Structural Characterization of the Whisker System of the Rat

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***Abstract*—Vibrissae or tactile hairs, commonly known as whiskers, are the mechanical gates of special mechano-sensitive organs. In terrestrial mammals, they carry various functions, especially object determination and texture discrimination. We hypothesise that the characteristic morphology and structure of whiskers is a primary morphological condition for their mechano-sensitive functions. To constitute mathematical models on the systematic but different mechanical behavior of the main types of whisker hairs (micro vibrissae, macro vibrissae, straddlers), information is lacking on the distribution of properties in a field of all three types of hairs, taken from one and the same animal. Referring to sets taken from five individuals, geometry data is provided as one complete set for a female rat (*Rattus norvegicus*). Due to measurements of diameters along the length, the shape of whiskers in rats is confirmed to resemble a cone, which may be overlaid by some convexity or concavity. Additionally, the surface and internal structure of different vibrissae were examined by scanning electron microscopy. The cuticle of the rat whisker consists of flat scales, overlapping like roofing slates. A cross section reveals up to 20 superposed layers of cuticular scales. The longitudinal dimension of one scale is shorter in whiskers compared with body hairs. A hollow medulla is observed from the base to approximately half of the overall length, which is then partially filled by compact tissue, until it disappears completely near the tip. An extraordinarily thick cortex probably rules the characteristic bending features, and the multilayer cuticle probably has a mainly protective function.**

***Index Terms*—Biomimetics, rat vibrissae, structure, tactile sensors, whiskers.**

I. Introduction

VIBRISSAE form the first mechanical element of a complex mechano-sensitive organ, which beneath a lot of other hypothetized functions allows mammals to localize objects and to discriminate their surface structure (cf. the overview in [20]). To understand the observed physiological behavior of whiskers, the underlying control laws acting on the follicle sinus complexes (FSCs) as active bearings of the hairs, and at last at biomimetic transfer into technical sensor principles, we try to constitute mathematical models of the mechanical behavior of vibrissae.

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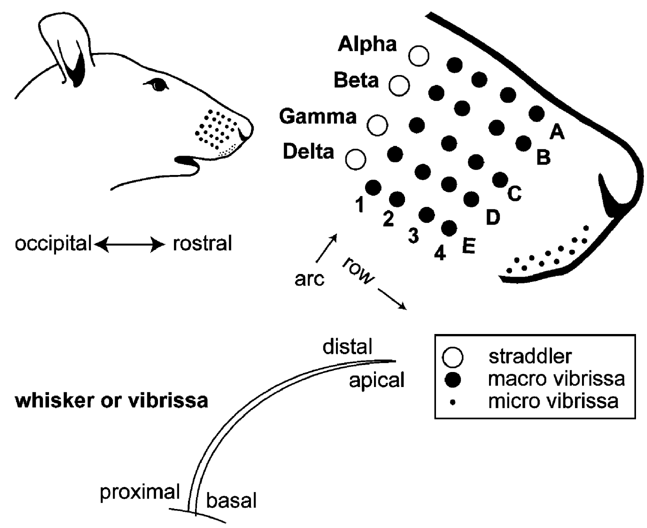

Fig. 1. Morphological designation of mystacial vibrissae. The individual of *Rattus norvegicus* described owned four rows of macro vibrissae numbered 1 to 4 from occipital to rostral, and five arcs of macro vibrissae called A (near *Dorsum nasi*) to E (near the mouth). Straddlers situated occipital between the rows of macro vibrissae are identified by Greek letters Alpha to Delta corresponding to the next nasal row of macro vibrissae. Micro vibrissae are named following an analogous sequence from MicroA to MicroE.

From literature, no set of data necessary for this task, describing morphology, structure, and material properties of a complete array of mystacial vibrissae of a terrestrial/arboreal mammal is available. Thus, in a first step, we provide data on the outer and inner geometry of mystacial vibrissae of a rat, addressed via their location in the fields of macro vibrissae, micro vibrissae, and straddlers (see Fig. 1 for that terminology).

The morphological features of various types of hair are used for their characterization in widely varying branches of science [17]. In addition to the macroscopic features of form, size, profile and color, microscopic characteristics are gaining in significance, an observation that applies both to the distinction of different hair types of one species and the comparison of those of different species [21]. The crucial characteristics are the shape, the varying cross section, and the surface texture. To microscopic characteristics belong the form and size of the cuticular scales, as well as the nature of the medulla. The properties of any hair are modified by a number of environmental influences which complicate general characterization, such as climate, habitat, ectoparasites, or nutrition [9].

