JASs ***R**eports*

Journal of Anthropological Sciences
Vol. 84 (2006), pp. 147-160

From Verheyen to Bookstein: history of colobids and superimpositions

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Summary – *Currently, the morphology and taxonomy of the African colobids is rather uncertain and scarcely investigated. Modern morphometrics deals mostly with landmark data, coordinates, and shape analysis. Primatology was one of the first disciplines to adopt the methods of geometric morphometrics. Superimpositions represent a set of procedures aimed at standardizing shapes and forms to make them comparable in terms of geometry. More than 30 years before the development of geometric morphometric techniques, W. Verheyen, a Belgian zoologist, evaluated the morphological variation in the African colobids by using a baseline superimposition to compare cranial forms. The present paper is aimed at discussing some topics in relation to colobid cranial morphology, by presenting methodological comments on different kinds of superimpositions, and providing homage to Verheyen's pioneer work . His data, published in 1957 and 1962, were sampled and analysed using baseline and Procrustes superimpositions. The large proportion of differences between* Piliocolobus *and* Procolobus *are probably size-related, while the differences between Piliocolobus and Colobus are probably associated with non-allometric structural changes. Nevertheless,* Piliocolobus *shows a downward rotation of the foramen magnum which is not detected in the other genera. In general, an integrative use of Procrustes and baseline superimpositions is rather useful in analysing shape variation both in terms of overall similarity and of structural relationships.*

Keywords – *shape analysis, primatology, skull, African colobids.*

Introduction

Taxonomy and systematics are rarely as uncertain and debated as in primatology, in which difficulties arise starting with the definition of what a primate is (Martin, 1990). Within this Order, the colobids are one of the most neglected groups (Oates & Davis, 1994; Oates *et al.*, 1994). Often regarded as a subfamily of the Cercopithecids (Groves, 2001; Grubb *et al.,* 2003), this taxon is relatively homogeneous, sharing a large number of traits and structures (Fleagle, 1998; Ankel-Simons, 2000). Both the morphological (Strasser & Delson, 1987) and genetic (Page *et al.,* 1999; Xing *et al.,* 2005) evidence show that the group is probably monophyletic. The earliest morphs that present such a composition of characters are found in the Middle Miocene in Africa (Conroy, 1990). Accordingly, taking into account the morphological and ecological distinctiveness, and the monophyly of this taxon, I prefer to consider the Colobids a family. While our knowledge of Colobids' natural history is poor, they are rather endangered because of their habitat requirements, since they are strictly associated (mostly in Africa) with primary and rain forests. These premises lead to a certain urgency concerning the development of both research and management programs for these taxa.

Historically, primatology has always been rather sensitive to morphometrics and to shape analysis, and it was one of the first disciplines to undergo the "morphometric revolution" (Rohlf & Marcus, 1993; Lynch *et al.,* 1996). The multivariate statistics of landmark data and the superimposition procedures quickly became the most important analytical tool for morphologists in the '90s, and geometric morphometrics is presently the basic framework of many morphological studies (Adams *et al.*, 2004).

Briefly, geometric morphometrics relies upon the sampling of two- or three-dimensional Euclidean coordinates from physical or digital objects using a given configuration of points, the registration of all the coordinate systems according to a certain criterion to normalise the geometric variation, and the multivariate analysis of the residuals after such process of normalisation (see Zelditch *et al.,* 2004). Differences between specimens, group means, or along multivariate vectors, can be visualised as shifting of points, chromatic maps, or by using the distortion grids introduced by D'Arcy Wentworth Thompson in the first half of the 20th century (Thompson, 1942). Spatial quantification of the differences are computed through interpolant functions such as the *thin-plate spline*, imported into morphometrics by Fred Bookstein at the end of the '80s (Bookstein, 1991).

Registration and normalisation of the shape coordinates are performed through superimposition procedures. Generally, superimpositions are aimed at eliminating or controlling the effect of size and position of the different specimens, computing a translation, rotation, and scaling of the coordinates so as to make all the specimens comparable. Different registration procedures are based on different assumptions and give different results. Therefore, the choice of a given superimposition is a rather basic requirement.

The baseline approach (also known as the *Bookstein superimposition*) superimposes in two dimensions all the systems of landmarks according to the same diameter, defined by two anatomical points. The configuration is translated, rotated, and scaled, so as to shift the first point to the position 0,0, and the second to the position 0,1. That is, the first point is moved to the origin of the axis, the baseline is oriented along the abscissa, and the diameter is normalised to 1. This is a rather useful approach when the baseline represents a functional or structural reference, and we want to know the ways in which the morphology varies in relation to this reference.

The *Procrustes superimposition* is the most applied registration procedure, and a large amount of literature is devoted to the description of this approach. The centroids of each coordinate system (that is, the average coordinates of each specimen) are translated to a common centroid at the origin of the axes, and then the configurations are scaled to unitary centroid size (the square root of the summed square distances of each landmark from the centroid of the configuration) and rotated so as to minimise the least square residuals between corresponding landmarks. For more than two specimens, this approach is computed iteratively using an average shape until the process reaches sufficient stability. Actually, it is more accurate to call this procedure partial Procrustes superimposition, because a full Procrustes procedure requires another scaling step to minimise the residuals further (Zelditch *et al.*, 2004). It is commonly stated that this procedure eliminates size from the overall form, leaving the shape to be fully investigated. Nevertheless, considering the tight relationship between size and shape, and some theoretical and pragmatic critiques of this approach (Richtsmeier *et al.*, 2002), it would be better to say that the Procrustes transformation standardises the shape component in relation to unit centroid size. Procrustes analysis has one key advantage over all other superimposition methods in that, when variations in landmark coordinates are independent and isotropic, it will yield an isotropic distribution of specimens in the resulting (statistically well understood and well behaved) Kendall's shape space (Rohlf, 2003). Consequently, Procrustes registration is the method of choice when there is no strong *a priori* reason, based on the biological question at hand, for baseline or other superimpositions, which in practice entails most situations.

