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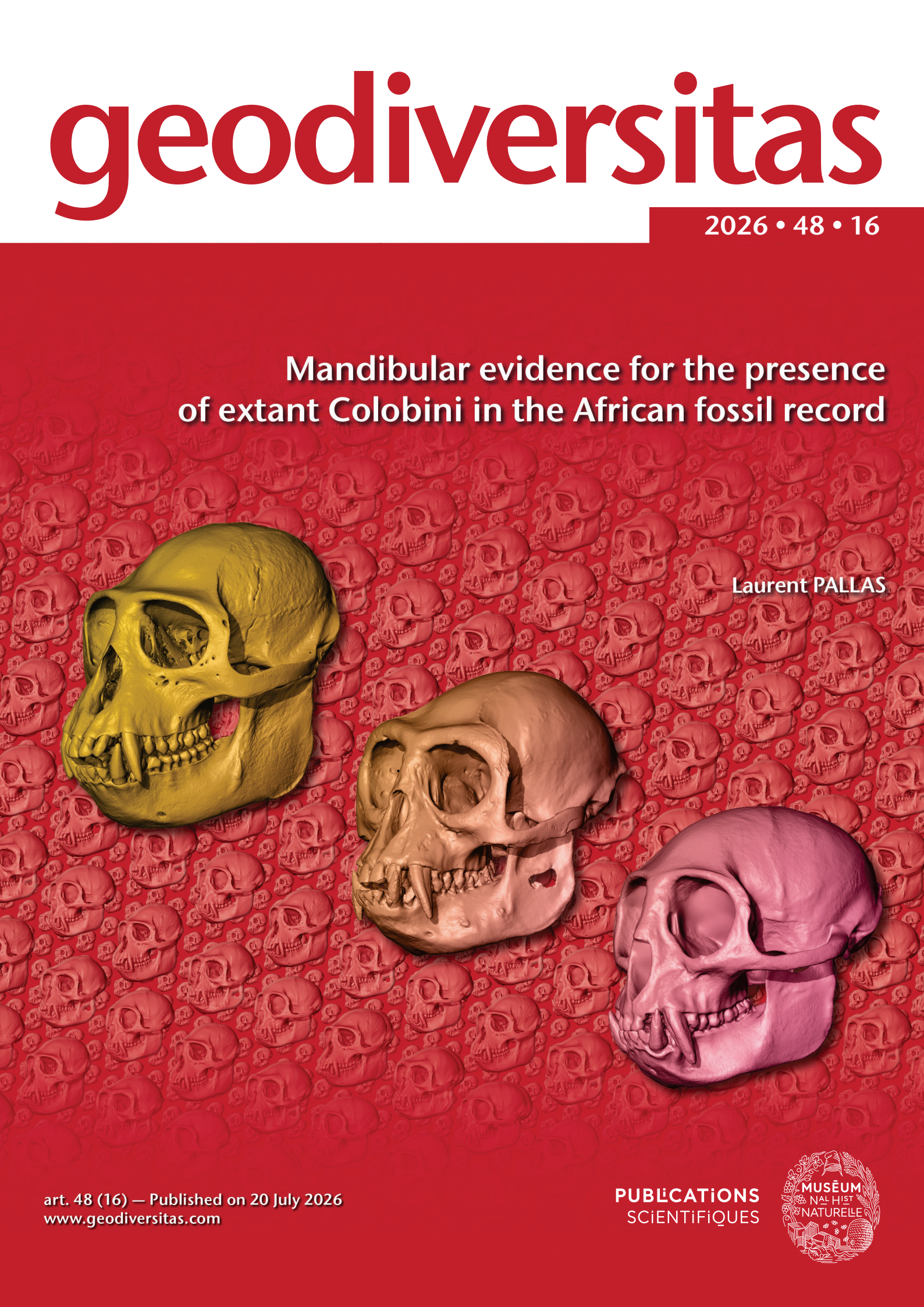
Laurent PALLAS



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Mandibular evidence for the presence of extant Colobini in the African fossil record

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ABSTRACT
Piliocolobus Rochebrune, 1877 and *Procolobus* Rochebrune, 1877 are key members of the primate community from eastern and central Africa but their presence in the fossil record has yet to be documented, hampering our knowledge of their evolutionary history. Using a combination of morphometric ratio, exploratory and discriminant multivariate analyses as well as hierarchical clustering on mandibular teeth, symphysis and corpus shape and dimensions, the phenetic affinity of small colobines from Asbole and Koobi Fora with *Piliocolobus* and *Colobus* Illiger, 1811 is demonstrated. This determination provides new evidence for the assessment of the paleobiogeography and evolution of extant African colobines.

KEY WORDS
Colobini,
Asbole,
Pleistocene,
mandibles,
symphysis,
corpus,
morphometry.

RÉSUMÉ
Preuves mandibulaires de la présence de colobinés actuels dans le registre fossile africain.
Piliocolobus Rochebrune, 1877 et *Procolobus* Rochebrune, 1877 sont des membres clés de la communauté des primates d'Afrique centrale et orientale, mais leur présence dans les archives fossiles n'a pas encore été documentée, ce qui entrave notre connaissance de leur histoire évolutive. En utilisant une combinaison de ratios morphométriques, d'analyses multivariées exploratoires et discriminantes ainsi qu'un regroupement hiérarchique sur les dents mandibulaires, la symphyse et la forme et les dimensions du corpus, l'affinité phénétique de petits colobes d'Asbole et de Koobi Fora avec *Piliocolobus* et *Colobus* Illiger, 1811 est ici démontrée. Ces nouvelles hypothèses taxonomiques apportent de nouvelles données sur la paléobiogéographie et l'évolution des colobinés africains actuels.

MOTS CLÉS
Colobini,
Asbole,
Pléistocène,
mandibules,
symphyses,
corpus,
morphométrie.

INTRODUCTION

Colobines from the equatorial forests of Africa form a monophyletic group (Fig. 1; Colobini Jerdon, 1867) of three genera (*Colobus* Illiger, 1811, *Piliocolobus* Rochebrune, 1877, and *Procolobus* Rochebrune, 1877) that likely play a role of seed dispersers (Matsuda *et al.* 2013) and are documented as a source of subsistence for chimpanzees (Bugir *et al.* 2021). Molecular data characterized *Colobus* as the sister taxon to the *Piliocolobus-Procolobus* clade (Ting 2008; Perelman *et al.* 2011; Kuderna *et al.* 2023), with both clades documented sympatrically in western, central and eastern Africa (Fig. 1; Kingdon & Groves 2013). When documented in sympatry, eco-ethological data from the Taï Forest (Ivory Coast) highlighted that climbing and leaping is more frequent in *Piliocolobus badius* Kerr, 1792 than in *Colobus polykomos* Zimmermann, 1780, and leaf consumption higher in *Pi. badius* compared to the specialized granivory and the processing of tough and fibrous food by *Co. polykomos* (McGraw 1998; Daegling & McGraw 2001). Skeletal traits diagnostic of the *Colobus* and *Piliocolobus-Procolobus* clades were identified on the dental, mandibular, cranial, and postcranial anatomy (Schultz 1958; Verheyen 1962; Strasser 1992; Groves 2007; Cardini & Elton 2009a, b; Koyabu & Endo 2009; Dunham *et al.* 2015). Recent advances in the last decades were notably done in the identification of diagnostic dental and mandibular traits (Groves 2007; Hlusko *et al.* 2016; Pallas *et al.* 2019; Brasil *et al.* 2023; Pallas *et al.* 2024a, b). Among others, these studies highlighted the large lateral prominences of the corpus and the large inferior transverse torus of the symphysis, the angulated symphysis, the reduced area of the P_4 relative to the M_1 area, and the large tuberculum sextum (C6) of *Piliocolobus* and *Procolobus* compared to *Colobus*. Despite those diagnostic morphological and eco-ethological traits, the evolutionary history of extant Colobini is poorly known. This is especially true for the absence of fossil record for *Piliocolobus* and *Procolobus*, contrasting with the presence of *Colobus* remains in eastern African fossil deposits (Fig. 1; Frost 2001; Jablonski & Frost 2010).

Leaving aside scarce remains where taxonomy was established on isolated teeth (Eck 1977; Leakey 1987) or sites with dubious dating (Harrison & Harris 1996), a fossil species of *Colobus*, *Colobus freedmani* Jablonski & Leakey, 2008, which includes a female partial skeleton in its hypodigm along with a fairly complete putative male mandible (KNM-ER 6025), is known from the *c.* 1.9-1.4 Ma Okote and KBS members of the Koobi Fora Formation (Jablonski & Leakey 2008). An indeterminate *Colobus* species, hypothesized as related to extant *Colobus angolensis* Sclater, 1860*,* is documented in the *c.* 600 Ka site of Asbole from a substantial collection of mandibular remains (Frost & Alemseged 2007). A large collection of *Colobus* specimens, likened to *Co. guereza* Rüppell, 1835, from the Middle Awash research area is also known from the *c.* 100 Ka Faro Daba beds of the Daiwaitoli Formation in Ethiopia (Brasil *et al.* 2023). Another fossil population, partially described in Frost (2001) and possibly related to *Colobus angolensis* given its poorly dimorphic canines and heteromorphic incisors*,* is known from "Andalee" (see Brasil *et al.* [2023] for further information on site denomination and chronostratigraphic context). Finally, an isolated skull of *Co. guereza* from Wadi Medani in central Sudan (Simons 1967; Jablonski & Frost 2010) and an undescribed partial skull from the Shungura Formation that may represent *Colobus* (Assefa *et al.* 2008) complete our knowledge of the *Colobus* fossil record.

Relationships between fossil *Colobus* populations have been seldomly investigated and controversy remains regarding the taxonomic homogeneity of the *Co. freedmani* sample from Koobi Fora and the taxonomic status of the Asbole specimens. Indeed, the Koobi Fora sample was described as *Colobus* by Jablonski & Leakey (2008) but previously regarded as *Procolobus* by Frost & Alemseged (2007), mainly based on the corpus robustness. In contrast, Jablonski & Leakey (2008) considered the robust corpus of the putative male KNM-ER 6025 as part of the range of variation of *Colobus*. Similarly, the colobine sample from Asbole was initially described as belonging to the *Procolobus-Piliocolobus* clade by Alemseged & Geraads (2000) and later revised to *Colobus* by Frost & Alemseged (2007). The species status of Asbole is indeterminate and its affinity with *Co. angolensis* established primarily on biogeographical data and poor canine dimorphism. It has been recently suggested that the *Colobus* cf. *guereza* samples from Faro Daba and Asbole may represent a chronolineage (Brasil *et al.* 2023), giving support for population continuity in the northern part of Ethiopia during the last 600 Ka in addition to recognizing that the Asbole sample may include the earliest members of the *Colobus guereza* lineage. Resolving the taxonomic affinity of the Asbole and Koobi Fora sample has hence implications on faunal dispersal along the East African Rift System during the Pleistocene, a time and place that witnesses the emergence of *Homo sapiens* Linnaeus, 1758.

Here, the mandibular colobine fossil record from Asbole and Koobi Fora is used to evaluate the possible presence of traits diagnostic of extant Colobini taxa that were previously disregarded. Univariate and multivariate analyses (exploratory and discriminant) are used along with hierarchical clustering established on lower teeth dimensions, symphyseal dimensions, and corpus shape to test the hypothesis that the specimens are phenetically closer to *Colobus* than to *Procolobus* and *Piliocolobus*. An alternative hypothesis would posit that the Asbole and Koobi Fora samples each represent a distinct taxon or, for the large collection from Asbole, a mix of different taxa. The range of variation present within the corpus morphology of the Asbole specimens is assessed using bootstrap analyses to test the hypothesis that only one taxon is present and whether sexual dimorphism can explain differences in corpus shape between fossil specimens, as proposed by Jablonski & Leakey (2008).

MATERIAL AND METHODS

Extant and fossil samples

The dimensions of the lower canine, premolars, and molars of n = 113 specimens and the symphyseal dimensions of n = 119 specimens extant Colobini were measured. The depth of the corpus, at mid-M_1, of n = 233 extant Colobini specimens

