THE UNIVERSITY OF CALGARY

METRICAL FEATURES OF *PAPIO* HAIR

BY

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE

DEGREE OF MASTER OF ARTS

DEPARTMENT OF ANTHROPOLOGY

CALGARY, ALBERTA

FEBRUARY, 1987

ISBN Ø-315-35969-2

THE UNIVERSITY OF CALGARY

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Metrical Features of Papio Hair", submitted by Elke I. Tenor in partial fulfillment of the requirements for the degree of Master of Arts.

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ABSTRACT

As an antecedent to heat transfer studies through the hair coat of the olive baboon (Papio cyncocephalus anubis), several coat and hair structural parameters, necessary components of heat transfer equations, were determined. A skin sample with 146 hairs attached to it was excised from the nape area of an eight year old P. c. anubis male. The hairs were removed from the skin, tied together, embedded in Epon and serially sectioned at 50 microns. The hair cross-sections in every eighth section were photographed. The resulting slides were projected onto paper, and the hair and medulla outlines were traced with pencil. The areas of both hair and medulla cross-sections were measured via planimetry. Using the obtained areas and the length for each hair, its volume was calculated using Simpson's rule of integration. The minor and major diameters of the base and also of the midshaft region of each hair were used to derive hair indices for both locations on the hairshaft. The base areas were recalculated using either the minor or major diameter, or the geometric mean of the two, and the relative errors incurred in deriving the areas using these measurements were calculated. The data were analyzed using multiple regression techniques.

The skin from which the hair sample had been taken was fixed, embedded in Paraplast, sectioned, stained with hematoxylin and eosin Y, mounted, and photographed.

The hair sample proved divisible into fully grown hairs and new growth. The grown hairs were further categorized according to medullary configuration and hair pigmentation pattern. The medulla in grown hairs was either absent, fragmental, or initially fragmental and then becoming continuous.

Multiple regression equations were derived separately for the grown hairs and for the new growth. The best predictor of hair volume in grown hairs was the midhair cross-sectional area, and in the new growth, hair length and midhair area.

The hairs proved to be elliptical, and thus the lowest error was incurred by using using the geometric mean to calculate cross-sectional area. The hair density of the coat was found to be relatively low, and follicle groupings followed both the linear perfect independent, and the linear imperfect, patterns.

Thermal transfer through the hair coat in terms of coat structure was briefly discussed. It was concluded that the hair pigmentation pattern, coupled with postural variation, might allow a more precise regulation of heat gain or loss by the animal.

ACKNOWLEDGEMENTS

I consider myself fortunate to have had as my supervisor Dr. J. D. Paterson. I particulary appreciated his inhuman patience with my extended efforts to overcome the technical difficulties encountered in the course of this study. I am indebted to him for his sound advice, his encouragement during some very bleak moments, and his faith in my capabilities. I also would like to thank him for introducing me to the stimulating field of primate thermoregulation, the nuances and complexities of which have hardly been realized as yet.

I wish to thank Ms. Judi Smith, a long-time friend who not only knew I could, but also that I would, and told me so more than once. The occasional financial injection administered by Ms. Smith was also greatly appreciated.

I am particulary grateful to my dear friend Bryan Rooney, who wrote the initial Fortran programs, and also provided encouragement and feedback, especially during the final stages of thesis preparation. Without his help, this thesis would have been a more arduous undertaking.

FOR MORGAN,

who caught me when I fell.

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INTRODUCTION

Animal Hair Coats as Insulators

The normal body temperature of homeotherms is $35^{\circ} \pm 3^{\circ}$ C. In general, an adjustment to the ambient thermal environment is not solely effected by an adjustment in body temperature (Swan, 1974). Rather, a homeotherm varies its metabolism, its insulative covering (hair, fur, feathers, fleece, clothing), its posture or position (Paterson, 1982, 1986), or all of these. Metabolic heat must be conserved or dissipated in some manner, or more accurately, heat absorption and dissipation must be regulated to maintain a relatively constant internal body temperature. It is a major function of the coats of homeothermic animals to regulate the thermal energy exchange between the body of the animal and its environment.

Most research into primate thermoregulation has concerned itself with either the physiological (Funkhouser, Higgins, Adams & Snow, 1967) or the behavioral (Stelzner & Hausfater, 1986; Paterson - in preparation) mechanisms involved. Behavioral studies tend to seek correlations between environmental variables such as air temperature, solar radiation, wind velocity, etc., and the animal's posture, position, or orientation relative to the sun.

However, the effects of the thermal properties of the hair coat on the animal's rate of heat exchange have been largely neglected. Since it is well known that both the insulative quality and the pigmentation of the coat play significant thermoregulatory roles, at least in animals other than primates (Cena & Clark, 1973; Lustick, Battersby & Kelty, 1978; Walsberg, Campbell & King, 1978), the inclusion of such factors would provide a more detailed and complete energy budget for any species under investigation.

The fur, or hair coat of an animal may be thought of as a fibrous insulator, composed of hair fibres and the air pervading the spaces between these fibres. Only one study (Scholander, Walters, Hock & Irving, 1950) has investigated the insulative value of non-human primate hair coats, but only in 2 of 200 species. A considerable lack of data exists on the insulative properties of hair, then, for use in ecological research involving the calculation of energy budgets for non-human primates. An indication of the importance of this natural insulator in the thermoregulation of one species is given in the aforementioned study by Scholander et al. (1950): The coat of the arctic fox is such an efficient insulator that only a resting level metabolism is necessary to maintain a constant body temperature at environmental temperatures as low as $-40^{\circ}C$.

It follows, therefore, that the insulative value of the coat must be taken into account when calculating an animal's energy budget; but before this can be done, the thermal properties of the coat must be determined. This involves the investigation of a number of complex factors involved in the transfer of thermal energy.

Briefly, in a solid substance, heat transfer occurs by conduction alone. In a gas, additional modes of heat transfer include convection and radiation. In a porous or fibrous material, which is part solid and part gas, all three mechanisms play a role in thermal transfer. Which of these three predominates in animal hair coats is dependent on the structure of the coat -- that is, whether the hair is coarse or fine, dense or sparse, straight or crimped, long or short. In sparse coats, those of less than 1000 hairs/cm^2, radiative transfer between hairs becomes a relatively important mode of heat transfer (Strong, Bundy & Bovenkerk, 1960), whereas in denser coats, free convection predominates. For example, convection would be an important factor in the coat of Humboldt's woolly monkey (Lagothrix lagotricha), since the hair density on the back of this species is 2,446 hairs/cm^2 (Schultz, 1931). On the other hand, radiative transfer would predominate in the back hairs of the blackhanded spider monkey (Ateles geoffroyi), the hair density here being only approximately

651 hairs/cm^2 (Schultz, 1931). A minor factor is also introduced by thermal conduction through hair shafts. According to Cena and Monteith (1975), in order to assess the radiative transfer between hairs it is necessary to know the mean length and diameter of the hairs, the mean depth of the coat, and the number of hairs per unit skin area. Moreover, in order to determine the thermal conductivity, the volume of the solid components (i. e. the hairs) of the insulator must be known (Pelanne,1978). The thermal conductivity encompasses all three modes of heat transfer and their interactions, and is defined as the heat flow per unit area of the insulator per unit time, divided by the temperature gradient across the insulator.

Importance of Coat Structural Parameters

A number of studies have dealt with variables such as hair density, length, diameter, and growth patterns in different species of mammals. Usually attempts at phylogenetic classification of the various species have been made, based on their relative hair densities (Schultz, 1931), on hair diameters (Rosen, 1969), or on hair growth patterns (Perkins, Smith & Ford, 1969). It has been stressed by Hausman (1930) and Wynkoop (1929) that hair measurement must be standardized : diameter measurements

must be done at midshaft, and the area of the body from which the hair sample was taken must be reported. More recently, Reuer (1976) has determined that 100 is the absolute minimum sample size that will accurately represent the population from which it was taken. While Hausman (1930) was aware that the extreme variability of hair made a sizeable sample necessary, the results of other studies (Wynkoop, (1929); Kneberg, 1935) are based on 3 and 5 hairs per individual, respectively. Rosen (1969) and Vernall (1961) based their choice of sample sizes (3 and 4 hairs per subject, respectively) on "a previous unpublished study" (Rosen, 1969, p. 36), and on a "preliminary statistical analysis" (Vernall, 1961 p. 346). Neither author provides pertinent details of either document. Rosen utilized 42 non-human primate species, represented by 118 individuals. Approximately half the species were represented by only a single individual, and 3 hairs per individual were measured. A comparison of average rhesus macaque (Macaca mulatta) head hair areas as measured by Rosen (based on 8 animals, 3 hairs per individual) and by Reuer (1971) (based on 26 animals, 109 - 165 hairs per individual) provides support for Reuer's position. The average hairshaft area, according to Rosen, is 4910.32 μm^2, whereas Reuer found it to be 1233.00 μm^2. Although Rosen measured his samples at midshaft, and Reuer measured within

5 mm of the hair base, it seems unlikely that such a large discrepancy could be due merely to a difference in measurement locations along the hairshaft.

Another group of researchers (Massa, Durante & Monchietto, 1981) cite Rosen's mean Macaca hair index, 81.3. The hair index is a calculation of ellipticity: the minor diameter of the hairshaft is divided by its major diameter, and the result multiplied by 100. A hair index of 100 indicates a perfectly circular hair. Massa et al. measured 5 dorsal surface hairs each from 32 Japanese macaques (Macaca fuscata). They give no indication of where on the hairshafts the measurements were performed, and they are apparently unaware that Rosen measured cephalic, not dorsum, hairs. At any rate, they report the average hair index for their sample as falling "within the range already observed by Rosen (1974) for macaques" (p. 47). The "range" Massa et al. are referring to is, in fact, the standard deviation of Rosen's hair indices. According to a recalculation of the raw data given by Rosen (1969), the mean hair index for Macaca fuscata specifically appears to be somewhat lower than that given for macaques in general. The range of values given by Massa et al. overlaps with Rosen's range, but does not fall within it. In addition, these researchers provide a multiple regression equation for cross-sectional area which is based

on 7 dependent variables. Of these, 6 are intercorrelated at least at .94, thus creating a substantial problem with multicollinearity and rendering the derived regression coefficients unstable.

It is clear, then, that three important factors to consider in the determination of the structural parameters of hair are the sample size, its location on the body, and the location along the hairshaft at which the cross-sectional areas or diameters are best measured. For example, when measuring diameters, Reuer (1976) states that a sample of 100 hairs is sufficient if the standard deviation in the sample does not exceed 15 μm. As for the location of the measurements, the hair base or the midshaft seems to be the choice of the majority of researchers.

Volumetric Determination of Hair Sample

A volumetric determination of hair has apparently not been done in primates or other animals. A simple means of accomplishing this would be to shave a large area of skin on a primate, submerge the hairs thus obtained in liquid and note the change in volume of the liquid. However, this renders the subject useless for field studies of thermoregulation, at least until the hair in the shaved area grows in again. Moreover, determination of other

pertinent structural features of the hair would still require hair-by-hair measurement.

The most accurate estimation of volume would be via the areal measurement of histological serial sections of an adequately sized sample. It is relatively simple to embed a single hair and obtain serial sections of it, but it would not be feasible to embed over 100 hairs, one at a time, and to section each one. Therefore, it appears to be most efficient to embed the entire hair sample at once, keeping all hairs relatively straight and with their long axes as parallel as possible in order to ensure that the subsequent cross-sections can be cut perpendicular to all hairshafts. It should be noted, however, that even when sections are taken from fibres oriented at more than 25 degrees from the vertical, the average cross-sectional area is overestimated by only approximately 3% (Clancy & Herlihy, 1978). In addition, it is extremely important that no sections be lost or ruined, and that all hair cross-sections remain in their embedding matrix, and not fall out during handling. Should everything proceed smoothly, it is then necessary to trace the course of each hair through its entire length, remembering that each sample cross-section may contain up to 200 hair cross-sections. Each hair must be identified relative to all others, so that its volume can be reconstructed from

its serial cross-sections. Unfortunately, the hairs are unlikely to retain their positions relative to each other throughout the entire set of serial sections, thus making the task of identification a particularly tedious and difficult one. Given these inherent problems, it is little wonder that such a study has not previously been undertaken.

It has already been stated that the volume of the hairs is a necessary prerequisite for the development of accurate heat transfer equations. The purpose of the present thesis, therefore, is to determine the volume of a sample of at least 100 Papio cynocephalus anubis hairs, as well as the length, base and midshaft diameters, and the number of hairs present per unit area of skin in order to provide the necessary base data for such equations. Most hairs contain a central medulla, portions of which are composed of large, vacuolated cells. It is therefore necessary to determine the portion of each hair occupied by its medulla, since the presence of air in an otherwise solid conductor may complicate the heat transfer within this structure. Accordingly, the medullary volumes of the hairs will also be estimated.

The common, or savanna baboon, of which P. c. anubis is considered a variant, is of interest in that this species inhabits a broad range of ecological and climatic

zones, "from closed canopy forests in central Africa to arid thorn scrub in Ethiopia" (Bramblett, 1976, p. 141). It would be interesting to calculate energy budgets for the species under these various climatic conditions. In addition, according to Montagna and Yun (1962), P. c. anubis has more eccrine than apocrine sweat glands. However, it is unlikely that eccrine glands actually play a role in the thermoregulation of any primate other than humans, since Montagna (1972) failed to induce sweating in response to thermal stress in the chimpanzee, vervet, or rhesus monkey. Although sweating has been reported in P. cynocephalus under such stress, the "sweating during the heat exposure was estimated subjectively" (Funkhouser, Higgins, Adams & Snow, 1967, p. 1616), and the amount of perspired fluid was not measured.

METHOD

The methods chosen to conduct this study of Papio cynocephalus anubis hair are essentially those described in the introduction. That is, a sample of between 100 and 200 hairs from the dorsal surface of a P. c. anubis skin was embedded, sectioned and measured according to the following detailed procedure.

Sample Acquisition

The hair sample was obtained from the dorsal surface of a Papio cynocephalus anubis coat. The skin was removed from a healthy eight year old male subject sacrificed in the course of arteriosclerosis research at the Southwest Research Foundation (San Antonio, Texas) and shipped to the University of Calgary in a freshly frozen state.

The skin was partially thawed, and a .5 x 1.0 cm sample with hairs attached was excised at the midline, 3 cm below the inion. The hairs were cut with a razor blade to within .5 mm of the skin surface. The excised skin sample, minus its hairs, was re-frozen for subsequent histological processing.

The hairs were gathered together with their bases as nearly aligned as possible, and the resultant hair bundle

was clamped at its base. Several long human hairs, used because of their distinctly different and hence identifiable structure, were then knotted together end to end, and two such lengths of hair were wound around the Papio hairs in criss-cross fashion, beginning at their bases, and ending at the tips of the longest hairs. The result was a compact bundle, able to withstand considerable handling during the embedding procedure.