Another approach, the *resistant fit superimposition*, computes a similar transformation by iteratively using the medians from the Euclidean distance matrix (the matrix of the physical distances of each landmark from all the other landmarks). Procrustes superimposition distributes the differences at each landmark equally throughout the configuration. This may lead to an unsatisfactory registration in terms of the fitting of corresponding structures, if some landmarks are much more variable than others (also known as the "Pinocchio effect": the nose gets longer, the face remains the same, and the variation at the nose will be incorrectly distributed all through the head). The resistant fit approach limits the problems related to such outliers, by working on the medians in order to distribute the variation more properly.

The resistant fit, like the Bookstein baseline superimposition, does not however lead to the specimens' being represented in Kendall's shape space. While this might have few practical repercussions with respect to subsequent statistical analyses and interpretations if the variations are very small, there will be subtle differences, which will become increasingly more important as the variations increase and which will require added care in the interpretation of any results.

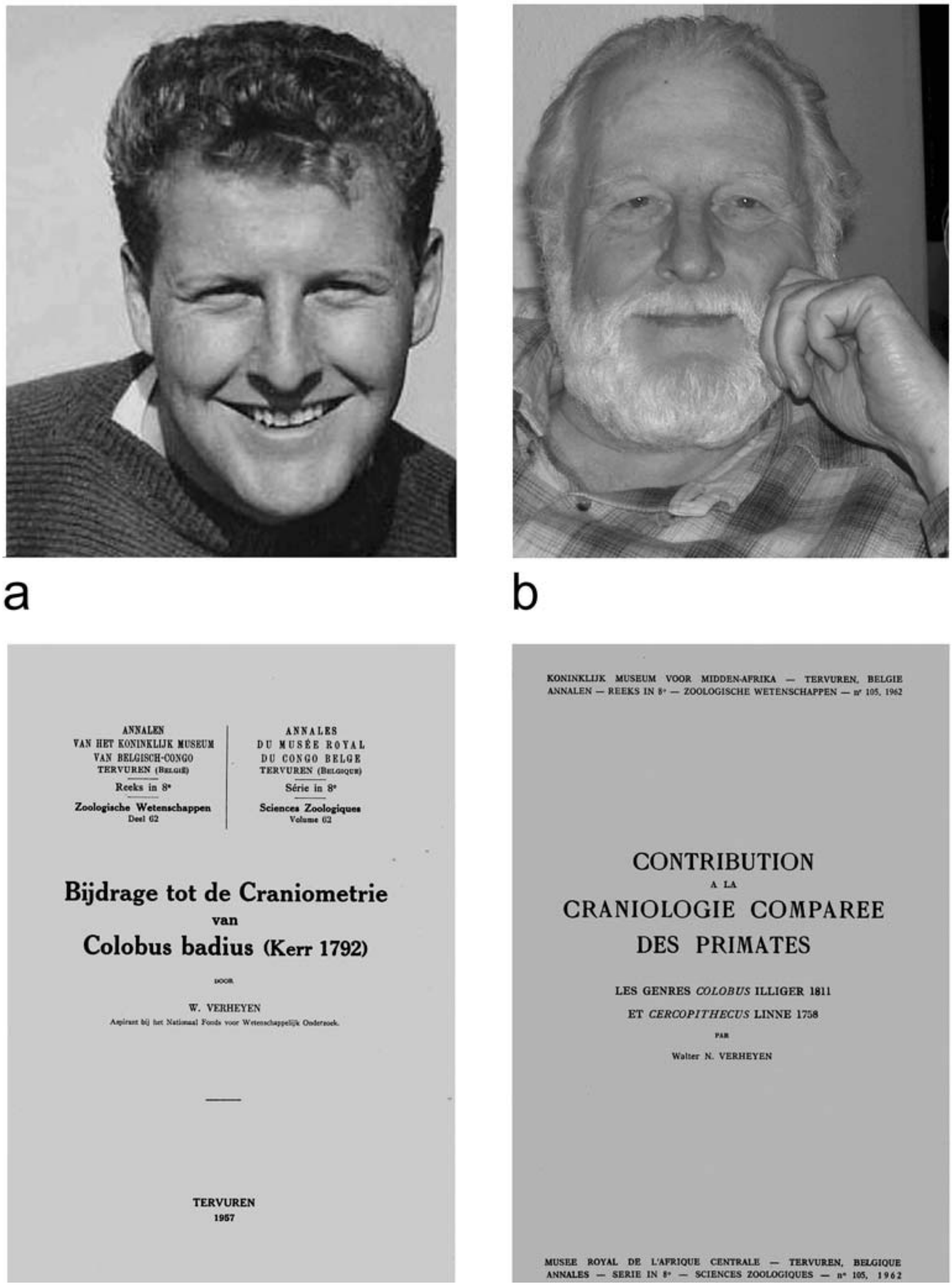
As stressed before, Primatology was one of the first disciplines to undergo the morphometric revolution, and the application of these techniques is now well established in the whole field, including the studies of colobid cranial variation (O'Higgins & Pan, 2004; Pan & Groves, 2004).

Many years before the introduction of such techniques and a thorough understanding of shape spaces, many scholars applied different superimpositions in an attempt to examine the morphological variation within a standardised framework. It is well worth noting that one of the earlier and more valuable attempts in this direction concerned colobid cranial morphology, thanks to the pioneering studies of Walter Verheyen (Verheyen, 1957, 1962).

