

CRANIAL MORPHOLOGY AND ANATOMY OF TWO ADULT FEMALES OF *PILIOCOLOBUS GORDONORUM* (UDZUNGWA RED COLOBUS) (MAMMALIA, PRIMATES: COLOBIDAE)

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ABSTRACT Taxonomy of the African Red Colobus group is currently unresolved. The single species *Procolobus badius* has been split into different taxa, but the relationships between the morphotypes are poorly understood, often due to a lack of specimens. One of these taxa, the endangered *Piliocolobus gordonorum* (Udzungwa Red Colobus) is restricted to the Udzungwa Mountains of southern Tanzania. In this paper, two adult female skulls of *P. gordonorum* are described comparing morphological features and metrics available from the literature. The two crania are extremely similar, showing very limited differences. The general morphology and metrics show a clear phenotypic affinity to *P. badius*, with some specific characters (e.g. shape of the occipital foramen, and shape of the mandibular notch) that must be further investigated. Size is only slightly larger than the *P. badius* mean, and metrics and general anatomy are comparable with this taxon. In contrast, the two skulls display a shorter anterior muzzle and larger neurocranium. Although these data are preliminary and descriptive, they represent a further step in the analysis of this endangered taxon.

KEY WORDS African colobids, skull, morphology, Udzungwa

INTRODUCTION

The fourteen taxa of 'Red Colobus' occur in a patchy allopatric distribution across tropical Africa from Senegal to Zanzibar (Oates et al., 1994). Most populations are primarily adapted to mature low and medium-altitude rain, riverine and groundwater forests (Struhsaker, 1975). Four allopatric taxa of Red Colobus occur in East Africa (Rodgers et al., 1982; Kingdon, 1997). The Udzungwa Red Colobus, *Piliocolobus gordonorum* Matschie, 1900, is one of the rarest and most endangered. Its distribution is restricted to montane forests of the Udzungwa Mountains of South-eastern Tanzania, and a few small groundwater and riverine forests in the nearby Kilombero Valley, between 300 and 2,300 m (Decker, 1994; Struhsaker et al., 2004; Jones, original data). Adequate data for estimating remaining numbers are not yet available. The largest populations are found within the well protected Udzungwa Mountains National Park (Mwanihana, Luhomero and Matundu Forests). Outside of the Park, the species is threatened by habitat loss and degradation, in spite of many of the habitats' nominal status as Forest Reserves. For example, the Kalunga Forest Reserve has recently been completely destroyed for firewood and charcoal, and the unique groundwater Magombera Forest was threatened with destruction in 2002 by a proposed resettlement in the forest of 2-300 people from adjacent land belonging to the Kilombero Sugar Company, and is currently heavily exploited (Pucci & Jones, pers. obs.). The Udzungwa Red Colobus is listed as African Convention Class A, CITES Appendix 2, IUCN Vulnerable (IUCN, 2006).

The body of the Udzungwa Red Colobus is dark,

tricoloured (red, black and white) with a thin, shaggy coat, with a tendency to darker tones (Fig. 1). They form large "multi-male multi-female" groups of up to 83 animals, though group size shows great variation across its range (Struhsaker et al., 2004). The Udzungwa Red Colobus is selective of the plant types and parts that form the principal components of its diet, though it eats many species in the course of the day. It feeds especially on young leaves, mature leaves, buds, petioles and fruits. Groups show a high tendency towards association with the other diurnal monkey species of the Udzungwas, in particular the Angolan Black-and-White Colobus, *Colobus angolensis* P. Sclater, 1860 (Pucci & Jones, original data).

African colobid systematics has never shown a sufficient taxonomic stability, largely because of the scarce information available on their biology and overall variation (see Oates et al., 1994). Taxonomy is



Fig. 1 Adult male of *Piliocolobus gordonorum* (photo by T. Jones).