Embedding

The hair bundle was soaked for two hours in a thermosetting epoxy resin compound of the following proportions:

Epon 812 (Shell Chemical Co.)	12.40 ml
DDSA (dodecenyl succinic anhydride)	20.00 ml
DMP-30 (2,4,6-tri(dimethylaminomethyl)phenol)	.55 ml

The bundle was then removed, and an approximately 10 cm long piece of thread was tied around its base, and another such piece, around its tip. The bundle was placed in an ordinary plastic drinking straw, 20 cm long and 3 mm in diameter, which had had approximately one third of its longitudinal surface removed, but leaving 2 cm at each end intact. The threads at each end of the bundle were pulled

through the open ends of the straw; one end was clamped shut, the thread at the other end was gently pulled until the hair bundle was straight, and this opening was also clamped. The straw boat was then filled with more of the Epon compound, and subjected to a low vacuum (300 mm Hg) for one hour. This proved sufficient to eliminate any air bubbles trapped between the hairs in the bundle. The exposed surface of the Epon-filled straw was covered with a sheet of plastic film (Saran wrap, Dow Chemical Co.), and the entire assembly was placed in a controlled-temperature oven for the three-stage curing cycle suggested by Luft (1961): 24 hours each at 35° C, 45° C, and 60° C.

At the end of the curing period, the straw casing was peeled from the hair bundle, now completely encased in hardened Epon. The bundle was then cut into 14 mm lengths with a razor blade. The blade was stabilized by inserting it into a holder constructed from an ordinary 6 cm long door hinge (see Figure 1). It was necessary to use a fresh area of the blade edge for each cut. It was not possible to use a scalpel, knife, or other more convenient cutting implement, since their wide cutting edges and even wider backs tended to fracture or shatter the Epon, resulting in an uneven cut, or tearing of the hair bundle.

The 14 mm pieces of hair bundle were next embedded in no.1 gelatin capsules which already contained a hardened

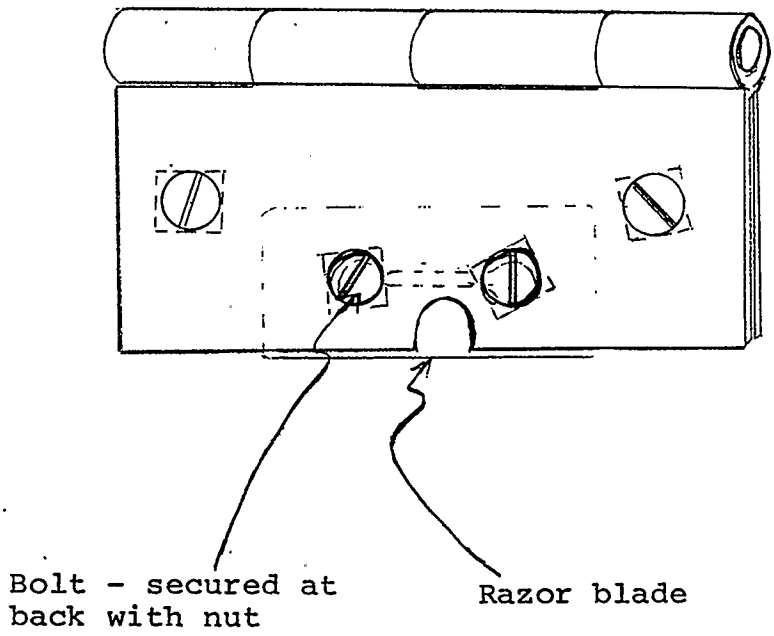


Figure 1. Razor blade holder. The cut-out in the bottom edge is only slightly wider than the gelatin capsule used to embed the hair sample.

base of Epon, and subjected to the same three-stage curing cycle. The Epon bases were prepared as follows: the bottom end of each capsule was tapped once or twice on the surface of a hot plate, just enough to flatten the curved bottom slightly. This capsule was then forced gently into the open bottom half of a second, intact capsule. The top of the first capsule was removed, a needle probe inserted, and the weakened bottom punched out. The longer capsule created in this way was then inverted, and the debris in its bottom shaken out. All prepared capsules were then placed upright into holes drilled in a piece of rigid plastic (preferred to wood because wood, unless oven-cured first, contains a certain amount of moisture, and this interferes with the proper cure of the Epon (Spurr, 1969). A numbered slip of paper was inserted into the bottom of each capsule in order to identify it, the capsules were filled to a depth of 1 cm with Epon, and cured.

When these bases were hardened, one 14 mm piece of hairbundle was placed in each capsule, beginning with the base of the hair sample in capsule no.1, the piece next to it in capsule no.2, and so on. The capsules were then filled with Epon, each hairbundle piece was maneuvered into a vertical position inside its capsule, the tops were placed on the capsules, and they were cured. After the three-day cure cycle, the gelatin was washed off the

hardened plastic. Each Epon capsule was placed in the chuck of a clinical microtome (American Optical Co.) and sectioned transversely at 50 micron intervals. The thick plastic sections cut in this way were lifted off the microtome knife with double-sided adhesive tape, applied to microscope slides with the tape side down, and pressed down firmly with wax paper. Each section was covered with a drop of Epon (the same formulation used throughtout the study), and a coverslip was applied. The Epon was allowed to set for four days to prevent shifting of the coverslips. (An attempt to cure the slides in the same way as the hair samples proved unsuccessful - considerable warping of the plastic embedding matrix and shifting of the hair cross-sections within it ensued.)

Determination of Measurement Interval

At this point it is necessary to address the problem that arises in connection with any attempt at volume determination through the use of serial sections: how many sections must be measured in order to obtain an accurate estimate of the volume of the structure? What is the least number of sections that can safely be measured without a concomitant rise in error?

According to Zilles, Schleicher, and Pehleman (1982), 20 equidistant sections will suffice to determine the volume of even an irregularly shaped structure, with a resultant error of less than 5%. In order to establish the least number of sections that needed to be measured in the present study, and before the actual sample used in this study was removed from its site, a single hair was cut from the Papio skin close to the eventual sample site. This hair was selected due to its 'average' appearance; that is, under the dissecting microscope, it resembled most of the other hairs in its vicinity. (In fact, later comparison with the sample hairs showed it to be approximately average in length, and above average in base area.) The hair was then processed similarly to the actual sample. It was embedded in Epon, cured, sectioned at 50 microns, and the area of every fifth section was measured with a planimeter. The volume (based on all 420 measured sections and considered the true volume) was calculated and recorded. The volume was then repeatedly re-calculated, using only 210 equidistant areas, then only 140, and so on. For each volume calculation, the relative error was determined:

$$\text{relative error} = \frac{\text{calculated volume} - \text{true volume}}{\text{true volume}}$$

The relative errors were graphed (Figure 2), and based on these results, and an estimation that the shortest hair in any sample was likely to be not much less than 20 mm long, it was decided to measure the actual sample at 2 mm intervals. This would then provide ten equidistant measurements for the shortest hairs, and a much greater number of measurements for the longest hairs. The average error for the entire sample would therefore depend directly on the actual lengths of the hairs in it, but would be considerably less than the almost 5% shown in Figure 2 for only ten measurements. (In fact, the shortest hair in the actual sample was 17.6 mm long, the average hair length was 90.28 mm, giving an average of 45.14 measurements per hair, and therefore, according to Figure 2, a relative error well within 1% of true volume. The actual calculated average relative error was .65%.)

Data Collection

Having obtained an orderly series of cross-sections from the base of the hair bundle to its tip, every fortieth section (40 x 50 = 2000 microns = 2 mm) was placed under a Nikon S-KE II light microscope fitted with a compensated 10x objective. The sections were photographed at 100x magnification with a Nikon EM 35mm camera loaded with Kodak

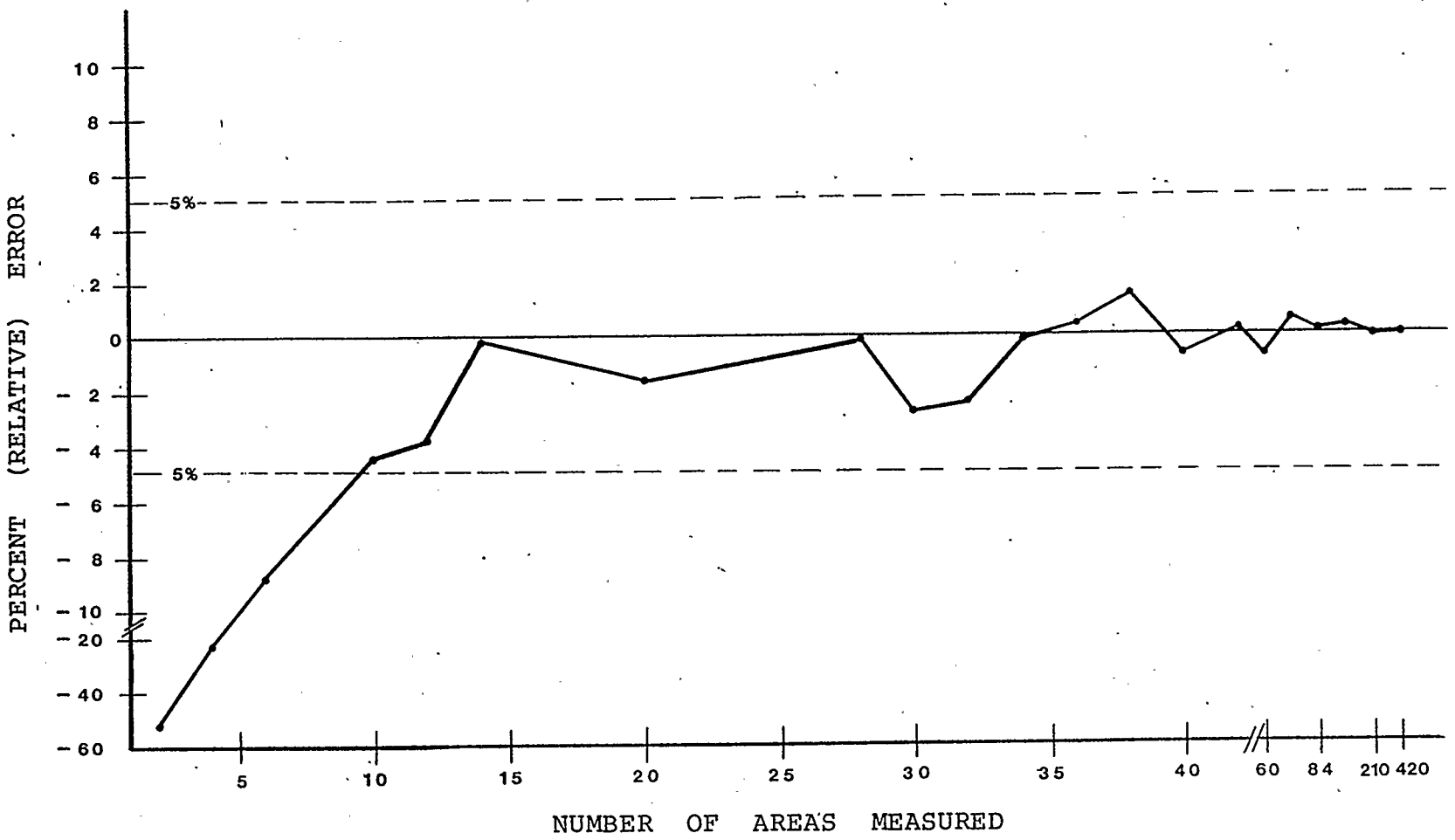


Figure 2. Plot of relative errors of calculated volumes of test hair versus number of areas measured.

Kodachrome 25 color slide film. See Figure 3 for a print of one such slide. Each slide was projected at 500x magnification onto a large sheet of paper, and the outline of each hair cross-section and also its medulla (if present) was traced in pencil.

Beginning with the first sheet of paper (containing the tracings of the bases of the hairs in the hairbundle), each hair cross-section on it was assigned a number. Then, with the film slide of these in the projector, the next film slide in the series in a hand slide viewer, and the intervening microscope slides in the microscope, the course of each hair was followed until the location of its next cross-section on the next sheet of paper could be determined and assigned the same number. Since the intervening distance (2 mm) is relatively great, considerable searching was often necessary, as the hairs were shifted in their positions relative to one another.

Measurement

When all hair cross-section tracings had been identified and numbered, the area of each (and its medulla, if present) was measured with a Lasico model N-42 polar compensating planimeter. This method of area measurement was chosen over others because of its superior accuracy

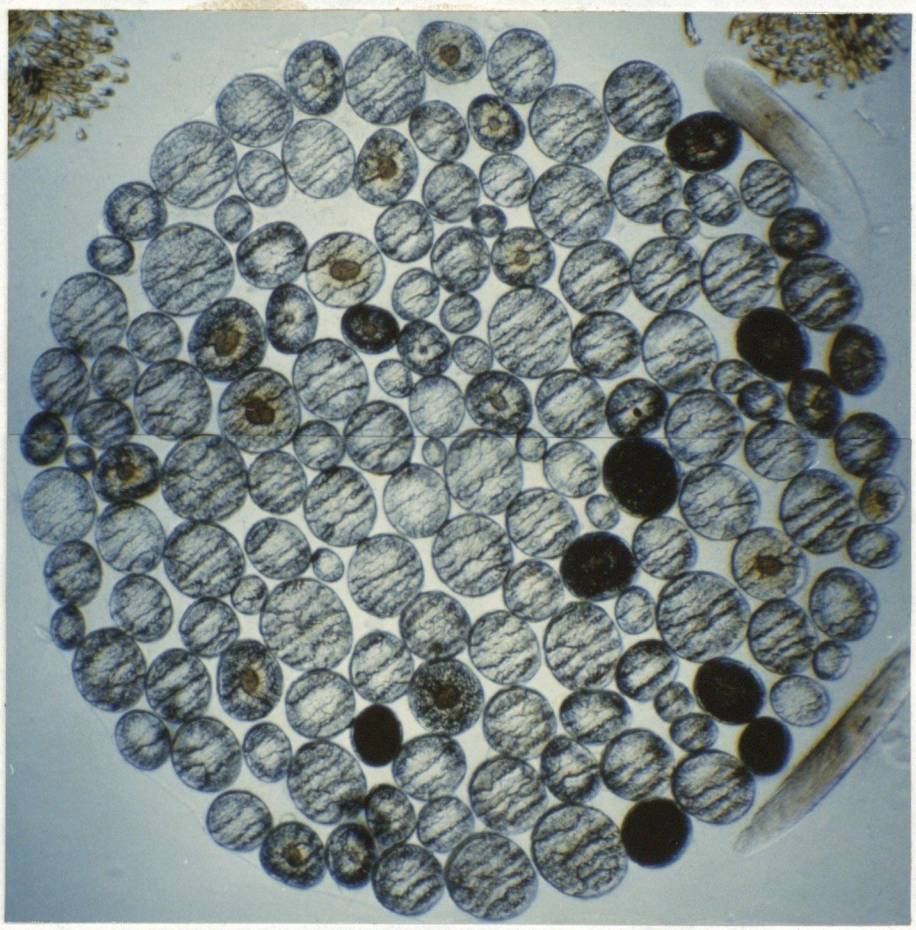


Figure 3. Micrograph of dorsum hair cross-sections (x100).

