

Craniometric investigations on *Mesopithecus* in comparison with two recent colobines

Kraniometrische Untersuchungen an *Mesopithecus* im Vergleich zu zwei rezenten Colobinen

by

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Abstract

Craniometric measurements were taken on *Mesopithecus pentelicus* from the Miocene of Pikermi (Greece). Landmark distances and angle measurements were obtained to the skull, while mesiodistal length and trigonid width were used as tooth measurements. A number of indices were calculated that are less significant in discrimination analysis than direct measurements.

The same set of measurements was carried out on archetypic representatives of the recent African (*Procolobus badius*) and Asiatic (*Presbytis entellus*) colobine monkeys. These were compared to the fossil species in order to elucidate phenetic relationships. Sexual dimorphism is demonstrated in various characters using uni- and multivariate statistical methods; the mesiodistal length of the canines playing an especially important role. It is furthermore possible to differentiate between species using the length of the upper canines.

Morphological relationships are determined by calculating generalized distances. *Mesopithecus pentelicus* differs equally from both recent forms in skull measurements, but its dental measurements show a stronger relationship to the Asiatic form.

Keywords: *Mesopithecus*, Colobines, Craniometry, Analysis of Variance, Discriminant Analysis.

Zusammenfassung

An *Mesopithecus pentelicus* aus dem Miozän von Pikermi wurden kraniometrische Messungen durchgeführt, wobei am Schädel die gebräuchliche Methode der Landmarken und Winkelmessungen Verwendung fanden, während bei den Zähnen die

mesiodistalen Längen und trigonalen Breiten erfaßt wurden. Weiters konnten auch verschiedene Indizes berechnet werden, die sich in den folgenden Analysen als weniger aussagekräftig als die Einzelmerkmale erwiesen.

Als Vergleich zur fossilen Art wurden an jeweils einem Vertreter der afrikanischen (*Procolobus badius*) und asiatischen (*Presbytis entellus*) Colobinen die gleichen Messungen durchgeführt, um die phänetischen Verwandtschaftsbeziehungen aufzuklären. Mittels uni- und multivariater statistischer Verfahren konnten die Geschlechtsunterschiede anhand verschiedener Merkmale untermauert werden, wobei die mesiodistale Länge der Caninen eine wesentliche Rolle spielt. Die Länge des oberen Canins kann darüber hinaus auch zur Trennung der Arten herangezogen werden.

Verwandtschaftliche Beziehungen, die auf der Morphologie basieren, ließen sich durch Berechnung der Generalisierten Distanzen ermitteln. Während bei den reinen Schädelmessungen *Mesopithecus pentelicus* von den beiden rezenten Vertretern in einem ähnlichen Grade verschieden ist, ergeben sich bei den Zahnmessungen stärkere Konnexen zwischen der asiatischen und der fossilen Form.

Problem

Craniometric methods for comparisons within the cercopithecids (compare HULL, 1979) were applied within a project on the osteology and dentition of *Mesopithecus*. Compared to other fossil catarrhines, the tooth and skull remains of *Mesopithecus* are numerous, thus allowing statistical evaluations. This does not hold true for the poorly documented postcranial skeleton.

Mesopithecus, well known since GAUDRY (1862), has more recently been studied by DELSON (1973, 1975). New data concerning geographic distribution, which can deliver important clues to phylo-

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genetic relationships, are now available. In addition to the classic locality of Pikermi near Athens (GAUDRY 1862), further Eastern European localities are known from Bulgaria, Macedonia and southern Russia. The distribution of *Mesopithecus* also reached across Hungary up to the "Dinotheriensande" of Hessen in SW-Germany. All finds are of Turolian age (Miocene) with the exception of the "Dinotheriensande", which are dated as Vallesian. Of especial importance from the standpoint of biogeography are the localities of Maragha, Persia (MECQUENEM 1925) and the region of Kabul, Afghanistan (BRUNET et al. 1982), which are similarly dated as Turolian in age. Here the distribution of *Mesopithecus* is contiguous with the Asiatic colobine monkeys. The relationship of *Mesopithecus* to the Asiatic as well as to the African representatives of recent colobine monkeys is problematic due to the postulated faunal boundary in the Turolian between northern Eurasia and India (HEINTZ & BRUNET 1982).

Another open question is which metric character of the skull and dentition (additional to the canines, which are not always present) can be used in order to differentiate between the sexes of *Mesopithecus*, and how these characters behave in recent colobine monkeys.

Material and methods

Material and measurements

Only those skulls, jaws or teeth of *Mesopithecus* were analyzed which originate from the type locality in the valley of the Megalorhema Creek at Pikermi near Athens (Greece). The finds come from numerous European collections including Athens, Basel, Munich, Paris, Stuttgart and Vienna. The material studied originates from the same stratigraphic level of the classic locality (Turolian, Miocene). Thus the individuals belong to a fossil population with a restricted area of origin (compare BACHMAYER et al. 1982 for the formation of the bonebed of Pikermi). In further investigations only those *Mesopithecus* remains were included which could be identified as males or females by canine tooth height.

One species each of Asiatic and African colobine monkey was used for comparison (Plate 1). The 20 complete skulls (10 males, 10 females) of the African red colobus (*Procolobus badius*) from the collections of the NHM Wien all originate from the Ituri forest (NE Zaire, Grauer collections), so that they can be considered as being members of a single geographic population.

The skulls of the Asiatic Hanuman langur (*Presbytis entellus*) originate, on the other hand, from different collections. In addition to skulls from the Zo-

ologisches Museum der Universität Hamburg, other collections (Munich, Stuttgart and Frankfurt) were drawn upon for comparison. Thus they originate from different populations within the distribution area of this species. Some of the individuals originate from NE India (Assam), the larger part lived in Western and Southern India and Sri Lanka.

The skull characters chosen for measurement varied according to the state of preservation of the *Mesopithecus* skull. These are always deformed to some extent by sediment compaction, so that some, often important, dimensions could not be taken at all. Thus only those dimensions of recent colobine monkey skulls were measured which were also intact in *Mesopithecus*. Primarily, those dimensions were taken as defined in detail by OPPENHEIM et al. 1927. Exceptions are the biorbital width, interorbital width, orbital rim thickness and palatine width (SCHULTZ 1958, p.81).

The longest mesio-distal length was taken as an attribute characterizing the dentition. Within the molars, trigonid (trigon) width was measured perpendicular to the length, whereas the largest crown width was taken for the premolars. The length of the tooth rows (premolars, molars and dental lengths) are to be understood as the shortest mesio-distal lengths. Tooth measurements presented little difficulty. In *Mesopithecus*, however, the length dimensions of the tooth rows can also be affected by deformation.

Statistical methods

All six groups (3 species with different sexes) had approximately the same number of specimens (9–14 individuals). The variances can thus be better compared when using parametric methods. The skull and jaws of the fossil *Mesopithecus* are rarely associated. It was thus impossible to consider the skull and the jaws as a unified set within the multivariate analysis, which handles all characters together. This results in 4 parallel multivariate analyses, with the skull and lower jaw proportions and the teeth of the upper and lower jaws each being analyzed independently from one another. Whereas all characters (with the exception of certain teeth dimensions) of the recent *Procolobus badius* and *Presbytis entellus* are measurable, this is not the case for *Mesopithecus pentelicus*. If it was not possible to measure more than half of the specimen of *Mesopithecus*, then these characters were deleted in the subsequent multivariate analyses. Otherwise the missing measurements were estimated using step-wise multivariate regressions (DILLON & GOLDSTEIN, 1984). The characters with the least missing measurements were the first to be supplemented. A comparison of both the correlation matrices (original and supplemented

characters) proves the correctness of this procedure.

The normal distribution of individual characters was tested with the Kolmogoroff-Smirnov-test (see Tables 1 to 3). With few exceptions (some angle measurements of the skull and jaw) all variables show a good agreement with the normal distribution. Thus the following parametric methods are justified. Variance analyses were used to prove the differences in the individual characters between the six groups. With only few exceptions (some incisor lengths in the upper and lower jaws) all were highly significant (see Tables 4–14). Following the variance analyses, a Student-Newman-Keuls test (compare SOKAL & ROHLF 1969) was applied, allowing a pairwise comparison between the different groups (see Tables 4–14).

The variables important for distinguishing groups can be determined through a multivariate discriminant analysis, using the Mahalanobis method for extraction. A step-wise reduction to the significant differentiating variables followed. The advantage of this method is that the differences between groups can be shown in distances (Mahalanobis-Distances, see Table 17). These represent the degree of morphological similarity. The conversion of the multivariate F-values between the groups to Mahalanobis-Distances follows the equation of DILLON & GOLDSTEIN (1984, p.367). In the discriminant analysis only direct and no derived measurements (indices), as in the univariate analysis, were included.

An advantage of discriminant equations is that new forms, not incorporated in the analyses before, can be assigned to the group with the highest similarity. This occurs by the appointment of the characters' measurements in the discriminant equations, which include as parameters the classification function coefficients (Table 15) for the individual groups.

Results

The statistical parameters for each character of the six groups are presented in Tables 1–3. All characters of the tooth dimensions show a normal distribution. Within the skull and lower jaw characters, the angle measurements tend to deviate from a normal distribution. As far as the facial skull is concerned, only the profile angle of the male Hanuman langur is not normally distributed. The females of this species and the remaining two studied species (both sexes) always show normal distribution. The bicondylar width and the mandibular length of *Mesopithecus pentelicus* was only measured in a few cases. A test for normal distribution of this character is thus superfluous. The mandibular angle does not show a normal distribution for both sexes of *Presbytis* and for the female red colobus. Within *Mesopithecus* females this character also shows tendencies to an

asymmetric distribution. The same is true for the tooth row angle. The deviation from the normal distribution in this character is highly significant only for Hanuman langur females. This approaches to the significance threshold of 5% probability of error for the male red colobus, male *Presbytis* and female *Mesopithecus*.

A test for homogeneity of variances between the 6 groups revealed correspondences in only a few skull characters (see Tables 4–14), these being the thickness of the orbital rim and the nasal width. Some angle measurements of the lower jaw also show uniform variances. Furthermore the homogeneity of variances can be determined for most of the index calculations.

Within tooth measurements, only the lengths of the lower premolars are similar as far as variances are concerned. All other characters show a significant statistical inhomogeneity. This is caused by the comparatively high variances of male and female *Presbytis* (with the exception of the mesio-distal lengths of the upper and lower canines). A higher variance of the mesio-distal lengths of the canines is shown by the males of all species.

Similar differences are also responsible for the inhomogeneity of the variances of the skull and lower jaw dimensions. The variances in male and female Hanuman langurs are distinctly higher than in other groups. A possible explanation for these inhomogeneities is that the *Procolobus* individuals originate from a more or less uniform population. Similar population uniformity can be assumed for the fossil *Mesopithecus* specimens as all originate from a single "fossil population". Population homogeneity can be excluded for the *Presbytis* skulls. This could explain the relatively uniform variances in *Procolobus* as well as *Mesopithecus* for most dimensions.

The homogeneity in the variances of most indices can be explained as follows: When no correlation between direct measurements exists, the variances of the calculated characters (indices) are higher than the variances of both the single characters. The correlations between the characters used in the index calculations are high, the variances of the relationships of both measurements have to remain small and therefore homogeneity within the variances of indices results.

