vibrissae (whiskers), bristle hairs (domestic pig), overhairs, and underhairs, more than one type often occurring on the same animal. Vibrissae are readily recognized, their structure being very similar in different species. Most vibrissae are circular in cross-section, and they are the only hairs to taper all the way from the base to the tip. Since the value of this type of hair for identification purposes is limited, it is not included in the keys. The spines of the Western hedgehog are greatly enlarged and strongly modified hairs. Possible interspecies differences due to age, diet, disease, environment, or season, will not be taken into consideration here.
Due to the absence of GH 1 and GH 2 (see 4.1) in very young animals, identification of these is almost impossible.

3 Geographic area and species studied

This study covers all wild terrestrial mammals of the western part of Europe – including Denmark, Germany, The Netherlands, Belgium, Luxembourg, the northern part of France, Great Britain, and Ireland – except for a few species running wild in Great Britain, sika deer (*Sika nippon* (Temminck)), muntjac (*Muntiacus muntjac* (Zimmerman)), reindeer (*Rangifer tarandus* (L.)), and the genet (*Genetta genetta* (L.)), which is seen occasionally. The agricultural domestic mammals such as the horse, cow, pig, and sheep are not dealt with. A list of the animals included, with their scientific names and common names in English, German, French, Danish, and Dutch, is given at the end of this book.

Part I

How to identify hairs

4 Features with importance for identification and terminology

4.1 Hair profile

As already mentioned, an animal's coat is composed of several types of hair, the main components being the overhair and the underhair (Fig. 4).

Overhair is the long and stiff hair (called guard hair) with a thickening in the distal part called the shield and a thinner proximal part, the shaft (distal = toward the tip, proximal = toward the base of a hair). Underhair is made up much thinner and less stiff and has an undulating appearance. Although the transition from the longest overhair to the shortest underhair is more or less gradual, four main groups can be distinguished, three of them belonging to the overhair (GH 0, GH 1, and GH 2). The scarce GH 0 is a long, firm, and, as a rule, straight hair with an elongated, sharp tip. The diameter of the thickest part of the shield is generally smaller than that in GH 1 and GH 2. This type of hair is most characteristic in the Rodentia (Fig. 4).

The GH 1 hair is usually straight and stiff too but its occurrence is much more frequent (by a factor of some dozens) than that of GH 0. Moreover, the distal part of the shield is less elongated than in GH 0, and this means that the thickest part of the GH 1 shield is a little closer to the tip (Fig. 4). In some species, GH 1 may be slightly wavy or even bent (see species numbers 10 and 49 in the atlas section).

In GH 2, the shield and shaft usually form an angle with each other. The shaft is rather straight as a rule, but may be wavy or zigzag in some groups and/or species (Figs. 56a and 60; species number 55 in atlas section). In other species, GH 2 is rather similar to GH 1, and, in such cases, the smaller type of GH 1 is classified as GH 2. This often occurs in the somewhat larger animals such as the badger (*Meles meles*), wild boar (*Sus scrofa*), and deer (*Cervidae*). The GH 2 type is always more numerous than GH 1.

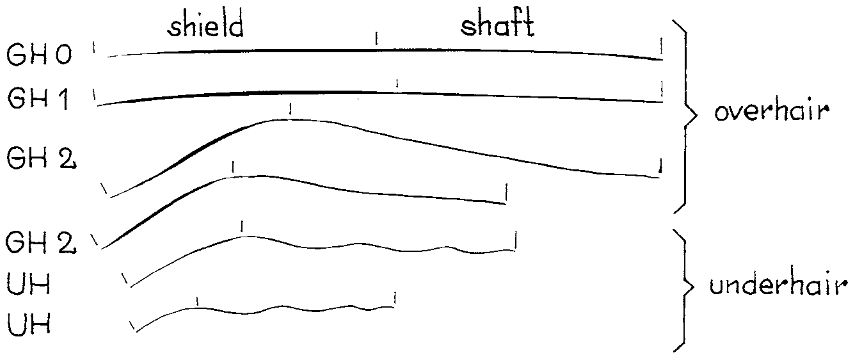


Fig. 4.
Types of hair (the tip of the hair points to the left).