Walter Norbert Verheyen (Fig. 1a,b) was born at Wilrijk, Belgium, on the 15th of December 1932. He married Adriana De Vos, and had three children. He studied at the State University of Ghent, where he became Doctor of Sciences in 1959 with a dissertation in Zoology entitled "Bijdrage tot de Craniologie van de Primaten genera Colobus Illiger 1911 en Cercopithecus Linnaeus 1758" (Contribution to the craniology of the primate genera *Colobus Illiger* 1911 and *Cercopithecus* Linnaeus 1758). He became Assistant Researcher at the Royal Museum for Central Africa in Tervuren in 1958, and taught at the State University of Ghent from 1962 to 1965. From 1965 he taught at the State University Centre of Antwerp. W. Verheyen was a member of several scientific societies, of the editorial board of many scientific journals, and was chairman and director of laboratories and national commissions in zoology, nature conservation, and biology, organising and participating many scientific zoological expeditions in Zaire, Togo, Ivory Coast, Cameroun, Morocco, Algeria, South-Africa, Ghana, Ruanda, Burundi, Gabon, Tanzania, Kenya, and Papua-New Guinea. At the end of the '80s, he was project leader of the Tanzania-Belgium Rodent Research Project. He died at the end of 2005. In 1957, a first monograph by Walter Verheyen concerning the cranial diversity of the African colobids was published*: "Bijdrage tot de Craniometrie van Colobus badius (Kerr 1792)"* (Fig. 1c). In this monograph Verheyen provided a large morphological and morphometric survey on the Colobids of the Congo basin, discussing the results in terms of phylogeny, taxonomy, and biogeography. He analysed 115 skulls from the Museé Royal du Congo Belge and from the Institut Royal des Sciences Naturelles de Belgique, considering 63 diameters and describing the morphological variation of important structural areas such as the metopic and pteric surfaces.

A second book followed in 1962 which provided a large analysis of the difference within colobids and cercopithecids: *Contribution a la craniologie comparee des Primates. Les genres* Colobus *Illiger 1811 et* Cercopithecus *Linne 1758*" (Fig. 1d). In this work, he considered a wide taxonomic variation of the genera *Colobus* and *Cercopithecus*, using a large set of metrics (44 diameters, 55 indexes) to discuss sexual dimorphism, phylogeny, and ontogeny. The total sample numbered 1085 adult skulls and 303 subadult specimens, including collections from Bruxelles, Tervuren, London, New York, Birchington, Paris, Leiden, Gent, and Berlin.

In these monographs, together with a detailed analysis of cranial anatomy, conventional craniograms, and traditional morphometrics, Verheyen promoted a geometric comparison of two-dimensional coordinates computed trigonometrically by using the available interlandmark distances (*craniotrigonograms*). The mean configurations for each species or ontogenetic stage were compared through the alignment of the baseline nasion-basion, and the subsequent translation along this axis to a common basion (Fig. 2). No scaling was performed and each configuration kept its original size. Accordingly, the analysis concerned the comparison of forms, and not shapes. The nasion-basion baseline represents an important functional and structural reference, being the interface between the neurocranium and the splanchnocranium.



ANNALEN
VAN HET KONINKLIJK MUSEUM
VAN BELGISCH-CONGO
TERVUREN (BELGIË)
Reeks in 8°
Zoologische Wetenschappen
Deel 62

ANNALES
DU MUSÉE ROYAL
DU CONGO BELGE
TERVUREN (BELGIQUE)
Série in 8°
Sciences Zoologiques
Volume 62

Bijdrage tot de Craniometrie
van
Colobus badius (Kerr 1792)

DOOR

W. VERHEYEN
Aspirant bij het Nationaal Fonds voor Wetenschappelijk Onderzoek.

TERVUREN
1957

KONINKLIJK MUSEUM VOOR MIDDEN-AFRIKA — TERVUREN, BELGIE
ANNALEN — REEKS IN 8° — ZOOLOGISCHE WETENSCHAPPEN — n° 105, 1962

CONTRIBUTION
A LA
CRANIOLOGIE COMPAREE
DES PRIMATES

LES GENRES *COLOBUS* ILLIGER 1811
ET *CERCOPITHECUS* LINNE 1758
PAR
Walter N. VERHEYEN

MUSEE ROYAL DE L'AFRIQUE CENTRALE — TERVUREN, BELGIQUE
ANNALES — SERIE IN 8° — SCIENCES ZOOLOGIQUES — n° 105, 1962

Fig. 1 – Walter Verheyen at the time of the publication of the two monographs (a), and in a recent photo (b), with the front covers of the two books on the primates skulls (c, d).