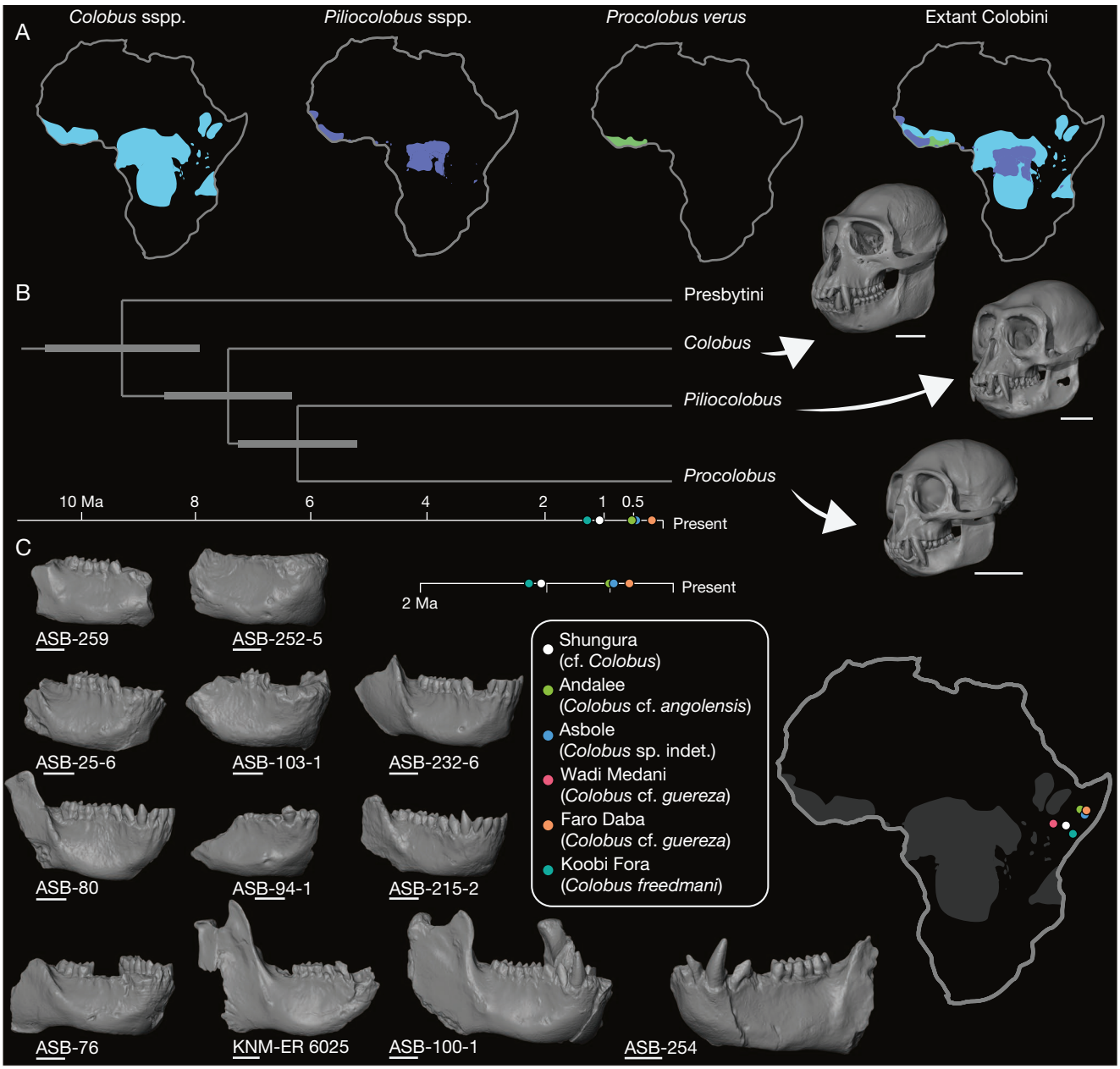

Fig. 1. — **A**, Geographic distribution of extant *Colobus* Illiger, 1811, *Piliocolobus* Rochebrune, 1877 and *Procolobus* Rochebrune, 1877; **B**, chronocladogram of extant Colobini with uncertainty in divergence dates modeled as a gray rectangle; **C**, chronostratigraphic frame of fossil Colobini (**upper panel**) along with 3D generated surfaces of Asbole and Koobi Fora mandibles discussed in the text (**central panel**) and geographic locations of fossiliferous deposits discussed in the text along the geographic range of extant Colobini (**right panel**). Scale bars: B, 20 mm; C, 10 mm. Illustration and photos: Laurent Pallas.

were also measured along with landmark digitization on the transverse cross-section of $n = 178$ corpus of extant Colobini. A list of the extant and fossil specimens used in this study is provided in Appendix 1. Only adult specimens were included in the analysis, and their adult status was asserted using the M_3 eruption. Extant and fossil Colobini specimens were collected from the National Museums of Ethiopia (Addis-Abeba), the National Museums of Kenya (KNM, Nairobi), the Muséum national d'Histoire naturelle (MNHN, Paris), the Royal Museum for Central Africa (RMCA, Tervuren), the Bavarian State Collection of Zoology (ZSM, Munich), the Center for the Evolutionary Origins of Human Behavior (EHUB, Kyoto University, Inuyama), the Zoological Collection of the Kyoto University, the Smithsonian National Museum of Natural History (USNM, Washington), the American Museum of Natural History (New York), the Stony Brook University (New York), and the PALEVOPRIM Laboratory (University of Poitiers).

Data acquisition and morphometry

Fossil and extant specimens integrated in this study were scanned using the Artec Space Spider and Einscan Pro 2X surface scanners as well as using photogrammetry given photographs obtained with a Panasonic Lumix DC-GX9 camera. For the dental fossil data, I measured dental dimensions from

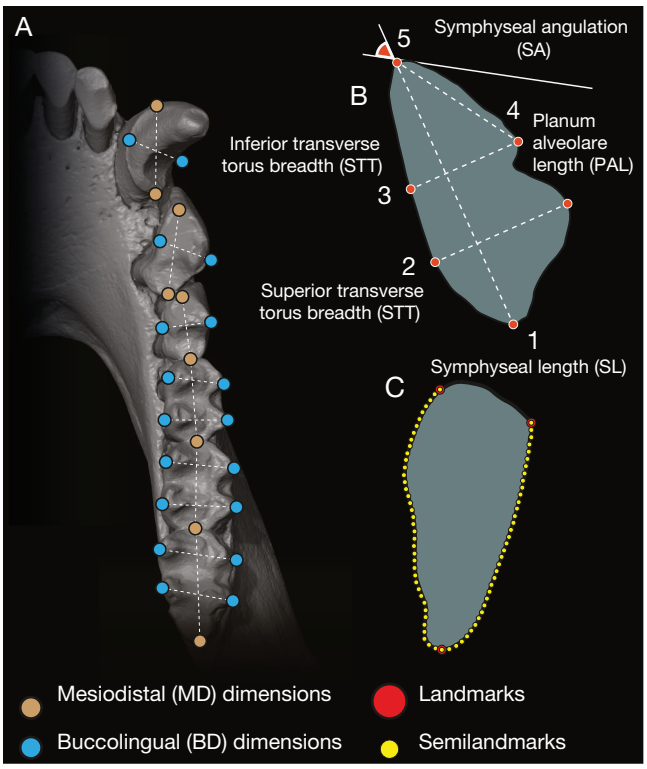

Fig. 2. — Morphometric protocols for quantifying: **A**, dental dimensions; **B**, symphyseal dimensions; **C**, shape of the corpus. Illustration and photos: Laurent Pallas.

3D-generated surfaces using Avizo v7.0. The mesiodistal (MD) and buccolingual (BD) dimensions of the lower canine, premolars, and molars were measured to the nearest tenth of millimeters following the protocol illustrated in Figure 2A. Three dental ratios were used to evaluate the phenetic similarity between extant and fossil taxa. Precisely, these ratios quantify the MD elongation of the lower canine relative to the M_2 area, the area of the P_4 relative to that of the M_1 and the length of the M_3 relative to the M_2 area.

The length of the symphysis, the breadth of the symphyseal transverse tori and the angulation of the symphysis relative to occlusal plane (Fig. 2B) were measured from pictures of sagittal cross-section of symphysis using ImageJ (Schneider *et al.* 2012) and following the protocol presented in Pallas *et al.* 2024a. In addition to differences in absolute angulation of the symphysis, the ratio of the symphyseal transverse torus (STT) breadth over the breadth of the symphyseal inferior torus (ITT) was used to investigate phenetic similarity between extant and fossil sample.

Three landmarks and seventy-five semilandmarks (Fig. 2C) were digitized on transverse cross-sections of the corpus of extant and fossil colobines following the protocol presented in Pallas *et al.* (2024b). To summarize, cross-section images at the M_1/M_2 junction were obtained using Avizo with landmarks and semilandmarks digitization done using tpsDig (Rohlf 2006). Three landmarks were placed at the 1) most proximal and buccal point of the corpus; 2) most inferior point of the corpus; and 3) most proximal and lingual point of the corpus. Seventy-five semilandmarks were then digitized equidistally along the corpus outline.

Repeatability of morphometric analyses

To verify the repeatability of the new protocol proposed here for the symphyseal morphometric analyses, four colobine specimens belonging to four different taxa (*Nasalis larvatus* Geoffroy, 1812; *Colobus satanas* Waterhouse, 1838; *Piliocolobus badius* Kerr, 1972; *Procolobus verus* Van Beneden, 1838) were measured five times each for each measurement by the same observer (LP). The measurement error estimate follows the computation presented in White & Folkens (2005) and a maximum error threshold of 5% was adopted. Briefly, the average value of the five replicates was calculated and then subtracted from each replicate value. The resulting cumulative differences were then divided by the number of measurements, which was five in this case, to obtain a percentage of error.

All results for replicability of the symphyseal measurements are presented in Appendix 2. The range of measurement error for symphyseal length (0.4-2.0%), breadth of the superior transverse torus (0.2-3.9%), breadth of the inferior transverse torus (0.4-0.9%), planum alveolare length (1.4-3.8%), and symphyseal angulation (2.6-5%) never exceeded 5% of error and are considered as repeatable.

A different approach was used to test for the repeatability of the 2D geometric morphometric analysis of the corpus shape. Repeatability is here considered as the proportion of the between taxa variance compared to the total observed variance (between and within taxa). Landmarks and semilandmarks were digitized by the same observer (LP) on four specimens of four different colobine taxa (same as previously). Landmarks and semilandmarks coordinates were subjected to a Generalized Procrustes Analysis and a principal component analysis (PCA) was run on the Procrustes coordinates (see below subsection below for more details). Repeatability was assessed on PCA scores using the rptGaussian function of rptR (Stoffel *et al.* 2017). For each PC scores, the within taxa variation is extremely low and nearly all the variation is explained by the between taxa variation for PC1 (95% confidence interval [CI] = 0.99-1), PC2 (95% CI = 0.98-1), and PC3 scores (95% CI = 0.97-0.99). This result is confirmed graphically in Appendix 3.

Statistical analysis

All statistical analyses were done using R v.4.4.1 (R Core Team 2024) and the interface RStudio v.2023.12.0 (RStudio Team 2020). All the packages and functions used can be found in Table 1.

Univariate analyses: First, phenetic similarity was evaluated by comparing dental ratio values between fossil specimens and extant Colobini. The formulas for the dental ratios can be found in Table 2. Such ratios were previously recognized as significantly distinct between extant Colobini taxa but given that additional specimens were added compared to Pallas *et al.* (2019), new statistical tests were computed to evaluate whether differences are still significant. Significance was evaluated using a one-way parametric analysis of variance (ANOVA) and non-parametric Kruskall-Wallis. Normality and homoscedasticity of the model residuals were evaluated

TABLE 1. — List of the R package and associated functions in this article.

Analyses	Packages	Functions	References
GPA	geomorph	gpagen	Adams *et al.* 2024
PCA on Procrustes coordinates (corpus)	geomorph	gm.prcomp	–
PCA on linear dimensions (dental and symphysis)	stats	prcomp	R Core Team 2024
ANOVA	stats	aov	–
Kruskal-Wallis	stats	kruskal.test	–
MANOVA	stats	manova	–
Shapiro-Wilk	stats	shapiro.test	–
Bartlett	stats	bartlett.test	–
Tukey HSD	stats	TukeyHSD	–
Hierarchical Clustering	stats	hclust	–
PERMANOVA	vegan	adonis	Oksanen *et al.* 2001
Multivariate Shapiro-Wilk	rstatix	mshapiro_test	Kassambara 2023
Box M	rstatix	box_m	–
Dunn	FSA	dunnTest	Ogle *et al.* 2023
rptR	rptR	rptGaussian	Stoffel *et al.* 2017
LDA	MASS	lda	Venables & Ripley 1997

TABLE 2. — Formulas of the dental ratios. Used formula: C_1 MD/(M_2MBL × M_2DBL).

	Descriptive statistics	
Relative canine elongation	*Colobus*	0.18 (0.02)
	Piliocolobus	0.21 (0.04)
	Procolobus	0.27 (0.05)
	Asbole	0.20 (0.04)
P_4 area/M_1 area	*Colobus*	0.70 (0.06)
	Piliocolobus	0.64 (0.05)
	Procolobus	0.61 (0.06)
	Asbole	0.65 (0.05)
Relative length of M_3	*Colobus*	0.22 (0.02)
	Piliocolobus	0.27 (0.02)
	Procolobus	0.32 (0.03)
	Asbole	0.26 (0.03)

prior to the ANOVAs using the Shapiro-Wilk and Bartlett tests, respectively. To identify pairs of taxa that differ significantly, the Tukey Honest Significant Differences (HSD) post-hoc test following ANOVA and the Dunn test following Kruskall-Wallis were used.

Principal Component Analyses and Generalized Procrustes Analysis: Following comparison of univariate data, a principal component analysis (PCA) was used to explore and order variation within the dental, symphyseal and corpus datasets. Data was transformed using the log-shape ratio method prior to PCA for the dental and symphyseal data while a Generalized Procrustes Analysis (GPA) was used for the corpus landmark dataset. The log-shape ratio method standardizes data and mitigates the confounding effect of size (Mosimann 1970). The GPA was applied on the 2D landmarks and semi-landmarks coordinates, permitting retaining shape data only by translating, scaling, and rotating the landmarks and semi-landmarks coordinates of each specimen.

Significant differences in PC scores between extant genera were examined using the parametric multivariate analysis of variance (MANOVA) and the non-parametric permutational multivariate analysis of variance (PERMANOVA). Normality and homoscedasticity were evaluated prior to MANOVA and PERMANOVA using the multivariate Shapiro-Wilk and Box M tests, respectively. Differences in PC scores between pairs of taxa were evaluated using Tukey HSD and Dunn post-hoc tests.

Sexual dimorphism in corpus shape: To evaluate sexual dimorphism in corpus shape, a MANOVA on the scores of the three PCs of the aligned Procrustes coordinates was run. Multivariate normality and homogeneity of covariances were evaluated prior to MANOVA using the multivariate Shapiro-Wilk and Box M tests, respectively. The MANOVA was followed by a Tukey HSD test to identify pairs of significantly distinct taxa.

Linear Discriminant Analyses (LDA): Following exploration and ordination of the variation, a linear discriminant analysis was used on the first four PCs of the dental, symphyseal and corpus PCAs to taxonomically classify fossil specimens and to highlight their phenetic affinities towards *Colobus*, *Piliocolobus* or *Procolobus*. Prior to inclusion of fossil specimens, a jackknife analysis was used to evaluate the accuracy of the model to correctly classify extant specimens.

Hierarchical clustering: Hierarchical clustering was used to assess the phenetic affinity of the Asbole specimens. A distance matrix was first computed using Euclidean distance on the scaled and centered values of the first two mean PC scores of dental shapes of the three extant Colobini genera in addition to the first two PC scores of corpus shape and the first three PC scores of symphyseal shape. The hierarchical clustering was computed using the Ward clustering method.

Two different hierarchical clustering were done given different operational taxonomic unit (OTU) for the Asbole specimens. The first clustering incorporates the mean value of all Asbole specimens for dental, corpus, and symphyseal shape. This view hence recognizes the Asbole colobine specimens as part of a single taxon. The second clustering includes only ASB-232-6 and ASB-100-1 from which a complete dataset for dental, corpus, and symphyseal shape is available.