Latzke [11] suggests a structural classification:

- cross-sectional shape: round or with another profile (e.g., angular, lobed, dentate, etc.);
- cross-sectional shape: filled (solid) or hollow (mono- or multitubular);

- surface finish: smooth or structured (fibrillate, grooved, scaled, etc.).

These structural characteristics of hairs of different species play an important role in the comparison of species and zoological systematization, in criminology and forensic medicine. Thus, there have been some attempts to use scale, form and arrangement for the identification of the species of a mammal [12]. Morphology, however, serves the purposes not only of systematization and classification, but also of the analysis of numerous functional characteristics. It is for that reason that this study of the structural characteristics of the vibrissae system is offered.

Vibrissae grow on different body regions, but are limited to certain areas [10] and perform special sensory functions. In this study, we concentrate on mystacial vibrissae (facial vibrissae, whiskers), arranged around the snouts of terrestrial/arboreal mammals (Fig. 1). Macro vibrissae, long, thick hairs of the snout region, clearly visible to the human eye, are used for distance detection in object localization and the estimation of an object's size and shape [2], [5]. Micro vibrissae are shorter tactile hairs at upper and lower lip, which enable an animal to detect surface texture and material properties [8]. The surface texture is perceived at very high resolution. Rats, for example, can differentiate rough and smooth surfaces, if the grooves are as little as 30 μm deep [3]. "Straddlers are the four caudal-most whiskers of the mystacial pads, and are found only in rodents." [2].

It is the aim of this study to characterize the morphology and structure of rat whiskers (which especially in this species are also sometimes called sinus hairs), to support identification of structure-function-correlations.

II. Material and Methods

A. Biological Material

Vibrissae of five different rats were examined, in two individuals the complete whisker arrays were analyzed. These rats were female Wistar Hannover rats from the same clade, and had died from natural causes at an average age of approximately 14 months at a farm for laboratory animals. In the case of rat 1, the postmortem sampling took place using tweezers to pull each whisker of the mystacial pad (Fig. 1) out of its follicle. The whisker was gripped as close as possible to the skin in order to minimize damage through the pressure of the tweezers. With rat 2, the whisker was held with tweezers and the shaft was cut off close to the follicle. Since the first method according to microscopic inspection provoked less damage, this method also was chosen for rats 3 to 5. For comparison, some body hairs were taken from each rat's back.

B. Analyzing Length and Diameter

The external geometrical parameters of the vibrissae were first determined, to provide information on the shape and dimension of whiskers. The overall length of the vibrissae was measured with a ruler, against which the whisker was laid with contact at base and tip and as far as possible parallel. For this purpose, the natural bending of whiskers was straightened by slightly squeezing the hair with a second ruler against the first one. The diameters were measured at five defined measuring points (Fig. 2). Procedures were repeated three times each.

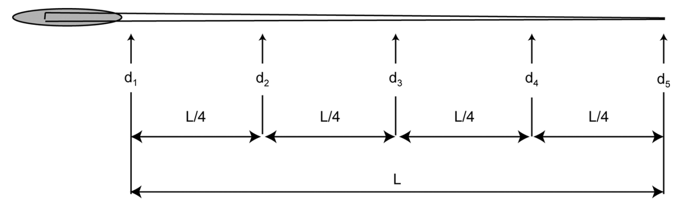

Fig. 2. Diameter measuring points along a vibrissa.

The first measuring point was directly after the follicle at the point of skin exit of the hair. The remaining four values were measured at points in quarter steps of the length of the particular whisker.

For these measurements of the diameter a "Militast 1083" micrometer gauge with a cylinder diameter of 1 mm was used as measuring probe. Tweezers were used to fix the hairs to a sample table and the probe tip was attached to the vibrissae at the selected measuring point. Accuracy to approximately 1 μm can be achieved by this means.

C. Making Cross Sections

Cross sections were made with the aid of a micro laser (P.A.L.M. Microlaser Technologies, Carl Zeiss® AG) to enable more exact statements about the morphology of the three hair layers, cuticula, cortex, and medulla to be made. The microlaser makes it possible to cut the tactile hair precisely and under small demand. Cross sections with a thickness of only a few μm can be produced and observed immediately under an inverse optical microscope (Carl Zeiss® AG). For the analysis of the cross sections in a scanning electron microscope (SEM) hair segments between 5 and 10 mm of length were made, fastened on a sample holder, and fixed perpendicularly to the electron beam in the SEM.