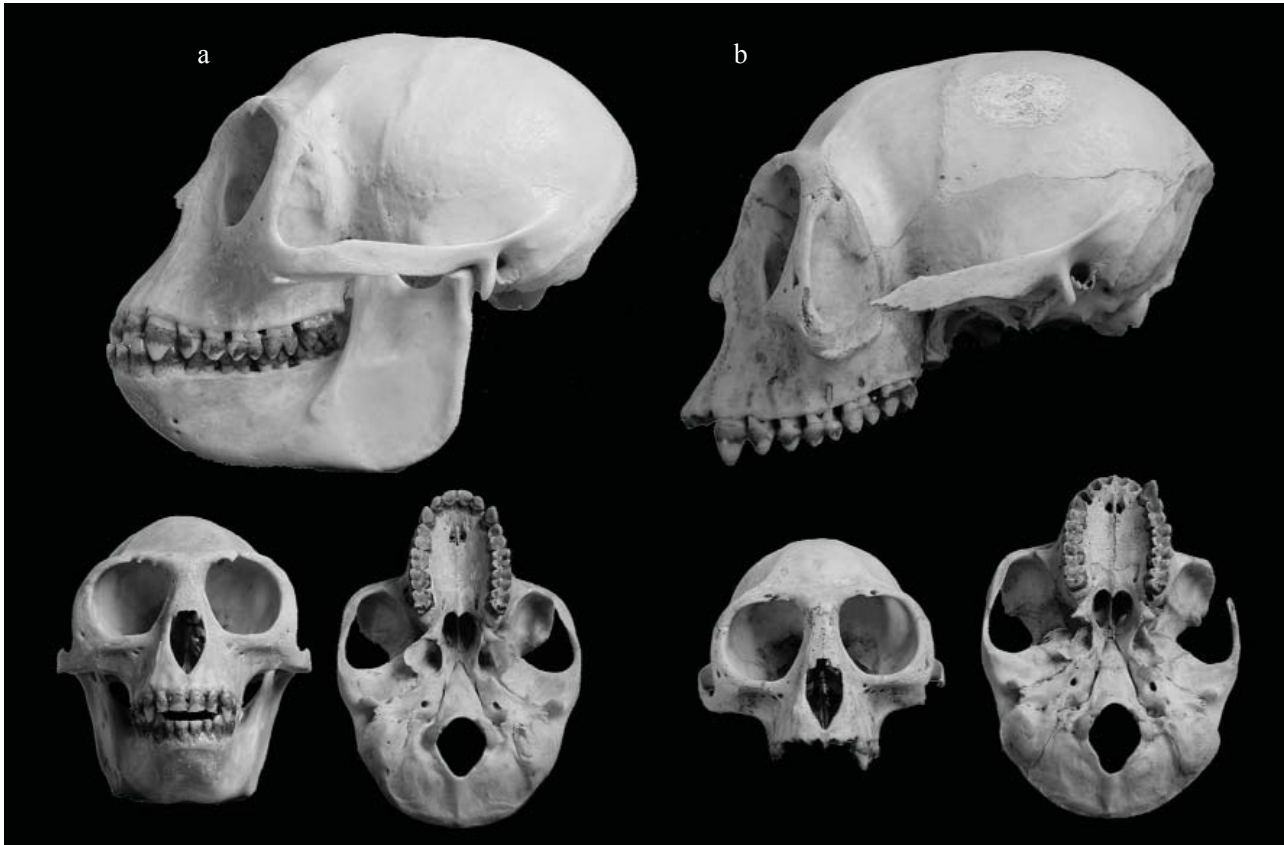


Fig. 2 The two *Piliocolobus gordonorum* skulls.

further confounded by the fact that all the Red Colobus taxa are allopatric. Recently, the Red Colobus group (formerly *Procolobus badius* (Kerr, 1792)) has been split into several different species, based on geographical and morphological characterisation (Groves, 2001a; but see Grubb et al., 2003). The genus *Procolobus* Rochebrune, 1887 has been restricted to *P. verus* (Van Beneden, 1838) (Green or Olive Colobus), while all the "classic" Red Colobus taxa have been placed in the genus *Piliocolobus* Rochebrune, 1887. The different groups included in the *Piliocolobus badius* complex (red colobids) have been then distinguished as different species. This splitting approach at the species level can be convenient for conservation biology purposes, isolating endemic and localised morphotypes (Groves, 2001b). According to this systematic approach, the Udzungwa Red Colobus has been raised from the subspecific rank of *Procolobus badius* (Kerr, 1792) to the specific level as *Piliocolobus gordonorum* Matschie, 1900 (Groves, 2001a).