Bootstrap analyses: To evaluate whether the range of variation of the corpus shape of the Asbole sample and the combined Asbole and Koobi Fora samples can be accommodated in the same genus, a bootstrap analysis was carried out based on comparison of the coefficient of variation. To this end, 10.000 random distributions were generated for *Colobus*, *Procolobus*, and *Piliocolobus* based on PC1 and PC2 scores obtained from the original dataset. Then, 10.000 random distributions were generated based on $n = 6$ and $n = 7$ specimens randomly selected for each extant genus. The number of specimens randomly selected corresponds to the number of specimens included in the Asbole sample ($n = 6$) and the combined Asbole and Koobi Fora samples ($n = 7$). Finally, coefficient of variation (i.e., standard deviation/mean) for each of the generated distribution of extant Colobini genera were computed and compared with that of the fossil sample.

TABLE 3. — Results of the statistical tests of the dental and symphyseal ratios.

	Normality (Shapiro-Wilk)	Homoscedasticity (Bartlett)	Model (ANOVA or Kruskal-Wallis)	Post-Hoc (Tukey HSD or Dunn)	p. val.
Relative elongation of C_1	W = 1, p. val. < 0.05	K^2 = 33, p. val. < 0.01	Kruskal-Wallis	*Colobus-Piliocolobus*	< 0.001
			X^2 = 50,	*Colobus-Procolobus*	< 0.001
			p. val. < 0.01	*Piliocolobus-Procolobus*	< 0.01
P_4 area/M_1 area	W = 1, p. val. = 0.4	K^2 = 0.8, p. val. = 0.8	ANOVA	*Colobus-Piliocolobus*	< 0.001
			F = 25.9,	*Colobus-Procolobus*	< 0.001
			p. val. < 0.001	*Piliocolobus-Procolobus*	= 0.24
Relative length of M_3	W = 1, p. val. = 0.7	K^2 = 6, p. val. = 0.06	ANOVA	*Colobus-Piliocolobus*	= 0.06
			F = 171,	*Colobus-Procolobus*	= 0.11
			p. val. < 0.001	*Piliocolobus-Procolobus*	= 0.06
Symphyseal tori breadth differential	W = 10.9, p. val. < 0.001	K^2 = 16, p. val. < 0.001	Kruskal-Wallis	*Colobus-Piliocolobus*	< 0.001
			X^2 = 63,	*Colobus-Procolobus*	< 0.001
			p. val. < 0.01	*Piliocolobus-Procolobus*	= 0.24
Symphyseal angulation	W = 1, p. val. = 0.3	K^2 = 5, p. val. = 0.07	ANOVA	*Colobus-Piliocolobus*	= 0.001
			F = 10,	*Colobus-Procolobus*	= 0.392
			p. val. < 0.001	*Piliocolobus-Procolobus*	< 0.001

A bootstrap analysis was also generated using corpus height below mid-M_1 as many specimens from Asbole (n = 10) preserves this dimension. Compared to the corpus shape bootstrap, that of the mid-M_1 depth of the corpus was evaluated at species level using n = 7 species of Colobini: *Co. angolensis*, *Co. guereza*, *Co. polykomos*, *Pi. langi* Allen, 1925, *Pi. parmentieri* Colyn & Verheyen, 1987, *Pi. tholloni* Milne-Edwards, 1886, and *Pro. verus*. Corpus depth at M_1 is also reported for the Faro Daba *Co. guereza* specimens (Brasil *et al.* 2023), and its coefficient of variation compared to a combined Faro Daba, Koobi Fora and Asbole sample and also to the coefficient of variation of extant Colobini species.

ABBREVIATIONS

Institutions

AMNH	American Museum of Natural History, New York;
MNHN	Muséum national d'Histoire naturelle, Paris;
KAS	Osteological colletion of the Physical Anthropology Laboratory of the Kyoto University;
KUPRI	Kyoto University, Primate Research Institute;
MCZ	Harvard University, Museum of Comparative Zoology, Cambridge;
KNM-OM	Kenya National Museum, Osteology collection;
RMCA	Royal Museum for Central Africa, Tervuren;
SBU RS	Stony Brook University, Randal Susman collection;
SNSB-ZSM	Staatliche Naturwissenschaftliche Sammlungen Bayerns;
USNM	Smithsonian Institution, National Museum of Natural History, Washington.

Collections

F	MNHN, fossil collection;
ZM	MNHN, mammal collection.

Other abbreviations

MD	mesiodistal;
BL	buccolingual ;
STT	superior transverse torus;
ITT	inferior transverse torus;
PCA	principal component analysis;
GPA	generalized procrustes analysis;
ANOVA	analysis of variance;
PC	principal component;
LDA	linear discriminant analysis.

RESULTS

UNIVARIATE AND MULTIVARIATE DENTAL ANALYSES

Relative canine elongation: The index of the MD length of the canine relative to the M_2 area statistically discriminates *Procolobus* and *Piliocolobus* from *Colobus* (Fig. 3A; Table 3). The canines of the former are mesiodistally elongated compared to the M_2 area, having significantly higher index values (Table 3), and mesiodistally longer canines than *Colobus*. This condition reaches an extreme level in *Procolobus*, which has significantly longer canines relative to the M_2 area than those of *Colobus* and *Piliocolobus*. The position of the Asbole colobines is ambiguous and apart from ASB-254, they occupy an intermediate position between the interquartile range of *Piliocolobus* and *Colobus* (Fig. 3A). Precisely, ASB-100-1 and ASB-232-6 have index values consistent with the interquartile of *Piliocolobus* and *Colobus* while ASB-80 and ASB-215-2 fall in the interquartile range of *Colobus* only and in the upper range of variation of *Piliocolobus*.

Area of the P_4 relative to the area of the M_1: The index of the area of the P_4 relative to the area of the M_1 statistically discriminate *Procolobus* and *Piliocolobus* from *Colobus* (Fig. 3B and Table 3), with the former two genera having a reduced P_4 relative to M_1 dimensions, and hence statistically lower index values compared to *Colobus* (Table 3). The Asbole colobine sample has a mean index value consistent with the interquartile range of *Procolobus* and *Piliocolobus*. Precisely, ASB-215-2 and ASB-232-6 are falling in the interquartile range of *Piliocolobus* and *Procolobus* while ASB-100-1 and ASB-25-6 are fitting with the interquartile range of *Colobus* (Fig. 3B). Similarly, *Colobus freedmani* KNM-ER 6025 falls in the interquartile range of *Piliocolobus* and *Procolobus* and in the first quartile of *Colobus*.

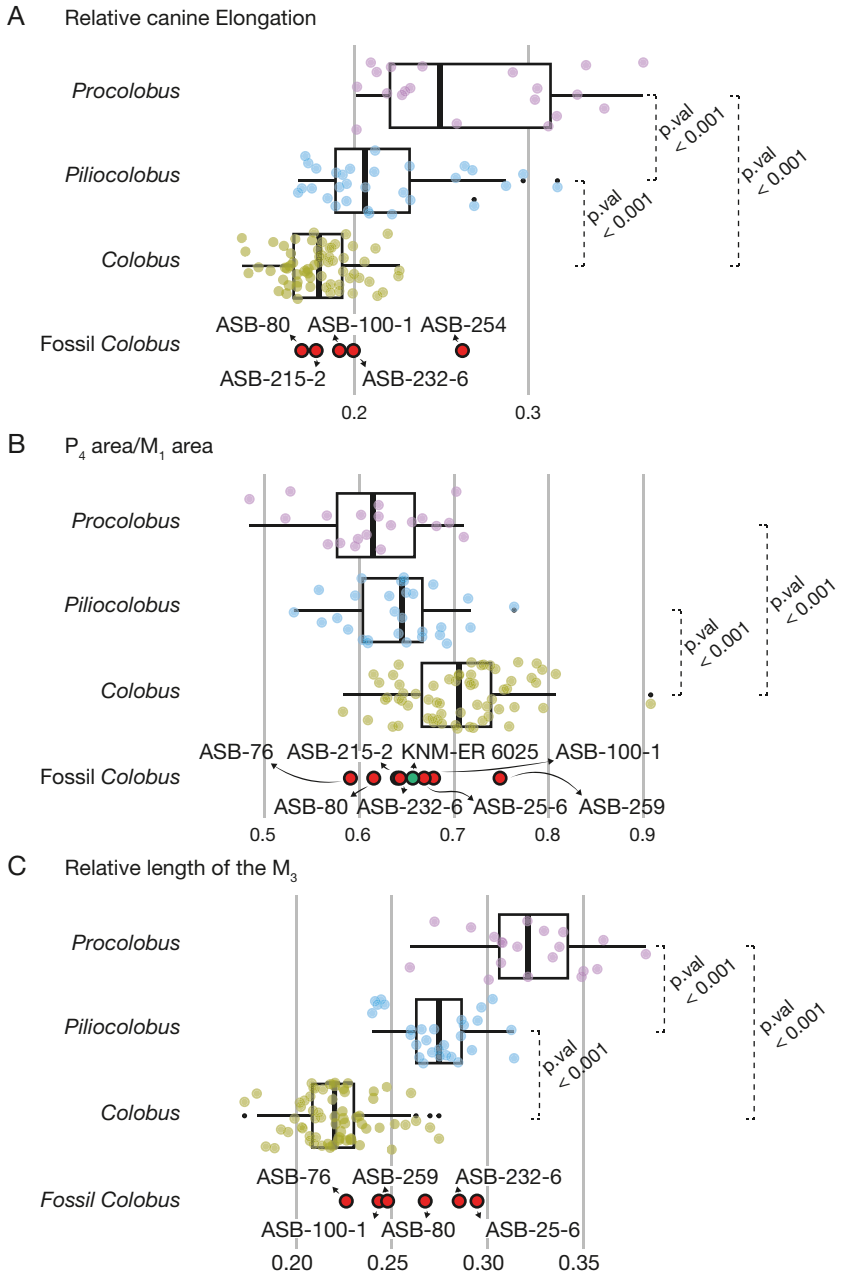

FIG. 3. — **A**, Boxplots of the relative canine elongation of extant and fossil colobines; **B**, boxplots of the P_4 area/M_1 area ratio of extant and fossil colobines; **C**, boxplots of the relative length of the M_3 of extant and fossil colobines. All boxplots with median (**black bar**), outliers (**black dot**), first quartile and third quartile. Illustration: Laurent Pallas.

Relative M_3 elongation: MD length of the M_3 relative to the M_2 area statistically discriminates *Piliocolobus* and *Procolobus* from *Colobus* (Fig. 3C and Table 3). *Piliocolobus* and *Procolobus* have significantly higher index values compared to *Colobus*, illustrating their longer M_3 compared to the M_2 area. The M_3 of *Procolobus* is even longer, relative to the M_2 area, than that of *Piliocolobus*. While ASB-76 conforms to the interquartile range of *Colobus*, the specimens ASB-232-6, ASB-80, and ASB-25-6 are within or close to the interquartile range of *Piliocolobus*. ASB-259 and ASB-100-1 are included in the range of variation of both *Piliocolobus* and *Colobus*.

PCA of dental dimensions

PC1 and PC2 account for *c.* 47% of the variance (Fig. 4). PC1 scores discriminate *Piliocolobus* from *Colobus*, although interquartile ranges of variation greatly overlap, and PC2 scores discriminate *Piliocolobus* and *Procolobus* from *Colobus* (Table 4). Positive scores on PC1 are driven by P_3 and C_1 dimensions while negative scores are driven by the molars BL breadth (Fig. 4). Positive scores on PC2 are influenced by the MD length of the molars and by the BL breadth of the P_4 and the BL breadth of the anterior loph of M_1 and M_2. *Piliocolobus* and *Procolobus* have significantly higher scores on PC2 than *Colobus* (Table 4). The Asbole colobines

TABLE 4. — Results of the statistical tests of the dental and symphyseal PCA.

	Multivariate Normality (Shapiro-Wilk multivariate extension)	Homogeneity of covariance	Model (MANOVA or Kruskal-Wallis)	Post-Hoc (Tukey HSD or Dunn)	p. val.
PCA Scores Dental	p. val. = 0.0013	p. val. = 0.023	MANOVA PC1	NA	–
			F val. = 0.47, p. val. = 0.63	–	–
				–	–
			MANOVA PC2	*Piliocolobus-Colobus*	< 0.001
			F val. = 38.6, p. val. < 0.001	*Piliocolobus-Procolobus*	< 0.05
				Procolobus-Colobus	< 0.001
				–	–
			MANOVA PC3	*Piliocolobus-Colobus*	–
			F val. = 14.8, p. val. < 0.001	*Piliocolobus-Procolobus*	< 0.05
				Procolobus-Colobus	< 0.001
PCA Scores Symphysis	p. val. < 0.001	p. val. = 0.07	PERMANOVA PC1	*Piliocolobus-Colobus*	< 0.001
			X^2 = 68, p. val. < 0.001	*Piliocolobus-Procolobus*	< 0.05
				Procolobus-Colobus	< 0.001
				–	–
			PERMANOVA PC2	*Piliocolobus-Colobus*	< 0.001
			X^2 = 61, p. val. < 0.001	*Piliocolobus-Procolobus*	< 0.001
				Procolobus-Colobus	< 0.01
				–	–
			PERMANOVA PC3	NA	–
			X^2 = 0.1, p. val. = 0.7	–	–

TABLE 5. — Posterior probabilities of the Asbole specimens belonging to each extant Colobini genera, based on dental PCA scores.

Specimen	Taxon	*Colobus*	*Piliocolobus*	*Procolobus*
ASB-80	*Colobus* sp. indet.	38%	58%	4%
ASB-100-1		67%	14%	33%
ASB-232-6		35%	60%	5%

TABLE 6. — Descriptive statistics, per genus, for the symphyseal ratio and raw symphyseal measurement with standard deviation given in brackets.

	Formula	Descriptive statistics	
Torus transverse breadth differential	STT breadth/ ITT breadth	*Colobus*	1.61 (0.25)
		Piliocolobus	1.14 (0.14)
		Procolobus	1.25 (0.27)
		Asbole	1.30 (0.05)
Symphyseal angulation	Raw data	*Colobus*	46.88 (3.66)
		Piliocolobus	44.06 (3.15)
		Procolobus	48.10 (4.82)
		Asbole	49.75 (3.13)

have negative scores on PC1 and, apart from ASB-100-1, positive scores on PC2, hence better conforming with the *Piliocolobus* – *Procolobus* pattern on PC2 (Fig. 4). Discrimination between extant taxa is observed on PC2 with no overlap in interquartile ranges, underlining the phenetic affinity of the fossil ASB-100-1 with *Colobus* given its inclusion in the interquartile range of *Colobus* on PC2. However, none of the Asbole colobines are outside the range of variation of any extant Colobini. PC3, accounting for *c.* 11% of the variance, distinguishes *Procolobus* from *Piliocolobus* and *Colobus*. The positive scores of *Procolobus* can be explained by the mesial and distal breadth of M_3 and the distal breadth of M_2. While ASB-100-1 and ASB-80 correspond to the interquartile range of *Piliocolobus* and *Colobus*, ASB-232-6 aligns with the interquartile range of *Procolobus*, although it remains within the range of variation of all extant Colobini.