Group differentiation

The results of the univariate variance analyses show that only few characters are useful in separating species or genera. Within the characters of the facial skull the nasion-prosthion length shows a significantly high F-value. The relationships between the individual groups are, however, not clear. Palatine breadth shows even higher F-values (with similar number of degrees of freedom). This parameter

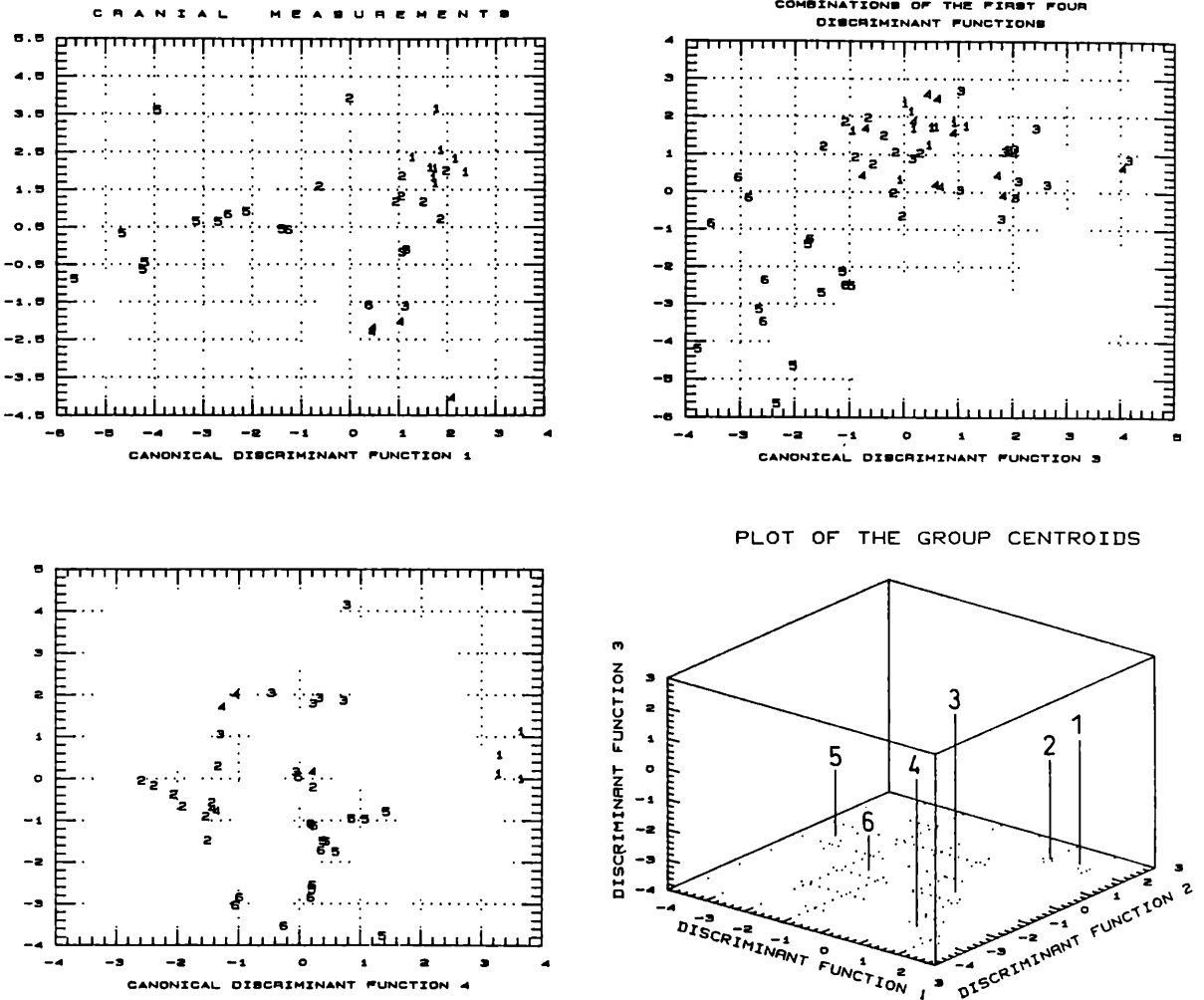


Fig. 1. Discriminant analysis by facial skull characters. Position of individuals and group centroids within the first three canonical discriminant functions indicated by numbers corresponding to group numbers of Plate 1.

separates *Presbytis* from *Procolobus* and *Mesopithecus*. Within the variance analyses of the facial skull characters, the orbital rim thickness shows the highest F-values. In each species male individuals are separated from females. Although the dental length of the skull shows a lower F-value than the previously described parameters, *Presbytis* is separated from both the other species.

It is noteworthy that only those indices whose elements already allow clear differentiations as individual characters also allow a discrimination of the groups. This is true for the index palatine breadth/nasion-prosthion height, which orders the female *Presbytis* to *Mesopithecus*. The *Presbytis* male shows no differences to *Procolobus*, which has uniform characters amongst the sexes. All other indices, with the exception of molar-premolar length/nasion-prosthion height, show little or absolutely no differences between the groups. They are thus less suitable than the directly measured charac-

ters in differentiating between the groups. Furthermore they could not be important for all multivariate analyses.

Lower jaw measurements show similar results. The best differentiations can be made with the characters chin height, dental (molar-premolar) and molar length. The highest chin height values are found within both sexes of *Presbytis*, followed by *Procolobus*. *Mesopithecus* is characterized by the lowest values. The values are not significantly different between either the males or females of *Presbytis* and *Procolobus*. *Mesopithecus*, however, is distinctly different in the sexes. The variability in chin height of the *Mesopithecus* male falls within the range of both recent female forms. Dental and molar length show similar properties. Both the *Presbytis* sexes can be separated from the relatively uniform *Procolobus-Mesopithecus* group.

As far as derived characters are concerned, the index corpus height/molar length joins all male and

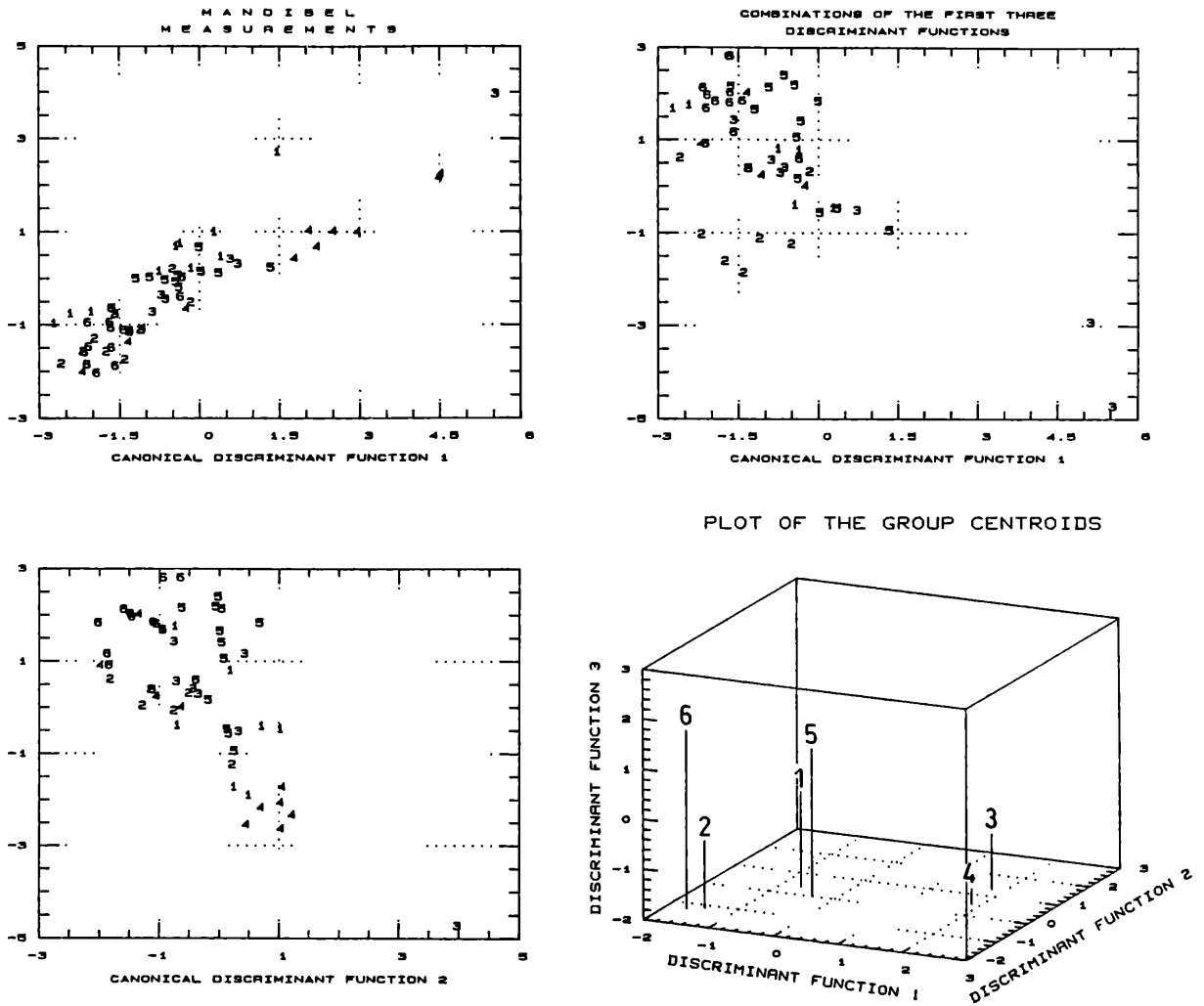


Fig. 2. Discriminant analysis by mandibular characters. Position of individuals and group centroids within the first three canonical discriminant functions indicated by numbers corresponding to group numbers of Plate 1.

female individuals of the three species, although significantly separating the sexes. All further indices are even worse separators than the individual characters from which they are computed.

The trend revealed by individual characters and indices is that *Mesopithecus* is closer to *Procolobus* than to *Presbytis* as far as facial skull and lower jaw characters are concerned.

The tooth measurements show, as opposed to the skull measurements, higher F-values in variance analyses between the groups. Therefore the number of separating characters is higher. The best result is provided by mesiodistal length of the superior canine, which significantly differentiates between all groups. Further useful characters are the breadth of the P4 sup., the M1 sup. and the M2 sup., which separates all *Procolobus* specimens (with smaller values) from the *Mesopithecus-Presbytis* group. The length of M1 sup. and M3 sup. show a different relationship: here, *Presbytis* is separated with higher values

from the *Procolobus-Mesopithecus* group.

Only few significant differences between the groups are recognizable based on the remaining maxillar teeth characters. The lengths of both upper premolars are especially unsuitable for differentiation. Even the lengths of both upper incisors do not allow any differentiations.

The mandibular teeth show similar results to those of the maxillar teeth. Here, the mesiodistal length of the canine is also especially suitable for separating the sexes. *Procolobus* is always separated from the uniform *Mesopithecus-Presbytis* group in the breadth of molars M1 inf., M2 inf. and M3 inf.