(Zilles et al. , 1982; Aherne & Dunnill, 1982; Williams, 1977). Each outline was traced twice with the planimeter needle, and the average of the two measurements was recorded as the area for that particular hair/medulla cross-section.

In addition to the areas of all cross-sections, the minimum and maximum caliper diameter of the base and midshaft cross-section of each hair were recorded.

Calculations

Most of the following calculations were performed by Fortran programs written especially for the particular task at hand, and run on the Honeywell DPS 8/70 M computer installation of the University of Calgary.

Hair Length

Hair length was composed of three parts (Figure 4): the base lengths (that part of each hair which extends beyond the first photographed and measured cross-section of the hairbundle), the tip lengths (that part of each hair extending beyond the last cross-section) - neither of these can be more than 2 mm long, since in that case there would have been another cross-section photographed and measured - and the length of the main body of the hair. The number of

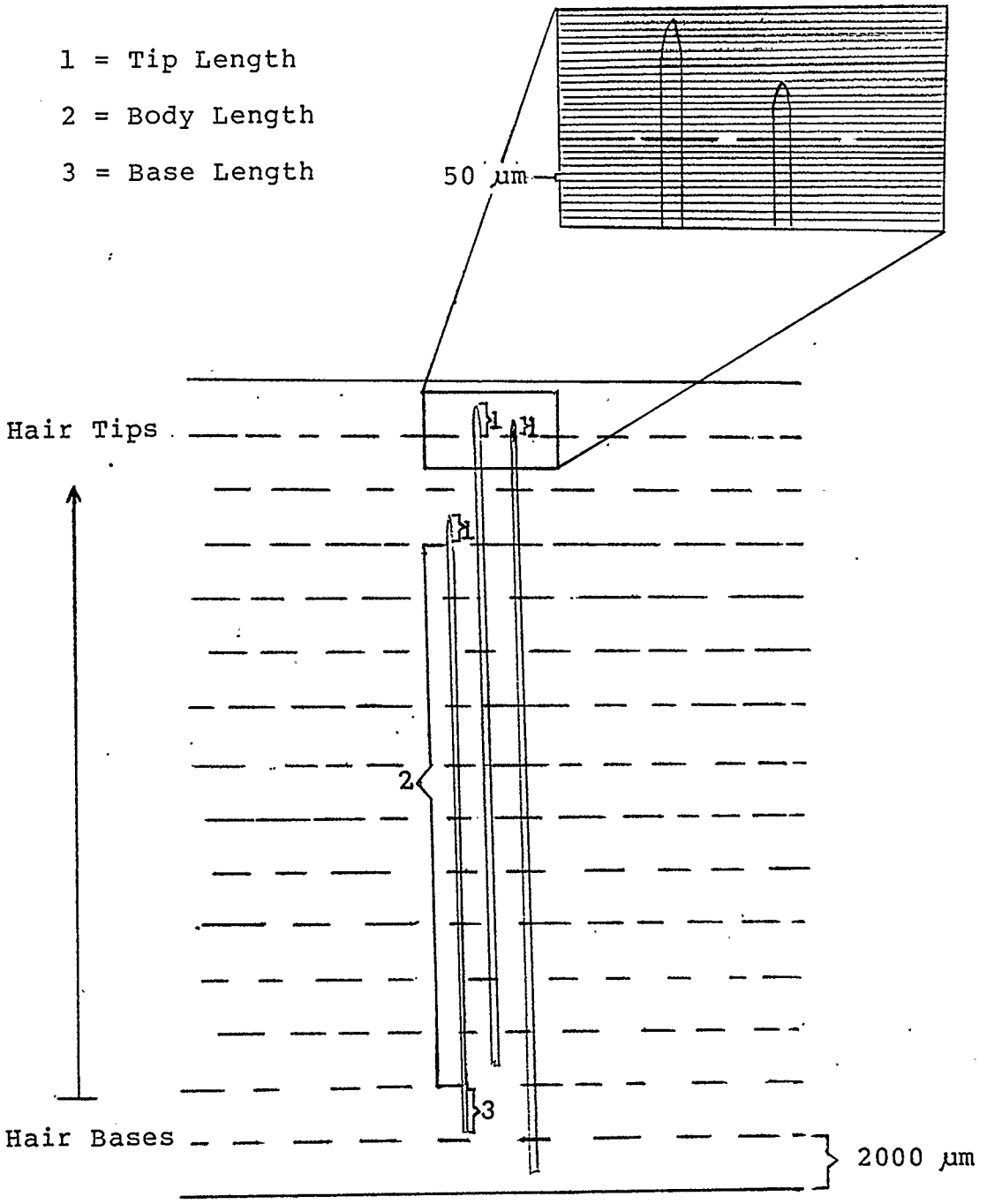


Figure 4. Diagrammatic representation of three embedded hairs, showing measurement intervals.

sections in the tip and base were multiplied by 50 microns, since this was the thickness of each section, and the main body segments, by 2000 microns (since only every 40th section was measured, and, of course, 40x50=2000). Therefore, the number of sections below the first measured cross-section x 50 = base length, the number of sections above the last measured cross-section x 50 = tip length, the number of measured sections in the main body minus one section (because the interval between cross-sections is always one less than the number of cross-sections, and it is the interval that is being assessed) x 2000 = main body length, and adding all three lengths = length of the entire hair.

Hair Volume

The volume of the main body of the hair was calculated using Simpson's rule of integration (Leithold, 1976; Aherne, 1982). The formula is

$$V = 1/3\ 1\ [(a_0+a_n)+4(a_1+a_3+\ldots a_{n-1})+2(a_2+a_4+\ldots a_{n-2})]$$

where 1 = length of interval = 2000 microns

a = area of cross-section

The formula requires an even number of areas, but approximately half the hairs in the sample had been sectioned into an odd number of cross-sections. In these

hairs, the extra bit of volume between the last and second-last measured areas was calculated according to the formula for the frustrum of a cone (Leithold, 1976):

$$V = 1/3 \pi l (r_1^2 + r_2^2 + r_1 r_2)$$

where l = 50 microns

The volume of the base of each hair was also calculated using the frustrum formula, and a variation thereof was used to calculate the tip volume:

$$V = 1/3 \pi r^2 l$$

where l = 50 microns

This, of course, is simply the volume formula for a cone.

Finally, the results of all three (or, in the case of hairs with an uneven number of measured cross-sections, four) calculations were added to produce the total volume of any given hair. All hair volumes were then added to give the volume of the entire sample.

Medulla Length

The length of each medulla was calculated by adding the number of cross- sections in which a medulla was evident, subtracting one, and multiplying by 2000 microns. The result was considered an approximation only, since the error was found to be quite high - see below.

Medulla Volume

The volume of each medulla segment between two measured areas was calculated using the frustrum formula. Again, the results are considered only approximate.

Hair Index

The degree of ellipticity of each hair was assessed both at the base and at midhair, using the formula

$$\text{hair index} = \frac{\text{minimum diameter (base or midhair)}}{\text{maximum diameter (at base or midhair)}} \times 100$$

The percent difference between the index at the base and at midhair was calculated according to the formula

$$\% \text{ difference} = \frac{\text{hair index (base)} - \text{hair index (midhair)}}{\text{hair index (base)} + \text{hair index (midhair)}/2}$$

Base Areas

The area of the base of each hair was re-calculated using the minimum and maximum base diameter and several different area formulas:

Area based on the geometric mean of the min/max caliper diameters = $(\pi/4) \times Dd$

Area based on maximum caliper diameter only = $(\pi/4) \times D$

Area based on minimum caliper diameter only = $(\pi/4) \times d$

Percent (Relative) Error

The percent error was established for each re-calculation of the base areas, relative to the base areas as measured by planimetry. For example:

$$\% \text{ Error} = \frac{-\left(\frac{\text{base area (geometric mean)}}{\text{base area (planimetry)}}\right)}{\text{base area (planimetry)}} \times 100$$

$$\text{Average Error} = \frac{\Sigma\,|\%\ \text{error}|}{\text{no. of hairs}}$$

Here, of course, the area as measured with a planimeter is considered the 'true', or most accurate estimation of the area.

Statistics

SPSS (v.9) was used to calculate a multiple regression coefficient (R), with hair volume as the dependent variable, and base area, midhair area and hair length as independent (or predictor) variables. Bivariate correlation coefficients and scatterplots were also derived for all possible pairs of variables. Since SPSS cannot process extremely large numbers, hair volumes and medulla volumes were divided by 10,000.

Frequency distributions and descriptive statistics were produced for all variables.

Histology

The frozen skin sample was processed in the following manner:

formol saline	5%	48 hrs
alcohol (isopropyl)	100%	24 hrs
fresh " "	"	"
xylene	100%	24 hrs
fresh "	"	"
fresh "	"	"
xylene/Paraplast	50/50	1 hr at 57°C
Paraplast		1 hr at 60°C
fresh "		" " "

The sample was then embedded in fresh Paraplast in a tinfoil embedding form floated on cold water. When solid, the embedded sample was removed from the foil, attached to a mounting block, placed in the specimen clamp of a clinical microtome, and sectioned at 30 microns. Sections were unfolded on very warm water, floated onto untreated microscope slides, and dried at 57°C for 24 hours. They

were then removed from the slides, and sandwiched between two tightly stretched sheets of netting secured at the edges by a small frame (analogous to an embroidery hoop). The rather rough treatment that the sections were subjected to during subsequent staining made it necessary to secure them in some manner. The sections were further processed as follows:

xylene	100%	60 mins
xylene/isopropyl	50/50	2 mins
isopropyl	100%	3 mins
"	"	"
isopropyl	90%	3 mins
distilled H_2O		3 mins

((modified) procedure No. HHS (Sigma Chemical Co.) follows):

hematoxylin		10 mins
tap water (running)		3 mins
acid alcohol	1%	10 seconds
tap water (running)		3 mins
lithium carbonate	.5%	30 seconds
tap water (running)		10 mins
eosin Y		90 seconds
isopropyl	95%	3 mins

fresh "	"	"
isopropyl	100%	3 mins
xylene	100%	5 mins

The sections were then removed from their net casings, placed on slides, coverslipped with Permount, and photographed at 10x magnification with a Nikon EM 35mm camera fitted with extension rings and a Nikon 55mm macro lens, and loaded with Kodak EKtachrome 100 ASA color print film.

RESULTS AND DISCUSSION

Sample Composition

The sample consisted of 146 hairs, giving a hair density of 292 hairs/cm^2. Schultz (1931) cites a value of 405 hairs/cm^2 for juvenile Papio cynocephalus. However, the hair samples used in the Schultz study were taken from preserved skins, and it is possible that shrinkage due to the preservation process resulted in a higher hair density than if the samples had been obtained from fresh skins. This, coupled with the observation that hair density decreases with age (Schultz, 1931), may explain the lower density obtained in the present study, which utilized the skin of an adult animal.

The follicle groupings were assessed from histological sections of the skin sample (Figure 5). The hair follicle arrangement follows, for the most part, the linear perfect independent categorization used by Perkins, Smith and Ford (1969) to describe the follicle groupings in both P. anubis and P. papio. However, hair follicle groups distributed according to the linear imperfect categorization are also evident in Figure 5.

Of the total sample, 30 hairs were clearly identified as new growth. These hairs are hereafter referred to as

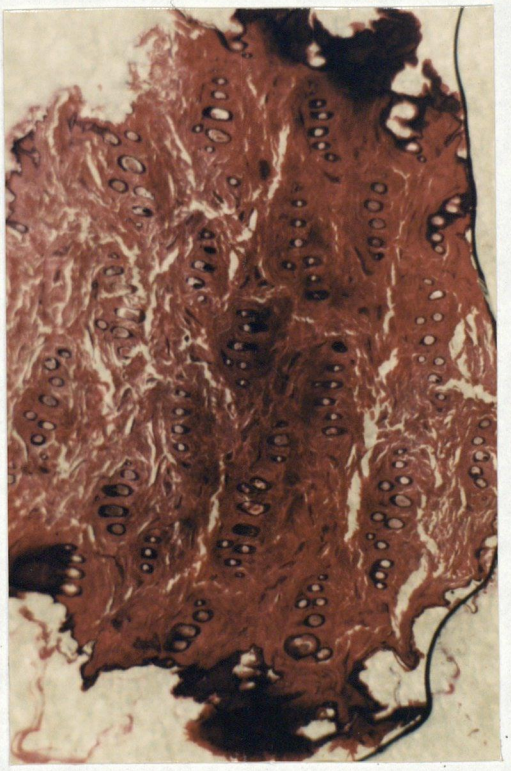


Figure 5. Follicle groupings in P. c. anubis dorsal skin (hematoxylin and eosin, x 10).

group 1 hairs. The remaining 116 hairs, which will be referred to as group 2, were divisible into three distinct types based on the presence or absence of a medulla as well as its structure.

The scatterplots of hair length versus base area (Figure 6) and versus midhair area (Figure 7) show that hairs less than 73,000 μm long and with base areas greater than 5,400 μm^2, or midhair areas greater than 3,550 μm^2 diverge from the main curve. The same trend is evident when length, base area and midhair area are plotted relative to hair volume (Figures 8, 9, and 10). In Figure 8 it can be seen that relative to the main portion of the curve, volume increases more rapidly than length within the approximate range of 14,958 μm^3 to 58,072 μm^3. If this rise in volume is not accounted for by length, then it must be accounted for by area, since these are the two essential components used in the volume calculations (page 24). This is confirmed by Figures 9 and 10, where, within the same range of values, area increases more rapidly than volume. In all scatterplots, these offshoots from the main curve represent group 1 hairs. When hair length is linearized via an inverse log transformation ($10^{length/100,000}$) the divergence between group 1 and group 2 hairs becomes even more obvious (Figures 11, 12, and 13). Moreover, group 1 and group 2 hairs were found to be statistically distinct.