LDA of dental dimensions

Colobus can be distinguished from *Procolobus* and *Piliocolobus* based on its positive scores on LD1 (Fig. 5). The positive scores of *Procolobus* on LD2 distinguish it from *Piliocolobus*. While ASB-232-6 and ASB-80 show a combination of negative LD1 scores and positive LD2 scores like *Piliocolobus*, ASB-100-1 has a null LD1 score and negative LD2 score more similar to *Colobus* (Fig. 5). According to the jackknife analysis, dental dimensions correctly classify the generic attribution of 71% of the extant specimens randomly included in the training dataset. Classification for the fossil specimens ASB-80, ASB-100-1 and ASB-232-6 are ambiguous and does not go over 67% of posterior probability (Table 5). However, it permits to highlight that ASB-100-1 has a greater phenetic affinity with *Colobus*, with a posterior probability of 67%, than with *Procolobus* and *Piliocolobus*, a view consistent with its negative scores on PC2. On the contrary, ASB-80 has a posterior probability of 62% to belong to the *Procolobus-Piliocolobus* while ASB-232-6 has a posterior probability of 65% (Table 5).

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Breadth differential of the transverse tori: The differences in breadth between the STT and ITT differentiate extant Colobini, with *Piliocolobus* and *Procolobus* having tori of nearly equal breadth, and hence a significantly lower index compared to the marked breadth differential of the transverse tori of

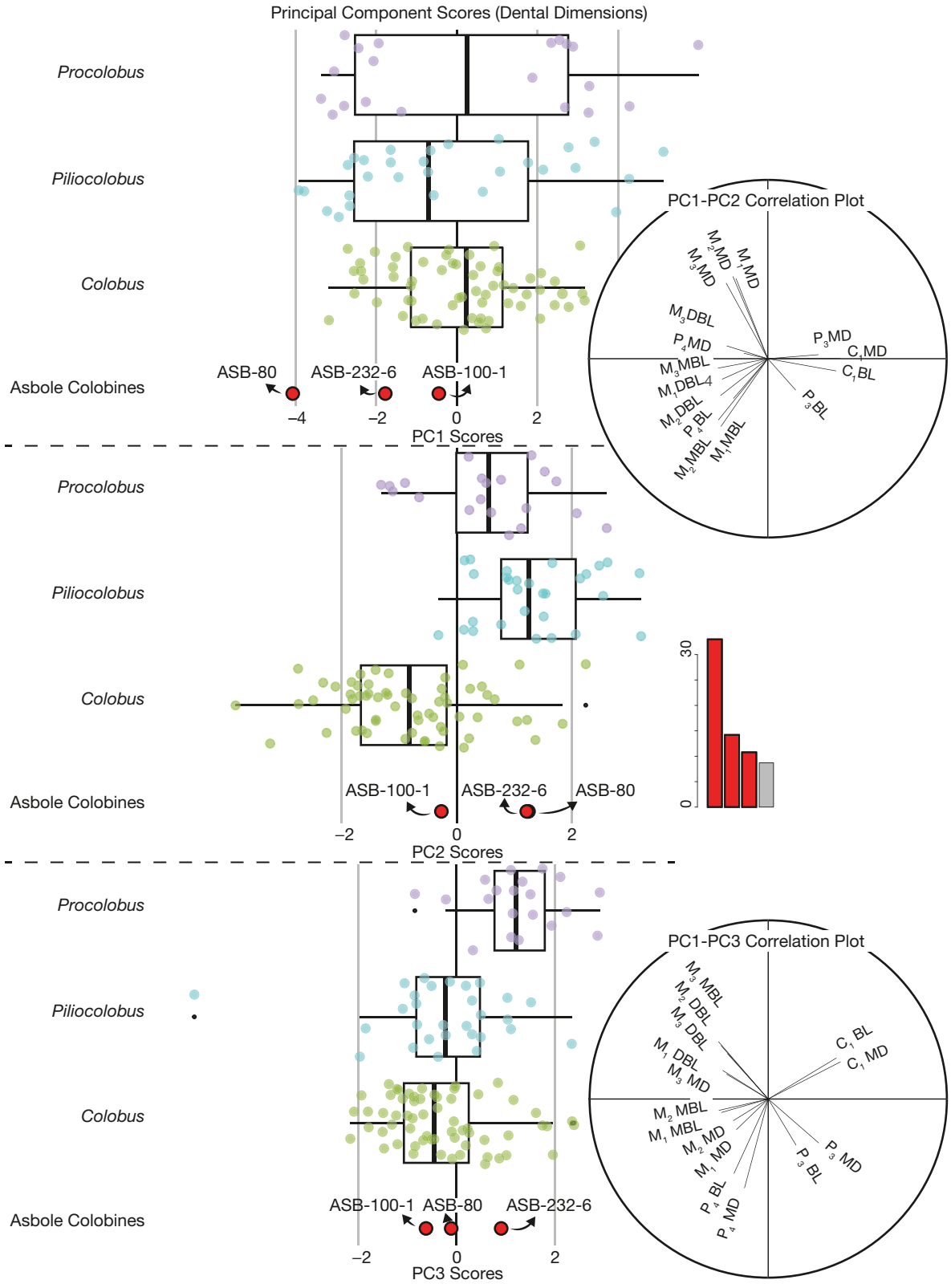

FIG. 4. — Boxplots of PC1 scores on the left panel and PC2 scores on the right panel of the PCA established on dental dimensions. A barplot illustrating the relative contribution of the first four PCs, in %, to the total variance is given on the central panel, along with a correlation circle for the PC1-PC2 biplot. Illustrations: Laurent Pallas.

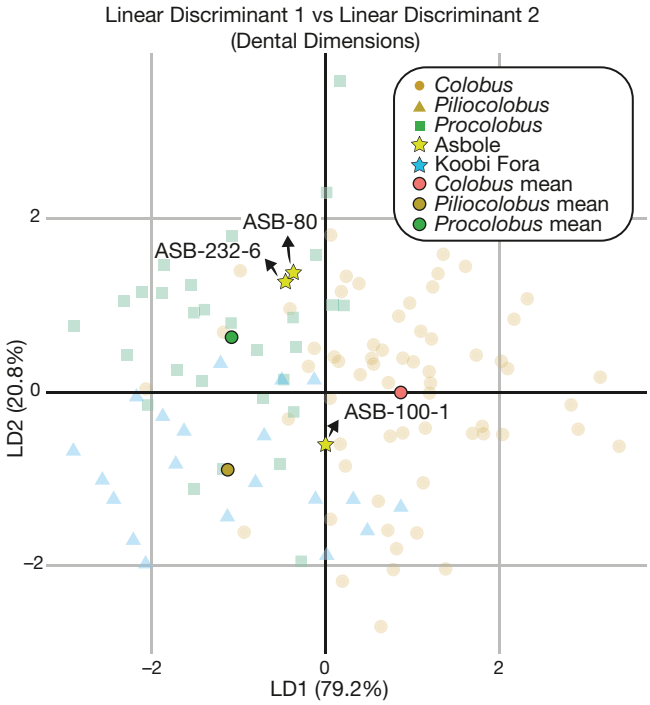

Fig. 5. — Biplot of the LD1-LD2 scores of the LDA established on PC scores of the dental dimensions. Illustration: Laurent Pallas.

Colobus (Fig. 6A, Table 6 and Table 3). The Asbole colobines occupy an intermediate position, falling in the third quartile of *Piliocolobus* and first quartile of *Colobus*. However, they fall in the interquartile range of variation of *Procolobus*.

Symphyseal angulation: The symphysis of *Piliocolobus* is significantly more inclined than that of *Colobus* and *Procolobus* (Fig. 6B, Table 3 and Table 6). Apart from the obtuse symphysis of ASB-100-1, all other Asbole colobines have an inclination of the symphysis fitting with the interquartile range of variation of *Procolobus* and *Colobus*.

PCA of symphyseal dimensions

PC1 and PC2 account for 75% of the variance (Fig. 7). Positive scores on PC1 are influenced by the breadth of the STT, the length of the planum alveolare and the length of the symphysis while negative scores are due to the breadth of the ITT and angulation of the symphysis. Positive scores on PC2 are influenced by the length of the symphysis and breadth of the ITT whereas negative scores are due to the angulation of the symphysis. All Colobini genera can be significantly discriminated on PC1 scores, with positive scores for *Colobus*, slightly negative scores for *Piliocolobus* and highly negative scores for *Procolobus* (Fig. 7 and Table 4). Similarly, Colobini genera can be significantly discriminated on PC2 scores with *Piliocolobus* having positive scores, *Colobus* slightly negative scores and *Procolobus* lower scores relative to *Colobus*. Asbole colobines present an intermediate position on PC1, with ASB-100-1, ASB-232-6 and ASB-215-2 having negative scores like *Piliocolobus*, and ASB-94-1 a positive score like *Colobus* (Fig. 7). Asbole colobines better conforms with *Colobus* on PC2 with ASB-100-1, ASB-251-2 and ASB-232-6 showing slightly negative scores falling in the interquartile range of the former.

Table 7. — Posterior probabilities of the Asbole specimens belonging to each extant Colobini genera, based on symphyseal PCA scores.

Specimen	Taxon	*Colobus*	*Piliocolobus*	*Procolobus*
ASB-232-6	*Colobus* sp. indet.	31%	51%	18%
ASB-215-2		51%	41%	8%
ASB-94-1		53%	46%	1%
ASB-100-1		58%	35%	7%

LDA of symphyseal dimensions

On the LD1-LD2 biplot, *Colobus* specimens are typified by negative LD1 scores and positive LD2 scores, contrasting with the positive LD1 scores and negative LD2 scores of *Piliocolobus* (Fig. 8).

The jackknife analysis drawn from the symphyseal dimensions correctly classified the generic attribution of 92% of the extant specimens included in the training dataset. ASB-232-6 has a posterior probability of 69% to belong to the *Procolobus-Piliocolobus* clade while ASB-100-1 has a posterior probability of 58% to belong to *Colobus* (Table 7). These results contrast with the more ambiguous generic attribution of ASB-215-2 and ASB-94-1 which have posterior probabilities of 51% and 53%, respectively, to belong to the genus *Colobus* (Table 7).

Univariate and multivariate analyses of the mandibular corpus

Taxonomic discrimination based on corpus shape: PC1 and PC2 account for 72% of the variance (Fig. 9). *Colobus* and *Procolobus* shows, on average, slightly negative scores on PC1 compared to the slightly positive scores of *Piliocolobus*. On PC2, *Colobus* has, on average, slightly negative scores, and contrast with the slightly positive scores of *Piliocolobus* and *Procolobus* (Table 8). Shape changes along PC1 (Fig. 9) are explained by an overall gracility of the corpus (high and thin in contrast to short and broad) from low scores (gracile corpus) to positive scores (robust corpus). Shape changes along PC2 (Fig. 9) rather reflects the development of the lateral prominences (positive scores) and the development of the submandibular fossa (negative scores). On PC1, the Asbole colobines have greatly (e.g., ASB-232-6) or slightly positive scores (e.g., ASB-25-6), hence better conforming with the *Piliocolobus-Procolobus* mean scores and its robust corpus (Fig. 9). A similar observation can be made for KNM-ER 6025. On PC2, the Asbole colobines also have greatly (e.g., ASB-80) or slightly (e.g., ASB-25-6) positive scores. KNM-ER 6025 has the highest positive scores of all the fossil colobines on PC2. Overall, the positive scores of the Asbole specimens and KNM-ER 6025 on PC2 demonstrate their enlarged lateral prominences, like *Piliocolobus-Procolobus* but distinct from *Colobus* (Fig. 9).

Sexual dimorphism of the corpus shape

Sexual dimorphism, as expressed by significant differences in PC scores, is not visible on PC1 scores although female *Piliocolobus* are significantly distinct from both male and female *Colobus* and male *Procolobus* are significantly distinct from male and female *Piliocolobus* (Table 8). Sexual dimorphism is significant on PC2 scores for *Colobus*, with significantly

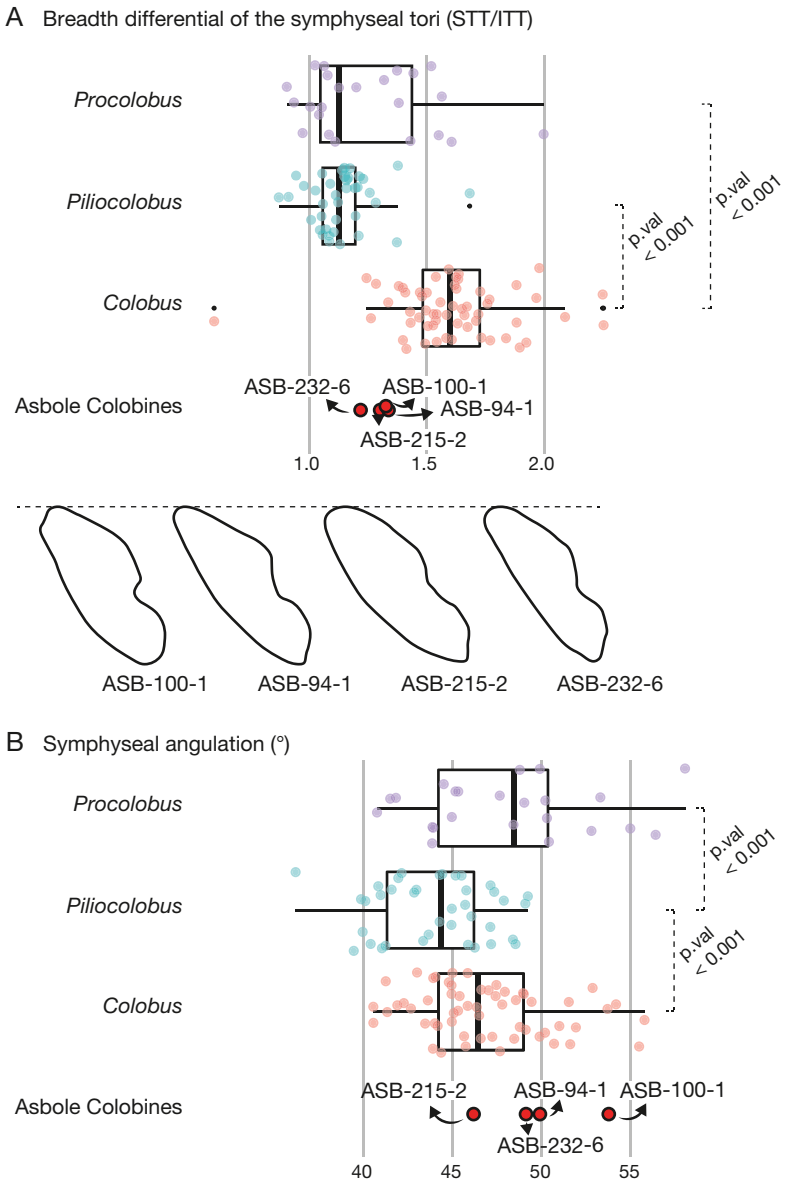

FIG. 6. — **A**, Boxplots of the breadth differential of the symphyseal tori of extant and fossil colobines; **B**, boxplots of the symphyseal angulation of extant and fossil colobines. All boxplots with median (**black bar**), outliers (**black dot**), first quartile and third quartile. Outlines of the symphysis of the Asbole colobines are given in the central panel. Illustrations: Laurent Pallas.