M1 inf. and M2 inf. lengths separates *Presbytis* from the remaining species. An especially good character for species discrimination is the length of M3 inf. Although no significant differences are found between the sexes of the species, the differences between the species are highly significant. These good diagnostic characters stands in opposition to the pa-

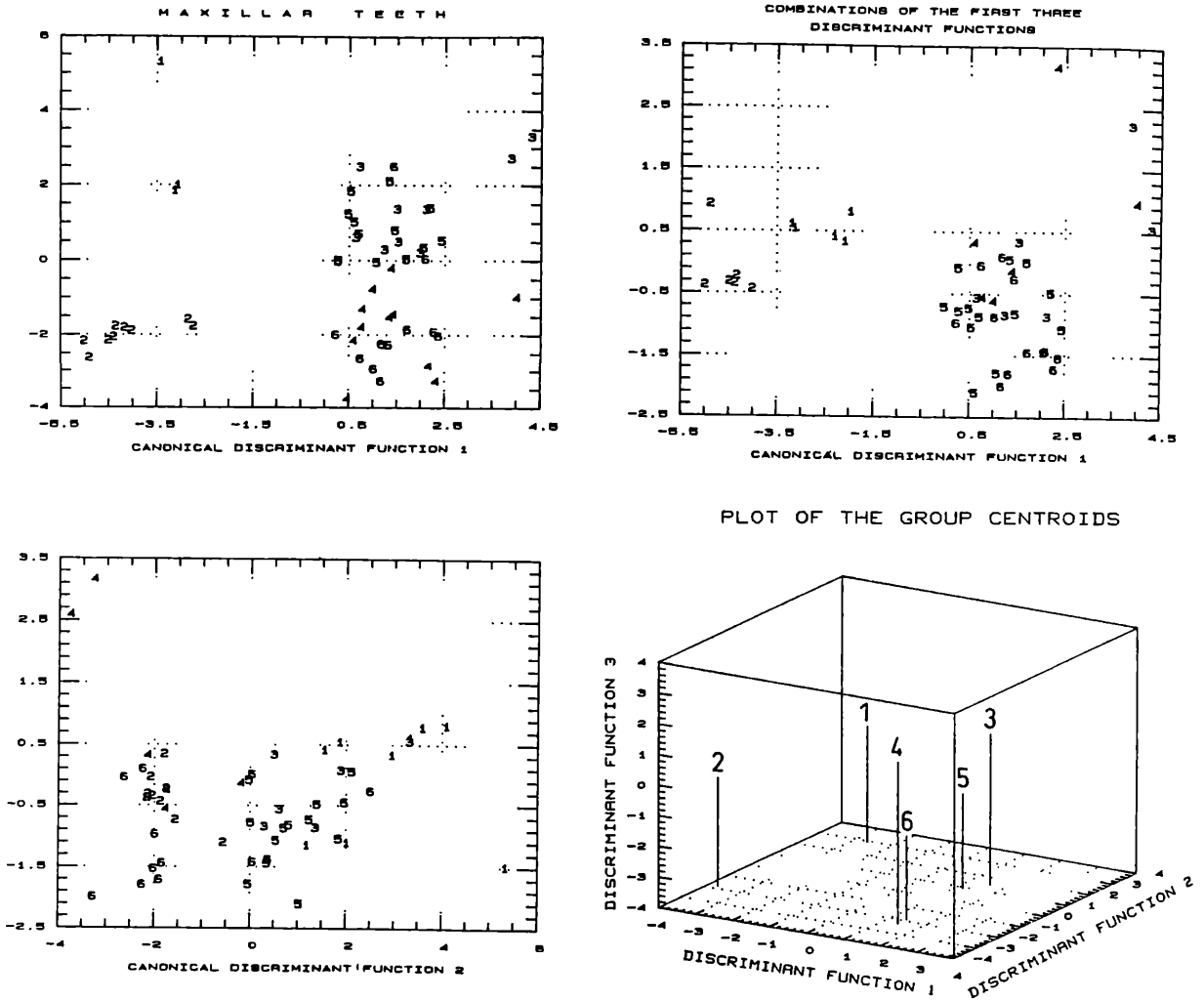


Fig. 3. Discriminant analysis by maxillary teeth characters. Position of individuals and group centroids within the first three canonical discriminant functions indicated by numbers corresponding to group numbers of Plate 1.

rameters I2 inf. length and P4 inf. breadth, which do not allow a differentiation into groups.

The analysis of tooth characters allows the conclusion that *Mesopithecus* and *Presbytis* are the morphologically closer groups whereas *Procolobus* stands somewhat aside.

In order to determine which variables are important for group differentiation and how these groups are morphologically related, multiple discriminant analyses and the calculation of Mahalanobis distances must be employed.

Only those skull dimensions which could be measured in all specimens were used for the discriminant analysis. Thus only 7 characters were used in the analysis (basion-prosthion length, nasion-prosthion height, interorbital width, palatine breadth, orbital rim thickness, nasal width, dental length). The step-wise reduction of the characters shows that all 7 characters are important for group differentiation. From the 5 discriminant functions the first 4 are of impor-

tance. Whereas the 1st function is highly correlated with the character nasal width, the 2nd function is determined to the same extent from all the variables. The 3rd function shows high correlation with the variables orbital rim thickness, basion-prosthion length and palatine breadth. The 4th function is highly correlated with nasion-prosthion height.

Identifications of the individuals using the classification functions resulted in a very high number (97.06%) of correctly classified individuals. Some female Hanuman langurs and *Mesopithecus* are incorrectly identified as the male of the same species.

The variables for the lower jaw do not show such promising results. The following characters were used in the multivariate analysis: symphyseal width, chin height, corpus height, mandibular angle, chin angle, dental length and molar length. All variables are important for the discrimination of the groups. A difference to the skull measurements is that only the first three discriminant functions are significant.

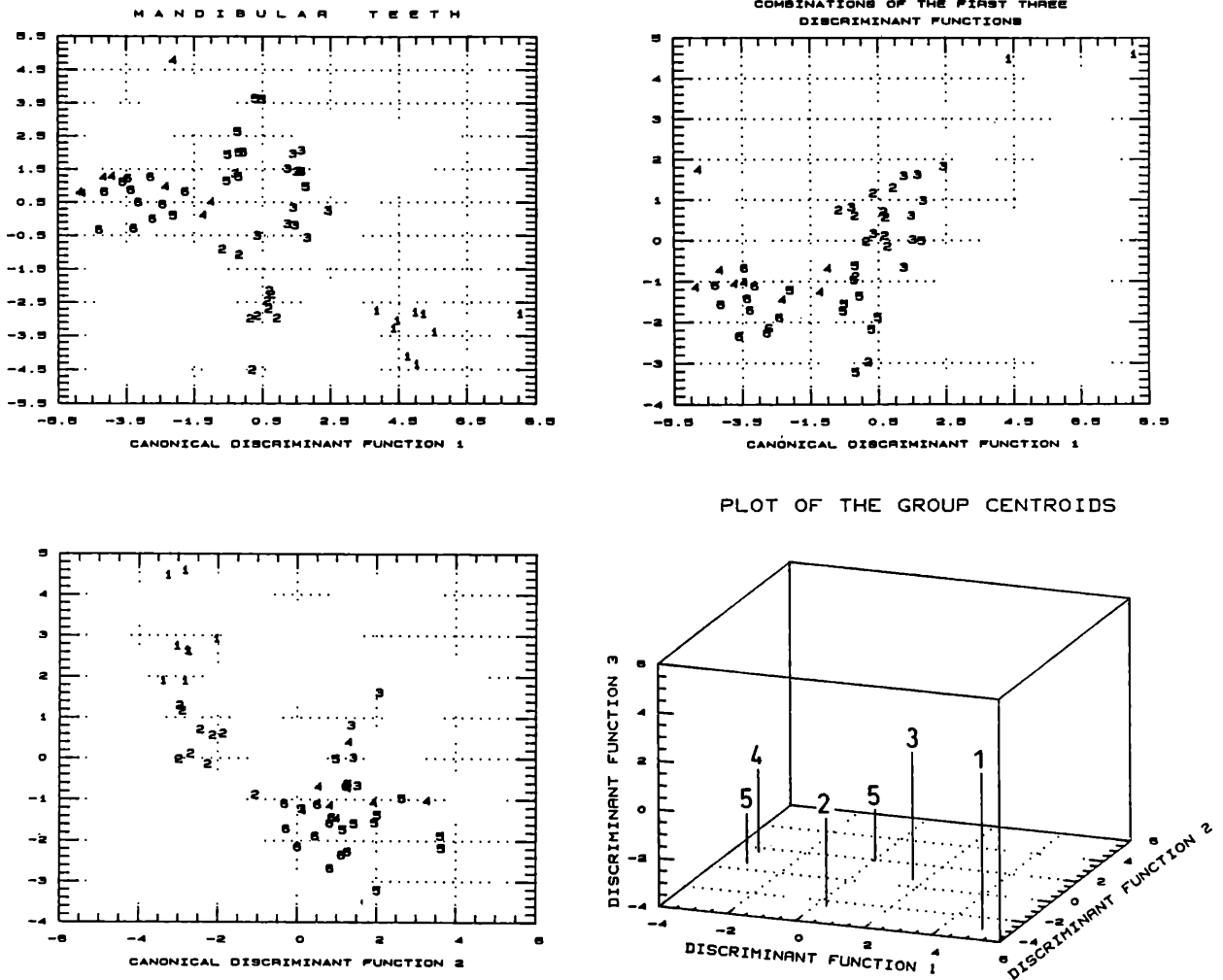


Fig. 4. Discriminant analysis by mandibular teeth characters. Position of individuals and group centroids within the first three canonical discriminant functions indicated by numbers corresponding to group numbers of Plate 1.

Whereas the first function is highly correlated with all variables, the 2nd function is determined by chin angle. All other variables are correlated with the 3rd discriminant function.

The identification of individuals using the classification functions yielded a lower percent of correct classifications (59.15%) than the skull measurements. The highest number of correct classifications are found in the fossil species. The classification of the male red colobus monkey was especially poor.

The results of univariate analysis demonstrate that tooth measurements are suitable for species separation. This becomes more apparent in the multivariate analysis through a distinctly better identification of the individuals. Using the step-wise reduction of the variables in the discriminant analyses within the maxillar teeth, it can be shown that the mesiodistal lengths of P4 sup., M1 sup. and M2 sup. as well as the breadth of P4 sup. are not necessary for discrimination. The remaining characters are highly correlated

with the discriminant functions and thus prove their importance for group separation.

The first and most important function is determined by the breadth of P3 sup., M1 sup. and M2 sup. The 2nd discriminant function is determined solely by the mesiodistal length of the Caninus sup. The 3rd function is determined by the length of M3 sup., the 4th by its breadth. All remaining variables are correlated with the irrelevant 5th function. The classification of the individuals using the classification functions yielded a high percentage (86.48%) of correctly identified individuals.

The analysis of mandibular teeth provided almost identical results. Only the length of I2 inf. and M2 inf. as well as the breadth of M1 inf. were removed. Of the three significant discriminant functions the first is correlated with the remaining variables. The second function shows a high correlation to the length of Caninus inf. and to the breadth of M2 inf. and M3 inf. With the exception of P4 inf.

and M1 inf. breadth, all other measurements are correlated with the 3rd discriminant function. An even better result (89.86%) is obtained for the classification of the individuals than using maxillary teeth. Even the sexes of *Procolobus* were correctly classified.

The relationships between groups can be shown using the false classifications. According to mandibular teeth, incorrectly classified male *Presbytis* individuals belong to male *Mesopithecus*, whereas the incorrectly associated females are placed within *Mesopithecus* females. The same holds true for the maxillary teeth. Incorrectly classified male *Presbytis* are associated with *Mesopithecus* males; female *Presbytis* tend to be placed within female *Mesopithecus*.

In order to determine differences and relationships between groups, a graphic method can be used. The mean of the discriminant function values for each group can be depicted in space, which is determined by the first three discriminant functions (see Figures 1-4). The following relationships between the species and sexes can be recognized from the distances of the skull measurements: Greatest affinities (shortest distances) exist between the sexes of each species. They are especially separated by the 3rd discriminant function. All species show comparable degrees of similarity among themselves (Figure 1).

Clearly structured relationships are evident according to lower jaw distances between group centroids. In this case, *Procolobus* and *Mesopithecus* are more similar to one another than *Presbytis*, which clearly stands aside (Figure 2).

The distances of the maxillary teeth demonstrate the following morphological affinities: The closest association occurs between males of *Presbytis* and *Mesopithecus* as well as between the females of both species (Figure 3). The sexes of *Procolobus* are clearly separated from the other species. The 2nd discriminant function again has the strongest influence in the separation of the sexes.

Similar relationships are evident according to the mandibular teeth. *Presbytis* and *Mesopithecus* females are in close contact, whereas male *Mesopithecus* show a stronger connection to the *Presbytis* males. *Procolobus* females are drawn to the neighborhood of male *Presbytis* and male *Mesopithecus*; the *Procolobus* male, however, stand clearly aside. (Figure 4).