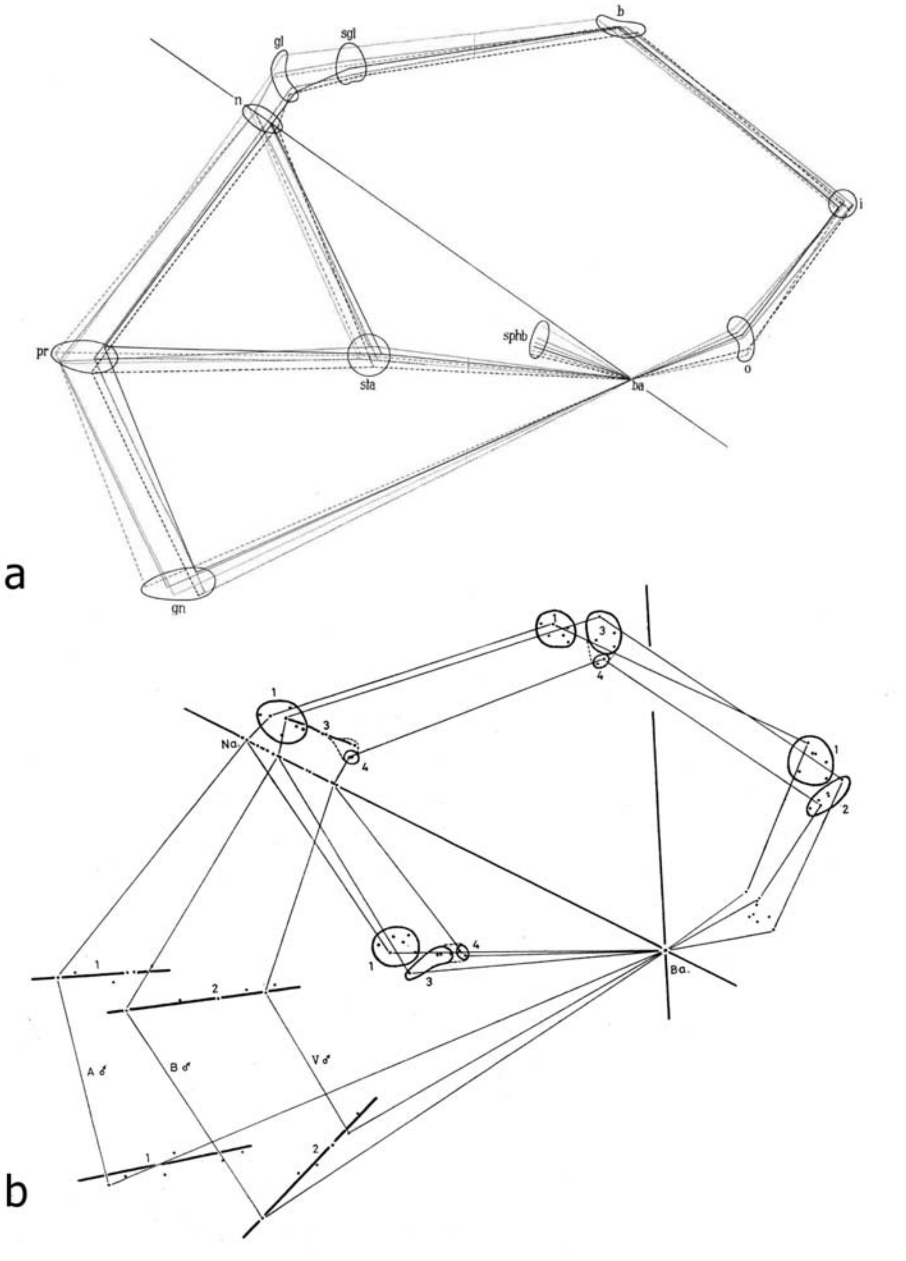


Fig. 2 – Coordinates and configurations published by W. Verheyen in 1957 to compare different **P. badius** *groups (a), and in 1962 to compare* **Colobus abyssinicus** *(now* **Colobus guereza***),* **Colobus badius** *(now* **Piliocolobus badius***), and* **Colobus verus** *(now* **Procolobus verus***) (b).*

Among the geometric comparisons, he performed a superimposition using averaged coordinates from *Colobus guereza, Procolobus badius*, and *Procolobus verus*. In the present paper, these coordinates have been resampled, and compared by using the thin-plate spline interpolant function to compute transformation grids and the Procrustes and Bookstein superimpositions.

Materials and Methods

The two-dimensional coordinates published by Verheyen in 1962 to compare the three main colobid genera were directly resampled with TPSDIG 1.20 (Rohlf, 1998a). The configuration numbers nine landmarks, namely prosthion, nasion, glabella, bregma, inion, opisthion, basion, staphylion, and gnathion (Fig. 3). Three coordinate systems represent the average shapes from *Colobus guereza* (formerly *Colobus abyssinicus*), *Procolobus badius*, and *Procolobus verus*. Here, *Procolobus badius* is referred to the genus *Piliocolobus*, as suggested by a recent taxonomy (Groves, 2001). At the time of Verheyen's monographs, instead, the differences within the *badius* group were not known. As a consequence of the current recognition of three genera describing the black, red, and green African colobids respectively, and because of the large cranial differences among these three groups described since Verheyen's publications, three means will be used to promote a comparison between *Colobus, Piliocolobus*, and *Procolobus*. Coordinates were superimposed and visualised using MORPHEUS ET AL. (Slice, 2000).

The superimposition performed by Verheyen was visualised by using deformation grids. As described previously, he used the nasion-basion baseline to align the specimens, shifting the configuration to a common basion while keeping its original size.

The three configurations were then compared by using the partial Procrustes superimposition. The differences among the shapes were quantified by using the bending energy by TPSSPLINE 1.15 (Rohlf, 1997) and by reporting the Procrustes distances by TPSSMALL 1.19 (Rohlf, 1998b). Figure 4 shows the superimpositions following the Verheyen and Procrustes procedures.