We agree with the taxonomic approach separating *Colobus* Illiger, 1811, *Piliocolobus*, and *Procolobus*, recognising these three genera as quite distinguishable biological models both in terms of size (large-, medium- and small-bodied African colobids respectively) and general appearance ("black, red, and

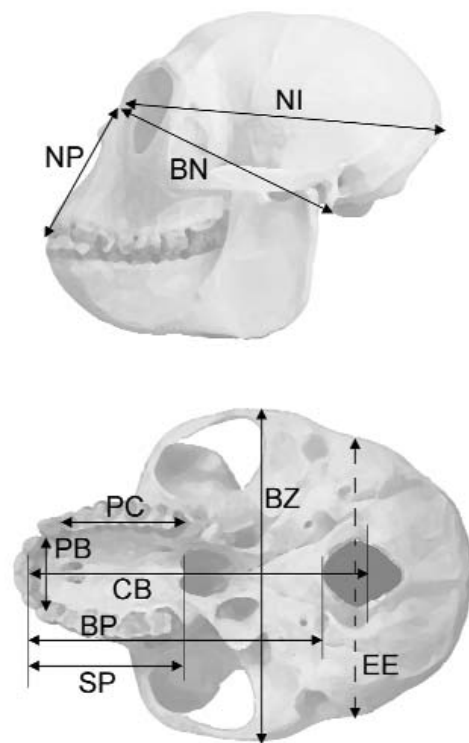


Fig. 3 Metric variables used to compare the two *P. gordonorum* skull with data available on literature (see tab. 1 for labels).

green" African colobids respectively). Considering the lack of information available on the colobids' skull anatomy (when compared with other primate taxa), and considering the endemic and endangered status of *P. gordonorum*, we present a description and analysis of two available female skulls of this species. As far as we know, the cranial morphology of this taxon is not yet described.

MATERIALS AND METHODS

The first cranium (PG1) is entirely preserved, including the mandible (Fig. 2a). It is an adult female. The whole body was found at about 700 m a.s.l. close to the Mizimu camp, Mwanihana Forest, Udzungwa Mountains National Park (UMNP), partially eviscerated. She was probably killed by an african crowned eagle (*Stephanoaetus coronatus*(Linnaeus, 1766)). After the decomposition of the soft tissues, the skull was cleaned and studied. The second specimen (PG2) is represented by the cranium alone (Fig. 2b). It was found without any other remains or soft tissues, next to a stream close to the Sanje Falls, Mwanihana Forest, UMNP (700 m a.s.l.). It is an adult individual, and it shows only some minor damages (lack of the incisors, lack of the right canine, fracture at the left zygomatic arch, damages at the right temporal fossa, and at the orbito-ethmoidal areas). Both crania show a complete fusion of the sphenoccipital suture, and must be interpreted as fully adult specimens. The two skulls are extremely similar, showing only very subtle differences both in size and morphology. Because of this high degree of morphological affinity between the two crania, we assume this second specimen may be a female too.

Both skulls were photographed and measured directly at the Udzungwa Mountains National Park. The skulls have been checked and compared with anatomical traits and 10 metrical variables available in the literature (Fig. 3), used to characterise the african colobids' crania (Bibus, 1967; Emer & Swindler, 1992). The inter-landmarks diameters from the two *P. gordonorum* (PG) specimens have been compared with the average female values from *Procolobus verus* (PV), *Piliocolobus badius* (PB), and *Colobus polykomos* (Zimmermann, 1780) (CP). For a general metric approach, raw values were used to compute the ratio between the PG mean value and the averages from the other species. The euclidean distance matrix has been used for a clustering procedure by unweighted pair-group method using arithmetic averages (UPGMA), to quantify the general phenotypic affinity.

It is worth noting that the data reported in literature for *Piliocolobus badius* are biased because of the past taxonomic interpretation. The data available on

	label	PV*	PB*	CP*	PG1	PG2
Condilo-basal length	CB	65	79	89	77	81
Basion-Prosthion	BP	58	70	81	69	72
Basion-Nasion	BN	55	60	66	60	63
Nasion-Prosthion	NP	33	39	40	38	38
Staphylion-Prosthion	SP	30	38	44	34	36
Eurion-Eurion	EE	52	54	59	57	58
Bizygomatic breadth	BZ	65	71	77	74	76
Premaxillar breadth	PB	24	25	29	24	25
post-canine length (maxilla)	PC	23	28	30	29	29
Nasion-Inion	NI	70	77	82	80	82
Mean		47	54	60	54	56

*data from Bibus (1967)

Tab. 1 Metric values (mm) of colobids (abbreviations of taxa as in fig. 4).