Methods which allow the intensity of relationships to be shown - such as the Mahalanobis distance - are even more suitable for the determination of morphological relationships. The relations between the groups can be shown in the form of distance matrices (Table 17). An interpretation of the degree of morphological relationships using Mahalanobis distances is included in the discussion below.

Sexual differentiation

Sexual dimorphism in *Mesopithecus pentelicus* is clearly developed not only in the canines but also in other tooth and skull dimensions. With the exception of the variables palatine width and dental length, all those facial skull dimensions representing direct measurements can be drawn upon to distinguish the sexes. Within the indices only the relationship dental length/nasion-prosthion height are suitable for differentiation. Correct assignment to sex using individual characters is not possible because of strong variance overlap.

The discriminant analysis between the sexes (Table 16) of *Mesopithecus* shows that optimal separation is reached by using only 2 variables: basion-prosthion length and orbital rim thickness. A 100% assignment of the individuals is attained using these two characters with the classification coefficients of the discriminant functions.

Direct lower jaw measurements are much less suitable for the discrimination of sex in *Mesopithecus* than skull characters. Only three characters (chin height, corpus height below the M2 inf. and mandibular angle) show significant differences (Tables 6-7). As far as the indices are concerned, the relationships corpus height/molar length and corpus height/dental length show sexual differences.

The discriminant functions again allow a 100% assignment despite the rather poor differentiation possibilities using the single characters. The combination of the variables symphyseal width, chin height, corpus height, mandibular angle and dental length allow this optimal discrimination. It is also demonstrated that the remaining characters (chin angle and molar length) add little more to this differentiation as they are highly correlated with a number of variables.

Both of the recent colobine monkey species show a 100% assignment of the individuals in the discriminant analysis which separates the sexes. The genera, however, show differences in the importance of the variables providing the base for these discriminations. Within the facial skull measurements, *Presbytis* shows a closer correspondence with *Mesopithecus*: here, both the basion-prosthion length and the orbital rim thickness contribute to the discrimination of sex. Of additional importance for the discrimination are palatine width and interorbital width. The palatine breadth and nasal width are also important for the separation of the sexes in *Procolobus*. The basion-prosthion length which is important in *Mesopithecus* only play a small role in the discrimination of the *Procolobus* sexes.

The differences in the importance of lower jaw characters for separating the sexes in the studied colobine monkeys are not so large. Almost all variables are important for the discrimination of the

groups, so that large conformity between the genera is also present (Table 16).

When tooth measurements are taken into consideration in form of univariate analyses, then only the mesiodistal length of the upper and lower canines is suitable for a differentiation of the *Mesopithecus* sexes. A definite assignment is difficult due to the strong overlap of variances. The discriminant analyses confirm the importance of these characters, as a high correlation exists between the discriminant function and canine length. Among the maxillary teeth measurements, the lengths of P3 sup., M1 sup. and of M2 sup. as well as the breadth of M1 sup. are important for the differentiation of the sexes, although this is not apparent from the univariate analyses.

In addition to the lower canines lengths, the lengths of I2 inf., P4 inf. and M2 inf. and the width of P3 inf. of the mandibular teeth are also important for the discrimination of the sexes (Table 16). With the exception of a single false result for the maxillary teeth, the classification of the individuals is optimal using the classification function coefficient for all teeth measurements.

Recent and fossil species are to a large extent similar in character discrimination. All *Presbytis* females have an average higher value than the males, with the exception of P3 sup. length, and M3 sup. breadth. The opposite is true for *Mesopithecus*, where in most cases the average maxillary teeth measurements are larger in the male. This is also true for mandibular teeth dimensions. Here Hanuman langur females also show higher values, with the exception of P3 inf. length and P3 inf. and P4 inf. breadths. Finally, in contrast to *Mesopithecus*, the length and breadths of P3 inf. in *Presbytis* is significantly different between the sexes. *Procolobus badius* shows a similar relationship between the sexes. In most parameters the males surpass the females. Exceptions are the lengths of P4 sup., M2 sup., I1 inf., and I2 inf. as well as the breadth of P4 inf., M1 inf. and M3 inf. Sexual dimorphism, however, has not been statistically confirmed. This contradicts the observations of YAMADA & SAKAI (1983), who found significant differences in *Procolobus badius* with respect to the lengths and breadth of P3 inf. Additionally, the tooth dimensions of the postcanine dentition are always larger in the female than the male.

The importance of the mesiodistal canine length for the separation of the sexes is once again proven by multivariate discriminant analysis. Other important characters of *Presbytis entellus* are restricted, in the upper jaw, to the lengths of P4 sup. and M3 sup. All other dimensions are of less importance for an optimal discrimination. Equally important as in *Mesopithecus* for separating the sexes are the lengths of I2 inf., P3 inf. and M3 inf. as well as the breadths

of P3 inf. and M3 inf.

In *Procolobus* the maxillary teeth play an equally dominant role in discriminant analysis as do the canines. Important are further the lengths of P3 sup. and M1 sup. as well as the breadths of P3 sup., P4 sup., M1 sup. and M2 sup. The role of canine lengths is distinctly more important in the lower jaw of *Procolobus badius*. In addition to P3 inf. and P4 inf. lengths the length of I2 inf. is also important.

The importance of I2 inf. length for the discrimination of sexes is thus documented for all of the studied colobine monkeys. Additionally, both measurements of P3 inf. are useful in the separation of sexes within these colobines.

Discussion

Cranial measurements

The relationship of both sexes in *Mesopithecus* to recent colobine monkeys using Mahalanobis distances (Table 17) indicates phenetic relationships. The correspondence in the measurements does not necessarily represent the degree of phylogenetic relationship.

As far as skull measurements of *Presbytis* and *Mesopithecus* are concerned, the highest similarities occur between the sexes. In *Procolobus*, however, distinct sexual dimorphism is indicated by a much smaller degree of similarity (more than twice the Mahalanobis distance) between the sexes. Relationships between the genera and species are demonstrated by the shortest distance for both male and female *Mesopithecus* to female *Procolobus*. Relationships with the same degree occur between the males of *Mesopithecus* and *Presbytis* as well as between *Mesopithecus* females and both sexes of *Presbytis*.

The lower jaw dimensions show no such clear relationships between sexes and species. This is additionally expressed in the higher proportion of false classifications within the discriminant analyses. Similarities between the sexes of the species, as shown by the skull measurements, are not present. The sexes of *Mesopithecus* are very similar (small Mahalanobis distances), but the *Mesopithecus* male shows a corresponding degree of similarity (with even smaller distance values) with the *Presbytis* male. The *Mesopithecus* female shows virtually the same distances to the other sex on the one hand and to the *Presbytis* female on the other hand. The red colobus again differs here from other species. Highest similarity occur between the female red colobus and the Hanuman langur female. The *Procolobus* male also shows a closer connection to the *Presbytis* male than to the *Procolobus* female.

Considering the skull measurements as a whole, the greatest similarity is present between the sexes of *Mesopithecus*, whereby in almost all measurements

the males are larger than the females. This is also true for the measurements of *Procolobus* and *Presbytis*.

The skull of the *Mesopithecus* female is somewhat more similar to the *Procolobus* female than to the *Presbytis* female. For the male the opposite is true; here *Mesopithecus* and *Presbytis* are clearly more similar to one another than to the specialized *Procolobus*.

If these morphological similarities are interpreted as phylogenetic relationships, then the fossil species must be interpreted as being the primitive form from which both recent forms have developed to almost the same extent. *Procolobus* and *Mesopithecus* are similar in those characters that pertain solely to the facial skull. If the braincase and the lower jaw are also considered, then the connection between *Mesopithecus* and *Presbytis* is somewhat stronger. Characteristic for these differences is also the development of a sagittal crest, which is only present in the *Procolobus* male. Within the *Procolobus* and *Colobus* species, however, this character varies considerably (compare SCHULTZ 1958).

It must be stressed once again that all *Mesopithecus pentelicus* measurements were made on individuals belonging to a uniform fossil population. Thus the variances in the characters remained relatively small, being equal to those seen in recent populations (*Procolobus badius*). Multivariate differences in characters can be highly significant between species of a colobine monkey genus. This has been shown in the black and white colobus species, where statistically significant differences are found even in the subspecies (compare HULL 1979). Considering the large distribution area of *Mesopithecus* (ranging from the Mediterranean area across Asia Minor to Afghanistan), the development of subspecies or even species, significantly differing in craniometric characters, would be expected. The large variances shown by *Presbytis entellus* represent the scatter of the whole species. In comparison, the small variances of *Mesopithecus* from Pikermi could be a clue to the existence of further species or subspecies.

Tooth measurements

Phenetic relationships of the species were analyzed using Mahalanobis distances. The sexual differences in teeth dimensions are clearly greater than the differences between the species. This is in contrast to the skull dimensions, where, with the exception of *Procolobus*, the sexes of a species show the greatest similarities (Table 17).

Based on the maxillary teeth of *Mesopithecus* the largest similarities occur between the male of this species and the *Presbytis* male. The *Mesopithecus* female is most similar first to the opposite sex and

then to the *Presbytis* female. The red colobus stand clearly aside. Closest connections are present between the males of *Procolobus* and *Mesopithecus* on the one hand and between the *Procolobus* female and the male of the fossil species on the other hand. The very large Mahalanobis distances correspond to 2 to 4 times the value between *Presbytis* and *Mesopithecus*.

Mandibular teeth reveal the same relationships. Here the *Mesopithecus* female shows the greatest similarity first to the *Presbytis* female and then to the *Mesopithecus* male. The connections between the *Mesopithecus* and *Presbytis* males are also very close, although somewhat larger similarities occur between male and female *Mesopithecus*.

Again the red colobus monkey stands clearly aside as far as mandibular teeth dimensions are concerned. Large morphological differences exist between all groups and sexes, even within the same species.

The results of the multiple discriminant analyses and the Mahalanobis distances allow the following interpretation. The differentiation of the sexes according to dental measurements is very clear. The strong phenetic relationship between *Mesopithecus* and *Presbytis* points to a similar method of food gathering. *Mesopithecus* is interpreted to be a ground dweller; *Presbytis* often collects food on the ground. *Procolobus*, however, is a tree inhabitant and leaf eater, in the case of the red colobus monkey also fruit consumer. The result is a recognizable specialization of the dentition. Gradational differences are also recognizable within the African colobine monkeys. Thus the black-white *Guereza* (genus *Colobus*) – a pure leaf consumer – is the most specialized representative of its genus group (compare LEUTENEGGER 1971, YAMADA & SAKAI 1983). It differs in its sexual and intraspecific differentiation even more clearly from the studied red colobus monkeys as well as from the *Nasalis* group of equally highly specialized leaf consumers within the Asiatic representatives (compare SWINDLER & ORLOSKY 1974). Thus according to tooth measurements the phenetic relationships between *Mesopithecus* and *Presbytis* are even closer than between the fossil species and *Procolobus badius*.

If both recent species are considered as archetypal representatives of their genus, and if they are phylogenetically linked to *Mesopithecus*, then the following hypothesis can be forwarded:

Mesopithecus pentelicus stands close to the primitive form of the African and Asiatic colobine monkeys (compare DELSON 1973, 1975, STRASSER & DELSON 1987, FLEAGLE 1988). A relationship of the European *Mesopithecus* to the Asiatic colobine monkeys can be assumed. *Mesopithecus* more strongly resembles the Asiatic colobine monkeys in the facial skull and tooth measurements than

the specialized, leaf-consuming African representatives. The somewhat closer relationship of *Mesopithecus* to the *Presbytis* group was already assumed earlier (compare DELSON 1973, SIMONS 1971) and has since been confirmed through studies on tooth prism structure (DOSTAL & ZAPFE 1986).