Finally, the three average shapes were compared through Bookstein superimposition using three different baselines: nasion-basion, nasion-inion, prosthion-basion (Fig. 5). The first registration uses the same points used by Verheyen, while scaling the baseline to the same length. Accordingly, the differences can be discussed relatively to the nasion-basion length and position. The nasion-inion

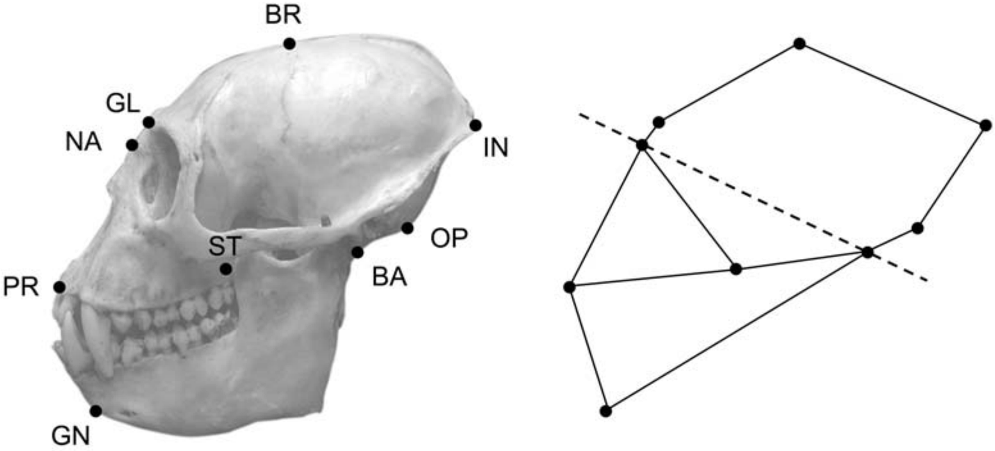


Fig. 3 – Landmarks and configuration used by Verheyen in 1957 and 1962, and in the present analysis, shown on a* Colobus *skull (left) and with the relative wireframe (right); PR: prosthion; NA: nasion; GL: glabella: BR: bregma; IN: inion; OP: opisthion; BA: basion; ST: staphylion: GN: gnathion.

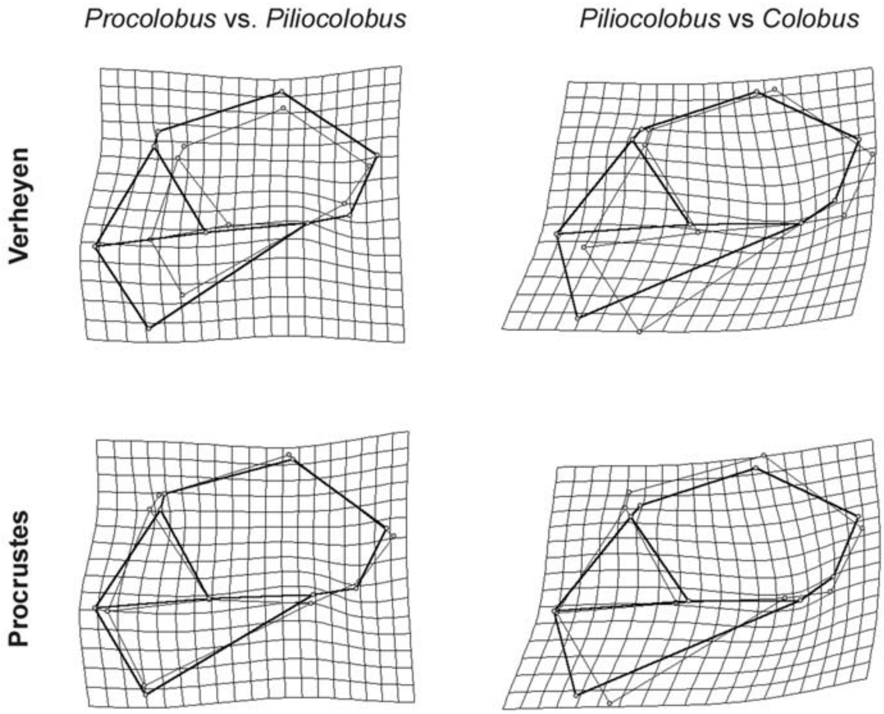


Fig. 4 – Pairwise average comparisons computed using the superimposition of W. Verheyen and the Procrustes superimposition, visualised through thin-plates spline and distortion grids, from **Procolobus verus** ***to*** **Piliocolobus badius** ***and from*** **Piliocolobus badius** ***to*** **Colobus guereza** ***(reference form: thin links; target form: bold links).***

superimposition allows us to compare the specimens according to the same neurocranial length and orientation. The prosthion-basion baseline (often referred to as one of the condilo-basal lengths), instead, allows us to compare the sample according to the length and position of the palatal and basicranial structures.

The pairwise differences will be described from the smaller to the largest taxon, that is from *Procolobus* to *Piliocolobus*, and from *Piliocolobus* to *Colobus*.

Results

Verheyen superimposition

Procolobus vs *Piliocolobus.* The skull of *Piliocolobus* is larger than the skull of *Procolobus*, with the difference in size increasing from vault, to face, to mandible. The neurocranial shape is rather similar in the two genera, but *Piliocolobus* shows a marked rotation of the foramen magnum which becomes increasingly oriented downward. The face and the mandible show a general isometric enlargement, increasing in size without displaying clear differences in the condylo-basal orientation or inclination of the mandibular symphysis (at least as described using the gnathion and prosthion positions).