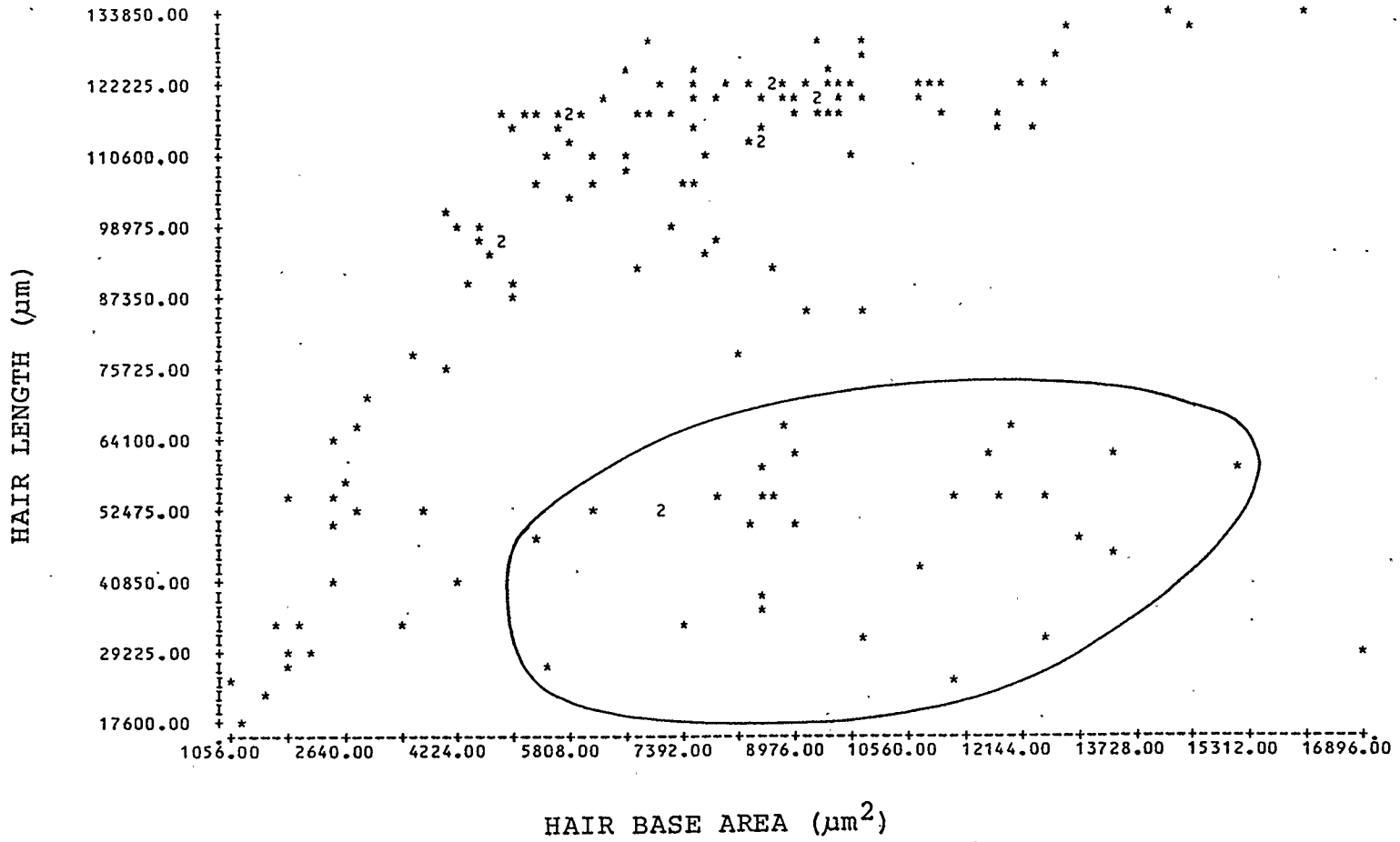


Figure 6. Plot of hair length versus base area showing deviation of group 1 hairs from main portion of curve. Group 1 hairs are circled.

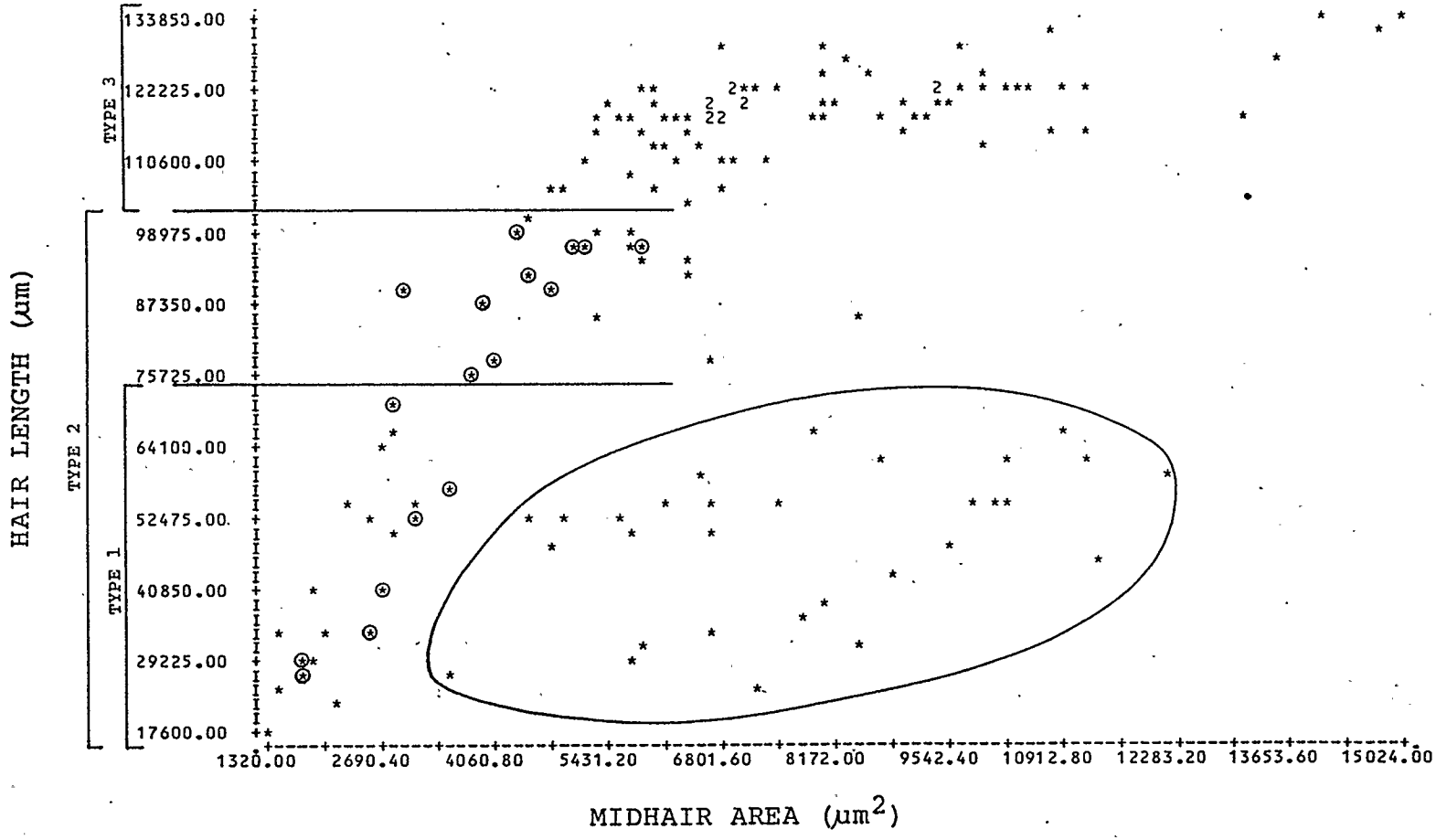


Figure 7. Plot of hair length versus midhair area. Group 1 hairs are circled. Circled points represent group 2, type 2 hairs. Group 2 hairs are divided into type 1 (medulla absent), type 2 (medulla fragmental) and type 3 (medulla initially fragmental, then becoming continuous).

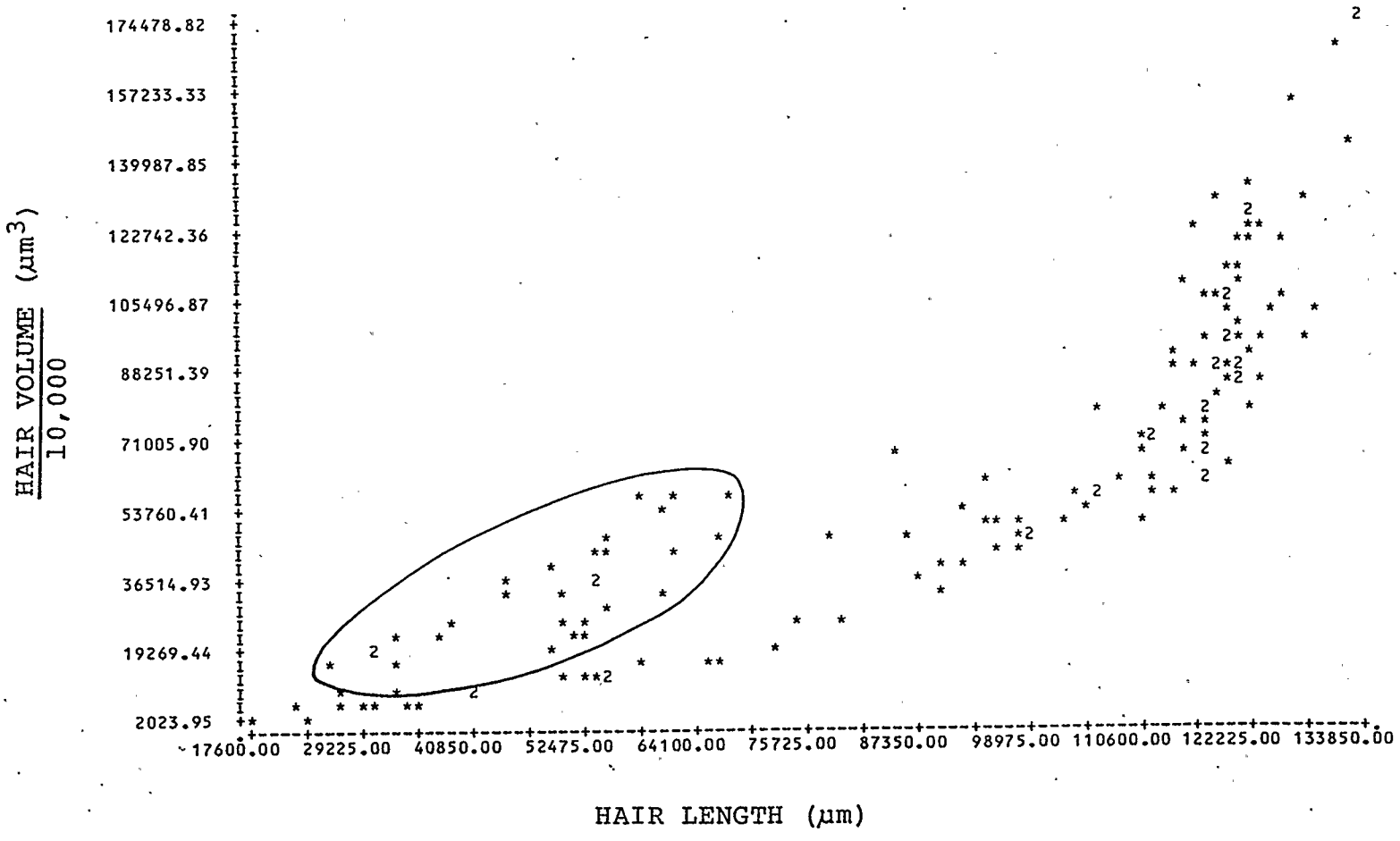


Figure 8. Plot of hair volume versus hair length. Group 1 hairs are circled.

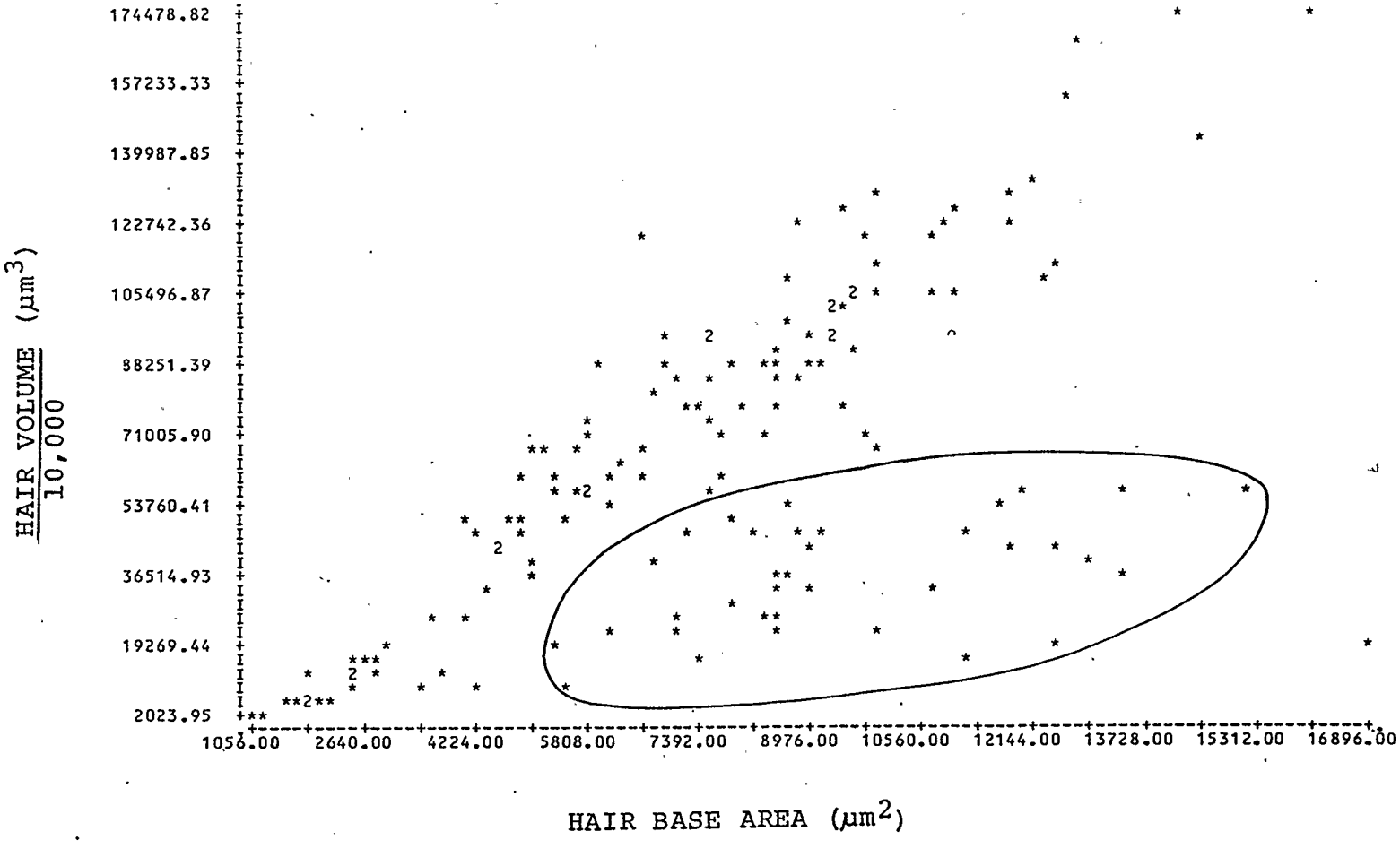


Figure 9. Plot of hair volume versus base area. Group 1 hairs are circled.