lower PC2 scores for females compared to males. Negative PC2 in female *Colobus* is associated with poorly developed lateral prominences and larger submandibular fossa compared to males. In contrast, no significant sexual dimorphism was detected for *Piliocolobus* and *Procolobus.* On PC2, male *Colobus* and *Procolobus* show higher scores than female specimens. On PC2, the Asbole and Koobi Fora colobines have positive scores and are above the interquartile range of variation of female *Colobus* but are still within the range of variation of male *Colobus* (Fig. 10). ASB-80 and ASB-232-6 were considered as female *Colobus* by Frost & Alemseged (2007), presumably based on canine size, but they are outside the range of variation of female *Colobus* on PC2 scores but fall in the third quartile range of female *Piliocolobus*.

LDA of corpus shape

Colobus shows negative LD1 scores and null LD2 scores distinct from the positive LD1 scores and more negative LD2 scores of *Piliocolobus* (Fig. 9).

The jackknife analysis drawn from the corpus shape correctly classified the generic attribution of 76% of the extant specimens included in the training dataset. Posterior probability of belonging to *Colobus* is high and above 75% for ASB-100-1, ASB-259, and ASB-254 (Table 9). In contrast, posterior probability of belonging to the *Piliocolobus-Procolobus* clade is high for KNM-ER 6025 with a value of 74% (addition of the posterior probability obtained for *Procolobus* and *Piliocolobus*). Other Asbole specimens show posterior probability inferior to 75% and are thus treated as ambiguous (Table 9).

TABLE 8. — Results of the statistical tests of the corpus shape PCA Scores Corpus (PC1+PC2+PC3 ~ Sex*Genera).

Multivariate Normality (Shapiro-Wilk multivariate extension)	Homogeneity of covariance	Model (MANOVA or Kruskal-Wallis)	Post-Hoc (Tukey HSD or Dunn)	p. val.
p. val. = 0.06	p. val. = 0.7	**MANOVA PC1**	–	–
		Sex F val. = 3.38, p. val. = 0.07	–	–
		Genera F val. = 8.62, p. val. < 0.001	*Piliocolobus*-*Colobus*	< 0.001
			Procolobus-*Colobus*	= 1
			Procolobus-*Piliocolobus*	< 0.01
		Sex*Genera F val. = 2.67, p. val. = 0.07	F *Piliocolobus*-F *Colobus*	= 0.03
			F *Piliocolobus*-M *Colobus*	= 0.01
			M *Procolobus*-F *Piliocolobus*	< 0.01
			M *Procolobus*-M *Piliocolobus*	= 0.01
		MANOVA PC2	–	–
		Sex F val. = 28.19, p. val. < 0.001	–	–
		Genera F val. = 19.60, p. val. < 0.001	*Piliocolobus*-*Colobus*	< 0.001
			Procolobus-*Colobus*	< 0.001
			Procolobus-*Piliocolobus*	= 0.96
		Sex*Genera F val. = 0.67, p. val. = 0.5	M *Colobus*-F *Colobus*	< 0.001
			M *Piliocolobus*-F *Piliocolobus*	= 0.7
			M *Procolobus*-F *Procolobus*	= 0.09
			F *Piliocolobus*-F *Colobus*	< 0.001
			M *Piliocolobus*-F *Colobus*	< 0.001
			M *Procolobus*-F *Colobus*	< 0.001
			M *Piliocolobus*-M *Colobus*	< 0.05
			M *Procolobus*-M *Colobus*	< 0.05
		MANOVA PC3	–	–
		Sex F val. = 0, p. val. = 1	–	–
		Genera F val. = 1.62, p. val. = 0.20	–	–
		Sex*Genera F val. = 2.67, p. val. = 0.13	–	–

Bootstrap analysis on corpus shape

The coefficient of variation of PC1 and PC2 scores of the Asbole sample and of the combined Asbole and Koobi Fora (i.e., KNM-ER 6025) sample never exceed that of any extant Colobini genera, demonstrating that, given corpus shape, they could be part of the same genus and that the sample from Asbole can be accommodated in one genus (Appendix 4).

Bootstrap analysis on the superoinferior dimension of the corpus at mid-M_1

When the Asbole specimens are considered as a single taxon, its coefficient of variation for corpus depth at mid-M_1 never significantly exceeds that of the seven considered extant Colobini species (Appendix 5). Similarly, when the coefficient of variation of the combined Asbole, Faro Daba and Koobi Fora sample is compared with that of the seven considered extant Colobini species, it does not significantly exceed it.

Hierarchical clustering

The hierarchical clustering including all Asbole specimens in a single taxon demonstrates that it is phenetically more like *Piliocolobus* than to *Procolobus* and *Colobus* (Fig. 11A). The mean values of the PC1 scores of the dental PCA and the PC3 scores of the symphyseal PCA of the Asbole colobines are quite unlike that of extant Colobini, but all other PC scores, especially those of the corpus PCA are consistent with those of *Piliocolobus*. When PC scores of the dental dimensions, symphyseal dimensions and corpus shape of ASB-232-6 and ASB-100-1 are considered distinctly in the hierarchical clustering analysis, it gave a distinct result, with ASB-232-6 as the sister taxon to *Piliocolobus* and ASB-100-1 as close to *Colobus* (Fig. 11A). The main differences between ASB-232-6 and ASB-100-1 are observed in the PC1 dental and PC3 symphyseal scores. ASB-100-1 is phenetically closer to *Colobus* on the PC1 and PC2 dental scores while ASB-232-6 is closer to *Piliocolobus* on the PC1 and PC3 symphyseal scores. When only corpus and dental data are considered, ASB-80 and ASB-232-6 are recovered as sister taxon to all other extant taxa. ASB-100-1 is nested within extant taxa but is clustered with *Procolobus* instead of *Colobus*. While ASB-100-1 is similar to extant Colobini in PC1 dental score, ASB-80 and ASB-232-6 are quite distinct from them.

Summary of the taxonomic attribution of the Asbole colobines

Overall, the hierarchical clustering established on dental, corpus, and symphyseal shape demonstrated that the Asbole colobines, when considered as a single population, are phenetically closer to *Piliocolobus* than to other extant Colobini genera (Fig. 11A). When the total evidence pattern (teeth, symphysis, and corpus) is considered for ASB-100-1 and ASB-232-6, it demonstrates the affinity of the former with *Colobus* and the affinity of the latter with *Piliocolobus*. When only the dental and corpus evidence are considered, a different result is reached, with ASB-80 as the sister taxon to ASB-232-6 outside of a cluster encompassing extant Colobini and ASB-100-1.

Regarding specific results obtained for morphometric ratios and discriminative analyses, the breadth differential

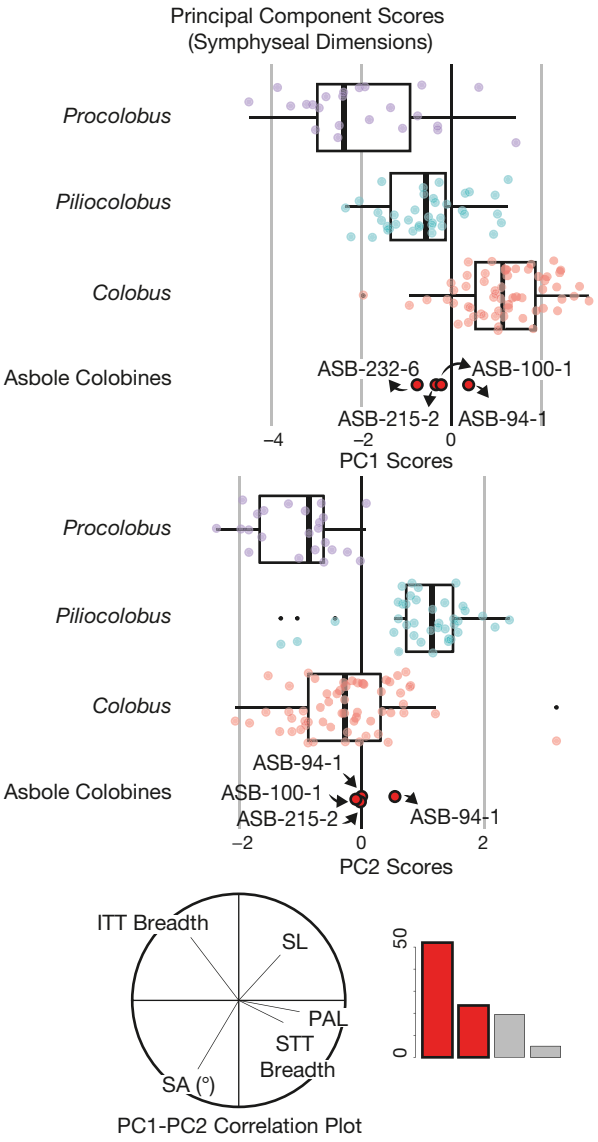

FIG. 7. — Boxplots of PC1 scores on the upper panel and PC2 scores on the lower panel of the PCA established on symphyseal dimensions. A barplot illustrating the relative contribution of the first four PCs, in %, to the total variance is given on the central panel, along with a correlation circle for the PC1-PC2 biplot. Illustrations: Laurent Pallas.

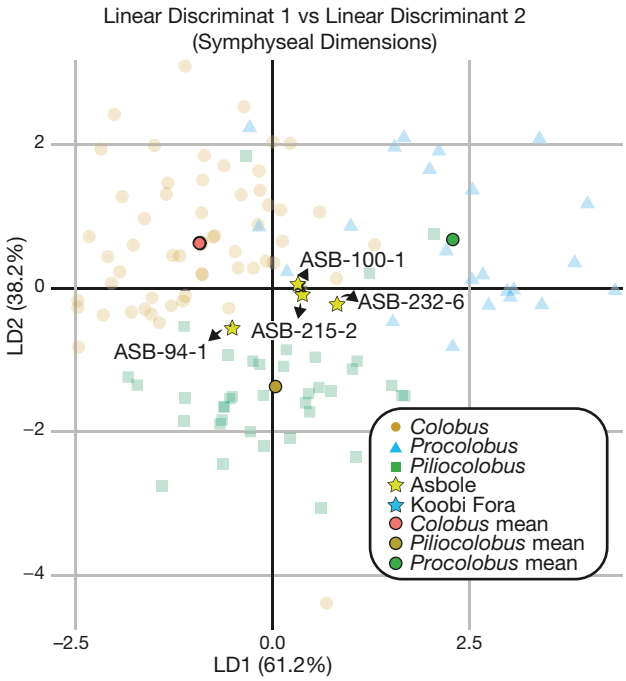

FIG. 8. — Biplot of the LD1-LD2 scores of the LDA established on PC scores of the symphyseal dimensions. Illustrations: Laurent Pallas.

TABLE 9. — Posterior probabilities of the Asbole specimens belonging to each extant Colobini genera based on corpus shape PCA scores.

		Colobus	*Piliocolobus*	*Procolobus*
KNM-ER 6025	*Colobus freedmani*	25%	50%	24%
ASB-100-1	*Colobus* sp. indet.	80%	7%	13%
ASB-232-6		53%	23%	24%
ASB-25-6		36%	42%	21%
ASB-254		77%	9%	14%
ASB-259		78%	11%	10%
ASB-80		59%	13%	28%

of the transverse tori of ASB-232-6 is more like *Procolobus* and *Piliocolobus* than *Colobus*, whereas the morphology of specimens ASB-94-1 and ASB-215-2 is less easily attributable to any extant Colobini taxa (Figs 6A; 11B; Table 10). In addition, the linear discriminant analysis established on symphyseal dimensions showed that ASB-232-6 has a high phenetic affinity with the *Procolobus-Piliocolobus* clade (Fig. 8). This result is consistent with the dental linear discriminant analysis which demonstrated that ASB-232-6 is classified as a member of the *Procolobus-Piliocolobus* clade, notably by showing a relatively long M_3 and a small P_4 (Figs 5; 11B; Table 10). However, the classification of the corpus shape of ASB-232-6 is more ambiguous and not as clear-cut as that of the symphysis. Similarities in classification results between dental dimensions and corpus shape is also observed for ASB-100-1, which is more similar to *Colobus* than to *Procolobus-Piliocolobus*. ASB-80 has a corpus like *Colobus* but a dentition more similar to *Procolobus-Piliocolobus* (Table 10). Classification results for the corpus shape indicate that ASB-259 and ASB-254 are more like *Colobus* while ASB-25-6 is more similar to *Piliocolobus-Procolobus*. As for ASB-232-6 (Fig. 11B), the specimen ASB-25-6 has a relatively long M_3 and a small P_4 similar to *Piliocolobus-Procolobus*, supporting its greater phenetic affinity with *Piliocolobus* and *Procolobus*. The *Colobus*-like corpus of ASB-259 is also consistent with its relatively large P_4 and short M_3, features more consistent with an allocation to *Colobus* than to *Piliocolobus* or *Procolobus*. Although ASB-232-6 and ASB-25-6 correspond well to representatives of the *Piliocolobus-Procolobus* clade for most of the traits studied, they still lack the median mental foramen typical of *Procolobus*, and for ASB-232-6, the elongated canine typical of *Procolobus*, hence supporting an assignment to *Piliocolobus*.