D. Light Microscopy

For an overview of surface and internal structure of the vibrissae they were analyzed with a light microscope: the research microscope AxioObserver (Carl Zeiss® AG) with high-performance lenses, permitting enlargements between fivefold and a hundredfold.

E. Scanning Electron Microscopy (SEM)

For detailed examination of surface and internal structure, a SEM was used (Philips® ESEM REM XL 30). SEM allows the imaging of objects with high depth of sharpness and a maximum enlargement of 100.000:1. The resolution is clearly finer than that of a light microscope. A coating with gold is unnecessary during sample analysis in the Environmental Scanning Electron Microscopy (ESEM) mode which is an advanced form of electron microscopy not requiring an absolute vacuum, and thus not requiring conductive samples.

Vibrissae were attached to a sample holder with an electrically conducting (C endowed dosed), double-sided tape. Photographs were taken in different enlargements and the vibrissae measured. The contour and size of the hair scales and how these altered along the hair were determined.

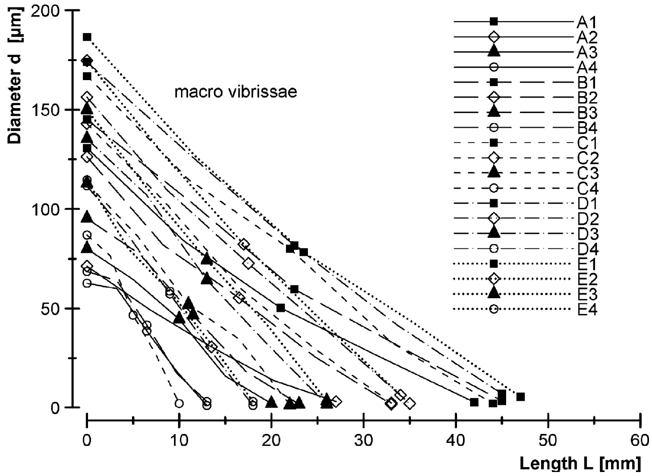

Fig. 3. *Rattus norvegicus* Wistar Hannover: Diameter over length (from hair-base to hair tip) of macro vibrissae. Identifiers of hairs correspond with Fig. 1.

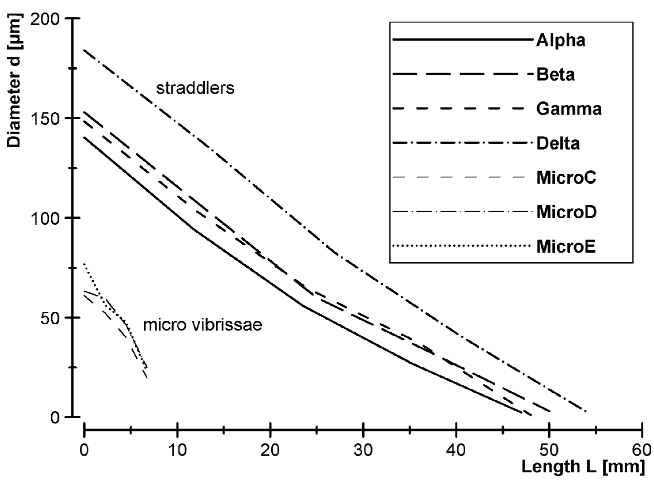

Fig. 4. *Rattus norvegicus* Wistar Hannover: Diameter over length (from hair base to hair tip) of straddlers and micro vibrissae. Identifiers of hairs correspond with Fig. 1.

III. Results

A. Length and Diameter

Even though geometrical values were taken from five individuals from an inbred stem (Wistar Hannover), lengths and diameters massively differed between corresponding hairs of different animals. On the other hand, intraindividually the geometrical descriptors showed systematic distribution in the mystacial field. Thus, geometrical data is reported for one individual, avoiding the overloading of figures by standard deviation bars.

Fig. 3 gives the diameter of macro vibrissae along the long axes of hairs from the "hair base" (the hair getting visible outside the skin, not the hair follicle, see above) to the tip. Fig. 4 reports this data for micro vibrissae and straddlers. The length of whiskers systematically decreases from straddlers (occipital) via macro vibrissae to micro vibrissae (rostral) (along rows), while the decrease from mouth to nasal roof (along arcs) is less systematic. In tendency, hairs are the "thicker" the longer they are. In combination, the "largest" hairs are the straddlers near the mouth, the "smallest" hairs the micro vibrissae near the nose. Due to the anatomy of a rat's head, this means that whisker increase their size steadily in the direction from nose to eye, forming the well-known "basket" of whiskers bent to the frontal.