Here the specialization of the African colobine monkeys in the metric characters of the facial skull and in the tooth measurements can be proven. A clear differentiation is shown from *Mesopithecus* on the one hand and from contemporary Asiatic genera (for example *Presbytis*) on the other hand.

Summary

Discrimination of sexes

As far as sex differentiation according to metric characters is concerned, *Mesopithecus pentelicus* shows a degree of differentiation similar to that of recent African (*Procolobus badius*) and Asiatic (*Presbytis entellus*) colobine monkeys. The species studied here show very similar skull and teeth dimensions. With the exception of orbital rim thickness, the facial skull characters vary in importance for sexual discrimination. The basion-prosthion length is important for the differentiation of the sexes in *Mesopithecus* and *Presbytis*; in *Procolobus badius* this role is taken over by palatine breadth. The male red colobus is additionally characterized by a sagittal crest.

Among the tooth dimensions the importance of the upper and lower canine lengths for sexual differentiation in all three species is notable. The length and breadth of P3 sup. and P3 inf. as well as the length of I2 inf. can also contribute to this separation.

Discrimination of species

Several characters are important for differentiating the studied species. No skull dimension is suitable for separating all three species in univariate analysis. For some characters at least one species is significantly different from the others two.

Another situation exists as far as the tooth measurements are concerned. Here the mesiodistal length of C sup. is suitable not only for separating the sexes, but also for species differentiation. While canine length in the lower jaw is significantly different in the sexes, the breadth of all lower molars is suitable for differentiating the specialized *Procolobus badius* from *Mesopithecus* and *Presbytis*. The importance of these variables in the separation of the species is also confirmed through multiple discriminant analysis.

The premolars and especially the lengths of the lower 2 incisors play a large role in the differentiation

of the sexes. These characters are totally unsuited for the separation of species.

The multivariate analyses determining the phenetic relationships show a great affinity between *Mesopithecus* and *Presbytis*, especially in the teeth measurements. *Procolobus badius* appears to be more clearly differentiated. *Procolobus* and *Presbytis* stand to one another in about the similar degree of phenetic relationship, as far as the skull measurements are concerned, and show almost identical distances to the fossil representative of the colobine monkeys, *Mesopithecus pentelicus*.

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Table 1. Craniometric characters and their statistical parameters in *Mesopithecus pentelicus*. Measurements in mm. \bar{x} = arithmetic mean, sd = standard deviation, P(z) = probability proving normal distribution, n = number of individuals.

	m a l e				f e m a l e			
	\bar{x}	sd	P(z)	n	\bar{x}	sd	P(z)	n
Basion-prosthion	85.45	4.19	.669	12	72.72	5.78	.963	9
Nasion-prosthion	39.05	5.13	.902	12	33.18	2.22	.870	9
Interorbital width	10.68	.97	.986	12	8.70	.59	.886	9
Palatine breadth	37.15	1.81	.983	12	34.93	1.50	.955	9
Biorbital breadth					65.00	.00		2
Orbital rim thickness	4.57	.36	.613	12	3.82	.60	.515	9
Nasal width	11.77	1.68	.927	12	10.22	.99	.485	9
Molar-premolar length	30.79	2.04	.504	12	30.42	1.01	.899	9
Sagittal crest height	1.00	1.16	.846	4	.00	.00		5
Profile angle	69.58	12.38	.227	12	63.33	8.12	.652	9
Interorbital width/ palatine breadth	29.15	2.15	.669	10	25.96	2.93	.997	5
Palatine breadth/ nasion-prosthion	97.26	13.79	.756	8	104.30	6.04	.931	5
Molar-premolar length/ nasion-prosthion	77.02	8.53	.385	11	89.20	8.85	.978	3
Nasion-prosthion/ biorbital breadth				1	50.35	.49		2
Interorbital width/ biorbital-breadth				1	14.65	.07		2
Symphysal width	19.89	1.13	.880	12	17.42	1.73	.983	13
Bicondylar width	71.50	4.95		2				
Chin height	25.50	1.67	.985	12	20.78	1.31	.344	13
Corpus height (below second molar)	20.19	1.28	.511	12	16.32	1.18	.534	13
Mandibular length	78.75	6.01		2	66.00	5.66		2
Mandibular angle	38.33	7.34	.475	12	31.39	1.94	.086	13
Tooth row angle	6.00	4.90	.682	6	9.33	8.33		3
Chin angle	56.00	4.37	.512	12	54.31	3.25	.335	13
Molar-premolar length	36.55	1.02	.941	12	34.54	.92	.899	13
Molar length	23.83	.89	.756	12	23.44	.56	.480	13
Corpus height/ chin height	78.91	4.77	.793	12	78.03	5.11	.550	12
Corpus height/ symphysis width	102.00	13.25	.928	8	96.93	13.27	.739	4
Corpus height/ molar length	84.50	7.75	.914	10	69.62	5.08	.597	9
Corpus height/ molar-premolar length	55.22	4.15	.991	9	46.92	2.78	.749	9
Symphysis width/ molar-premolar length	53.40	3.97	.873	7	47.75	7.67	.838	4

Continuation Table 1

	m a l e				f e m a l e			
	\bar{x}	sd	P(z)	n	\bar{x}	sd	P(z)	n
Maxillary teeth								
Length central incisor	5.18	.21	.640	17	4.95	.18	.975	11
Length lateral incisor	4.42	.41	.572	17	4.26	.27	.964	11
Length canine	8.49	.81	.643	17	6.30	.82	.873	11
Length first premolar	5.21	.44	.797	17	4.84	.28	.879	11
Breadth first premolar	5.75	.38	.502	17	5.80	.36	.794	11
Length second premolar	5.21	.36	.776	17	5.00	.27	.897	11
Breadth second premolar	6.38	.33	.970	17	6.43	.21	.826	11
Length first molar	7.01	.38	.888	17	7.02	.19	.792	11
Breadth first molar	6.99	.24	.352	17	6.95	.26	.975	11
Length second molar	7.78	.33	.377	17	7.49	.16	.743	11
Breadth second molar	7.75	.35	.692	17	7.64	.20	.517	11
Length third molar	7.34	.56	.694	17	7.09	.36	.677	11
Breadth third molar	7.31	.33	.879	17	7.02	.23	.792	11
Length molar-premolar	31.31	1.50	.951	16	29.88	.95	.965	10
Length molar	21.96	.92	.360	16	20.85	.69	.840	10
Length premolar	9.99	.73	.979	16	9.66	.66	.999	11
Mandibular teeth								
Length central incisor	3.10	.21	.819	12	3.29	.33	.561	11
Length lateral incisor	3.78	.27	.248	12	3.63	.23	.907	11
Length canine	7.47	.73	.843	12	5.45	.45	.838	11
Length first premolar	7.48	.91	.957	12	6.73	.81	.757	11
Breadth first premolar	4.12	.20	.231	12	3.81	.25	.702	11
Length second premolar	6.19	.42	.781	12	5.86	.52	.443	11
Breadth second premolar	4.64	.22	.871	12	4.79	.26	.964	11
Length first molar	7.08	.38	.422	12	6.82	.35	.847	11
Breadth first molar	5.82	.39	.813	12	5.65	.23	.968	11
Length second molar	7.68	.43	.481	12	7.45	.31	.985	11
Breadth second molar	6.74	.39	.952	12	6.55	.23	.990	11
Length third molar	9.38	.40	.391	12	9.22	.49	.174	11
Breadth third molar	6.82	.44	.339	12	6.53	.23	.907	11
Length molar-premolar	36.48	1.18	.989	12	34.76	.83	.643	8
Length molar	23.86	.99	.987	12	23.46	.67	.496	8
Length premolar	12.79	.67	.888	12	11.56	.53	.998	11

Table 2. Craniometric characters and their statistical parameters in *Procolobus badius*. Measurements in mm. \bar{x} = arithmetic mean, sd = standard deviation, P(z) = probability proving normal distribution by Kolmogoroff-Smirnov test, n = number of individuals.

	m a l e				f e m a l e			
	\bar{x}	sd	P(z)	n	\bar{x}	sd	P(z)	n
Basion-prosthion	79.01	2.48	.969	10	70.51	3.81	.861	10
Nasion-prosthion	44.61	2.42	.820	10	39.37	2.56	.991	10
Interorbital width	11.15	.98	.618	10	10.09	1.09	.701	10
Palatine breadth	35.08	1.32	.962	10	32.38	.66	.951	10
Biorbital breadth	66.73	3.39	.711	10	59.88	1.56	.998	10
Orbital rim thickness	5.48	.55	.719	10	2.90	.52	.791	10
Nasal width	10.30	.82	.600	10	9.54	1.25	.899	10
Molar-premolar length	29.58	1.69	.878	10	29.09	1.41	.873	10
Sagittal crest height	4.12	1.74	.878	10	.25	.42	.057	10
Profile angle	58.80	4.26	.921	10	60.80	2.57	.708	10
Interorbital width/ palatine breadth	31.75	2.75	.907	10	31.10	3.15	.919	10
Palatine breadth/ nasion-prosthion	78.70	3.35	.955	10	82.54	6.01	.814	10
Molar-premolar length/ nasion-prosthion	66.20	2.68	.926	10	74.05	5.02	.928	10
Nasion-prosthion/ biorbital breadth	66.93	4.68	.929	10	65.72	4.40	.924	10
Interorbital width/ biorbital-breadth	16.64	1.06	.805	10	16.20	2.56	.886	10
Symphysal width	21.66	1.83	.685	10	18.45	1.60	.380	10
Bicondylar width	66.47	3.92	.868	10	62.23	2.61	.899	10
Chin height	29.17	3.14	.393	10	25.08	1.60	.935	10
Corpus height (below second molar)	19.38	1.33	.977	10	16.24	1.62	.719	10
Mandibular length	81.15	3.96	.489	10	71.92	3.01	.844	10
Mandibular angle	36.50	4.74	.130	10	31.70	3.65	.020	10
Tooth row angle	8.50	4.74	.055	10	3.50	4.74	.130	10
Chin angle	51.80	4.59	.523	10	45.40	3.86	.956	10
Molar-premolar length	36.79	2.73	.946	10	34.40	1.63	.342	10
Molar length	22.09	1.18	.800	10	22.48	.98	.831	10
Corpus height/ chin height	66.68	3.80	.983	10	64.69	4.50	.972	10
Corpus height/ symphysis width	89.61	4.35	.998	10	88.09	6.55	.987	10
Corpus height/ molar length	87.70	4.15	.829	10	72.30	7.71	.998	10
Corpus height/ molar-premolar length	52.72	2.76	.907	10	47.24	4.91	.999	10
Symphysis width/ molar-premolar length	58.81	1.93	.820	10	53.64	4.30	.812	10

Continuation Table 2.