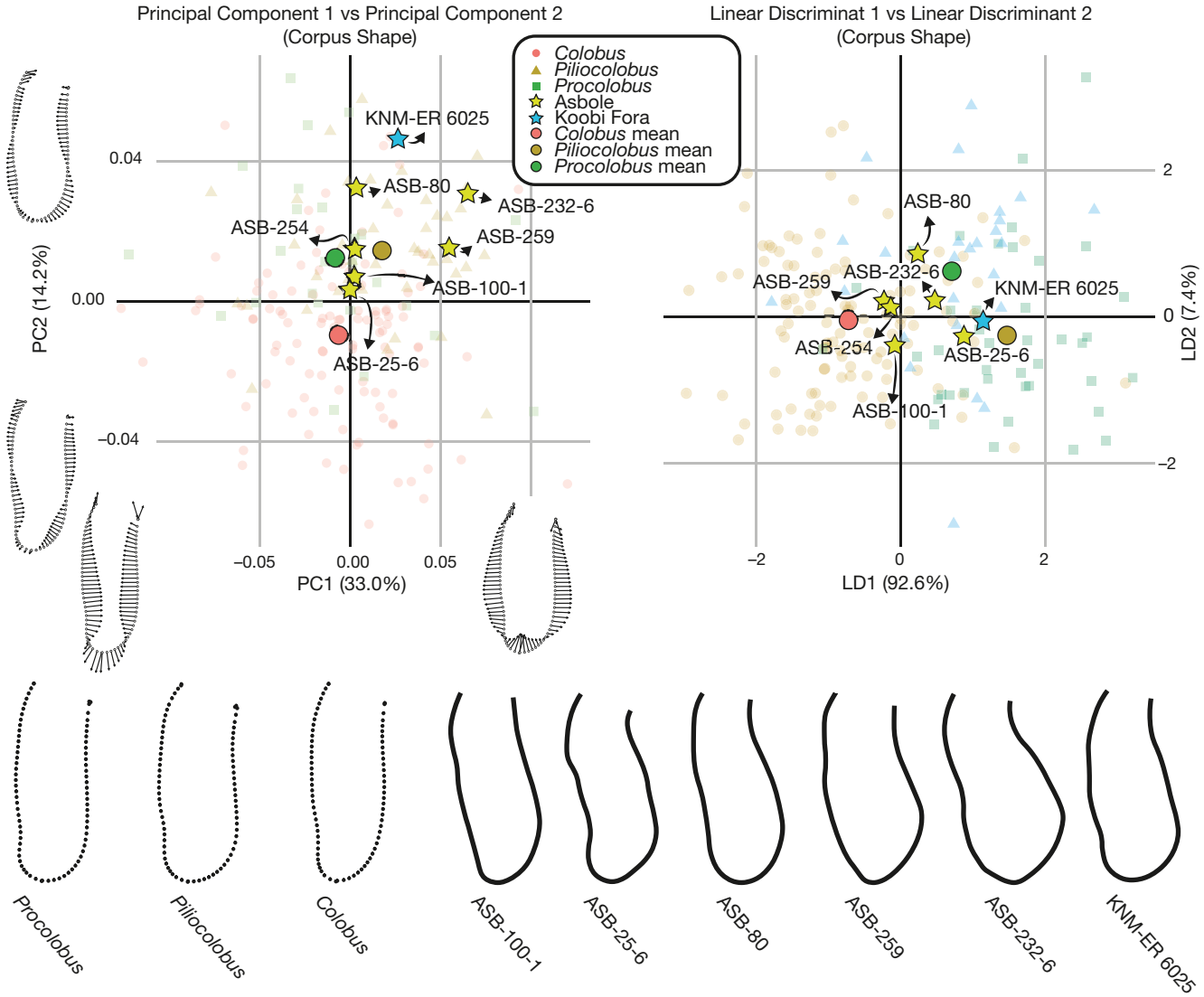

FIG. 9. — Biplot of the PC1-PC2 scores of the PCA established on aligned Procrustes coordinates of the corpus on the left panel. Shape changes associated with PC scores are given at the extrema of each PC axis. On the left panel, a biplot of the LD1-LD2 scores of the LDA established on PC scores of the corpus shape is given. On the lower panel, the mean shape of extant Colobini is given next to the corpus outline of fossil colobines discussed in the text. Illustrations: Laurent Pallas.

TABLE 10. — Summary table of the phenetic affinities of the considered Koobi Fora and Asbole colobines given each analysis. The rationale for assigning a specimen to a particular taxon is based on the absolute difference between the quantitative value of the specimen to the mean value of *Colobus* or *Piliocolobus*/*Procolobus*. Abbreviations: **C**, *Colobus*-like; **P**, *Piliocolobus*-like.

		KNM-ER 3065	ASB-100-1	ASB-232-6	ASB-25-6	ASB-254	ASB-259	ASB-80	ASB-215-2	ASB-94-1
Dental	Relative lower canine elongation	NA	C	P	NA	P	NA	C	C	NA
	P_4 area/M_1 area	P	C	P	P	P	C	P	P	NA
	Relative length of the M_3	NA	C	P	P	NA	P	P	NA	NA
	LDA on dental dimensions	NA	C	P	NA	NA	NA	P	NA	NA
Symphyseal	Breadth differential of the symphyseal tori	NA	P	P	NA	NA	NA	NA	P	P
	LDA on symphyseal dimensions	NA	C	P	NA	NA	NA	NA	C	C
Corpus	LDA on corpus shape	P	C	C	P	C	C	C	NA	NA

DISCUSSION

A reassessment of the taxonomy of *Colobus freedmani*

This study demonstrated that the relatively small P_4 and the corpus shape of *Co. freedmani* KNM-ER 6025 resemble *Piliocolobus* and *Procolobus* more than *Colobus*, although the fossil specimen still falls within the range of variation of extant *Colobus*. The initial justification for including KNM-ER 6025 to *Colobus* is dubious, as no traits clearly supporting its inclusion are provided in the original description of Jablonski & Leakey (2008). Sexual dimorphism in the development of the lateral prominences was advocated to explain the differences observed between the holotype of *Co. freedmani* (i.e., the damaged female mandible KNM-ER 44224) with the partial male mandible KNM-ER 6025 (Jablonski & Leakey 2008). The development of the lateral prominences of the corpus is indeed sexually dimorphic in extant *Colobus* as shown on the PC2 scores of the corpus outline analysis, but a trend (non-significant) for sexually dimorphic lateral prominences is also observed for *Procolobus verus*, demonstrating that this dimorphic pattern in corpus shape is not unique to *Colobus*. It was further hypothesized that *Co. freedmani* was more sexually dimorphic than extant *Colobus* in corpus shape to accommodate KNM-ER 6025 in the hypodigm of *Co. freedmani*. Unfortunately, no adequately preserved *Colobus* female specimens from Koobi Fora could have been integrated in our morphometric analysis to fully test this hypothesis. Moreover, assessing a level of dimorphism in a fossil population requires an extensive fossil sample and the Koobi Fora sample is currently too limited to test this hypothesis.

KNM-ER 6025 is an outlying specimen when compared to the range of variation of *Colobus* in corpus shape and its P_4 area/M_1 area ratio is also more consistent with that of *Piliocolobus-Procolobus* than with that of *Colobus*. Our data hence favor, on quantitative grounds, an attribution to the *Piliocolobus-Procolobus* clade for KNM-ER 6025 rather than to a male *Co. freedmani*, supporting the initial hypothesis of Frost & Alemseged (2007). However, the hypothesis that two distinct taxa occur at Koobi Fora cannot be rejected given the low number of mandibular specimens available, with one taxon attributable to *Colobus* (the female mandible KNM-ER 44224) and another one to *Piliocolobus* – *Procolobus* (KNM-ER 6025). The humerofemoral proportion (i.e., humeral length over femoral length) of the partial female *Co. freedmani* skeleton KNM-ER 5896 is more akin to that of *Colobus* than to that of *Piliocolobus-Procolobus*, highlighting the ambiguity of the taxonomic homogeneity of the small colobines from the Okote - KBS members of Koobi Fora (Pallas, in prep.). Future discoveries of small-sized colobines in the Okote, KBS, and Chari members of Koobi Fora or in penecontemporaneous fossil deposits of the Turkana Basin will be of prime value on this aspect. A closer look at postcranial traits distinguishing *Piliocolobus* from *Colobus* will also add more evidence to answer this question.

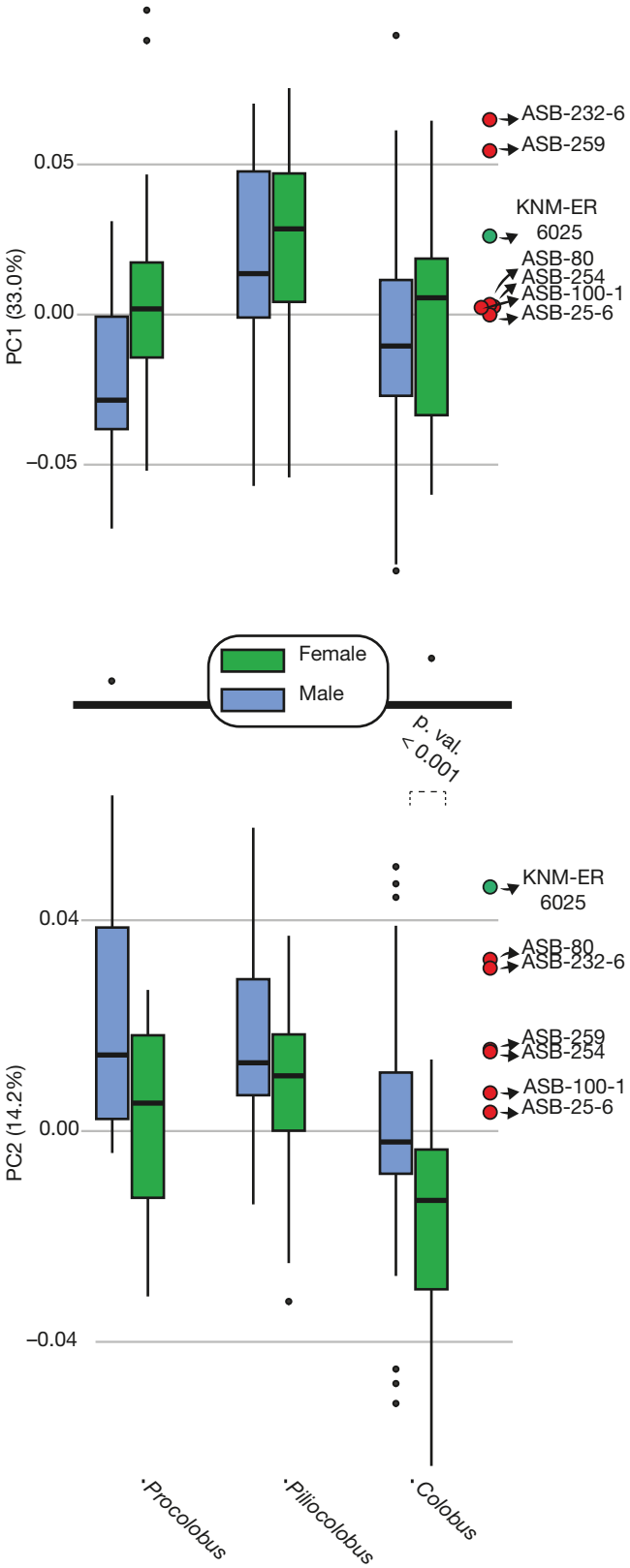

Fig. 10. — Boxplots of PC1 scores on the upper panel and PC2 scores on the lower panel of corpus shape per sex and genus. All boxplots with median (black bar), outliers (black dot), first quartile and third quartile. Illustrations: Laurent Pallas.