Underhair is the predominant type of hair in a coat but has limited taxonomic value. The shield, the distal articulation of this type of hair is insignificant and shows little or no thickening (Fig. 4).

4.2 Cuticula

The outermost layer, the cuticula (Fig. 2), is made up of a large number of overlapping transparent scales of keratin. The distal part of each scale lies over the proximal part of the next one, and, as a result, each hair has less resistance from base to tip than in the opposite direction. This property is useful for rapid determination of which end of a hair is the tip. When a hair is taken between the thumb and forefinger of each hand and pulled gently, the tip of the hair will be on the end that slips out of the fingers.

The size and shape of the scales vary according to the position on the hair. At the tip, the first scales to appear are small. On the widest part of the shield, the scales are much larger and lie transversely (Fig. 5). Many different shapes occur along the shaft. In general, these scales represent differences between species and/or groups better than those in the shield do. The last scales to be formed, i.e. those at the extreme base of the hair, are simple in form (Fig. 3), and are very similar in all species. The presence of this type shows that the growing stage has been completed (see under Note in Chapter 2).

The shape of the cuticular scales is very important for identification, but usually they can not or can hardly be seen with a light microscope without special preparation. This problem can be solved by making a gelatin impression of the hair (see Chapter 5 under *Material and techniques*), in which the outline of the scales can be seen as thin lines together forming what is called the scale pattern.

4.2.1 Scale position relative to the longitudinal axis of the hair

Transversa

These scales lie at right angles to the longitudinal axis and their width is greater than their length (Fig. 5, also Figs 8, 13, 15, 17, 18).

Longitudinal

The scales lie parallel to the longitudinal axis of the hair and their length is greater than their width (Fig. 6, also Figs 9 and 10).

Intermediate

In these scales the length is approximately the same as the width (Fig. 7, also Figs 11 and 12).

4.2.2 Cuticular patterns

Petal pattern

The general appearance of this pattern is similar to that formed by the overlapping petals of a flower (Wildman, 1954).

1. Broad petal pattern. This pattern is made up of wide scales (Fig. 8).
2. Elongate petal pattern. This pattern is intermediate between the broad and the diamond petal patterns (Fig. 9).

Diamond petal pattern

In this pattern the scales overlap in a way giving them a diamond shape. The pattern resembles that of a pine cone.

1. Narrow diamond petal. The scales are long and narrow (Fig. 10).
2. Broad diamond petal. The scales are rather short (Fig. 11).

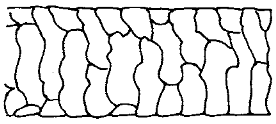
Mosaic pattern
The adjacent scales have rather straight margins (Fig. 12).

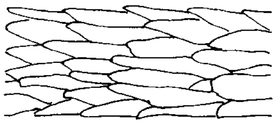
Waved pattern
The pattern is usually transverse with weakly to strongly undulating margins. We distinguish:

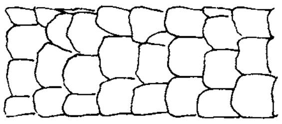
1. The regular wave: The scale always lies transversely. The waves are shallow (Fig. 13).
2. The irregular wave: The scale usually lies transversely (Fig. 5) and sometimes longitudinally (Fig. 6). The waves have deeper troughs and are less regular (Fig. 14).

Figs 5–22.
Cuticular patterns
(the tip of the hair points to the left).