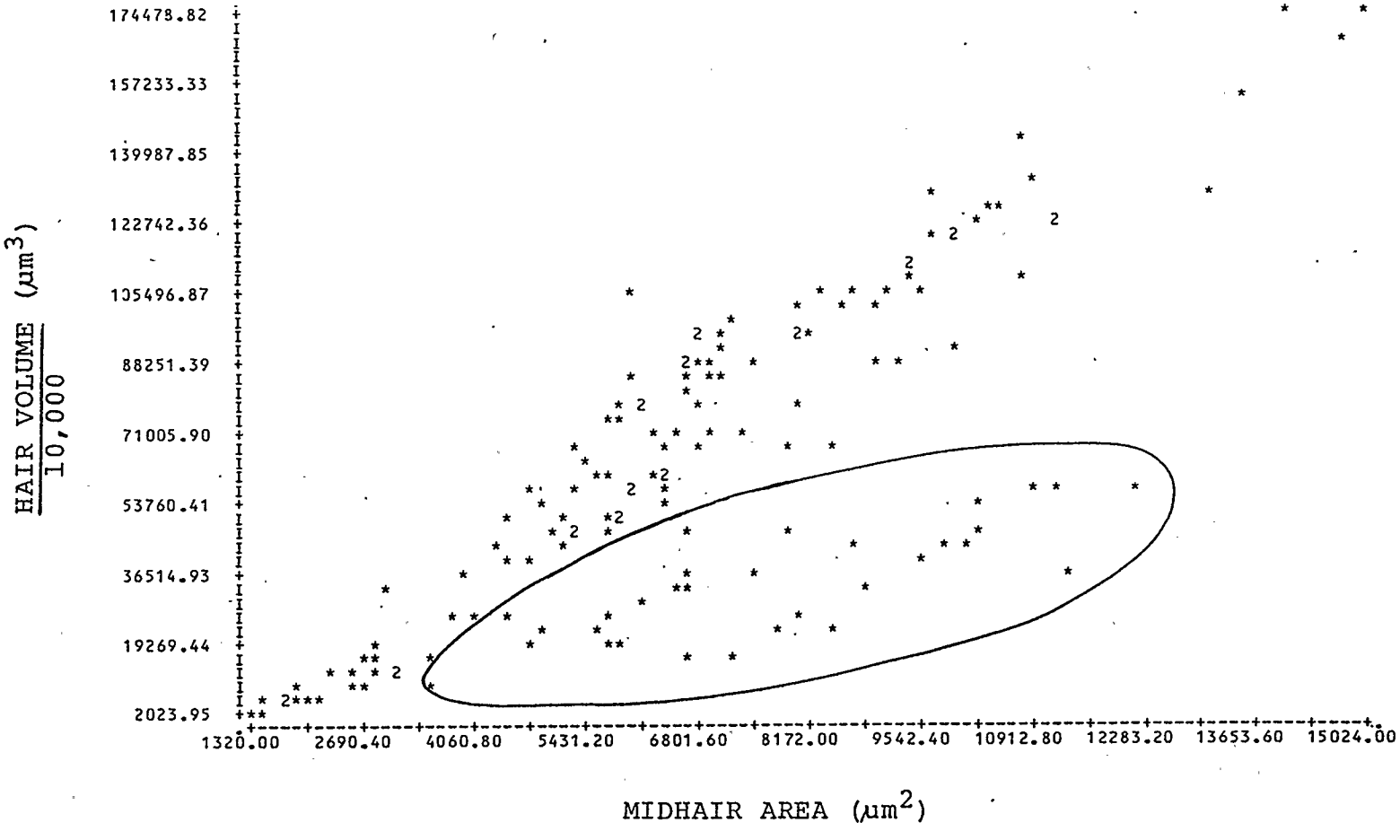


Figure 10. Plot of hair volume versus midhair area. Group 1 hairs are circled.

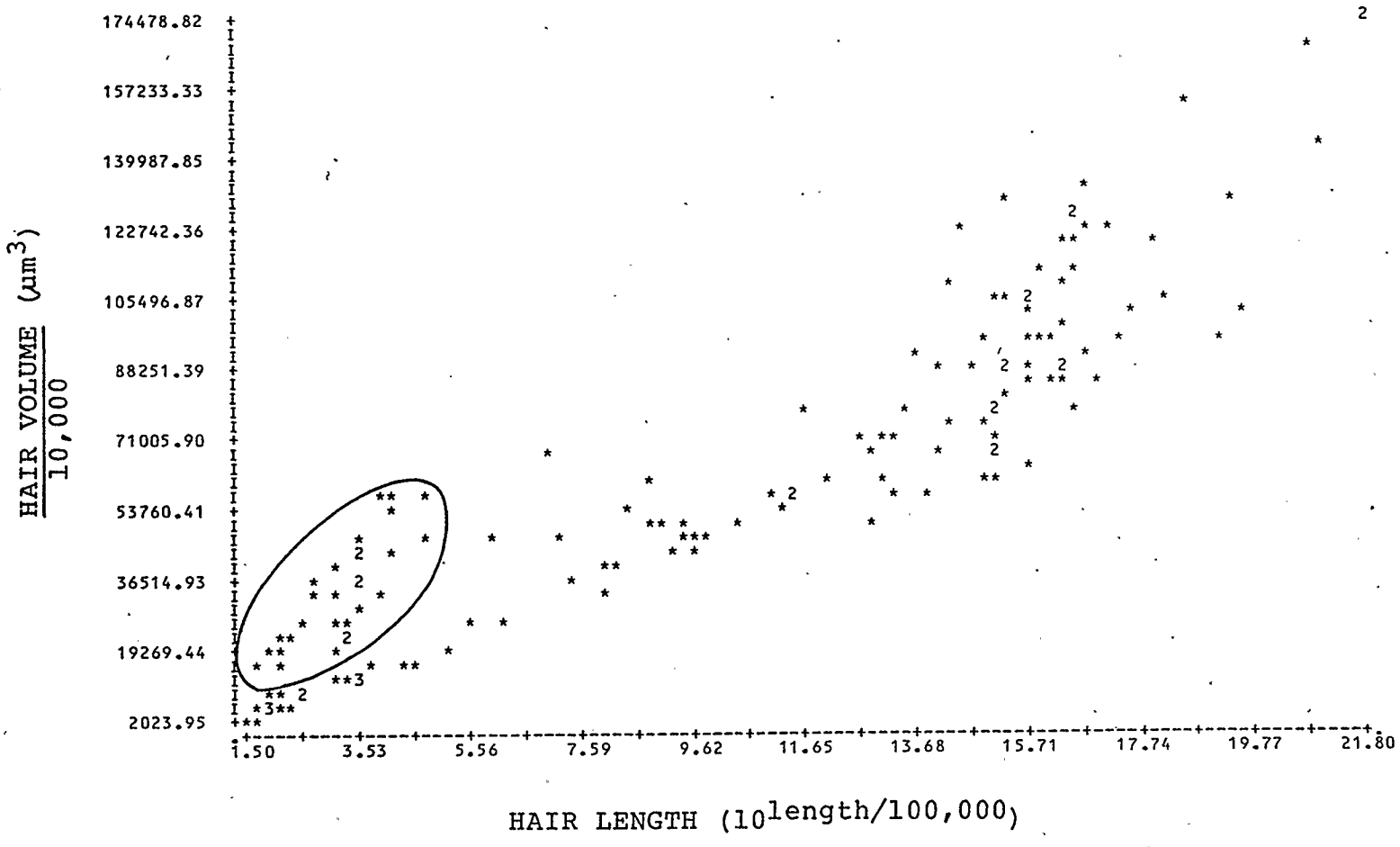


Figure 11. Plot of transformed hair length values versus hair volume showing divergence between group 1 hairs (circled) and group 2 hairs (main curve).

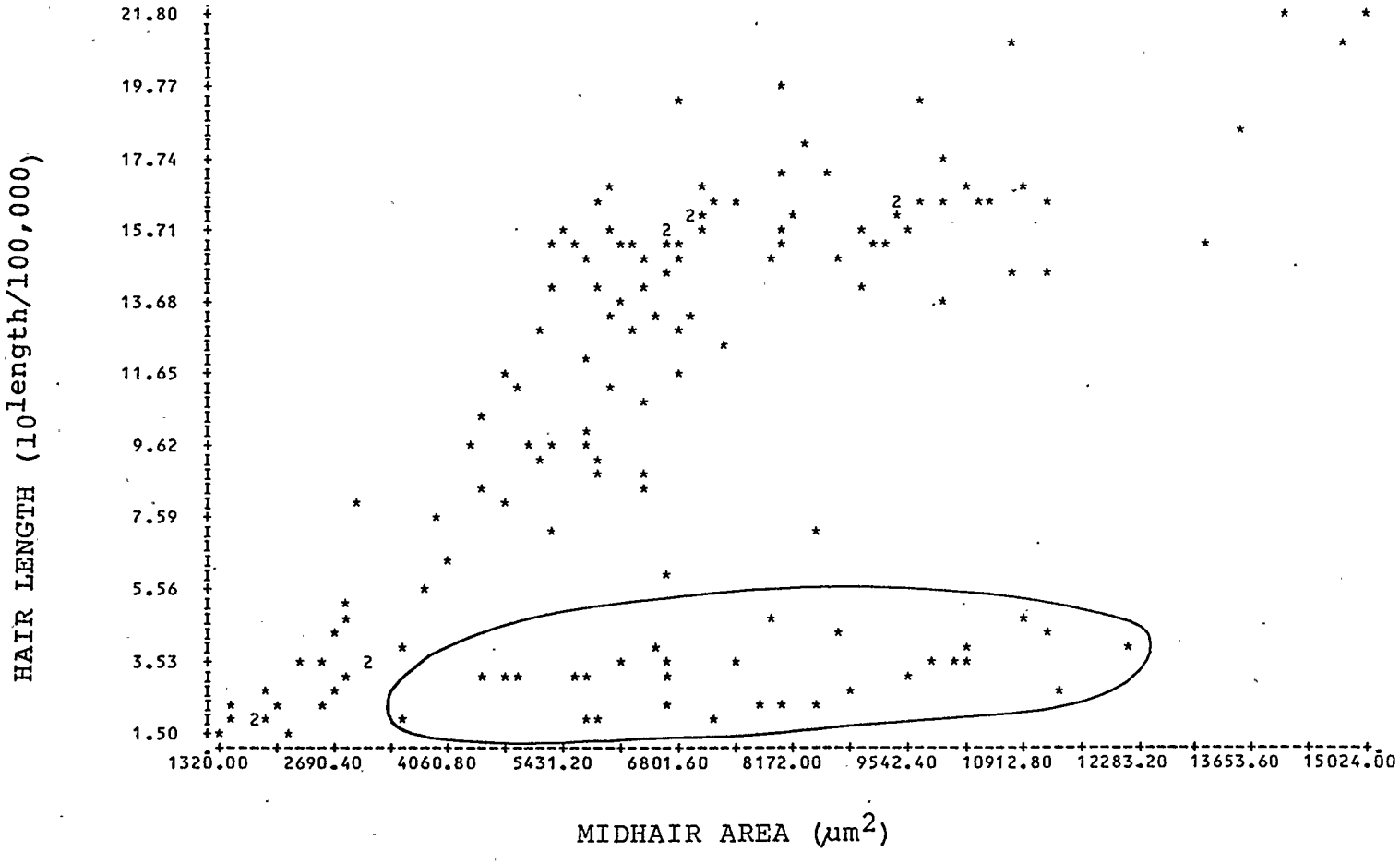


Figure 12. Plot of transformed hair length values versus midhair area showing divergence between group 1 hairs (circled) and group 2 hairs (main curve).