B. Possible Sources of Error

For the measurement of the overall hair length the following sources of error need to be taken into account. The biased error of the ruler is approximately ± 0.5 mm. Because of the preforming of the whisker, exact measurement of the length is quite difficult, and an allowance of approximately ± 2.0 mm is made. The accuracy of the diameter analysis by means of a micrometer gauge is $\pm 1\ \mu$m, but for the maximum diameter under the cylinder probe width of 1 mm. This error shows highest effect in the whiskers with the steepest cone shape, the micro vibrissae (cf. Fig. 4). Due to the high fragility of these whiskers, measurements with the cylinder probe at the "real" tip lead to breaking of the hair. Thus, for micro vibrissae, the absolute error of diameter measurement is maximal, but not exceeding $+3\ \mu$m.

The determination of the exact measuring point on the longitudinal axis is another potential source of error, arising from:

1) Choice of measuring position along the whisker.
2) Choice of measuring position across the width of the whisker.

A commercially available ruler was used to find the measuring position; this error is again estimated to be ± 2.0 mm. As to the hair width, the error arising from variation of the measuring position along the hair width is relatively small, especially in view of the fact that each diameter was measured three times. The coefficient of determination for linear regression shows that these errors have only a negligible influence on the overall result.

C. Surface Structure

The surface, i.e., the structure of the outermost hair layer (cuticle), of different vibrissae was examined by scanning electron microscopy. Fig. 5 gives as an example the surface textures of a macro vibrissa and of a micro vibrissa in comparison to that of a body hair. No differences were to be noted among the surface textures of different types of vibrissae.

The cuticle of the whisker consists of flat scales, overlapping like roofing slates. The free end of these scales points in the distal direction. The scales are arranged in an irregular pattern, which does not alter along the hair. Only the scale size varies, though this is without exhibiting any uniform dependence on hair diameter. The edge of the individual scales of different vibrissae is serrated to different depths.

Comparing the pattern and size of the scales of whiskers with those of normal body hairs from the same animals, clear differences are observable. From the large number of overlapping cells with serrated edges, the irregular whisker scale pattern resembles the cuticle of a human hair. The body hairs of rats, however, consists of a clearly smaller number of scales with small edges, in a regular arrangement. This sort of regularity is also described for the wool and the guard hairs of different breeds of rabbit [17]. The scales on rat body hair extend wider in the proximal-distal dimension, with an average length of 24.75 μm (standard deviation 2.22 μm) than in the lateral direction, while those of the whiskers are wider in the other direction ($\varnothing$ 5.43 μm in the proximal-distal dimension, with a standard deviation of