Piliocolobus vs *Colobus.* The difference in size is less relevant, while the differences in shape are more evident. In the neurocranium, *Piliocolobus* shows a rotation of the foramen magnum, and *Colobus* is characterised by a projection of the nasion in relation to the glabella. In the latter, both face and maxilla are projected anteriorly and flattened vertically. Such prognathism increases from the

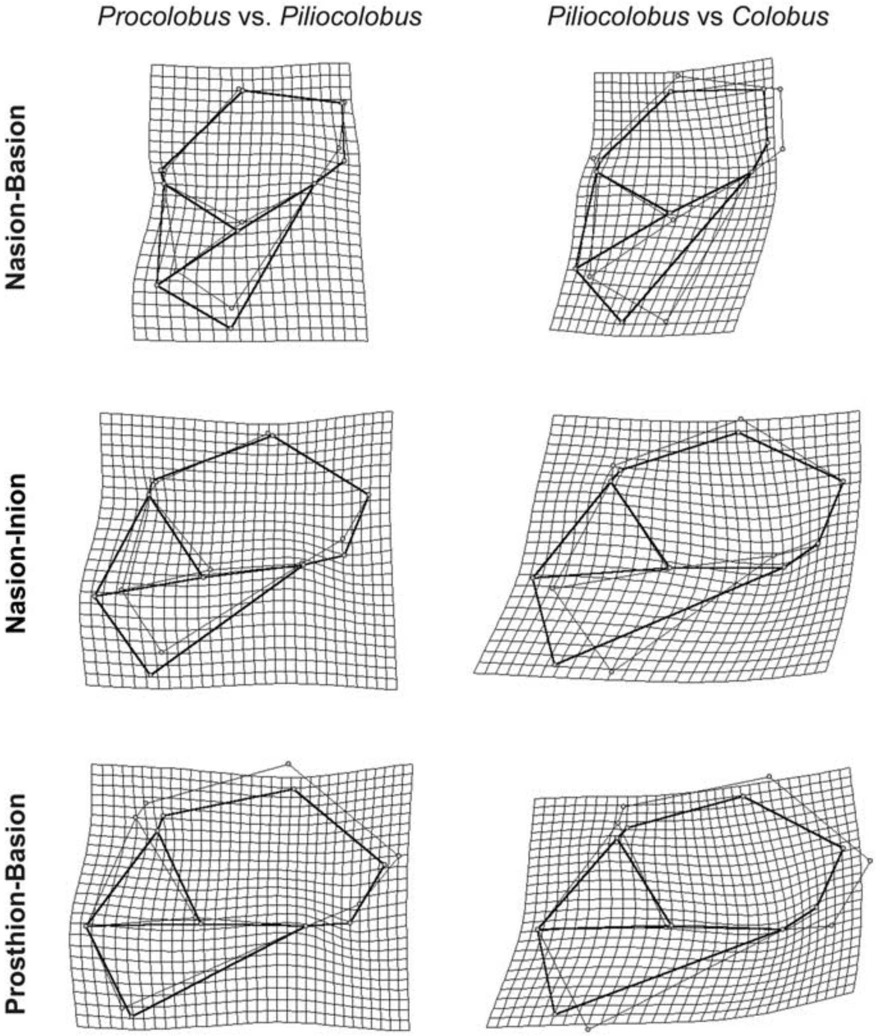


Fig. 5 – Pairwise average comparisons computed through Bookstein superimposition using nasion-basion, nasion-inion, and prosthion-basion as baselines, visualised through thin-plates spline and distortion grids, from* Procolobus verus *to* Piliocolobus badius *and from* Piliocolobus badius *to* Colobus guereza *(reference form: thin links; target form: bold links).

upper (glabella) to the lower (gnathion) parts of the skull, involving a minor angulation between the nasion-basion axis and the condylobasal diameter, and more vertical mandibular symphysis.

Procrustes superimposition

Procolobus vs *Piliocolobus*. Loading all the shape differences throughout the entire configuration by the Procrustes approach, *Procolobus* and *Piliocolobus* display a very similar morphology. The neurocranium is a bit shortened anteroposteriorly in the latter genus, which also shows a downward rotation of the foramen magnum. The face is more projected in *Piliocolobus*, and the mandible is relatively larger. The grids describe all these three

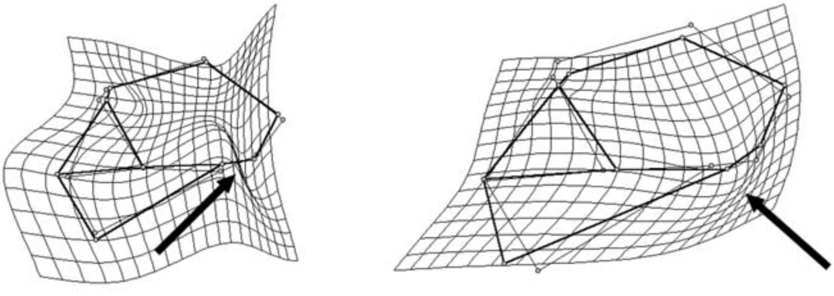


Fig. 6 – Pairwise average comparisons computed by Procrustes superimposition from* Procolobus verus *to* Piliocolobus badius *(left) and from* Piliocolobus badius *to* Colobus guereza *(right) are magnified x2 and x5 respectively, so as to emphasize the areas of principal folding of the distortion grids (arrows). Reference form: thin links; Target form: bold links;

components, namely (from *Procolobus* to *Piliocolobus*) the relative enlargement of the maxillary and mandibulary structures, the bending of the vault, and a localised crease at the foramen magnum (see Fig. 6).

Piliocolobus vs *Colobus.* The differences between *Piliocolobus* and *Colobus* are rather marked, with the second showing a relatively flattened vault, a posteriorly inclined foramen magnum, relatively lengthened facial and palatal structures, and a shorter and more inclined mandibular symphysis. The grids display an anterior flattening and posterior enlargement of the vault, a forward shifting of the mandible, and a compression at the nuchal area. Figure 6 shows the pairwise Procrustes superimpositions with the deformations of the transformation grids magnified so as to stress the main shape differences. Table 1 shows the bending energy values and the Procrustes distances for all the pairwise comparisons. Interestingly, the results are quite different. Concerning the bending energy, there are minor differences between *Procolobus* and *Colobus*, with *Piliocolobus* showing about 30% more stress in the deformation grids when compared with the other genera. Quantifying the differences according to Procrustes differences, instead, *Procolobus* and *Piliocolobus* are more similar, while *Colobus* shows 80% and 110% greater differences in relation to each genus respectively.