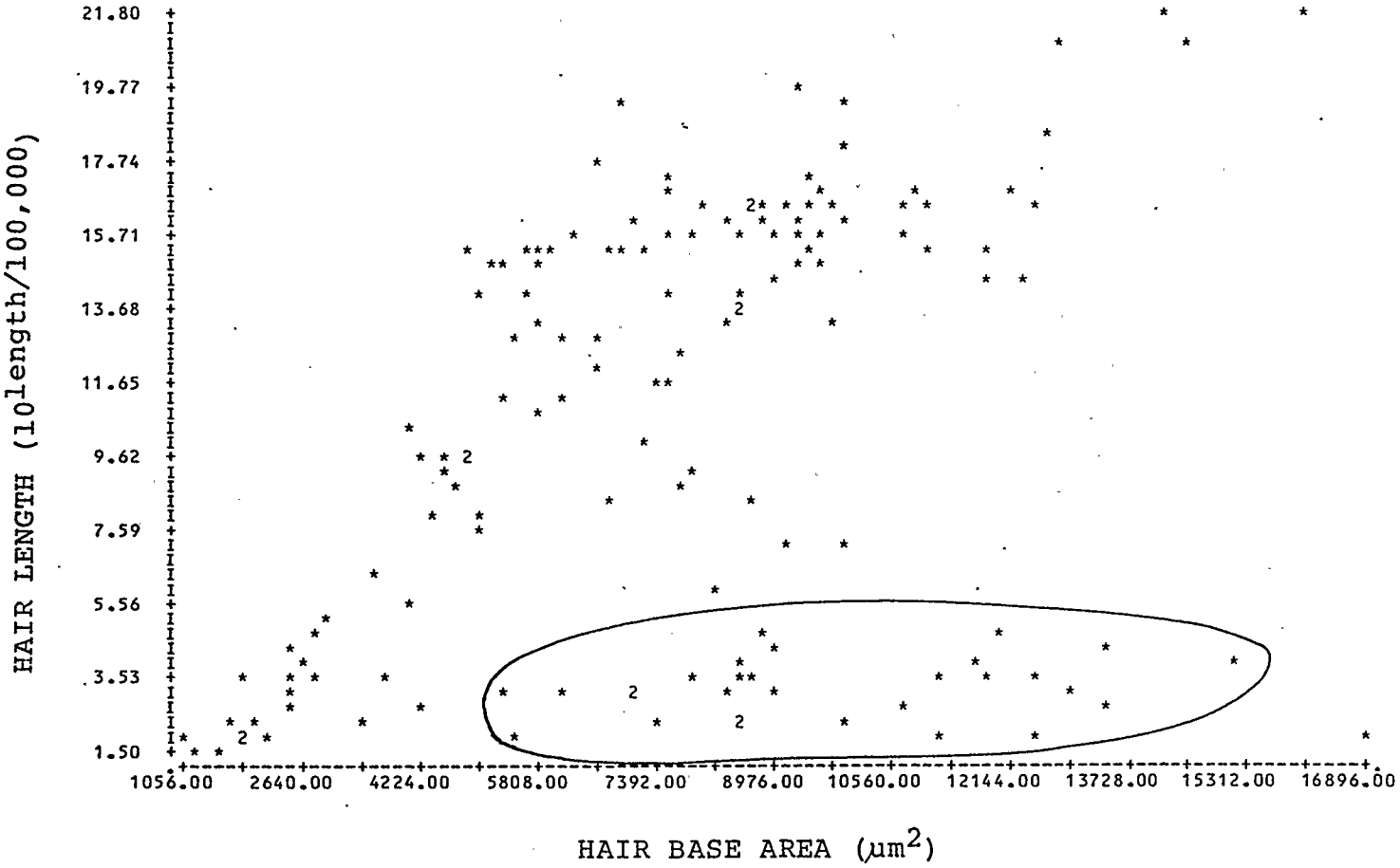
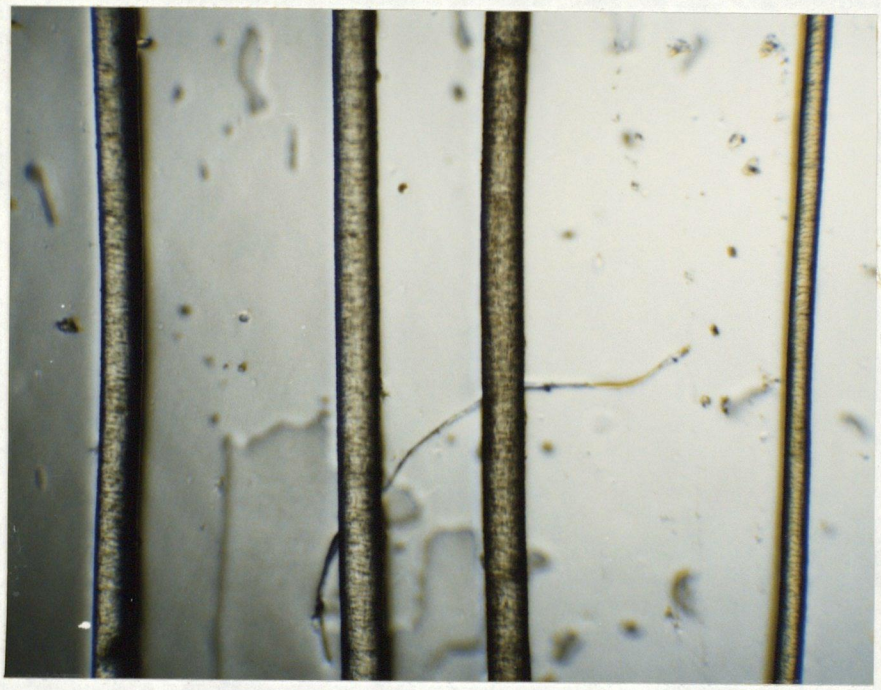


Figure 13. Plot of transformed hair length values versus hair base area showing divergence between group 1 hairs (circled) and group 2 hairs (main curve).

With respect to the relevant morphometric characteristics of hair length, base area, midhair area, volume and hair index, the differences between the means of group 1 and group 2 hair lengths ($t(120) = 14.84$, $p < .0005$), base areas ($t(144) = 4.51$, $p < .0005$), midhair areas ($t(144) = 1.98$, $p < .025$), volumes ($t(137) = 8.33$, $p < .0005$), and base hair indices ($t(144) = 7.51$, $p < .0005$) were all statistically significant.

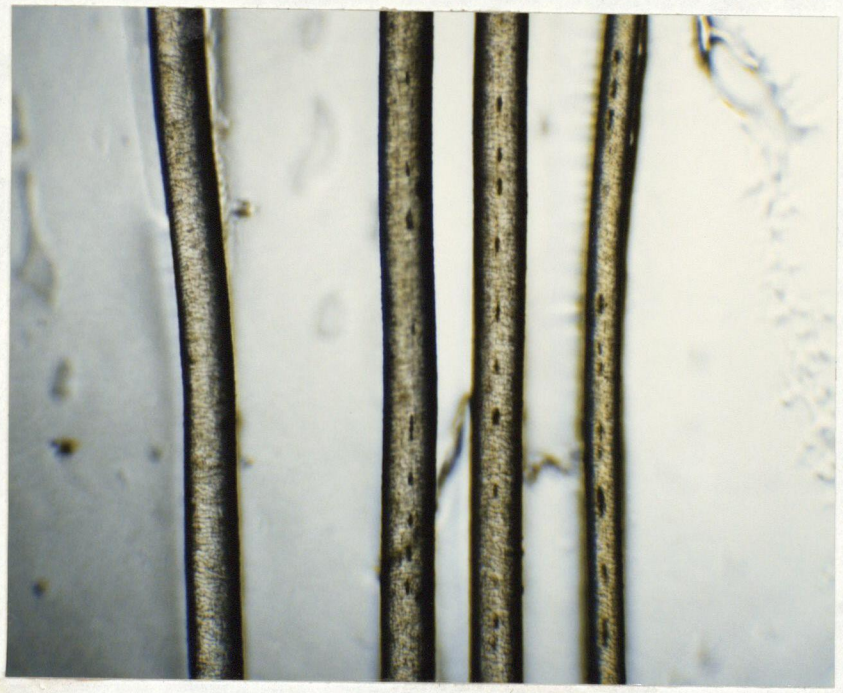
Medulla Types and Hair Pigmentation

In group 2 hairs, the medulla was either absent, or it assumed one of two configurations: fragmental and/or continuous. In 13 out of the 20 hairs less than 75,000 um long and having midhair areas less than 3550 μm^2 or base areas less than 5,400 μm^2, the medulla was absent (Figures 7 and 14). These hairs are relatively fine and are light grey in color, with a black tip. The second and third type of hairs both contain medullae which begin at some distance from the base and end short of the hair tip. Type 2 hairs contain a type of medulla described by Hausman (1930) as fragmental (Figure 15). These hairs attain a length of approximately 100,000 μm, and are somewhat coarser than type 1 hairs. They are an almost transparent white color at the base, turning light grey-brown further up the hair



Hair Base ——— ——— ———» Hair Tip

Figure 14. Sections removed from the base to the tip of a group 2, type 1 hair, showing no medulla.



Hair Base ——— ——— ——— ———» Hair Tip

Figure 15. Sections removed from the base to the tip of a group 2, type 2 hair, showing a fragmental medulla.

shaft. Approximately .5 - 1.0 cm before the tip, a white/yellow band is evident, and the tip itself is black. The third type of hair contains a medulla which is initally fragmental, but then becomes continuous (Figure 16). These hairs vary far more in base and midhair areas than in length (Figure 7). Type 3 hairs have a whitish, translucent base shading into light grey-brown, followed by dark grey-brown further up the shaft. Approximately at mid-shaft (in fully grown hairs) a roughly 1.0 cm wide dark yellow band is present, followed by a black section of shaft, a lighter yellow band and a black tip.

A typical raw data set for each of the three types of group 2 hairs is presented in Figure 17 a, b and c. A data set for a group 1 hair (Figure 17 d) demonstrates what is true for each of these 30 hairs: The medulla is already present at the base of the hair, which is not the case for any of the group 2 hairs. Furthermore, in each hair, the medulla is of the continuous type. This leads to the conclusion that group 1 hairs are, specifically, the new growth of group 2, type 3 hairs. If these were type 1 hairs, no medulla would be in evidence; if type 2, the medulla would be fragmented. Also, group 1 hairs display the strong black-yellow-black banding that is characteristic of group 2, type 3 hairs near their tips, and these bands are the same width as in fully grown hairs.

Hair Base ——— ——— ——— ———→ Hair Tip

Figure 16. Sections removed from the base to the tip of a group 2, type 3 hair, showing an initially fragmental, then continuous medulla.

(a) Group 2, type 1 data set - medulla absent.

2760	0
2230	0
2592	0
3048	0
3048	0
2832	0
3024	0
2952	0
3408	0
3432	0
3336	0
3216	0
2592	0
3096	0
3000	0
2904	0
2760	0
2304	0
2904	0
3120	0
2472	0
1968	0
2208	0
2184	0
2184	0
2160	0
2232	0
1752	0
1728	0
1656	0
1008	0
696	0
576	0
312	0

7488	504
7656	504
5688	384
5712	384
5472	480
6360	600
5880	504
6528	624
6624	600
5112	504
4512	312
4008	0
3432	0
2280	0
1344	0
1104	0
336	0

(d) Group 1 data set - continuous medulla - compare with last third of group 2, type 3 data set.

(b) Group 2, type 2 data set - medulla fragmental.

4800	0
5976	0
5376	0
5688	0
5184	0
5760	0
5544	0
5952	0
5112	0
5616	0
6000	0
6336	0
6960	0
5736	0
6264	0
5808	0
6858	0
5304	0
5280	0
5784	0
5808	24
5832	0
5496	24
5760	0
5232	0
4728	0
5352	0
5160	0
5736	24
5016	24
4896	48
4440	0
4608	0
4800	96
4512	96
4992	72
5040	72
4416	0
3216	48
3480	72
3456	0
3120	24
2952	24
2472	48
1920	0
1656	0
1344	0
1296	0
1152	0
552	0

(c) Group 2, type 3 data set - fragmental, then continous medulla.

5640	0
6264	0
5640	0
5640	0
6048	0
6120	0
5904	0
5952	0
6360	0
5976	0
6384	24
6312	0
5304	0
5376	0
5904	0
5928	0
6000	0
4848	0
5160	0
5280	0
5496	0
5136	24
5160	0
5064	0
4560	24
5112	0
5400	24
7248	456
7872	264
6936	0
8376	312
7992	48
8304	720
7656	360
7128	240
6192	360
6816	360
7200	240
7512	576
7872	504
6768	576
7704	552
6864	408
6456	312
6192	576
5712	672
6504	720
7056	720
7128	744
6984	816
5688	672
4584	0
4152	0
3600	0
2616	0
2088	0
1320	0
936	0

Figure 17. Typical raw data sets for group 1 and group 2 hairs, showing distribution of the medulla throughout the hair. Interval between measurements is 2000 µm.

In short, if one were to remove the top portion of a group 2, type 3 hair, then this top portion would be representative of a group 1 hair.

The new growth of group 2, type 1 and 2 hairs does not deviate from the main curve as do group 1 hairs, but rather, the new growth, half-grown, and fully grown hairs grade smoothly into each other, and new growth is therefore more difficult to identify. Of the 20 group 2 hairs which are less than 75,000 μm long, 7 were identified as type 2, and the remainder, as type 1 (see Figure 7). These 7 hairs, not having attained maximum length for type 2 hairs, could presumably be regarded as new growth, or at least, growing, type 2 hairs. However, more than these 4 may be present because, below a certain length, where only the tips of the hairs have grown beyond the skin surface, the new growth of types 1 and 2 hairs would be indistinguishable from each other, since their tips, where no medullary fragments would yet be present in type 2 hairs, would look very similar.

Dolnick (1969) found that in rhesus macaques, hair growth ceased completely in 3 out of the 4 body regions under investigation in spring, whereas an increased number of growing hairs was observed in summer. Possibly a seasonal cycle of hair growth also exists in P. c. anubis, and this would explain the gap between group 2 type 3 hairs

and group 1 hairs, where there is no gradation of hairs from new to old growth as there is in type 1 and type 2 hairs. This suggests that group 2 type 3 hair growth is seasonal, but growth of group 2, types 1 and 2 is not. However, had the subject used in the present study been sacrificed a few months later, the new growth might have been more advanced, and more of a gradation of type 3 hair lengths would then have been in evidence. Alternatively, had the animal been sacrificed a few months earlier, perhaps a more distinct division between the new and old growth of group 2, types 1 and 2 hairs would have been evident. A longitudinal study of a single animal, where hair samples from the same body region are examined at successive intervals throughout the year, appears to be the only way to resolve this problem.

Medulla Volume and Length

As stated earlier, the medulla volumes and lengths are considered approximations only. Their bases and tips were not traced beyond the first and last measured hair cross-sections in which they appeared, and consequently, in the worst possible case, the medulla in a given hair extends 1,950 µm past its reported base and 1,950 µm above its reported end. In addition, when the medulla is

fragmental, a similar extension into the empty space between fragments increases the error.

Again, group 1 hairs are clearly separated from group 2 on the basis of medulla volume and hair volume (Figure 18). The correlation of hair volumes with medulla volumes for all 146 hairs is .863. When the volumes of only group 1 hairs are correlated, however, r = .942, and when group 2 hairs are used, r = .928. The regression line for all 146 hairs passes between group 1 and group 2 hairs, and thus the scatter about the line is greater and produces a lower correlation coefficient than if a separate regression line is fitted to each group.

It is evident from these correlation coefficients that the larger the hair, the larger the medulla within it. There exists, however, an apparent upper limit on the cross-sectional area of the medulla relative to the cross-sectional area of the hair encompassing it. Figure 19 shows that as the cross-sectional area of the hair increases, the medulla area may assume a progressively larger range of values. Also, the larger the medulla area, the higher a percentage of the hair cross-sectional area is occupied by it (r = .934, Figure 20). However, the area of even the largest medulla accounts for only 17.70% of the hair cross-sectional area. The average percent of hair area occupied by medulla area is 3.02.