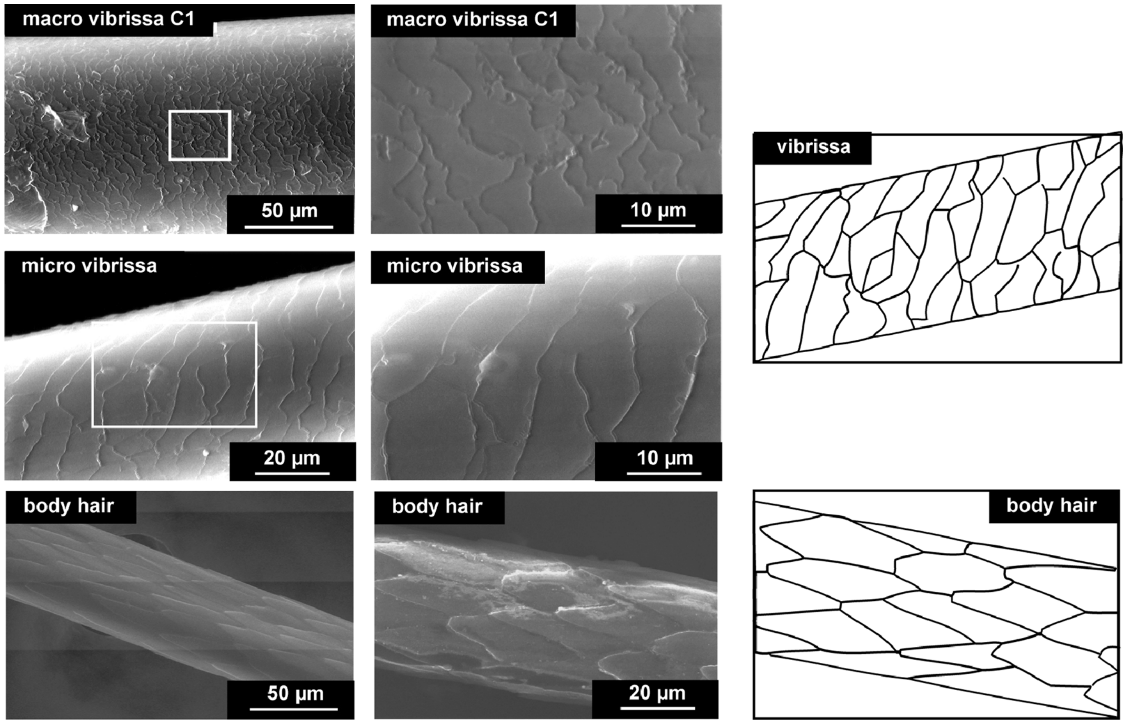

Fig. 5. SEM photographs of a macro vibrissa, a micro vibrissa and a body hair: surface texture (variously enlarged).

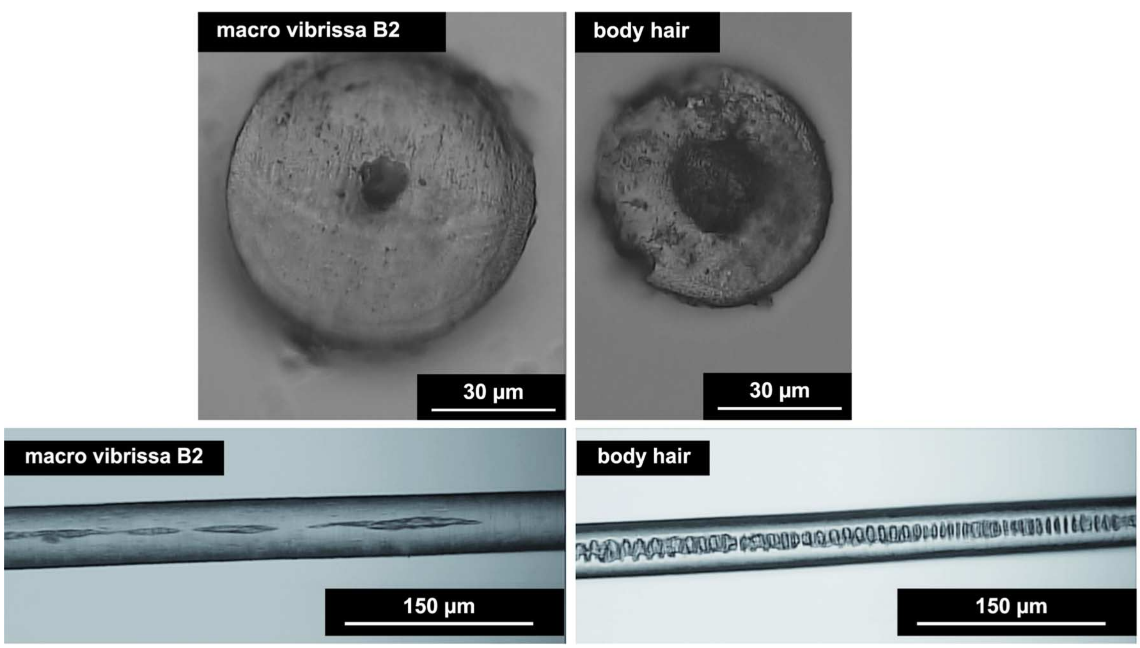

Fig. 6. Light-microscope photographs of the B2 macro vibrissa and a body hair. The dimensions of the cuticle and the cortex of the mystacial vibrissae are clearly much greater than those of body hair (and even of carpal vibrissae, own yet unpublished results). In contrast, it is the medulla of the body hairs which takes up the largest portion of the total cross section.

2.17 μm). Because of the very strongly serrated edge of some of the whisker scales, the width of scales varies, while the greatest width of the body hair scales is always to be found in a proximal-distal alignment, while whiskers to a helical, circumferential deviation of their long axes. A similar surface texture can also be found on the woolly hairs of different breeds of rabbit [17]. There is no significant correlation between the length of the scales and their distance from the base of the hair.