Nasion-basion baseline

Procolobus vs *Piliocolobus*. The shape of the nuerocranium is very similar, but for the rotation of the foramen magnum (and consequent changes of the nuchal area) in *Piliocolobus*. In this latter genus, both the face and mandible are relatively lengthened, without changes in the orientation of the condylobasal axis or mandibular symphysis. Accordingly, the facial complex is rather stretched antero-posteriorly, and the body of the mandible is longer and taller.

Piliocolobus vs *Colobus*. The differences are similar to those described previously, with *Colobus* showing a projection and vertical flattening of the facial and mandibular structures, and a more vertical symphysis. With the exception of the rotation of the foramen magnum described earlier, the neurocranium in *Colobus* is vertically flattened, and shortened antero-posteriorly in relation to the nasion-basion baseline.

Nasion-Inion (Neurocranial) baseline

Procolobus vs *Piliocolobus*. There are scarcely any differences in the neurocranium, but for the enlargement of the nuchal plane in *Piliocolobus* associated with lowering of the opisthion and a rotation of the foramen magnum. It is worth noting that the two basion almost coincide also when using the neurocranial baseline. Accordingly, the differences are almost the same as those discussed for the previous superimposition.

Tab.1 - Pairwise comparisons: bending energy (bE; lower matrix) and Procrustes distances (Pd; upper matrix).

bE\Pd	*Procolobus*	*Piliocolobus*	*Colobus*
Procolobus		0.074	0.158
Piliocolobus	0.078		0.137
Colobus	0.059	0.077	

Piliocolobus vs *Colobus*. Using this baseline, the opisthion and staphylion also almost coincide in the two shapes. The neurocranium is vertically flattened in *Colobus*, and the foramen magnum is posteriorly inclined because of the lower basion's position in relation to the neurocranial axis. The differences in face and mandible are the same as those described previously.

Prosthion-Basion (Condylobasal) baseline

Procolobus vs *Piliocolobus*. With respect to the condylobasal diameter, *Procolobus* shows a more bulging and rounded cranium (both face and neurocranium), while *Piliocolobus* shows a vertical flattening of the vault and more angled facial profile. The downward inclination of the foramen magnum in this latter genus is againstressed. The differences in the mandible are less marked, with *Piliocolobus* showing a taller mandibular corpus at the symphysis.

Piliocolobus vs *Colobus*. Considering the palatal and basicranial structures, the differences in the vault and mandible between the two genera are the same as those described previously. In contrast, the splanchnocranium shows scarce changes in the relative proportion and orientation, witha slight decrease in the vertical length of *Colobus's* face.

Discussion

The aim of the present paper is threefold: first to furnish a brief description and comment on some superimposition procedures, second to focus on some aspects of colobid cranial morphology, and third to provide homage to the pioneering work of W. Verheyen.

As a result of its statistical properties in relation to the geometry of the resulting shape space, Procrustes superimposition has been rapidly acknowledged as the default approach in morphometrics, from theory to software packages. Nevertheless, many different procedures are available (and often ignored), furnishing a large set of complementary tools to approach the functional and structural study of shape (see Zelditch *et al.*, 2004). It should be emphasised that these latter kind of transformations are algebraic procedures following models and assumptions, and must be properly interpreted within their theoretical frameworks in order to avoid misinterpretations and confounding effects (Richtsmeier *et al.*, 2002; Bruner, 2004). Aside from their role as preliminary steps towards more advanced and analytical investigations supplied by the multivariate statistics, the different superimposition techniques must be intended *per se* as heuristic tools to explore and collect information on forms and shapes. As shown through this simplified case-study, a large amount of information from different superimpositions is of course redundant, but small differences may be worth noting. This is particularly relevant when these differences refer to structural or functional axes. Superimpositions that do not scale the configurations such as the one used by Verheyen are useful to investigate the overall differences between forms, while the Bookstein transformations are necessary to describe differences relative to given biologically meaningful baselines. The Procrustes approach is required to compare shapes according to their minimal differences, and the resistant fit adjustment (not used in the present study) is useful when one or two landmarks bias the superimposition procedure prior to a visual interpretation.

It should be noted that another method of comparing differences in landmark configurations visually is afforded by transformation grids computed by using the thin-plate spline interpolant function. The distortion of the transformation grid is identical for each pair of comparisons, irrespective of the superimposition method used (Fig. 4-6). This is because transformation grids show deformations rather than relative locations, and these deformations are the same in character irrespective of translation, rotation and scale. That is, transformation grids are insensitive to differences in registration between configurations, and the thin-plate spline interpolation and visualisation does not require or assume any specific superimposition procedure. The function accounts for all the coordinate-wise differences between two sets of data. The thin-plate spline parameter estimates, treating coordinate-wise landmark differences as displacements of an infinite, infinitely thin metal plate above or below the plane (for 2D configurations) of the reference configuration, are computed to exactly fit the observed displacements while minimising the "bending" (double integrals of second-order partial derivatives) of the plate at between-landmark locations. Thus, any differences that could be attributable to misregistration of the configurations are also accounted for. This means that while various baseline superimpositions can be useful for visual interpretation of differences (though only paying great care with respect to any form of statistics), transformation grids can be a useful adjunct to ensure that we do not make serious errors of interpretation.