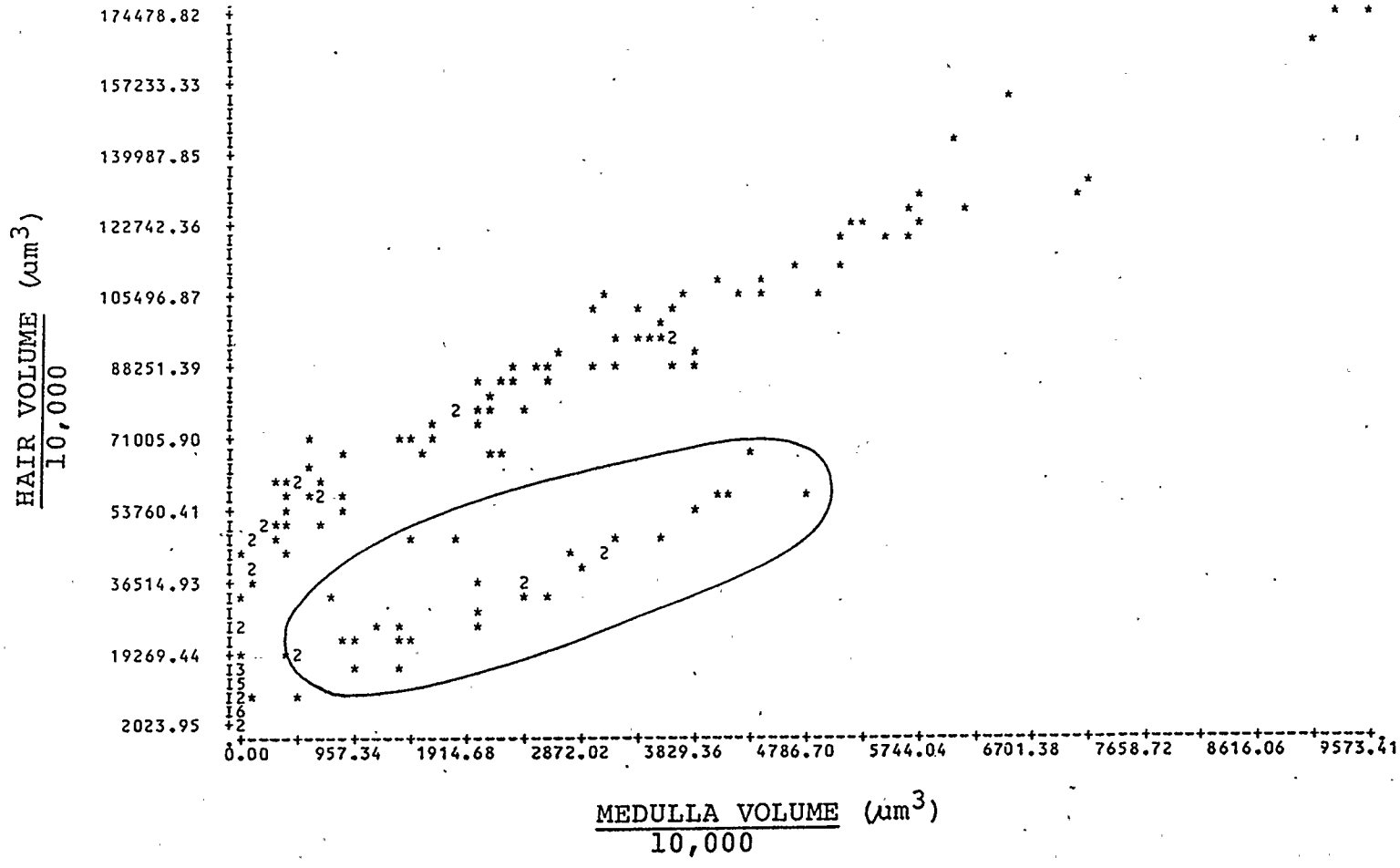


Figure 18. Plot of hair volume versus medulla volume, showing divergence of group 1 hairs (circled) from main body of curve.

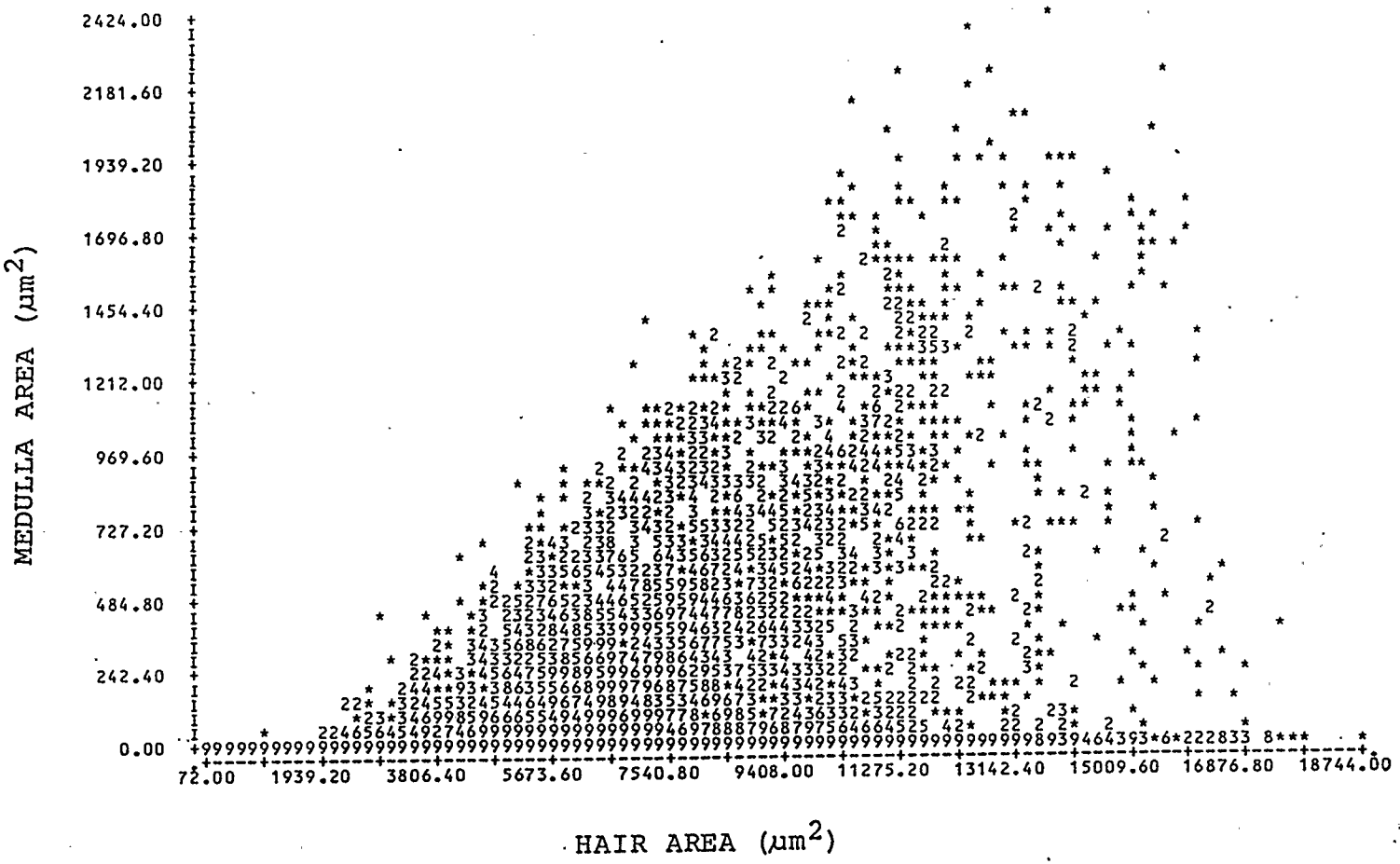


Figure 19. Plot of all measured medulla areas versus all measured hair areas (n=6592).

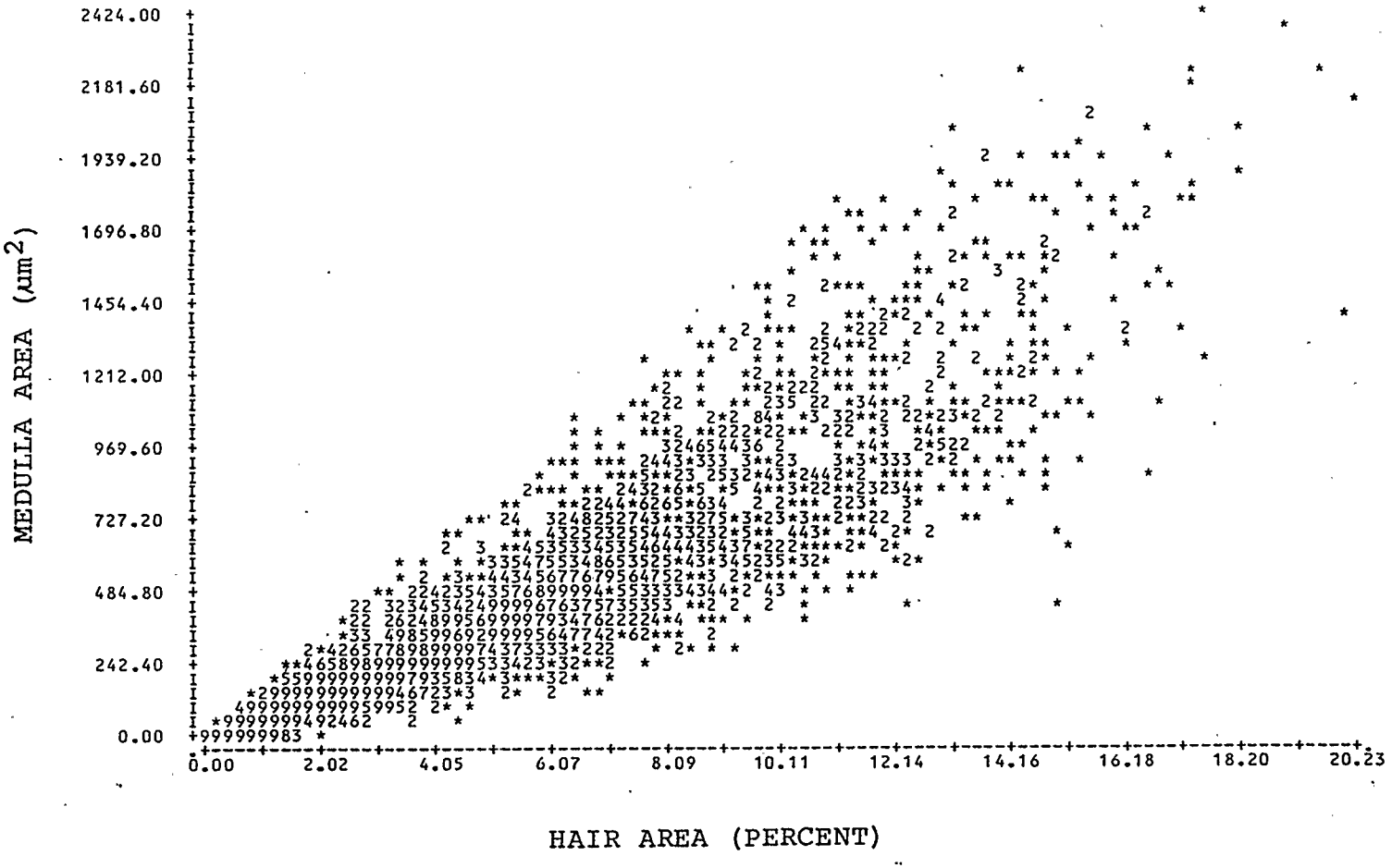


Figure 20. Plot of all measured medulla areas (n=6592) versus the percent of hair area each occupies.

Similarly, the medulla occupies an average of 2.99% of each hair volume, and at most, 8.57%. Of the entire hair sample, 3.45% of its volume is accounted for by the medullae. Even in the unlikely event that the medullary volume has been underestimated by as much as 100%, only approximately 7% of the hair sample volume would be occupied by medullae.

Coat Depth and Volume Fraction of Hair

The depth of the coat in the nape area, averaged over 10 measurements with a dial caliper, is 56.47 mm, and the average hair length is 90.28 mm (Table 1). The angle of the hairs relative to the skin surface is therefore

$$\text{sine } \theta = \frac{56.47 \text{ mm}}{90.28 \text{ mm}}$$

$$= .6255$$

$$= 39 \text{ degrees}$$

Given the coat depth of 56.47 mm, and the sum of all hair volumes (92,345,282,590.0 μm^3), the volume of the coat which is occupied by the hair is 32.7 mm^3/cm^3. If the coat is considered a fibrous insulator, then 3.27% of its volume is composed of fibres, and 96.73%, of air.

Table 1. Descriptive Statistics for Entire Sample (n=146)

	MEAN	ST. DEVIATION	MINIMUM	MAXIMUM	MEDIAN
Hair Volume	63,250.19	39,985.77	2,203.95	174,478.82	58,622.01
Hair Length	90,280.82	34,436.95	17,600.00	133,850.00	105,725.00
Medulla Length	58,947.37	28,088.15	2,000.00	96,000.00	67,500.00
Medulla Volume	2,423.77	2,107.09	4.80	9,573.40	2,067.82
HAIR BASE					
Cross-sectional Area	7,683.94	3,330.05	1,056.00	16,896.00	7,812.00
Major Diameter	101.88	25.32	37.00	162.00	106.00
Minor Diameter	91.99	22.22	30.00	143.00	96.17
Hair Index	90.68	7.08	70.27	100.00	92.06
MIDHAIR					
Cross-sectional Area	6,821.10	2,874.05	1,320.00	15,024.00	6,660.00
Major Diameter	98.90	21.29	46.00	147.00	100.25
Minor Diameter	84.49	20.50	38.00	132.00	85.25
Hair Index	85.15	6.99	65.59	100.00	84.79

Note. Lengths are given in μm, areas in μm^2, and volumes in μm^3. Hair volumes and medulla volumes were divided by 10,000. Medulla statistics are based on only the 133 hairs containing medullae.

Prediction of Volume

Using the Entire Sample to Predict Volume

Separately, the best predictors of hair volume were found to be hair length, midhair area and base area. These measurements are all relatively easy to obtain, and since the objective is to estimate volume without the time and effort involved in serial reconstruction, variables such as medulla volume, which correlate highly with hair volume but are as difficult to measure as hair volume itself, will not be used as components of the multiple regression equation.

The relationship between hair length and midhair area, length and base area, and length and hair volume is curvilinear (Figures 6, 7 and 8). Furthermore, the frequency distribution of hair length was found to be bimodal, and the major cause of the bimodality is new growth of type 3 hairs. The correlation between length and volume is .858 (Table 2), but when length is transformed ($10^{length/100,000}$) to linearize the relationship between it and the other variables, the length/volume correlation increases to .909.