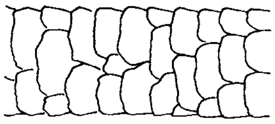
I SCALE POSITION IN RELATION TO LONGITUDINAL DIRECTION OF THE HAIR

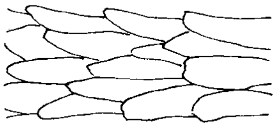

5. transversal

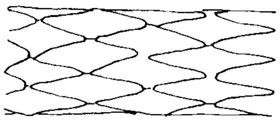

6. longitudinal

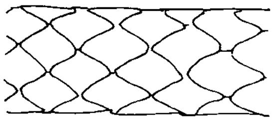

7. intermediate

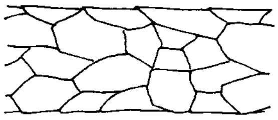
II SCALE PATTERNS

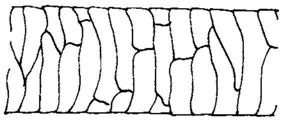

8. broad petal

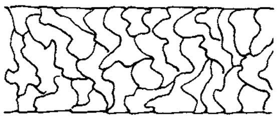

9. elongate petal

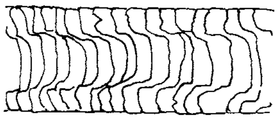

10. narrow diamond petal

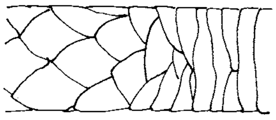

11. broad diamond petal


12 mosaic

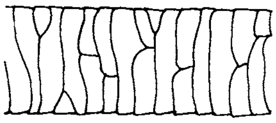

13. regular wave

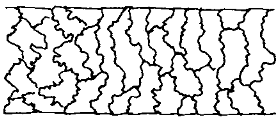

14. irregular wave

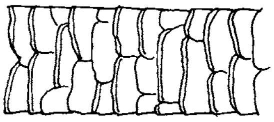

15. streaked


16. transitional

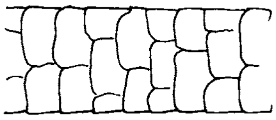
III STRUCTURE OF SCALE MARGINS

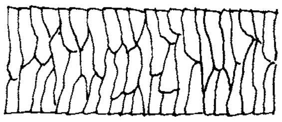

17. smooth

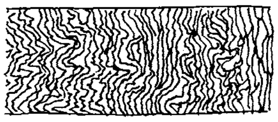

18. rippled


19. frilled

IV DISTANCE BETWEEN SCALE MARGINS


20. distant


21 . near


22. close

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3. The streaked pattern: This occurs in hairs with a longitudinal furrow in the shield (Fig.15).

Transitional pattern
Occurs between two patterns (see, e.g. Fig. 16), frequently occurs just distal to the lowest part of the shaft. A similar alteration can always be seen in the proximal part of the shield.

4.2.3 Structure of scale margins

Smooth: The margins of the scales show no indentations and appear as a smooth line (Fig. 17).

Rippled: There are small indentations along the margins, usually close together (Fig.18).

Frilled: This term is used for scales showing narrow borders (± 1 μm) along the distal part. Such borders may be rather smooth or dentated (Figs 19, 198a, 200b). The width of the border may increase up to 3 μm toward the tip in some species (Figs 198b and c), and in such cases half or more of the next scale may be covered.

4.2.4 Distance between scale margins

The distance between scale margins may vary considerably. To indicate such differences, the terms distant, near, and close (Figs 20–22) have been introduced.

4.3 Cortex

The central layer between the cuticula and the medulla, i.e. the cortex (Fig. 2), has been discussed by Hausman (1930, 1932). It is composed of longitudinal, cornified, and shrunken cells, which appear under the light microscope as a homogeneous, hyaline mass without any details, and is therefore of limited value for identification. In some cases, however, the thickness of the cortex relative to the total width of the hair can be important. Here, use will be made of the term CC/TW (expressed in μm), in which CC is the width of the combined cuticula and cortex and TW is the total width of the hair. Both CC and TW must be measured in the widest part of the shield (Fig. 96), using the medullar slide.

The pigments which are largely responsible for the hair colour may take the form of discrete granules, large amorphous masses, or diffuse stain (Hausman 1930). The majority of the granules are found in the cortex, whereas the other forms occur almost entirely in the medullary column. Because of the large variation, even within the same type of hair, the pigment granules are of little value for identification.