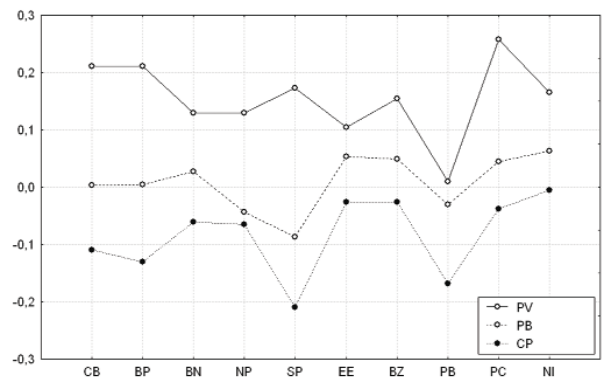


Fig. 4 Differences for each diameter (see Tab. 1) between the *P. gordonorum* mean and the averages from the other taxa, expressed as the ratio between the raw values (minus one, to show the percentage of variation). Values greater than zero indicates larger size in *P. gordonorum*, value less than zero indicates smaller size in *P. gordonorum*, and the zero baseline indicates no differences. CP = *Colobus polykomos*; PB = *Piliocolobus badius*; PV = *Procolobus verus*.

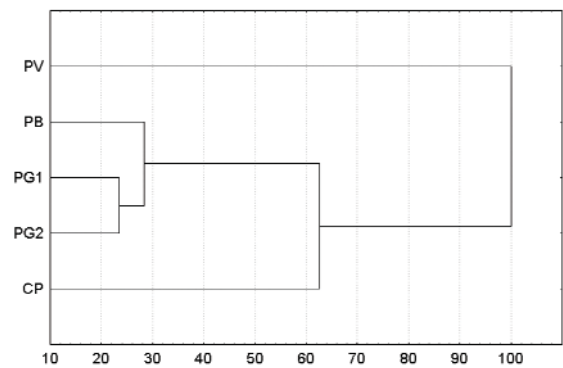


Fig. 5 Phenogram quantifying the morphological affinity between the two *P. gordonorum* (PG) specimens, and the female average values in *P. verus* (PV), *P. badius* (PB), e *C. polykomos* (CP). Groups have been clustered using a euclidean distance matrix and the UPGMA procedure (cophenetic correlation coefficient 0.93). Dissimilarity index was normalised to the longest branch.

anatomical traits (Bibus, 1967) derive from "*Procolobus badius badius*", and from the taxon currently recognised as *Piliocolobus badius*. In contrast, the morphometric data (Emer & Swindler, 1992) derive from the whole *Piliocolobus badius* complex, without species-specific differences. It is clear that they must be interpreted accordingly, representing general tendencies of the red colobids' variation.

RESULTS

In both skulls the premaxilla almost contacts superiorly the frontal bone, and the facial tract of the premaxillary suture is partially fused. In the pteric area the frontal bone contacts the temporal squama (fronto-temporal suture), although one of the two specimens (PG1) shows a unilateral limited speno-parietal joint. Some internasal bones are reported in both specimens, but to a limited degree of expression. The two crania show moderate supraorbital structures, and no sagittal crest. The infraorbital foramina are 3-4 on each side. The infraorbital fossa is quite marked. PG1 shows a light protrusion of the inferior incisive dentition onto the upper one (underbite). The occipital foramen does not show a clear anterior notch. In PG1 it is sub-romboidal, with the maximum axis developing backwards, while in PG2 the notch is developed at the posterior edge. In the PG1 mandible, the coronoid process is higher than the condyle, and the mandibular notch is deeper and narrower compared to the general red-colobids pattern. The median mental foramen is absent.

Tab. 1 shows the metric variables considered, with the mean female values for *P. verus*, *P. badius*, and *C. polykomos*, compared with the two PG specimens. The mean value shows that the size of the two PG skulls is more comparable to the PB female mean.

Fig. 4 shows the ratios between the PG mean value and the averages from the other species. PB shows the most similar values, not exceeding the 10% of differences. The main differences between PG and PB refer (in the former) to a shorter muzzle length (NP, SP), larger skull breadths (EE, BZ), longer neurocranium (NI) and longer postcanine teeth (PC). CP displays a similar pattern of variation between diameters, but scaled to larger size (up to about 20% of the PG values). PV shows a smaller size (up to 25% of difference with PG) and a distinct inter-diameters variation. The phenogram computed on the ten variables from the absolute values shows a phenotypic affinity between PG and PB, linked more to the CP morphotype than to the PV one (cophenetic correlation coefficient: 0.93; Fig. 5). Normalising the distances for the difference between PV and the other taxa, CP and

the red colobids show up to 60% of dissimilarity, and PB shows almost 30% of differences from the PG skulls.

DISCUSSION

The three genera of African colobids (*Colobus*, *Piliocolobus*, *Procolobus*) display different cranial structures, largely based on allometric and heterochronic variations but probably also including some size-independent features (Verheyen 1957, 1962; Bruner, 2006). This explorative analysis is aimed at characterising two skulls of *Piliocolobus gordonorum*, an endemic taxon of the Udzungwa Mountains. Although these two specimens cannot represent the true extent of variability within the group, their analysis adds to the very limited information available on this scarcely known and endangered taxon.