	m a l e				f e m a l e			
	\bar{x}	sd	P(z)	n	\bar{x}	sd	P(z)	n
Maxillary teeth								
Length central incisor	5.21	.55	.974	10	5.62	.40	.669	10
Length lateral incisor	4.33	.43	.680	10	4.29	.40	.571	11
Length canine	9.71	1.22	.943	11	6.27	.38	.994	11
Length first premolar	4.97	.61	.705	11	4.76	.56	.514	11
Breadth first premolar	5.33	.83	.788	11	5.00	.24	.215	11
Length second premolar	4.66	.38	.723	11	4.85	.32	.201	11
Breadth second premolar	5.59	.55	.303	11	5.45	.39	.860	11
Length first molar	6.74	.29	.960	11	6.56	.29	.988	11
Breadth first molar	5.95	.34	.823	11	5.84	.32	.861	11
Length second molar	6.85	.35	.756	11	7.12	.53	.987	11
Breadth second molar	6.42	.37	.981	11	6.20	.40	.969	11
Length third molar	7.13	.43	.807	11	6.99	.38	.571	11
Breadth third molar	6.34	.32	.983	11	6.25	.38	.909	11
Length molar-premolar	29.92	1.58	.595	11	29.20	1.31	.924	11
Length molar	20.45	.93	.351	11	20.28	.79	.998	11
Length premolar	9.62	.85	.815	11	9.44	.61	.852	11
Mandibular teeth								
Length central incisor	3.80	.37	.780	10	4.00	.30	.819	10
Length lateral incisor	3.71	.46	.990	10	3.94	.21	.277	10
Length canine	8.52	.87	.993	11	6.00	.29	.720	11
Length first premolar	9.72	1.29	.898	11	7.15	1.19	.306	11
Breadth first premolar	4.48	.38	.987	11	3.92	.58	.435	11
Length second premolar	5.63	.47	.426	11	5.55	.53	.911	11
Breadth second premolar	4.22	.23	.481	11	4.49	.89	.222	11
Length first molar	6.73	.37	.987	11	6.66	.63	.497	11
Breadth first molar	4.73	.31	.411	11	5.15	.90	.733	11
Length second molar	7.15	.45	.845	11	7.03	.57	.279	11
Breadth second molar	5.45	.27	.078	11	5.83	.95	.289	11
Length third molar	8.52	.60	.689	11	8.25	.93	.271	11
Breadth third molar	5.57	.34	.750	11	5.60	.26	.818	11
Length molar-premolar	36.84	2.48	.901	11	34.70	1.23	.910	11
Length molar	22.10	1.20	.801	11	22.45	.83	.947	11
Length premolar	14.78	1.38	.998	11	12.41	.90	.901	11

Table 3. Craniometric characters and their statistical parameters in *Presbytis entellus*. Measurements in mm. \bar{x} = arithmetic mean, sd = standard deviation, P(z) = probability proving normal distribution by Kolmogoroff-Smirnov test, n = number of individuals.

	m a l e				f e m a l e			
	\bar{x}	sd	P(z)	n	\bar{x}	sd	P(z)	n
Basion-prosthion	85.51	9.32	.941	13	77.19	8.89	.959	14
Nasion-prosthion	48.07	6.38	.828	13	43.34	6.30	.374	14
Interorbital width	12.77	1.70	.978	13	11.36	1.84	.522	14
Palatine breadth	40.12	3.95	.941	13	39.96	3.95	.918	14
Biorbital breadth	71.88	5.23	.783	13	66.41	3.45	.929	14
Orbital rim thickness	4.21	.82	.850	13	3.28	.78	.949	14
Nasal width	9.52	1.45	.808	13	8.51	1.35	.918	14
Molar-premolar length	33.92	3.69	.978	13	33.96	3.31	.806	14
Sagittal crest height	.00	.00		13	.00	.00		14
Profile angle	60.23	3.68	.056	13	63.00	2.94	.901	14
Interorbital width / palatine breadth	31.74	1.81	.987	13	28.28	2.68	.937	14
Palatine breadth/ nasion-prosthion	83.83	4.70	.865	13	92.89	6.87	.901	14
Molar-premolar length/ nasion-prosthion	70.83	4.47	.957	13	79.14	7.20	.832	14
Nasion-prosthion/ biorbital breadth	66.68	5.53	.449	13	65.00	7.14	.644	14
Interorbital width/ biorbital-breadth	17.67	1.36	.820	13	16.99	2.09	.885	14
Symphysal width	21.17	3.10	.823	12	19.48	2.36	.488	14
Bicondylar width	75.37	6.82	.887	12	73.50	8.31	.944	14
Chin height	29.92	4.40	.734	12	26.84	2.62	.990	14
Corpus height (below second molar)	20.93	3.08	.948	12	19.21	3.18	.980	14
Mandibular length	87.38	9.21	.868	12	80.71	8.70	.840	14
Mandibular angle	39.42	2.02	.002	12	37.14	4.69	.008	14
Tooth row angle	4.17	5.15	.070	12	9.64	3.08	.004	14
Chin angle	51.92	3.85	.855	12	46.57	4.05	.637	14
Molar-premolar length	40.82	4.32	.775	12	40.15	3.84	.820	14
Molar length	25.47	2.46	.855	12	26.48	2.36	.730	14
Corpus height/ chin height	70.04	4.72	.929	12	71.26	6.41	.957	14
Corpus height/ symphysis width	98.91	5.13	.437	12	98.58	9.98	.766	14
Corpus height/ molar length	81.90	6.46	.983	12	72.35	8.14	.994	14
Corpus height/ molar-premolar length	51.14	4.33	.958	12	47.76	5.07	.948	14
Symphysis width/ molar-premolar length	51.71	3.69	.784	12	48.47	2.93	.257	14

Continuation: Table 3.

	m a l e				f e m a l e			
	\bar{x}	sd	P(z)	n	\bar{x}	sd	P(z)	n
Maxillary teeth								
Length central incisor	5.35	.99	.978	11	5.38	.69	.996	10
Length lateral incisor	4.80	.76	.995	11	4.79	.58	.600	10
Length canine	9.50	1.42	.394	12	7.29	.66	.905	12
Length first premolar	5.53	.79	.939	12	5.52	.81	.871	11
Breadth first premolar	6.32	.58	.673	12	6.33	.82	.992	11
Length second premolar	5.29	.69	.988	12	5.37	.41	.739	11
Breadth second premolar	6.82	.78	.967	12	6.86	.69	.820	11
Length first molar	7.56	.77	.990	12	7.58	.59	.998	12
Breadth first molar	7.22	.82	.857	12	7.29	.89	.886	12
Length second molar	8.15	1.02	.576	12	8.53	.99	.978	12
Breadth second molar	8.18	.80	.998	12	8.20	.77	.945	12
Length third molar	8.31	.96	.625	12	8.45	.86	.514	12
Breadth third molar	7.98	.90	.693	12	7.95	.87	.781	12
Length molar-premolar	34.03	3.72	.910	12	34.38	3.21	.970	12
Length molar	23.81	2.51	.828	12	24.28	2.50	.970	12
Length premolar	10.93	1.45	.969	12	10.71	.96	.989	12
Mandibular teeth								
Length central incisor	3.63	.43	.844	11	3.72	.66	.896	11
Length lateral incisor	4.15	.57	.999	12	4.07	.51	.837	12
Length canine	8.59	1.24	.371	12	6.21	.58	.915	12
Length first premolar	10.26	1.13	.915	12	8.57	1.61	.611	12
Breadth first premolar	5.42	.89	.373	12	4.41	.61	.892	12
Length second premolar	6.63	.83	.776	12	6.73	.74	.753	12
Breadth second premolar	4.93	.63	.949	12	4.89	.58	.836	12
Length first molar	7.87	.86	.685	12	7.93	.68	.881	12
Breadth first molar	6.04	.55	.742	12	6.05	.60	.983	12
Length second molar	8.40	.97	.671	12	8.63	.76	.999	12
Breadth second molar	6.97	.57	.779	12	7.06	.75	.980	12
Length third molar	10.34	1.16	.932	12	10.58	1.04	.497	12
Breadth third molar	7.08	.66	.630	12	7.07	.77	.665	12
Length molar-premolar	41.93	4.92	.734	12	40.61	3.72	.854	12
Length molar	26.12	2.94	.904	12	26.71	2.16	.856	12
Length premolar	16.10	2.04	.982	12	14.22	1.59	.334	12

Table 4. Analyses of variance, X indicates significant differences (5% error estimation) in pairwise comparison.

Basion-prosthion						Nasion-prosthion					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .000					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	M	P	P	M		M	M	P	P	P
	r	e	r	r	e		e	e	r	r	r
	o	s	e	o	s		s	s	o	e	o
	f	f	f	m	m		f	m	f	f	m
Procl.fem.						Mesop.fem.					
Mesop.fem.	0					Mesop.mas.	X				
Presb.fem.	X	0				Procl.fem.	X	0			
Procl.mas.	X	0	0			Presb.fem.	X	0	0		
Mesop.mas.	X	X	X	X		Procl.mas.	X	X	X	0	
Presb.mas.	X	X	X	0	0	Presb.mas.	X	X	X	X	0

Interorbital width						Palatine breadth					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .011						Homogeneity of variances P(F) = .000					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	M	P	M	P	P		P	M	P	M	P
	e	r	e	r	r		r	e	r	e	r
	s	o	s	o	e		o	s	o	s	e
	f	f	m	m	f		f	f	m	m	f
Mesop.fem.						Procl.fem.					
Procl.fem.	X					Mesop.fem.	X				
Mesop.mas.	X	0				Procl.mas.	X	0			
Procl.fem.	X	0	0			Mesop.mas.	X	0	0		
Presb.fem.	X	0	0	0		Presb.fem.	X	X	X	X	
Presb.mas.	X	X	X	X	X	Presb.mas.	X	X	X	X	0

Biorbital breadth						Orbital rim thickness					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .009						Homogeneity of variances P(F) = .114					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	M	P	P			P	P	M	P	M
	r	e	r	r			r	r	e	r	e
	o	f	e	o			o	e	s	e	s
	f	f	f	m			f	f	f	m	m
Procl.fem.						Procl.fem.					
Mesop.fem.	0					Presb.fem.	0				
Presb.fem.	X	0				Mesop.fem.	X	0			
Procl.mas.	X	0	0			Presb.mas.	X	X	0		
Presb.mas.	X	0	X	X		Mesop.mas.	X	X	X	0	
						Procl.mas.	X	X	X	X	X

Table 5. Analyses of variance, X indicates significant differences (5% error estimation) in pairwise comparison.

Nasal width						Molar-premolar length					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .332						Homogeneity of variances P(F) = .001					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	P	M	P		P	P	M	M	P
	r	r	r	e	r		r	r	e	e	r
	e	e	0	s	o		o	o	s	s	e
	f	m	f	f	m		f	m	f	m	m
Presb.fem.						Procl.fem.					
Presb.mas.	0					Procl.mas.	0				
Procl.fem.	0	0				Mesop.fem.	0	0			
Mesop.fem.	X	0	0			Mesop.mas.	0	0	0		
Procl.mas.	X	0	0	0		Presb.mas.	X	X	X	X	
Mesop.mas.	X	X	X	X	X	Presb.fem.	X	X	X	X	0

Sagittal crest height						Profile angle					
P(F) between groups = .000						P(F) between groups = .004					
Homogeneity of variances P(F) = .001						Homogeneity of variances P(F) = .000					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	M	P	M		P	P	P	P	M
	r	r	e	r	e		r	r	r	r	e
	e	e	s	o	s		o	e	o	e	s
	m	f	f	f	m		m	m	f	f	f
Presb.mas.						Procl.mas.					
Presb.fem.	0					Presb.mas.	0				
Mesop.fem.	0	0				Procl.fem.	0	0			
Procl.fem.	0	0	0			Presb.fem.	0	0	0		
Mesop.mas.	0	0	0	0		Mesop.fem.	0	0	0	0	
Procl.mas.	X	X	X	X	X	Mesop.mas.	X	X	X	X	X

Interorbital width/palatine breadth						Palatine breadth/nasion prosthion					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .577						Homogeneity of variances P(F) = .002					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	M	P	M	P	P		P	P	P	P	M
	e	r	e	r	r		r	r	r	r	e
	s	e	s	o	e		o	o	e	e	s
	f	f	m	f	m		m	f	m	f	m
Mesop.fem.						Procl.mas.					
Presb.fem.	0					Procl.fem.	0				
Mesop.mas.	0	0				Presb.mas.	0	0			
Procl.fem.	X	X		0		Presb.fem.	X	X	X		
Presb.mas.	X	X	X	0		Mesop.mas.	X	X	X	0	
Procl.mas.	X	X	0	0	0	Mesop.fem.	X	X	X	X	0

Table 6. Analyses of variance. X indicates significant differences (5% error estimation) in pairwise comparison.