Base area correlates with volume at .613, but midhair area, at .785. Since base area and midhair area are intercorrelated at .858, only one of these can be used as a predictor. However, length and midhair area are

Table 2. Bivariate Correlation Coefficients for Entire Sample (n=146 *), Group 2 (n=116 **), and Group 1 (n=30 ***)

	HAIR BASE AREA	MIDHAIR AREA	MEDULLA VOLUME	HAIR VOLUME	MEDULLA LENGTH	HAIR LENGTH	HAIR LENGTH $(10^{length/100,000})$
HAIR BASE AREA	1.000	.858 *	.744	.613	.490	.299	.344
	1.000	.900 **	.856	.922	.825	.778	.813
	1.000	.679 ***	.466	.490	-.404	.029	---
MIDHAIR AREA		1.000	.891	.785	.599	.481	.523
		1.000	.920	.959	.778	.789	.837
		1.000	.852	.821	.052	.418	---
MEDULLA VOLUME			1.000	.863	.624	.513	.601
			1.000	.928	.675	.630	.748
			1.000	.942	.380	.675	---
HAIR VOLUME				1.000	.864	.858	.909
				1.000	.856	.858	.925
				1.000	.492	.820	---
MEDULLA LENGTH					1.000	.887	.892
					1.000	.909	.916
					1.000	.871	---
HAIR LENGTH						1.000	.969
						1.000	.957
						1.000	---
HAIR LENGTH $(10^{length/100,000})$							1.000
							1.000
							---

intercorrelated at only .481, making these the two most suitable variables to enter into the regression equation. With volume as the dependent variable and length and midhair area as the independent variables, a very high multiple R emerges (.97), but examination of residual plots indicates that the residual variance is a complex function of the independent variables, and is not homogeneous. Since this makes any regression equation derived from such a combination of independent variables too error-prone as a predictor of volume, the sample was divided into its component subgroups, each of which was analyzed separately.

Using Sample Subgroups to Predict Volume

Group 2

When the new growth is eliminated from the sample, correlations of midhair area and base area with volume increase (Table 2). The correlation of length with volume remains the same as for the entire sample, but transformation of the lengths increases r slightly more, from .909 when 146 hairs are used to .925 for only group 2 hairs. Both midhair area and base area show a marked increase in r, base area (from .613 to .922) relatively more so than midhair area (from .785 to .959).

However, midhair area remains the better predictor of volume, and given the high intercorrelations of length, base area and midhair area, this last is the only variable suitable for entry into the regression equation. The regression equation for group 2, using volume as the dependent variable and midhair area as the independent variable, is

$$\frac{\text{Hair Volume}}{10{,}000} = -16043.34295 + 13.22817(\text{midhair area})$$

Standard Error of Estimate = 11696.11885

Standard Error of B = 0.36737

Group 1

The correlation coefficients of base area and length with volume decrease, but midhair area r is even higher than if all 146 hairs had been used (Table 2). In this subgroup, length has a linear relationship with volume, midhair area and base area, and therefore a data transformation is not necessary. Length and midhair area are equally good predictors of volume (r = .820 and .821, respectively), and since they are intercorrelated at only .481, both can be used. The regression equation, with volume as dependent variable and length and midhair area as

independent variables, is

$$\frac{\text{Hair Volume}}{10{,}000} = -24324.12578 + 3.38654(\text{midhair area}) + 0.64502(\text{hair length})$$

Standard Error of Estimate = 3113.02000

Standard Error of B = 0.27906(midhair area) and 0.05330(hair length)

Ellipticity and Estimation of Cross-Sectional Area

Since the diameter of the hairshaft can be obtained simply by measuring the longitudinal profile of the hair, the determination of hair cross-sectional areas would be considerably faster if these could be accurately calculated using only the major or minor diameter, rather than both.

For the entire sample, very high negative correlations between ellipticity (hair index) and percent error using either minor diameter (r = -.919) or major diameter (r = -.915) were obtained. In other words, the more elliptic the hair, the higher the error incurred by using either the major or the minor diameter to calculate cross-sectional area.

With minor diameter as the only estimator of area in group 2 hairs, the average error is 7.07%, rising to 15.39%

in group 1. If the major diameter alone is used, the average error increases from 9.93% in group 2 hairs to 21.72% in group 1 hairs. This increase in percent error indicates that the base areas in group 1 hairs are more elliptic than in group 2 hairs: indeed, the mean hair index for the former is 83.39, whereas for the latter it is 92.57.

Essentially, the hair becomes more elliptic toward the tip. The mean base hair index of group 2 hairs is 92.57, whereas at midshaft, it is 85.96. In group 1 hairs, the mean index at the base is 83.39, and at midshaft, 82.02. It is evident that the midshaft areas for the two groups are more similar in ellipticity than the bases: 82.02 in group 1 and 85.96 in group 2. Furthermore, given that group 1 hairs are the new growth, their bases would more or less correspond with the midhair point in group 2 hairs (i. e. the base of a half-grown hair will, when the hair is fully grown out, be its midhair point), and hence the similarity in group 1 base, and group 2 midshaft, hair indices.

On the other hand, the average error using the geometric mean to calculate area is only 2.28% for all 146 hairs, 2.83% for group 1 hairs, and 2.14% for group 2. The geometric mean is therefore the best estimator of cross-sectional area, making it necessary to section the

hair transversely in order to measure the major and minor diameters in cross-section.

CONCLUSION

Two distinct groups of hair, containing three types of hairs were discernible in the Papio cynocephalus anubis hair sample under investigation. These were labeled group 2, type 1 hairs, containing no medulla, group 2, type 2 hairs, with a fragmental medulla, and group 2, type 3 hairs, with an initially fragmental, and then continuous medulla. Furthermore, of the total hair sample, a portion was distinguishable as new hair growth, and these hairs were labeled group 1. This new growth was distinguishable not only as an offshoot in scatterplots and with respect to type of medulla, but also proved to be statistically distinct from the main body of the sample.

A seasonal hair growth cycle was postulated, but a longitudinal study is necessary to test this. Although group 2, type 1 and 2 hairs did not display the discrepancy between new growth and old growth which was observed between group 2, type 3 and group 1 hairs, this does not mean that, at other times of the year, such a discrepancy might not be in evidence. Conversely, the divergence between group 2, type 3 and group 1 hairs might well disappear.

The present study indicates that, in P. c. anubis dorsum hairs, the best predictors of hair volume are the midhair

cross-sectional area and the hair length. The estimation of volume is best accomplished via the initial plotting of all independent variables of interest relative to each other. If growing hairs are present and do not grade smoothly into the hair sample as a whole, these can then be partitioned out for separate analysis.

It has been shown that, due to the ellipticity of the present hair sample, the calculation of cross-sectional area using either the major or the minor diameter of the hairshaft results in an unacceptable level of error. This is particularly true at midshaft, where the hairs were found to be even more elliptic than at the base. It is therefore deemed adviseable to embed the hair and obtain areal measurements from cross-sections. Although a planimeter will provide the most accurate evaluation of area, calculations using the geometric mean of the major and minor diameters were found to deviate from planimetric estimates by only a small percentage.

The hair itself was found to comprise only 3.27% of the volume of the insulating hair coat. The hair density of the Papio c. anubis coat is low, suggesting that radiative transfer between hairs should play a major part in thermal transfer. Approximately 3.5% to 7.0% of the hair sample volume is occupied by medulla volume. Since this is a relatively small portion, it is questionable

whether the medulla needs to be taken into account in heat transfer equations.

The hair coat of P. c. anubis seems to be fairly well adapted to a warm climate. The function of the solid component of a fibrous insulator is, essentially, to divide the air space into smaller pockets, and thus to inhibit heat transfer by free convection. The higher the hair density, the more such air pockets will exist in the hair coat of an animal. A layered type of insulation exists, given the shorter, finer underhairs (group 2, type 1), the somewhat longer intermediate hairs (group 2, type 2) and the long guard hairs (group 2, type 3). For animals which inhabit hot climatic zones, thermoregulation consists more of heat dissipation than heat conservation. The sun imposes a heat load on the animal that must be dealt with. The hair coat serves to absorb this heat, and thus shields the skin from direct sun exposure. A hair coat with a low proportion of underhair, as is the case in P. c. anubis, will facilitate convective heat transfer away from the skin. If, in addition, the hair coat is relatively sparse, fewer air pockets exist in the coat, and thus, again, very little impedance to convective heat transfer is present.

The pigmentation of the hairs, in addition to providing camouflage for the animal, plays a thermoregulatory role as well. Since radiative transfer

apparently plays the major role in heat transfer through sparse insulators (Strong, Bundy & Bovenkerk, 1960), and since pigmentation influences radiative transfer (Dawson & Brown, 1970; Hutchinson & Brown, 1969), it leads to speculation that sparse coats may generally show some type of banding or patterned pigmentation in order to allow control over radiative heat transfer, whereas denser hair coats would be more likely to be monochromatic, since the predominant mode of heat transfer is via convection, which is not influenced by pigmentation. An animal with such a patterned coat, which will expose differing amounts of dark or light pigmentation in the coat depending on its orientation to the sun could enhance backward (away from the skin) or forward (toward the skin) scattering of radiation by varying its posture with respect to the sun. In additon, according to Walsberg, Campbell and King (1978), and Hutchinson and Brown (1969), dark-colored coats incur a higher radiative heat load than do those of a lighter color. However, the light coat retains the heat better than the dark coat, particularly at higher wind speeds. A hair coat which combines both dark and light pigmentation could well permit more precise thermoregulation, particulary via posture, than would a monochromatic coat. In an environment where shade is scarce, such an enhanced thermoregulatory capacity would

certainly confer an adaptive advantage, in that it would allow more extensive use of said environment.

However, in order to confirm or deny these notions, heat transfer studies on primate hair coats must be done. Only then will a correlational analysis of environmental variables and behavior eludicate any relationships that may exist between behavior and thermoregulation.

REFERENCES

Aherne, W.A., & Dunnill, M.S. (1982). Morphometry. London: Edward Arnold.

Bramblett, C.A. (1976). Patterns of primate behavior. Palo Alto: Mayfield.

Cena, K., & Clark, J.A. (1973). Thermal radiation from animal hair coats: coat structure and measurements of radiative temperature. Physiological and Medical Biology, 18, 432.

Cena, K., & Monteith, J.L. (1975). Transfer processes in animal coats. I. Radiative transfer. Proceedings of the Royal Society of London, B188, 377.

Clancy, M.J., & Herlihy, P.D. (1978). Assessments of changes in myofibre size in muscle. In H. de Boer & J. Martin (Eds.), CEC Seminar on Patterns of Growth and Development in Cattle. The Hague: Nyhoff.

Dawson, T.J., & Brown, G.D. (1970). A comparison of the insulative and reflective properties of the fur of desert kangaroos. Comparative Biochemical Physiology, 37, 23.

Dolnick, E.H. (1969). Variability of hair growth in Macaca mulatta. In W. Montagna, & R.L. Dobson (Eds.), Hair growth. London: Pergamon Press.

Funkhouser, G.E., Higgins, E.A., Adams, T., & Snow, C.C. (1967). The response of the savannah baboon (Papio cynocephalus) to thermal stress. Life Sciences, 6, 1615.

Hausman, L.A. (1930). Recent studies of hair structure relationships. Science Monthly, 30, 258.

Hutchinson, J.C.D., & Brown, G.D. (1969). Penetrance of cattle coats by radiation. Journal of Applied Physiology, 26, 454.

Kneberg, M. (1935). Improved technique for hair examination. American Journal of Physical Anthropology, 20, 51.

Leithold, L. (1976). The calculus with analytic geometry. (3rd Ed.), New York: Harper & Row.

Luft, J.H. (1961). Improvements in epoxy resin embedding methods. Journal of Biophysical and Biochemical Cytology, 9, 409.

Lustick, S., Battersby, B., & Kelty, M. (1978). Behavioral thermoregulation: orientation to the sun in herring gulls. Science, 200, 81.

Massa, R.E., Durante, I., & Monchietto, M.J. (1981). Fur hair study in a colony of Macaca fuscata. Antropologia Contemporanea, 4, 47.

Montagna, W., & Yun, J.S. (1962). The skin of primates. VIII. The skin of the anubis baboon (Papio doguera). American Journal of Physical Anthropology, 20, 131.

Paterson, J.D. (1982). Thermoregulatory behaviour and ecological factors in primates. Canadian Review of Physical Anthropology, 3, 3.

Paterson, J.D. (1986). Shape as a factor in primate thermoregulation. In D. M. Taub & F. A. King (Eds.), Proceedings of the IXth Congress of the International Primatological Society. Vol. 1: Current Perspectives in Primate Social Dynamics. New York: Van Nostrand Reinhold, pp. 228-242.

Pelanne, C.M. (1978). Does the insulation have a thermal conductivity? In R.P. Tye (Ed.), Thermal transmission measurements of insulation, ASTM STP 660. American Society for Testing and Materials, 60.

Perkins, E.M., Smith, A.A., & Ford, D. (1969). A study of hair groupings in primates. In W. Montagna & R.L. Dobson (Eds.), Hair growth. London: Pergamon Press, p. 357-366.

Reuer, E. (1971). Dimension und Querschnittsform der Kopfhaare von Macaca mulatta. Proceedings of the 3rd International Congress of Primatology, Zurich, 1, 207.

Reuer, E. (1976). Pilometrische Methoden - Beiträge und Kritik. Anthropologischer Anzeiger, 35, 154.

Rosen, S.I. (1969). A comparative study of the microscopic anatomy of non-human primate head hair.

PhD thesis, University of Kansas. (University Microfilms, Inc. Ann Arbor, Michigan.)

Scholander, P.K., Walters, V., Hock, R., & Irving, L. (1950). Body insulation of some Arctic and tropical mammals and birds. Biological Bulletin, 99, 225.

Schultz, A.H. (1931). The density of hair in primates. Human Biology, 3, 303.

Spurr, A.R. (1969). A low-viscosity epoxy embedding medium for electron microscopy. Journal of Ultrastructure Research, 26, 31.

Stelzner, J.K. & Hausfater, G. (1986). Posture, microclimate, and thermoregulation in yellow baboons. Primates, 27, 449.

Strong, H.M., Bundy, F.P., & Bovenkerk, H.P. (1960). Flat panel vacuum thermal insulation. Journal of Applied Physics, 31(1), 39.

Swan, H. (1974). Thermoregulation and bioenergetics. New York: Elsevier.

Vernall, D.G. (1961). Study of the size and shape of cross sections of hair from four races of men. American Journal of Physical Anthroplogy, 19, 345.

Walsberg, G.E., Campbell, G.S., & King, J.R. (1978). Animal coat color and radiative heat gain: A re-evaluation. Journal of Comparative Physiology, 126, 211.

Williams, M.A. (1977). Quantitative methods in biology. In A.M. Glauert (Ed.), Practical methods in electron microscopy, (Vol. 6), New York: North-Holland.

Wynkoop, E.M. (1929). A study of the age correlations of the cuticular scales, medullas, and shaft diameters of human head hair. American Journal of Physical Anthropology, 13, 177.

Zilles, K., Schleicher, A., & Pehleman, F. (1982). How many sections must be measured in order to reconstruct the volume of a structure using serial sections? Microscopica ACTA, 86, 339.