The first specimen is a female, while the second is assumed to be a female because of the marked phenotypic affinity with the former. Data from the literature suggest a certain sexual dimorphism for the *P. badius* complex (e.g. Clutton-Brock et al., 1977; Harvey & Clutton-Brock, 1995). But splitting the data according to the taxa included in the *Procolobus-Piliocolobus* group, many species (*P. kirkii* (Gray, 1868), *Procolobus verus*, and especially *Piliocolobus badius*) show only a moderate body mass difference between sexes (Oates et al., 1994). Only *Piliocolobus tephrosceles* (Elliot, 1907) shows a more marked sexual dimorphism, comparable with *C. guereza* Rüppell, 1835. In particular, *P. kirkii* displays a ratio of 95% between the female and male average body mass (Davies & Oates, 1994). A significant amount of sexual differences in primates is largely developed through allometric and heterochronic processes (e.g. Leutenegger & Cheverud, 1982; Shea, 1986, 1992; Klingenberg, 1998), with males showing generally peramorphic variations compared to the females. Taking into account the close biological and phylogenetic relationship hypothesised between *P. kirkii* and *P. gordonorum*, we can assume their degree of sexual dimorphism to be comparable, and therefore rather limited in the Udzungwa Red Colobus. Clearly, the analysis of the male skull will be necessary to test this assumption.

Some anatomical traits have been considered to describe the colobids' cranial variation. The contact between the premaxilla and the frontal bone is a rare character found only in *P. badius*, and not in *P. verus* or *C. polykomos*. The proximity of the two sutures in the PG skulls likens their nasal morphology to the *P. badius* morphotype. The same conclusion can be inferred when considering the fusion of the premaxillary/maxillary suture, which is more frequently closed in

the *P. badius* specimens. This is a variable character, and its partial synostosis has also been noted in *C. guereza* skulls (Bruner, pers. obs.). An even more variable situation is known for the sutural pteric patterns, usually characterised by a heterogeneous variation. PG1 shows the fronto-temporal articulation, slightly more frequent in *P. badius*, while unilaterally PG2 shows the sphenoparietal contact, more frequent in *P. verus* and *C. polykomos*. The internasal bones show high prevalence in *P. verus*, but their expression in the two PG skulls is rather slight. A certain development of supraorbital structures and the presence of a sagittal crest are typical of the small colobids (red and olive colobids), but the lack of these features in the two *P. gordonorum* skulls can be related to sexual dimorphism.

Both skulls show a complete fusion of the sphenoccipital suture, representing a full morphogenetic stage. The presence of an infraorbital fossa is another shared character of the small African colobids, and it is strongly expressed in these PG specimens. The lack of the medial mental foramen is a probable derived feature, shared by the colobids with the exception of *P. verus* and some fossil species (Oates Davies, 1994).

The two PG crania have a size comparable with the *P. badius* group, and the overall diameters show a phenotypic affinity between the females of the two taxa. Nevertheless, some features seem to characterise both the PG specimens. The shape of the occipital foramen does not resemble the Red Colobus pattern, but the variability of this feature is scarcely investigated in this group. Compared with the *P. badius* female mean, the two specimens display a shorter muzzle. The premolar-molar length seems in contrast rather similar (if even larger). Accordingly, some differences could be associated with the premaxillary structures or with the canine development. Furthermore, the neurocranium is longer and wider in the two PG skulls compared with the *P. badius* female mean. In addition, the peculiarities of *P. verus* are once more evidenced, and a classification of the African colobids based on three different genera represents a useful approach. The use of mean values for the compared taxa is of course a major limit of this analysis. A more complete sample that better describes levels of intraspecific variation will be needed to quantify these differences. However, it is worth noting that the striking similarity between the two specimens suggests a well defined morphotype.

Studies on the biology of all the Red Colobus species are rather urgent, considering the current problems in their conservation and management (Rodgers & Homewood 1982; Struhsaker, 2005). The

clear phenotypic affinity between these two specimens and the mean characters of *P. badius* is not surprising, representing congeneric species. Nevertheless, some features may suggest a further characterisation for this morphotype. The present paper provides only a general description of these two specimens within the African colobids' variation, because of the limited information available both in terms of published data and osteological collections. Future efforts must therefore be directed towards increasing the sample size allowing a more robust approach to the intraspecific variation of this taxon, and to provide comparisons with the species currently recognised in the *Piliocolobus badius* complex.

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