Molar-premolar length/nasion prosthion						Nasion-prosthion/biorbital breadth					
P(F) between groups = .000						P(F) between groups = .013					
Homogeneity of variances P(F) = .019						Homogeneity of variances P(F) = .164					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	P	M	P		M	M	P	P	P
	r	r	r	e	r		e	e	r	r	r
	o	e	o	s	e		s	s	e	o	e
	m	m	f	m	f		f	m	f	f	m
Procl.mas.						Mesop.fem.					
Presb.mas.	0					Mesop.mas.	0				
Procl.fem.	X	0				Presb.fem.	X	0			
Mesop.mas.	X	X	0			Procl.fem.	X	0	0		
Presb.fem.	X	X	0	0		Presb.mas.	X	0	0	0	
Mesop.fem.	X	X	X	X	X	Procl.mas.	X	0	0	0	0
Interorbital width/biorbital breadth						Symphysal width					
P(F) between groups = .097						P(F) between groups = .000					
Homogeneity of variances P(F) = .011						Homogeneity of variances P(F) = .030					
Student-Newman-Keuls test						Student-Newman-Keuls test					
no differences between groups							M	P	P	M	P
							e	r	r	e	r
							e	o	e	s	e
							f	f	f	m	m
						Mesop.fem.					
						Procl.fem.	0				
						Presb.fem.	X	0			
						Mesop.mas.	X	0	0		
						Presb.mas.	X	X	0	0	
						Procl.mas.	X	X	0	0	0
Bicondylar width						Chin height					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .012						Homogeneity of variances P(F) = .000					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	M	P	P	M	P		M	P	M	P	P
	e	r	r	e	r		e	r	e	r	r
	s	o	o	s	e		e	o	s	e	o
	f	f	m	m	f		f	f	m	f	m
Mesop.fem.						Mesop.fem.					
Procl.fem.	0					Procl.fem.	X				
Procl.mas.	0	0				Mesop.mas.	X	0			
Mesop.mas.	0	0	0			Presb.fem.	X	0	0		
Presb.fem.	0	X	X	0		Procl.mas.	X	X	X	X	
Presb.mas.	0	X	X	0	0	Presb.mas.	X	X	X	X	0

Table 7. Analyses of variance. X indicates significant differences (5% error estimation) in pairwise comparison.

Corpus height						Mandibular length					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .019					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	M	P	P	M		M	P	M	P	P
	r	e	r	r	e		e	r	e	r	r
	o	s	e	o	s		s	o	s	e	o
	f	f	f	m	m		f	f	m	f	m
Procl.fem.						Mesop.fem.					
Mesop.fem.	0					Procl.fem.	0				
Presb.fem.	X	X				Mesop.mas.	0	0			
Procl.mas.	X	X	0			Presb.fem.	X	X	0		
Mesop.mas.	X	X	0	0		Procl.mas.	0	X	0	0	
Presb.mas.	X	X	0	0	0	Presb.mas.	X	X	0	0	X
Mandibular angle						Tooth row angle					
P(F) between groups = .000						P(F) between groups = .013					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .370					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	M	P	P	P	M		P	P	M	P	M
	e	r	r	r	e		r	r	e	r	e
	s	o	o	e	s		o	e	s	o	s
	f	f	m	f	m		f	m	m	m	f
Mesop.fem.						Procl.fem.					
Procl.fem.	0					Presb.mas.	0				
Procl.mas.	X	X				Mesop.mas.	0	0			
Presb.fem.	X	X	0			Procl.mas.	0	0	0		
Mesop.mas.	X	X	0	0		Mesop.fem.	0	0	0	0	
Presb.mas.	X	X	0	0	0	Presb.fem.	X	X	0	0	0
Chin angle						Molar-premolar length					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .917						Homogeneity of variances P(F) = .000					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	P	P	M		P	M	M	P	P
	r	r	r	r	e		r	e	e	r	r
	o	e	o	e	s		o	s	s	o	e
	f	f	m	m	f		f	f	m	m	f
Procl.fem.						Procl.fem.					
Presb.fem.	0					Mesop.fem.	0				
Procl.mas.	X	X				Mesop.mas.	0	0			
Presb.mas.	X	X	0			Procl.mas.	0	0	0		
Mesop.fem.	X	X	0	0		Presb.fem.	X	X	X	X	
Mesop.mas.	X	X	0	X	0	Presb.mas.	X	X	X	X	0

Table 8. Analyses of variance. X indicates significant differences (5% error estimation) in pairwise comparison.

Molar length						Corpus height/chin height					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .667					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	M	M	P		P	P	P	P	M
	r	r	e	e	r		r	r	r	r	e
	o	o	s	s	e		o	o	e	e	s
	m	f	f	m	m		f	m	m	f	f
Procl.mas.						Procl.fem.					
Procl.fem.	0					Procl.mas.	0				
Mesop.fem.	0	0				Presb.mas.	X	0			
Mesop.mas.	0	0	0			Presb.fem.	X	0	0		
Presb.mas.	X	X	X	X		Mesop.fem.	X	X	X	X	
Presb.fem.	X	X	X	X	0	Mesop.mas.	X	X	X	X	0
Corpus height/symphysal width						Corpus height/molar length					
P(F) between groups = .004						P(F) between groups = .000					
Homogeneity of variances P(F) = .007						Homogeneity of variances P(F) = .326					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	M	P	P		M	P	P	P	M
	r	r	e	r	r		e	r	r	r	e
	o	o	s	e	e		s	o	e	e	s
	f	m	f	f	m		f	f	f	m	m
Procl.fem.						Mesop.fem.					
Procl.mas.	0					Procl.fem.	0				
Mesop.fem.	0	0				Presb.fem.	0	0			
Presb.fem.	X	0	0			Presb.mas.	X	X	X		
Presb.mas.	X	0	0	0		Mesop.mas.	X	X	X	0	
Mesop mas.	X	X	0	0	0	Procl.mas.	X	X	X	0	0
Corpus height/molar-premolar length						Symphysis width/molar-premolar length					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .319						Homogeneity of variances P(F) = .039					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	M	P	P	P	P		M	P	P	M	P
	e	r	r	r	r		e	r	r	e	r
	s	o	e	e	o		s	e	e	s	o
	f	f	f	m	m		f	f	m	m	f
Mesop.fem.						Mesop.fem.					
Procl.fem.	0					Presb.fem.	0				
Presb.fem.	0	0	X			Presb.mas.	0	X			
Procl.mas.	X	X	X	0		Procl.fem.	0	X	0	0	
Mesop.mas.	X	X	X	0	0	Procl.mas.	X	X	X	X	X

Table 9. Analyses of variance. X indicates significant differences (5% error estimation) in pairwise comparison.

Length upper central incisor						Length upper lateral incisor					
P(F) between groups = .127						P(F) between groups = .027					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .030					
Student-Newman-Keuls test						Student-Newman-Keuls test					
no differences between groups						no differences between groups					
Length upper canine						Length upper first premolar					
P(F) between groups = .000						P(F) between groups = .007					
Homogeneity of variances P(F) = .002						Homogeneity of variances P(F) = .016					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	M	P	M	P		P	M	P	M	P
	r	e	r	e	r		r	e	r	e	r
	o	s	e	s	e		o	o	o	s	e
	f	f	f	m	m		f	f	m	m	f
Procl.fem.						Procl.fem.					
Mesop.fem.	0					Mesop.fem.	0				
Presb.fem.	X	X				Procl.mas.	0	0			
Mesop.mas.	X	X	X			Mesop.mas.	0	0	0		
Presb.mas.	X	X	X	X		Presb.fem.	X	X	0	0	
Procl.mas.	X	X	X	X	0	Presb.mas.	X	0	0	0	0
Breadth upper first premolar						Length upper second premolar					
P(F) between groups = .000						P(F) between groups = .001					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .030					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	M	M	P		P	P	M	M	P
	r	r	e	e	r		r	r	e	e	r
	o	o	s	s	e		o	o	s	s	e
	f	m	m	f	m		m	f	f	m	m
Procl.fem.						Procl.mas.					
Procl.mas.	0					Procl.fem.	0				
Mesop.mas.	X	0				Mesop.fem.	0	0			
Mesop.fem.	X	0	0			Mesop.mas.	X	0	0		
Presb.mas.	X	X	X	X		Presb.mas.	X	0	0	0	
Presb.fem.	X	X	X	0	0	Presb.fem.	X	X	0	0	0

Table 10. Analyses of variance. X indicates significant differences (5%error estimation) in pairwise comparison.

Breadth upper second premolar						Length upper first molar					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .001						Homogeneity of variances P(F) = .000					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	M	M	P		P	P	M	M	P
	r	r	e	e	r		r	r	e	e	r
	o	o	s	s	e		o	o	s	s	e
	f	m	m	f	m		f	m	m	f	m
Procl.fem.						Procl.fem.					
Procl.mas.	0					Procl.mas.	0				
Mesop.mas.	X	X				Mesop.mas.	0	0			
Mesop.fem.	X	X	0			Mesop.fem.	0	0	0		
Presb.mas.	X	X	0	0		Presb.mas.	X	X	X	X	
Presb.fem.	X	X	0	0	0	Presb.fem.	X	X	X	X	0

Breadth upper first molar						Length upper second molar					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .000					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	M	M	P		P	P	M	M	P
	r	r	e	e	r		r	r	e	e	r
	o	o	s	s	e		o	o	s	s	e
	f	m	f	m	m		m	f	f	m	m
Procl.fem.						Procl.mas.					
Procl.mas.	0					Procl.fem.	0				
Mesop.fem.	X	X				Mesop.fem.	0	0			
Mesop.mas.	X	X	0			Mesop.mas.	X	X	0		
Presb.mas.	X	X	0	0		Presb.mas.	X	X	X	0	
Presb.fem.	X	X	0	0	0	Presb.fem.	X	X	X	X	0

Breadth upper second molar						Length upper third molar					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .003					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	M	M	P		P	M	P	M	P
	r	r	e	e	r		r	e	r	e	r
	o	o	s	s	e		o	s	o	s	e
	f	m	f	m	m		f	f	m	m	m
Procl.fem.						Procl.fem.					
Procl.mas.	0					Mesop.fem.	0				
Mesop.fem.	X	X				Procl.mas.	0	0			
Mesop.mas.	X	X	0			Mesop.mas.	0	0	0		
Presb.mas.	X	X	X	X		Presb.mas.	X	X	X	X	
Presb.fem.	X	X	0	0	0	Presb.fem.	X	X	X	X	0

Table 11. Analyses of variance. X indicates significant differences (5%error estimation) in pairwise comparison.

Breadth upper third molar						Upper molar-premolar length					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .000					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	M	M	P		P	P	M	M	P
	r	r	e	e	r		r	r	e	e	r
	o	o	s	s	e		o	o	s	s	e
	f	m	f	m	f		f	m	f	m	m
Procl.fem.						Procl.fem.					
Procl.mas.	0					Procl.mas.	0				
Mesop.fem.	X	X				Mesop.fem.	0	0			
Mesop.mas.	X	X	0			Mesop.mas.	0	0	0		
Presb.fem.	X	X	X	X		Presb.fem.	X	X	X	X	
Presb.mas.	X	X	X	X	0	Presb.mas.	X	X	X	X	0

Upper molar length						Upper premolar length					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .037					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	M	M	P		P	P	M	M	P
	r	r	e	e	r		r	r	e	e	r
	o	o	s	s	e		o	o	s	s	e
	f	m	f	m	m		f	m	f	m	f
Procl.fem.						Procl.fem.					
Procl.mas.	0					Procl.mas.	0				
Mesop.fem.	0	0				Mesop.fem.	0	0			
Mesop.mas.	X	0	0			Mesop.mas.	0	0	0		
Presb.mas.	X	X	X	X		Presb.fem.	X	X	X	X	
Presb.fem.	X	X	X	X	0	Presb.mas.	X	X	X	X	0

Length lower central incisor						Length lower lateral incisor					
P(F) between groups = .000						P(F) between groups = .019					
Homogeneity of variances P(F) = .011						Homogeneity of variances P(F) = .004					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	M	M	P	P	P		M	P	M	P	P
	e	e	r	r	r		e	r	e	r	r
	s	s	e	e	o		s	o	e	o	e
	m	f	m	f	m		f	m	m	f	f
Mesop.mas.						Mesop.fem.					
Mesop.fem.	0					Procl.mas.	0				
Presb.mas.	X	0				Mesop.mas.	0	0			
Presb.fem.	X	X	0			Procl.fem.	0	0	0		
Procl.mas.	X	X	0	0		Presb.fem.	0	0	0	0	
Procl.fem.	X	X	0	0	0	Presb.mas.	X	0	0	0	0

Table 13. Analyses of variance. X indicates significant differences (5%error estimation) in pairwise comparison.