D. Internal Structure

The whiskers were analyzed with a light microscope to provide an initial overview of the internal morphology. These photographs already show clear changes along one vibrissa. A comparison with body hairs also reveals some special characteristics of the whiskers (Fig. 6). A channel is observed from the base to approximately the half the overall length, which is then partially filled by compact tissue, until it disappears

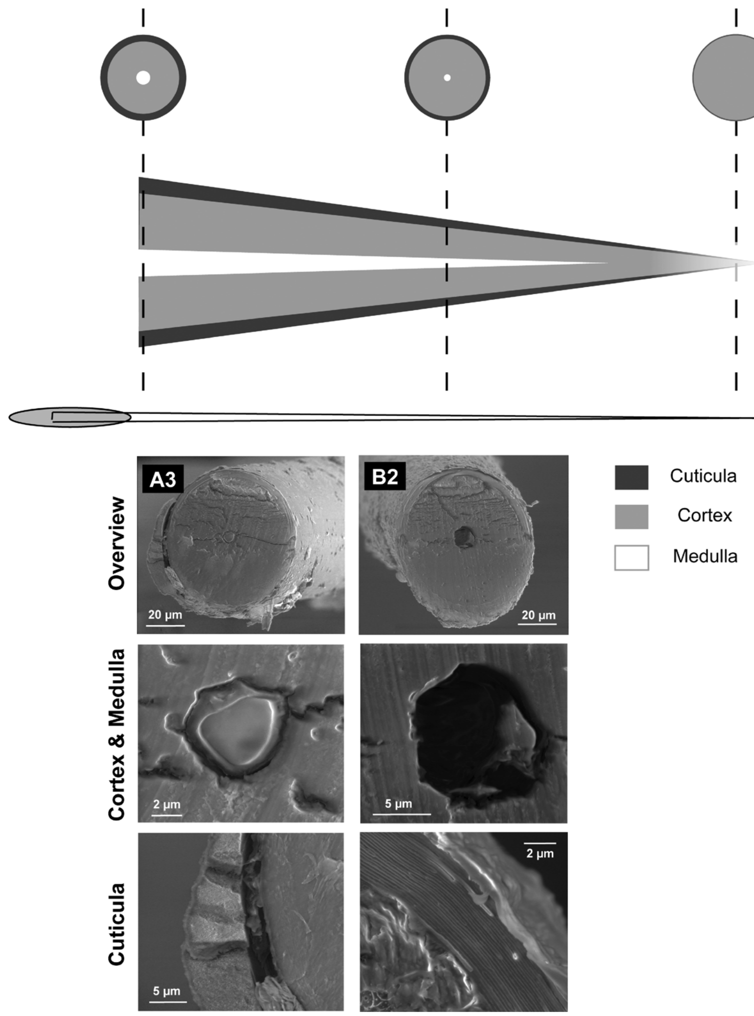

Fig. 7. Top: share of components of a macro vibrissa at base, mid and tip. Outer diameter unified to one (1) relative unit. Center: Virtual longitudinal section of a macro vibrissa, illustrating the change in share of components along the long axis of the hair. Scale factor transversal : longitudinal 100: 1 Bottom: SEM pictures of cross sections of two macro vibrissae, at base and mid length of whiskers. Cave: the absolute basal diameter of B2 (126 $\mu\mathrm{m}$) is larger than that of A2 (80 $\mu\mathrm{m}$), thus the cut through a "bubble" of the fragmented part of medulla in B2 shows larger absolute diameter than that through the base of medulla A2. This mirrors the ideal character of the virtual longitudinal section on top of the figure.

completely near the tip. However, the medulla of *body hairs is filled with cells, though it, also, is replaced close* to the tip by compact tissue.

In order to describe the morphology of the three layers (cuticle, cortex and medulla) in more detail, cross sections were analyzed using light and scanning electron microscopy. Already photographs at light-microscope scale make the differentiation of the three layers possible (Fig. 6, top).

Fig. 7 summarizes the results of structural analyses.

1) Cuticle: The cuticle's share of the total diameter is, at an average of 16%, quite considerable. This proportional thickness of cuticle decreases over the length of the whisker.

2) Cortex: The compact cortex represents the most pronounced layer over the entire length of the whisker, at 67% to 84% of the total diameter.