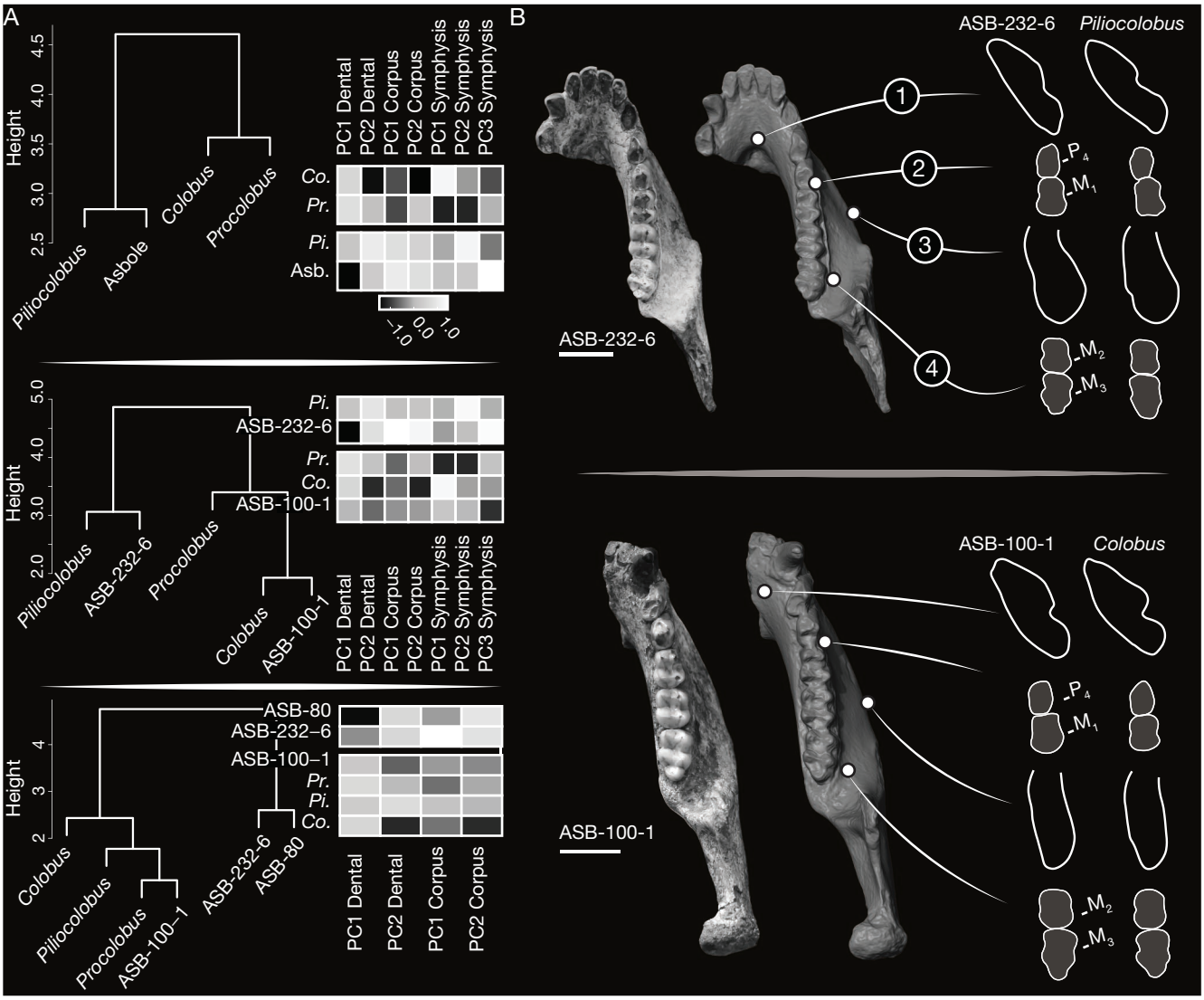

Fig. 11. — **A**, Dendrogram showing the results of the hierarchical clustering for the analysis taking into account Asbole specimens as a single OTU (**upper dendrogram**), taking into account dental, symphyseal, and corpus PCA scores of extant Colobini and the fossil ASB-232-6 and ASB-100-1 (**middle dendrogram**), and taking into account dental and corpus PCA scores of extant Colobini and the fossil ASB-232-6, ASB-100-1, and ASB-80; **B**, photographs and 3D generated surfaces of ASB-232-6 and ASB-100-1. ASB-232-6 is compared with *Piliocolobus* Rochebrune, 1877 and ASB-100-1 is compared with *Colobus* Illiger, 1811 on four traits: **1**, symphyseal outlines of fossil specimens compared with *Piliocolobus* and *Colobus*; **2**, outlines of P_4 and M_1 of fossil specimens compared with *Piliocolobus* and *Colobus*; **3**, corpus outlines of fossil specimens compared with *Piliocolobus* and *Colobus*; **4**, outlines of M_2 and M_3 of fossil specimens compared with *Piliocolobus* and *Colobus*. Scale bars: 10 mm. Illustration and photos: Laurent Pallas.

A reassessment of the taxonomy of *Colobus* from Asbole

Morphological similarities between the Asbole colobine specimens ASB-232-6 and ASB-256 with *Piliocolobus-Procolobus* and between ASB-100-1 and ASB-259 with *Colobus*, support their taxonomic allocation to the *Piliocolobus-Procolobus* clade and the *Colobus* clade, respectively.

Frost & Alemseged (2007) dismissed the attribution of *Piliocolobus* for the Asbole colobines based on the following traits : presence of infraorbital foramina of small diameters (foramina are larger in *Piliocolobus*), absence of maxillary fossae and ridges (present in *Piliocolobus*), gracile supraorbital tori (developed tori in male *Piliocolobus*), low and broad choanae (narrower in *Piliocolobus*), lack of a sagittal crest (present in male *Piliocolobus*), lack of a perforated pterygoid fossa (perforated fossae in *Piliocolobus*), deep mandibular corpus with expanded gonial area (shallower corpus in *Piliocolobus*), and absence of a median mental foramen (present in *Procolobus* but absent in *Piliocolobus*). In contrast, mandibular specimens of Asbole align with *Piliocolobus-Procolobus* and *Colobus* based on dental, corpus and symphyseal shape. Specifically, ASB-232-6 and ASB-25-6 support the presence of a colobine more similar to *Piliocolobus-Procolobus* at Asbole while ASB-100-1 and ASB-259 support the initial taxonomic hypothesis of Frost & Alemseged (2007). The bootstrap

analysis computed based on the PC scores of the corpus shape and superoinferior dimension of the corpus at mid-M_1 failed to demonstrate that the variation of the Asbole sample exceeds that of any extant Colobini genera, supporting the presence of a single taxon at Asbole. However, the combined dental, corpus, and symphysis evidence still provide support for the presence of a small colobine more like *Piliocolobus-Procolobus* than *Colobus*. Our data are also consistent with and complement those of Brasil *et al.* (2023) which demonstrated that the breadth - length proportions of the M_2 of the Asbole sample is more similar to *Piliocolobus* and that the length of the P_4 is greatly reduced compared to the length of the M_1, a result consistent with our P_4 area/M_1 area ratio. The hierarchical clustering based on PC scores of dental, symphysis, and corpus analyses also showed that ASB-232-6 has phenetic similarities with *Piliocolobus*.

To accommodate the observations of Frost & Alemseged (2007) on the cranial and maxillary specimens from Asbole and to account for the phenetic affinity of several mandibular specimens with *Colobus* (e.g., ASB 100-1), this study partly supports the hypothesis that two taxa occur at Asbole with affinities to *Piliocolobus-Procolobus* on one side and *Colobus* on the other side. Given that the present study is limited to mandibular remains, these taxa are not named, but it supports an inclusion of ASB-232-6 and ASB-25-6 to cf. *Piliocolobus* sp. indet., as previously suggested (Alemseged & Geraads 2000), but their precise taxonomic designation awaits additional postcranial and cranial quantitative evidence. Unfortunately, the association of the female maxilla ASB-204A and mandible ASB-204B as well as the male maxilla and mandible ASB-207-1A and ASB-207-1B is not clearly asserted in Frost & Alemseged (2007) and most of the specimens presented in the initial study are unprepared, leaving several anatomical characteristics unknown. Future discoveries of securely associated cranial and mandibular elements will provide decisive insights into the taxonomic conundrum of the Asbole colobines.

Conclusively, the recognition of a fossil taxon similar to *Piliocolobus-Procolobus* in mandibular anatomy in Asbole is consistent with our conclusion regarding the KNM-ER 6025 mandible from Koobi Fora. The Colobini taxonomic diversity highlighted here at Asbole and Koobi Fora has implications on our understanding of the emergence of extant African colobine genera.

The emergence of extant African colobine genera in the fossil record

It has been suggested that the *Colobus* sample from Asbole was ancestral to that from Faro Daba, implying population continuity between the *c.* 600 Ka *Colobus* population from Asbole and the *c.* 100 Ka *Colobus* population from Faro Daba (Brasil *et al.* 2023). Brasil *et al.* (2023) showed that the marked sexual dimorphism of the Asbole colobines in canine dimensions was inconsistent with that of the *Colobus* cf. *guereza* from Faro Daba and from that of extant *Co. guereza* species, hence suggesting that sexual dimorphism in canine dimensions was marked in the stem *Co. guereza* lineage represented at Asbole. However the identification of specimens more similar to *Procolobus-Piliocolobus* than *Colobus* at Asbole does not support population continuity at the colobine community level as no *Piliocolobus-Procolobus* specimens are recorded at Faro Daba. However, *Colobus* specimens sampled at Asbole (ASB-100-1 and ASB-259) could be part of the *Co. guereza* lineage and should be part of further analysis and comparison with *Co. guereza*.

Extant eastern African *Piliocolobus* species are considered as relictual populations and currently confined to limited geographical ranges in Kenya, Zanzibar and Tanzania (Cardini & Elton 2009b). The identification of *c.* 1.5 Ma and *c.* 600 Ka Ma mandibles similar to *Piliocolobus* at Asbole and Koobi Fora demonstrate that the geographical range of *Piliocolobus* could once have been more expansive and extended into northern Ethiopia. Moreover, the bootstrap analysis established on corpus shape did not provide evidence for a distinct taxonomic designation between the Koobi Fora mandible KNM-ER 6065 and the Asbole sample, at least at the generic level. Future studies should investigate whether the specimens similar to *Piliocolobus* from Asbole and Koobi Fora represent extant *Piliocolobus* species, notably *Pi. gordonorum* Matschie, 1900, *Pi. rufomitratus* Peters, 1879 or *Pi. kirkii* Gray, 1868, and alternatively a new species of *Piliocolobus*.

A large hiatus is present in the fossil record of extant Colobini. According to molecular data, *Colobus* should be present in *c.* 8 Ma fossil deposits and members of the *Piliocolobus-Procolobus* clade should be sampled after *c.* 6 Ma. Prior to *Co. freedmani* (*c.* 1.5 Ma), there is no consensus regarding the identification of fossil Colobini. At species level, the western African *Colobus satanas* diverged molecularly from other *Colobus* species at *c.* 3.5 Ma. Molecular divergence dates between extant *Piliocolobus* species are more problematic but eastern African *Piliocolobus* (i.e., *Pi. rufomitratus*, *Pi. gordonorum*, and *Pi. kirkii*) are part of the same clade which diverged from a central and western African clade at *c.* 3.5 Ma. Considering putative temporal lag between morphological speciation and molecular speciation, we should expect to identify *Colobus* and *Piliocolobus* specimens in eastern Africa after 3.5 Ma. A reevaluation of fossil specimens similar in size to extant Colobini after 3.5 Ma is needed to test whether *Colobus* and *Piliocolobus* are novel eastern African immigrants that appeared during the Pleistocene, as suggested by molecular data, or if older lineages could be identified in the eastern African fossil record. Considering that Colobini are forest-dependent taxa, extension of the geographical ranges of Colobini in the fossil record should also be correlated to paleoenvironmental changes and should hence track extension and contraction of forest covers along the East African Rift system. The identification of extant Colobini in the fossil record and the reevaluation of the small colobine fossil record has hence strong paleoenvironmental and evolutionary implications.

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Appendix 1. — List of the extant and fossil specimens used in this study.

Genus/Acc. n°
Dental analysis
Colobus
SNSB-ZSM 1911 2465
SNSB-ZSM 1911 2469
SNSB-ZSM 1911 2475
SNSB-ZSM 1911 2477
SNSB-ZSM 1912 1549
SNSB-ZSM 1951 263
SNSB-ZSM AM1269
SNSB-ZSM AM1270
SNSB-ZSM 1904 1542
SNSB-ZSM 1904 1543
SNSB-ZSM 1911 2470
SNSB-ZSM 1911 2471
SNSB-ZSM 1911 2476
SNSB-ZSM 1913 1168
SNSB-ZSM 1914 839
SNSB-ZSM 1914 847
SNSB-ZSM 1904 1541
SNSB-ZSM 1900 573
SNSB-ZSM 1909 P1
SNSB-ZSM 1904 1544
MNHN-ZM-AC-1983-97
MNHN-ZM-MO-1885-891
MNHN-ZM-AC-1983-98
MNHN-ZM-2009-359
MNHN-ZM-AC-1954-54
MNHN-ZM-MO-1939-702
MNHN-ZM-MO-1962-1390
MNHN-ZM-2009-358
MNHN-ZM-MO-1970-450
MNHN-ZM-MO-1962-2102
MNHN-ZM-2009-346
MNHN-ZM-MO-1939-701
MNHN-ZM-MO-1908-43
MNHN-ZM-MO-1970-60
MNHN-ZM-MO-1970-59
MNHN-ZM-MO-1890-194
MNHN-ZM-MO-1893-5
MNHN-ZM-MO-1962-123
MNHN-ZM-MO-1897-1505
MNHN-ZM-MO-1969-389
MNHN-ZM-MO-1969-379
MNHN-ZM-MO-1969-382
MNHN-ZM-MO-1969-384
MNHN-ZM-AC-1897-132
MNHN-ZM-MO-1969-380
MNHN-ZM-MO-1962-1398
MNHN-ZM-MO-1969-387
MNHN-ZM-MO-1969-386
MNHN-ZM-AC-1983-37
MNHN-ZM-MO-1908-191
MNHN-ZM-MO-1964-1517
MNHN-ZM-MO-1892-1010
MNHN-ZM-MO-1904-1960
MNHN-ZM-MO-1963-294
MNHN-ZM-MO-1892-1009
MNHN-ZM-MO-1892-1011
MNHN-ZM-MO-1962-986
MNHN-ZM-2009-345
MNHN-ZM-MO-1970-396
MNHN-ZM-MO-1886-108
MNHN-ZM-MO-1964-1514
MNHN-ZM-MO-1974-133
MNHN-ZM-MO-1892-1007
Piliocolobus
KUPRI 10129#524
KUPRI 10127#524
KUPRI 10125#520
KUPRI 10124#519

Genus/Acc. n°
Dental analysis,
Piliocolobus (continuation)
KUPRI 10123#518
KUPRI 10122#517
KUPRI 10109#504
KUPRI 10115#510
KUPRI 10110#505
KUPRI 10112#505
KUPRI 10067#462
KUPRI 10183#4786
KUPRI 10070#465
KUPRI 10184#4787
KUPRI 10082#477
KUPRI 10052#447
KUPRI 10001#396
KUPRI 10095#490
KUPRI 10046#441
KUPRI 10188#4791
MNHN-ZM-MO-2002-103
MNHN-ZM-MO-1895-9
MNHN-ZM-MO-1939-705
MNHN-ZM-MO-1908-45BIS
MNHN-ZM-MO-1939-706
MNHN-ZM-2009-288
MNHN-ZM-MO-1890-193
MNHN-ZM-MO-1961-114
MNHN-ZM-MO-1884-1428
Procolobus
KUPRI 10053#388
KUPRI 10057#392
KUPRI 10055#390
KUPRI 10056#391
KUPRI 10052#387
KUPRI 10043#378
KUPRI 10045#380
KUPRI 10028#363
KUPRI 10029#364
KUPRI 10030#365
KUPRI 10051#386
KUPRI 10058#393
KUPRI 10060#395
KUPRI 10039#374
KUPRI 10038#373
KUPRI 10042#377
KUPRI 10041#376
KUPRI 10035#370
KUPRI 10011#346
KUPRI 10013#348
Corpus depth analysis
Colobus
MNHN-ZM-MO-1970-60
MNHN-ZM-MO-1970-59
MNHN-ZM-MO-1890-194
MNHN-ZM-MO-1893-5
MNHN-ZM-MO-1962-123
MNHN-ZM-MO-1897-1505
MNHN-ZM-MO-1970-62
RMCA 8107
RMCA 9392
RMCA 9409
RMCA 9673
RMCA 9675
RMCA 10547
RMCA 11475
RMCA 13600
RMCA 22408
RMCA 22410
RMCA 28554
RMCA 28561
RMCA 28107