Breadth lower first molar						Length lower second molar					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .005					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	M	M	P		P	P	M	M	P
	r	r	e	e	r		r	r	e	e	r
	o	o	s	s	e		o	o	s	s	e
	m	f	f	m	m		f	m	f	m	m
Procl.mas.						Procl.fem.					
Procl.fem.	0					Procl.mas.	0				
Mesop.fem.	X	X				Mesop.fem.	0	0			
Mesop.mas.	X	X	0			Mesop.mas.	0	0	0		
Presb.mas.	X	X	0	0		Presb.mas.	X	X	X	X	
Presb.fem.	X	X	0	0	0	Presb.fem.	X	X	X	X	0
Breadth lower second molar						Length lower third molar					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .004					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	M	M	P		P	P	M	M	P
	r	r	e	e	r		r	r	e	e	r
	o	o	s	s	e		o	o	s	s	e
	m	f	f	m	m		f	m	f	m	m
Procl.mas.						Procl.fem.					
Procl.fem.	0					Procl.mas.	0				
Mesop.fem.	X	X				Mesop.fem.	X	0			
Mesop.mas.	X	X	0			Mesop.mas.	X	X	0		
Presb.mas.	X	X	0	0		Presb.mas.	X	X	X	X	
Presb.fem.	X	X	0	0	0	Presb.fem.	X	X	X	X	0
Breadth lower third molar						Lower molar-premolar length					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .000					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	M	M	P		P	M	M	P	P
	r	r	e	e	r		r	e	e	r	r
	o	o	s	s	e		o	s	s	o	e
	m	f	f	m	m		f	f	m	m	f
Procl.mas.						Procl.fem.					
Procl.fem.	0					Mesop.fem.	0				
Mesop.fem.	X	X				Mesop.mas.	0	0			
Mesop.mas.	X	X	0			Procl.mas.	0	0	0		
Presb.mas.	X	X	X	0		Presb.fem.	X	X	X	X	
Presb.fem.	X	x	0	0	0	Presb.mas.	X	X	X	X	0

Table 14. Analyses of variance. X indicates significant differences (5%error estimation) in pairwise comparison.

Lower molar length						Lower premolar length					
P(F) between groups = .000						P(F) between groups = .000					
Homogeneity of variances P(F) = .000						Homogeneity of variances P(F) = .000					
Student-Newman-Keuls test						Student-Newman-Keuls test					
	P	P	M	M	P		M	P	M	P	P
	r	r	e	e	r		e	r	e	r	r
	o	o	s	s	e		s	o	s	e	o
	m	f	f	m	m		f	f	m	f	m
Procl.mas.						Mesop.fem.					
Procl.fem.	0					Procl.fem.	0				
Mesop.fem.	0	0				Mesop.mas.	0	0			
Mesop.mas.	0	0	0			Presb.fem.	X	X	X		
Presb.mas.	X	X	X	X		Procl.mas.	X	X	X	0	
Presb.fem.	X	X	X	X	0	Presb.mas.	X	X	X	X	X

Table 15. Discriminant analyses. Classification function coefficients using Fisher's linear discriminant functions.

	Procolobus		Presbytis		Mesopithecus	
	male	female	male	female	male	female
Cranial measurements						
Basion-prosthion	.798	1.264	1.174	.911	2.700	1.992
Nasion-prosthion	-1.294	-1.652	-1.831	-2.172	-3.287	-3.240
Interorbital width	-2.826	-4.364	-3.809	-5.205	-7.257	-7.971
Palatine breadth	3.921	4.086	6.151	7.761	5.122	6.037
Orbital rim thickness	4.796	-3.062	-1.112	-3.283	-2.471	-2.589
Nasal width	-.045	.104	-2.418	-3.196	.786	.247
Molar-premolar length	2.257	2.627	2.372	2.827	2.164	3.037
Constant	-103.752	-92.252	-133.443	-144.413	-141.620	-133.783
Mandibular measurements						
Symphysal width	.723	-.188	-.930	-1.555	-.642	-.804
Chin height	1.704	1.647	1.268	.860	.090	-.434
Corpus height	.703	.053	1.474	1.246	3.039	2.104
Mandibular angle	2.174	1.745	2.250	1.975	2.204	1.731
Chin angle	5.488	5.032	5.762	5.449	6.126	5.885
Molar-premolar length	-3.155	-5.741	-4.170	-5.945	-6.054	-6.664
Molar length	13.888	19.514	18.281	22.613	20.623	23.030
Constant	-318.442	-283.618	-367.957	-353.751	-376.040	-349.213
Maxillary teeth measurements						
Length central incisor	4.666	8.999	-5.128	-4.949	-.791	-2.460
Length lateral incisor	3.773	3.369	10.991	13.498	8.584	11.248
Length canine	7.926	.500	5.469	-.282	4.927	.636
Length first premolar	-12.550	-6.163	-12.529	-7.987	-12.350	-9.925
Breadth first premolar	3.669	4.438	5.681	8.062	3.793	6.035
Breadth first molar	11.376	10.694	5.796	4.904	10.471	9.859
Breadth second molar	20.030	12.850	33.516	33.256	33.689	35.652
Length third molar	7.576	7.326	7.695	9.312	4.811	5.469
Breadth third molar	-13.273	-7.072	-11.640	-13.074	-14.924	-17.138
Constant	-121.791	-107.401	-165.597	-164.619	-148.572	-144.809
Mandibular teeth measurements						
Length central incisor	13.482	11.223	3.247	.946	-.116	.343
Length canine	10.158	1.066	3.962	-5.048	.875	-5.327
Length first premolar	1.704	-2.066	-1.054	-4.167	-4.104	-4.472
Breadth first premolar	-7.394	-10.672	-5.176	-10.114	-9.367	-10.202
Length second premolar	-1.134	5.045	4.606	11.057	8.776	10.702
Breadth second premolar	9.835	11.398	4.519	5.348	.417	5.969
Length first molar	16.991	19.824	17.486	17.665	13.751	14.489
Breadth second molar	5.062	5.939	11.559	12.877	14.658	11.213
Length third molar	-1.665	-1.098	.828	3.230	1.666	2.728
Breadth third molar	-10.948	-2.422	-2.019	6.198	7.227	9.286
Constant	-112.832	-110.660	-139.783	-152.376	-128.935	-128.053

Table 16. Discriminant analyses between sexes. Significance of variables between sexes after stepwise variable selection.

	Wilks'		Wilks'	
	λ	P (λ)	λ	P (λ)
<i>Mesopithecus pentelicus</i>				
Cranial measurements				
Basion-prosthion	.355	.000		
Orbital rim thickness	.275	.000		
Maxillary teeth measurements				
Canine length	.352	.000		
Length first premolar	.306	.000		
Breadth first molar	.259	.000		
Length first molar	.235	.000		
Length second molar	.220	.000		
Mandibular measurements				
Chin height	.269	.000		
Mandibular angle	.195	.000		
Corpus height	.160	.000		
Molar-premolar length	.143	.000		
Symphysal width	.124	.000		
Mandibular teeth measurements				
Canine length	.252	.000		
Length lateral incisor	.181	.000		
Breadth first premolar	.153	.000		
Length second molar	.126	.000		
Length second premolar	.118	.000		
<i>Presbytis entellus</i>				
Cranial measurements				
Orbital rim thickness	.733	.006		
Palatine breadth	.688	.011		
Basion-prosthion	.258	.000		
Interorbital width	.208	.000		
Maxillary teeth measurements				
Canine length	.437	.000		
Length third molar	.201	.000		
Length second premolar	.170	.000		
Mandibular measurements				
Chin angle	.671	.002		
Symphysal width	.391	.000		
Molar length	.287	.000		
Molar-premolar length	.206	.000		
Mandibular teeth measurements				
Canine length	.356	.000		
Breadth third molar	.188	.000		
Length first premolar	.126	.000		
Length second molar	.110	.000		
Breadth first premolar	.101	.000		
Length lateral incisor	.084	.000		
<i>Procolobus badius</i>				
Cranial measurements				
Orbital rim thickness	.133	.000		
Palatine breadth	.120	.000		
Nasal width	.107	.000		
Maxillary teeth measurements				
Canine length	.216	.000		
Length first premolar	.159	.000		
Breadth first premolar	.124	.000		
Length first molar	.101	.000		
Breadth second molar	.087	.000		
Breadth first molar	.080	.000		
Breadth second premolar	.070	.000		
Mandibular measurements				
Corpus height	.446	.000		
Chin angle	.343	.000		
Mandibular angle	.279	.000		
Molar length	.217	.000		
Molar-premolar length	.149	.000		
Chin height	.136	.000		
Mandibular teeth measurements				
Canine length	.202	.000		
Length second premolar	.101	.000		
Length lateral incisor	.078	.000		
Length first premolar	.056	.000		

Table 17. Generalized distances between groups

	Procolobus		Presbytis		Mesopithecus	
	male	female	male	female	male	female
Cranial measurements						
Procolobus male	0					
Procolobus female	25.84	0				
Presbytis male	25.42	20.13	0			
Presbytis female	55.96	33.08	9.89	0		
Mesopithecus male	45.97	34.72	37.45	53.53	0	
Mesopithecus female	55.70	31.43	36.32	34.83	11.49	0
Mandibular measurements						
Procolobus male	0					
Procolobus female	25.25	0				
Presbytis male	16.44	23.16	0			
Presbytis female	44.72	17.11	12.79	0		
Mesopithecus male	32.87	33.64	11.75	18.74	0	
Mesopithecus female	55.44	26.18	27.85	13.58	12.88	0
Maxillar teeth measurements						
Procolobus male	0					
Procolobus female	97.84	0				
Presbytis male	91.45	176.29	0			
Presbytis female	205.55	152.37	61.61	0		
Mesopithecus male	46.69	81.40	15.48	42.85	0	
Mesopithecus female	141.69	108.69	64.32	31.03	20.63	0
Mandibular teeth measurements						
Procolobus male	0					
Procolobus female	112.28	0				
Presbytis male	102.76	84.16	0			
Presbytis female	304.55	92.47	100.92	0		
Mesopithecus male	194.92	82.19	51.67	38.61	0	
Mesopithecus female	307.33	86.98	123.13	12.59	33.26	0

PLATE 1.

Complete skulls of selected colobine monkeys. Magnification 0.85 X.

- Fig. 1. *Procolobus badius*, male. Coll. Grauer, Naturhistorisches Museum, Wien.
 Fig. 2. *Procolobus badius*, female. Coll. Grauer, Naturhistorisches Museum, Wien.
 Fig. 3. *Presbytis entellus*, male. Zoologische Staatssammlung, München.
 Fig. 4. *Presbytis entellus*, female. Zoologische Staatssammlung, München.
 Fig. 5. *Mesopithecus pentelicus*, male. Naturhistorisches Museum, Wien.
 Fig. 6. *Mesopithecus pentelicus*, female. University of Athens, Greece.