3) Medulla: The medulla, just like the outer contour, is in the shape of a truncated cone (linearity $\mathrm{R}^2 = 0.93$), but with a sharper decrease. Thus, the medulla's share of the total diameter gets ever less from base to tip, until the medulla is no longer present. Depending on the type of whisker, it is present for between 50% and 75% of the overall length. At the hair base, the medulla takes up between 6% and 15% of the external diameter ($11.3\% + / - 2.9\%$). Compared with body hairs, where the medulla takes up to 38% of the hair diameter, this portion is small. For more detailed analysis, SEM is indispensable.

All the whiskers analyzed showed an approximately circular cross section. The cuticle is characterized by its unusual thickness. In comparison with human hair and its 5–10 layers of cuticular scales, whiskers have 15–20 overlapping layers of scales. Fig. 7 shows how markedly the individual scales of one layer overlap. The extraordinary extent of the cortex of the whiskers also indicates its strength. Depending upon the region from which the whisker was cut, different characteristics of the medulla were to be observed. Up to about half way along the whisker, there is a central, medullar channel, which is interrupted in the third quarter of the whisker length. In the last quarter, the medulla disappears completely.

IV. Discussion

Rats' whiskers, as specialized mechanically sensitive organs, exhibit many structural characteristics which differentiate them morphologically from body hair. While the body hairs of rats exhibit an almost cylindrical contour with a thinner portion at base and apex and a thicker central section, whiskers are characterized by their extraordinarily symmetrical, truncated cone-like form [20], [21], which for the rats analyzed in this study could be specified to deviate from the ideal linear cone shape by up to some 10% of diameter as well in the sense of bulging (convex) as of reduction (concave). Due to the curvature of the whole hair we were not able to securely identify possible asymmetries of these diameter deviations, indicating their possible origin in abrasion. Of the three groups under studies straddlers best fit to the model of a linearly limited cone, while micro vibrissae tend to bulged shape, and macro vibrissae vary from concave to convex shaped cones. The body hairs of mice, also, can be divided into three sections: a quite thin tip, a thicker center section and a tapering basal part [7], thus resembling the shape we observed for micro vibrissae in rats, perhaps indicating that the shaping under use may depend more from absolute size than from specialized function. On the other side, even human scalp hairs tend to have a cylindrical outer contour [18]. Thus, the characteristic contour of whiskers still may be hypothetized to be a primary morphological condition for the fulfilment of mechano-sensitive functions. In the range of diameters observed in whiskers of 23 species from 6 families by [21], the data we report on may be grouped in categories "D" (d less than 120 $\mu\mathrm{m}$) (micro vibrissae, rostral macro vibrissae) and "C" (d $=$ 120 to 200 $\mu\mathrm{m}$) (occipital macro vibrissae, straddlers).

In general, the diameters of macro vibrissae differ stronger between rows (cf. Fig. 1) than between arcs, showing an increase from rostral to occipital.

The information lack identified by [20] addressing the analysis of [1] that "'the tip tapers to a fine diameter in intact vibrissae,' but no diameter values are reported" [20, p. e8806] may partly be filled for rats: macro vibrissae and straddlers show tip diameters of 2.5 $\mu\mathrm{m} + / - 1\ \mu\mathrm{m}$ (Figs. 3, 4) with extremes of 1 and 7 $\mu\mathrm{m}$. Due to their fragility, the tip diameters of micro vibrissae could not be determined securely.

Following the classification of Latzke [11], the structural characteristics of vibrissae can be described as follows.

- Longitudinal aspect: The surface is scaly. The scales have edges which are serrated or even corrugated and overlap by an extent which is either small or proportionately large. The arrangement of the scales is irregularly wavelike, with a dip in the middle. The thickness of the scales is tiny: 3–9 $\mu\mathrm{m}$.
- Cross section: The whisker cross section is circular, with a diameter between up to 187 $\mu\mathrm{m}$ (maximum observed in five rats). The medulla, likewise, is circular and forms a channel in the first half, while being interrupted towards the tip ("fragmental" in the terminology of [6]) and disappearing at the apex.