Accordingly, the role of the thin-plate spline function is threefold: to compare the spatial differences, to interpolate the between-landmark changes, and (moving to the multivariate morphomerics - see Zeldtich *et al.*, 2004) to furnish a set of shape variables available for statistical investigation.

Back to the colobids considered in this analysis, all the three species do not show sexual differences in the facial shape, but males in *Piliocolobus* and *Colobus* are anyway larger than females (O'Higgins & Pan, 2004). The differences between *Procolobus* and *Piliocolobus* are largely due to the general larger size in the latter, with the maxillo-mandibular structures increasing more than the neurocranial ones. When size-adjusted, differences mainly involve prognathism. Aside from these general traits, *Piliocolobus* displays a marked relative downward rotation of the foramen magnum. Relative to the nasion-basion baseline (dividing the neurocranial from the splanchnocranial districts), the face and mandible are enlarged proportionally, the vault shows no differences at all, and the nuchal planum is enlarged accounting for the rotation of the foramen. The results do not change when accounting for the maximum neurocranial length, nasion, basion, and inion being almost coincident for the two genera. The condylobasal superimposition accounts for the more globural cranium in *Procolobus*.

In contrast, differences between *Piliocolobus* and *Colobus* are less related to size variation, suggesting direct shape involvements. The vault in *Colobus* is relatively flattened, mostly at the frontal squama. Face and mandible are also vertically flattened, stretched anteriorly with a relatively more vertical chin, and the foramen magnum is not rotated as in *Piliocolobus*. Nasion, inion, and basion, do not overlap, so the different orientation of the foramen magnum can be interpreted in terms of a more compressed occipital area with respect to the face to neurocranium relationship (nasion-basion baseline) and of a taller lower part of the braincase (distance from the neurocranial axis to the basion).

Verheyen (1962) recognised the similarities between *Piliocolobus* and *Procolobus*, stressing the phylogenetic interpretations given by prior scholars. According to his geometric comparison, he divided the colobids in two groups: those species with shorter nasion-basion axis, more caudal bregma, inion, and opisthion, longer facial cranium, caudal staphylion, more vertical frontal and occipital squama, and more flattened glabellar area (red and green colobids) from those species with the opposite pattern (black colobids). He also hypothesised that *Procolobus* could represent the less derived morphotype.

Considering the increase in size from *Procolobus,* to *Piliocolobus,* to *Colobus*, and their tight phylogenetic relationship, we may expect that a certain proportion of shape difference is due to allometry, associated with processes involving heterochrony and ontogenetic variations (Shea, 1992; Klingenberg, 1998). The facial variation of these three genera is mainly characterised by a size-related splanchnocranial enlargement, increasing from *Procolobus* to *Piliocolobus* to *Colobus* (O'Higgins & Pan, 2004). The same data also suggest that the last two genera are more similar, and share a large proportion of their ontogenetic trajectory. Accordingly, the main differences (at the orbits and premaxilla) may arise early during the development of facial morphology. Verheyen (1962) detected the basic differences between green/red and black colobids since the earliest ontogenetic stages of his sample, namely in the skulls with no permanent dentition.

In contrast, in considering the whole skull it seems that the mean shapes of *Procolobus* and *Piliocolobus* are more phenetically similar, showing an inferior amount of differences. The neurocranial morphology is often more conservative than the facial districts, which is sensitive to adaptations to diet and social/behavioural factors. Both *Colobus* and *Piliocolobus* are larger than *Procolobus*, and show size-based dimorphism. This is to be expected, considering the relationship between body size and dimorphism in primates (Clutton-Brock *et al.*, 1977; Leutenegger & Cheverud, 1982). In contrast, many lines of evidence suggest a phylogenetic relationship between *Piliocolobus* and *Procolobus*, formerly included in a single genus. This hypothesis is supported by both results, namely similar faces between the black and red groups, but similar overall cranial morphology between the red and green groups. Nevertheless, the differences between *Piliocolobus* and *Procolobus* are more localised, involving a larger bending energy. This increase in the stress of the transformation grid must be referred to the very localised changes at the foramen magnum in *Piliocolobus*, which contrast with the general and more gradual changes recorded throughout the rest of the skull. Of course, these data do not allow a full explanation of this process. The rotation of the foramen magnum from *Procolobus* to *Piliocolobus* could be the result of the allometric structural patterns related to brain size and to the cranial base angle (McCarthy, 2001; Ross *et al.*, 2004). In this case, the absence of such rotation in *Colobus* might be a derived and non-allometric trait. Or, conversely, the rotation of the foramen is not size-related, and the particular configuration in *Piliocolobus* is the result of a neomorphic adaptation.

This analysis is performed using the averaged metrics of Verheyen, and the main target is to furnish a further exploitation of those data after almost half century. Of course, while *Procolobus* is probably a monospecific genus, here we use *Colobus guereza* as representative of a polispecific and possibly variable genus. Such difficulties are even larger when considering the red African colobids, and the genus *Piliocolobus* is far from being resolved in terms of biogeography and taxonomy (Struhsaker, 1975, 2005; Bruner *et al.*, 2006).

As stated previously, this paper is mainly aimed at providing a useful overview of some problematic concerning superimposition from one side and colobids variation on the other. It should also serve as a reminder that in the late 1950s a Belgian zoologist provided pioneer work on both topics, publishing two memorable monographs. It is my pleasure to dedicate this commentary on primates, skulls, and morphology to him.

Acknowledgements

I am grateful to Erik Verheyen for his help and support during the preparation of this manuscript. Paul O'Higgins largely improved an early version of this paper. Dennis Slice provided many important comments. Marta Salustri explored the W. Verheyen monographs together with me. This work was partially supported by the Istituto Italiano di Antropologia.

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