4.4 Medulla

The pith of a hair, the medulla (Fig. 2), is composed, like the cortex, of closely packed, shrunken dead cells, but unlike the cortex they are clearly visible. These cells and the air-filled spaces between the intercellular connections are responsible for the specific character of the medulla.

In many cases, the medulla is so dark that structures can hardly be seen. Substantial improvement can be obtained by saturation of the hair with paraffin oil; this fills the air spaces, which become transparent (for technique, see Chapter 5). For identification, slides both with, and without, oil penetration are needed. In general, the medulla on the widest part of the shield is the most important structure, especially for identifying the orders. Morphologically, the medulla shows many different patterns. Some of them are very distinct, whereas others, for instance those formed by structures in the vicinity of the outer layer of the medulla in some carnivores, can only be seen after careful inspection.

The main patterns and the related terminology are discussed in the following section. In medullar drawings and photographs with both light and dark parts, the light area represents the situation after oil penetration and the dark part the situation without oil penetration.

Note
Sometimes the digestion process in the stomach and gut of a predator changes the medulla of the prey to a degree making identification of the original pattern difficult, but experience usually solves most of these problems.

4.4.1 Composition of the medulla

The cellular structure of the medulla can be unicellular or multicellular.

A. *Unicellular*: The medulla is composed of a single layer which is one cell wide, the pattern being regular (Fig. 23) or irregular (Fig. 24).

B. *Multicellular*: The medulla is composed of two or more layers of cells (Figs 25 and 26).

4.4.2 Structures of the medulla

The arrangement of the cells forming the medulla can take the following forms:

A. *The ladder pattern*: Between all cells there is a lighter area with almost the same dimensions, which creates a ladder effect (Figs 23 and 27). This pattern is usually restricted to the shaft. Sometimes there is a pattern resembling letters X, Y, V, M, N, or reversed (Fig. 24), which is brought about by air-filled spaces lying obliquely between contiguous cells.

B. *The intermediate pattern*: A ladder pattern is sometimes so indistinct that a sort of 'wreathy' pattern called intermediate arises. This phenomenon usually occurs in the shaft (Fig. 28).

C. *The cloisonné pattern*: Shrinking of the cells forms thin, intersecting thread-like lines giving rise to an angular network pattern called cloisonné. Within these partitions, some structured elements can be clearly observed. The spaces within these structures are transparent and are slightly lighter because of the absence of structure (Fig. 29, right side shows oil penetration).

D. *The reversed cloisonné pattern*: In this type of medullar pattern the cells are voluminous and the spaces between them form a thread-like pattern. The cells are granular, the thin spaces between them lack visible structure (Fig. 30). This pattern is multicellular but the cells do not lie in rows and the pattern often lacks strong contrasts.

E. *The isolated pattern*: The dark cells are occasionally contiguous but are usually separated to a variable degree and are easily recognized. The shape is circular up to oblong (Figs 25 and 31).