When the two types of surface texture are compared, further differences between the whiskers and the body hairs of rats are noticeable. While the whiskers have many irregularly arranged scales, the body hairs have regular scales with more marked elongation between base and apex. Following Latzke [11], one can speak of a smooth scale pattern for the body hairs of rats with broader overlap and a zig-zag scale arrangement. The types of surface texture of rats' vibrissae and of their body hairs are also found among the woolly hairs of various animals (sheep, alpaca, lama, camel, rabbit, etc.) [11]. The form and arrangement of the whisker scales is likewise found on human scalp hair [18]. The observed variability in the shape and form of scales and arrangement is usually morphologically interpreted [16] by type of hair growth and relation to hair length and hair diameter. On the other hand, it might be that an organization of the surface with narrow scales lying close together contributes to heightened flexural stiffness, or as a gear rack provoking the higher frequency of excitation in frictional whiskering of surface, complementary to the tuning of resonance frequencies by tapering [20, p. e8806]. This sort of scale arrangement is also described for rabbit whiskers [17] and the tactile hairs of cattle [22]. The fact that the degree of serration varies for the edges of the scales on different vibrissae could be an indicator of the demands placed on the individual whisker. A smooth edge (cp. Fig. 5) would suggest a less stressed or, perhaps, still young, whisker. In the case of human hair, such a change of the scale edge under the influence of different environmental conditions (sunlight, weather, etc.) has been described [18].

An extraordinary symmetry is found in the cross section: vibrissae are almost circular. Any minor deviations seem to be due to the preparation methods (influence of scalpel or micro laser). However, this round cross section is not, as such, a structural characteristic, since the same cross section is also found in the body hairs of the rat.

On detailed inspection, it is noticeable that the two external layers, the cuticle and the cortex of the whisker are particularly pronounced features of the cross section. With 15–20 layers of scales, the whisker cuticle is two to four times thicker than the body hair cuticle. For human hair, Robbins [15] describes only 5–10 superimposed layers. The whisker cortex is also particularly substantial, taking up to 84% of the total diameter. Such firmness in the outer layers of the vibrissa is one reason for the increased resistance of whiskers as against that of normal body hairs or human hairs. When the Young's moduli, also, are compared, significant differences appear. While the Young's modulus of whiskers is approximately 8 GPa, [15]–[17] describe a Young's modulus for human hair of 3.8 GPa. The hair with the sensory function (the whisker) therefore exhibits the higher stiffness. The stability derived already from the structure leads to a degree of flexural stiffness which is appropriate to the function of the whisker. Whiskers, which need to exhibit a higher flexural stiffness than hairs without sensory tasks, do so, and thus fulfill sensory functions such as object recognition and texture analysis. Furthermore, the higher number of cuticular scales increases the robustness of the stimulus-registering structure and supports high tolerance of environmental influences. As whiskers are subjected to considerable mechanical wear while performing their mechanical sensitive functions, they own "guaranteed" increased system lifetime by their high number of scale layers. The strongly defined outside layers enclose the medulla, which is on the whole, but variably hollow.

The cavity accounts for up to 15% of the total diameter near the base of the shaft. A similar distribution of the three layers is also described by Van den Broeck [17] for rabbit whiskers. In contrast, the medulla in body hairs without sensory functions is wider, taking up to 2/3 of the total diameter [4]. Furthermore, Chernova [4] postulates that the development of the medulla depends on the diameter of the hair. Thus, hairs with a $\text{diameter} < 10\ \mu\text{m}$ have no medulla, those between 10 μm and 75 μm have the medulla interrupted by the cortex, and it is only those with a thickness greater than 95 μm which possess a constant medulla. As regards function, it is possible to take different views of such a central channel. It might possibly influence the static and, above all, the dynamic characteristics of the hair shank, or it might only represent a saving in material. In the literature, the medulla is seen rather as serving the purposes of thermal isolation, than those of influencing the mechanical characteristics [4]. Seasonal changes in the extent of the medulla argue on behalf of this hypothesis [23]. This interpretation seems sound if one looks on the hairs as part of the total system. For an individual whisker, however, the medulla is credited with additional functions to do with mechanical transduction. Further analyses are necessary to test these hypotheses concerning the different functions, which would examine the bending behavior in relation to the dynamic characteristics.

Comparing structural characteristics of whiskers with those of body hairs, considerable differences are found. The assumption that the external, truncated cone-like form of the whiskers is of crucial functional importance is very probably correct. In addition, the substantial nature of the two external layers, the cuticle and the cortex contributes to the fulfilment of the sensory functions. The extraordinarily thick cortex probably contributes significantly to the characteristic bending features, and the multilayer cuticle probably has a mainly protective function. For a detailed functional interpretation of the structures described, further analyses of the sense organ as a whole are called for.

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