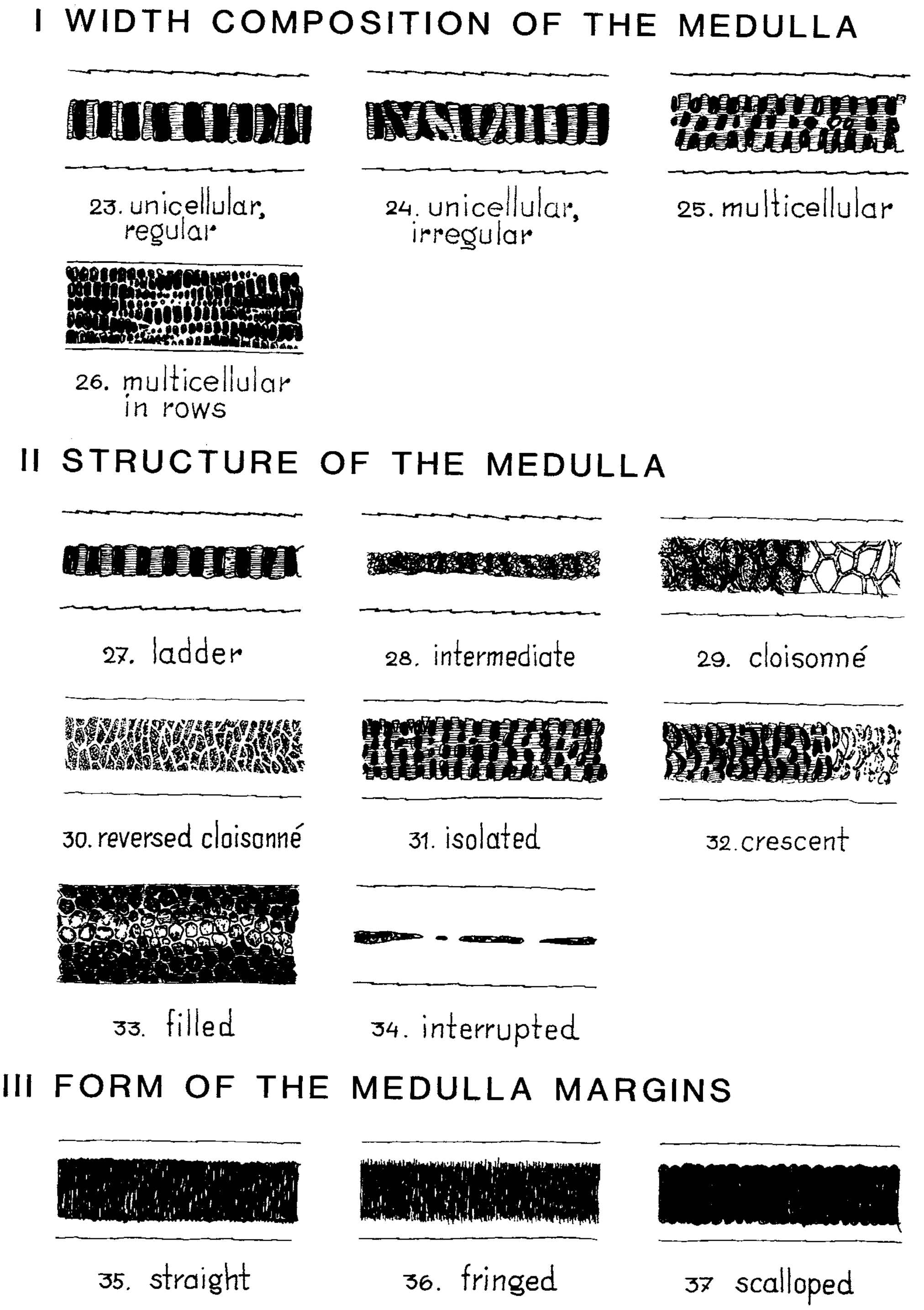
F. *The crescent pattern*: The dark cells form a pattern imposed by their shape. The cells are rather long and slightly curved, tapering at the ends. Many of them touch and overlap each other. The spaces between the curved cells have the shape of a banana or crescent (Fig. 32).

G. *The filled pattern*: Medullar cells seem to fill the entire width of the hair, and the cortex can hardly be distinguished (Fig. 33). The pattern is multicellular, but the cells do not lie in rows. A cloisonné becomes very distinct after the penetration of oil (Fig. 277).

H. *The interrupted pattern*: This pattern takes its name from the absence of the medulla at one or more sites (Fig. 34). If several, separate little pieces of the medulla are present, the pattern is called fragmental.

4.4.3 Margins of the medulla

Certain features of the margins of the medulla have importance for identification. These features can be seen most clearly before treatment of the hair with oil and concern only the widest part of the shield.



Figs 23–37.
Appearances of the medulla (the tip of the hair points to the left).