Genus/Acc. n°
Corpus depth analysis
Colobus (continuation)
RMCA 28110
RMCA 28106
RMCA 28789
RMCA 28790
RMCA 33621
RMCA 987
RMCA 1041
RMCA 1241
RMCA 1231
RMCA 1838
RMCA 1839
RMCA 2221
RMCA 6000
RMCA 8317
RMCA 8319
RMCA 8352
RMCA 8528
RMCA 8609
RMCA 10226
RMCA 37593
RMCA 8310
RMCA 14671
RMCA 19062
RMCA 20437
RMCA 28398
RMCA 37590
RMCA M6
RMCA 9912
RMCA 2147
RMCA 2202
MNHN-ZM-MO-1969-389
MNHN-ZM-MO-1969-379
MNHN-ZM-MO-1969-382
MNHN-ZM-MO-1969-384
MNHN-ZM-MO-1969-380
MNHN-ZM-MO-1962-1398
MNHN-ZM-MO-1969-387
MNHN-ZM-MO-1969-386
MNHN-ZM-MO-1969-383
MNHN-ZM-MO-1969-378
MNHN-ZM-MO-1902-1318
MNHN-ZM-AC-1983-37
MNHN-ZM-MO-1908-191
MNHN-ZM-MO-1972-350
MNHN-ZM-MO-1972-348
MNHN-ZM-AC-1897-132
RMCA 2800
MNHN-ZM-MO-1964-1517
MNHN-ZM-MO-1892-1010
MNHN-ZM-MO-1904-1960
MNHN-ZM-MO-1963-294
MNHN-ZM-MO-1892-1009
MNHN-ZM-MO-1892-1011
MNHN-ZM-MO-1962-986
MNHN-ZM-2009-345
MNHN-ZM-MO-1970-396
MNHN-ZM-MO-1886-108
MNHN-ZM-MO-1964-1514
MNHN-ZM-MO-1974-133
MNHN-ZM-MO-1892-1007
RMCA 2884
RMCA 3320
RMCA 3401
RMCA 3412
RMCA 5480
RMCA 5896
RMCA 8404
RMCA 8411
RMCA 8415

Genus/Acc. n°
Corpus depth analysis
Colobus (continuation)
RMCA 8417
RMCA 8418
RMCA 8443
RMCA 11164
RMCA M2
MNHN-ZM-AC-1954-54
MNHN-ZM-MO-1939-702
MNHN-ZM-2009-358
MNHN-ZM-MO-1970-450
MNHN-ZM-MO-1962-2102
MNHN-ZM-2009-346
MNHN-ZM-MO-1939-701
MNHN-ZM-2009-308
MNHN-ZM-MO-1961-411
MNHN-ZM-MO-1958-710
MNHN-ZM-MO-1992-320
MNHN-ZM-MO-1961-1017
MNHN-ZM-2009-350
MNHN-ZM-2009-312
SNSB-ZSM 1914
MNHN 19641530
MNHN-ZM-AC-1983-97
MNHN-ZM-MO-1885-891
MNHN-ZM-AC-1983-98
MNHN-ZM-2009-359
MNHN-ZM-MO-1962-1390
MNHN-ZM-MO-1908-43
Piliocolobus
MNHN-ZM-MO-1895-9
MNHN-ZM-MO-1939-705
MNHN-ZM-MO-1908-45BIS
MNHN-ZM-MO-1962-1195
MNHN-ZM-MO-1939-706
MNHN-ZM-2009-288
MNHN-ZM-MO-1908-421
MNHN-ZM-MO-1905-420
MNHN-ZM-MO-1890-193
RMCA 346
RMCA 348
RMCA 6011
MNHN-ZM-MO-1884-1428
RMCA 0001
RMCA 0003
RMCA 0004
RMCA 0005
RMCA 0011
RMCA 0012
RMCA 0013
RMCA 0015
RMCA 0017
RMCA 0018
RMCA 0019
RMCA 0022
RMCA 0024
RMCA 18042
RMCA 10408
RMCA 11172
RMCA 11822
RMCA 12340
RMCA 20399
RMCA 20400
RMCA 0004
RMCA 0007
RMCA 0008
RMCA 0009
RMCA 0011
RMCA 0015
RMCA 0019

Appendix 1. — Continuation.

Genus/Acc. n°
Corpus depth analysis
Piliocolobus (continuation)
RMCA 0020
RMCA 0024
RMCA 0032
RMCA 0033
RMCA 0037
RMCA 0045
MNHN-ZM-MO-1961-114
RMCA 22108
RMCA 26445
RMCA 9516
RMCA 9517
RMCA 9520
RMCA 10288
RMCA 10291
RMCA 10549
RMCA 10553
RMCA 10604
RMCA 10605
RMCA 12789
RMCA 12790
RMCA 13339
Procolobus
KUPRI 354
KUPRI 372
KUPRI 373
KUPRI 374
KUPRI 375
KUPRI 377
KUPRI 378
KUPRI 381
KUPRI 383
KUPRI 388
KUPRI 390
KUPRI 391
KUPRI 392
KUPRI 393
KUPRI 394
KUPRI 396
KUPRI 454
USNM 477327
Corpus shape analysis
Colobus
KAS 177
RMCA 5643
RMCA 8064
RMCA 8130
RMCA 9912
SBU RS 8110
SBU RS 8114
SBU RS 814
SBU RS 833
SBU RS 835
AMNH 52209
AMNH 52210
AMNH 52213
AMNH 52215
AMNH 52223
AMNH 52237
AMNH 52238
AMNH 52241
AMNH 52248
KUPRI 11372
KUPRI 8673
OM 3042
OM 3044
OM 3045
OM 3046
OM 3053

Genus/Acc. n°
Corpus shape analysis
Colobus (continuation)
OM 3059
OM 3079
OM 3085
OM 3097
OM 3125
KUPRI 28851
KUPRI 28852
KUPRI 28853
KUPRI 28856
KUPRI 28857
KUPRI 28859
KUPRI 31491
KUPRI 35126
KUPRI 1046
KUPRI 1053
KUPRI 1067
KUPRI 1071
KUPRI 1078
KUPRI 1085
KUPRI 1086
KUPRI 1087
KUPRI 1103
KUPRI 1105
KUPRI 1115
KUPRI 1118
KUPRI 1121
KUPRI 1127
KUPRI 1135
KUPRI 1136
KUPRI 1137
MCZ 22624
MCZ 22629
RMCA 28850
RMCA 35124
RMCA 7313M234
RMCA 8107M100
RMCA 8107M101
RMCA 8107M102
RMCA 8107M103
RMCA 8107M105
RMCA 8107M106
RMCA 8107M107
RMCA 8107M108
RMCA 8107M110
RMCA 8107M114
RMCA 8107M118
RMCA 8107M120
RMCA 8107M126
RMCA 8107M127
RMCA 8107M128
RMCA 8107M129
RMCA 8107M134
RMCA 8107M144
RMCA 8107M155
RMCA 8107M156
RMCA 8107M159
RMCA 8107M164
RMCA 8107M166
RMCA 8107M171
RMCA 8107M172
RMCA 8107M87
RMCA 8107M88
RMCA 8107M89
RMCA 8107M90
RMCA 8107M91
RMCA 8107M92
RMCA 8107M93
RMCA 8107M94
RMCA 8107M95

Genus/Acc. n°
Corpus shape analysis
Colobus (continuation)
RMCA 8107M96
RMCA 8107M99
RMCA 84037M38
USNM 477321
USNM 481784
USNM 481785
USNM 481786
SNSB-ZSM 1914263
Piliocolobus
AMNH ED5
KAS 175
KUPRI 396
KUPRI 441
KUPRI 447
KUPRI 454
KUPRI 456
KUPRI 458
KUPRI 462
KUPRI 464
KUPRI 465
KUPRI 477
KUPRI 4786
KUPRI 4787
KUPRI 4791
KUPRI 490
KUPRI 500
KUPRI 507
KUPRI 518
KUPRI 520
KUPRI 522
KUPRI 524
MCZ 24080
MCZ 24775
MCZ 25627
MCZ 25810
MCZ 26552
MCZ 26553
MCZ 27108
MCZ 31939
RMCA 8107M97
RMCA 8107M98
RMCA 91069
USNM 378673
USNM 378674
USNM 481792
USNM 481795
USNM 452546
OM 4356
KAS 176
KAS 178
USNM 452644
Procolobus
AMNH 89439
KUPRI 354
KUPRI 357
KUPRI 372
KUPRI 373
KUPRI 374
KUPRI 375
KUPRI 377
KUPRI 378
KUPRI 379
KUPRI 379 2
KUPRI 381
KUPRI 383
KUPRI 388
KUPRI 390
KUPRI 391

Genus/Acc. n°
Corpus shape analysis
Procolobus (continuation)
KUPRI 392
KUPRI 393
KUPRI 394
KUPRI 395
RMCA 02M66
RMCA 02M69
RMCA 84073 M176
USNM 477327
USNM 477331

Appendix 1. — Continuation.

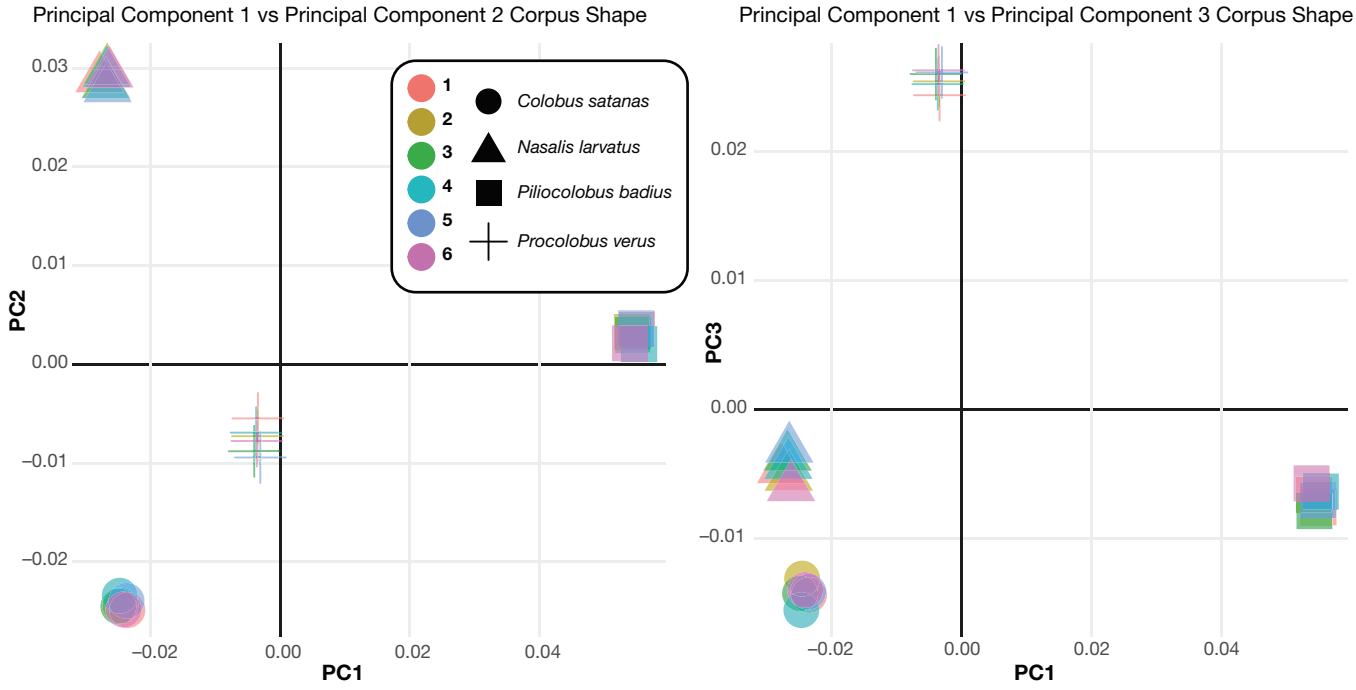
Genus/Acc. n°
Symphysis analysis
Colobus
MCZ 21151
MCZ 22624
MCZ 22626
MCZ 22629
MCZ 463680
RMCA 7313M234
RMCA 28851
RMCA 28852
RMCA 28853
RMCA 28856
RMCA 28857
RMCA 28859
RMCA 31491
RMCA 35126
KUPRI 1046
KUPRI 1067
KUPRI 1071
KUPRI 1085
KUPRI 1087
KUPRI 1103
KUPRI 1105
KUPRI 1121
KUPRI 1127
KUPRI 1053
KUPRI 1078
KUPRI 1086
KUPRI 1115
KUPRI 1118
KUPRI 1135
KUPRI 1136
KUPRI 1137
RMCA 5643
RMCA 8064
RMCA 8130
RMCA 9912
SBU-RS81-4
SBU-RS83-3
SBU-RS83-5
SBU-RS81-10
SBU-RS81-14
KAS 177
AMNH 52209
AMNH 52210
AMNH 52223
AMNH 52237
AMNH 52238
AMNH 52241
AMNH 52245
OM 3042
OM 3044
OM 3045
OM 3085
OM 3097
OM 3053
OM 3125
KUPRI 11372
KUPRI 8673
SNSB-ZSM 1914263

Genus/Acc. n°
Symphysis analysis
Piliocolobus
AMNH ED5
MCZ 24080
MCZ 24775
MCZ 25627
MCZ 25810
MCZ 26552
MCZ 26553
MCZ 27108
RMCA 91-060-M-0069
USNM 378673
USNM 378674
USNM 481792
USNM 481795
KAS175
KUPRI 454
KUPRI 456
KUPRI 458
KUPRI 464
KUPRI 500
KUPRI 507
KUPRI 518
KUPRI 520
KUPRI 522
KUPRI 524
KUPRI 396
KUPRI 441
KUPRI 447
KUPRI 462
KUPRI 465
KUPRI 477
KUPRI 490
KUPRI 4786
KUPRI 4787
KUPRI 4791
USNM 452646
USNM 452644
OM 3046
KAS 178
Procolobus
AMNH 89438
AMNH 89439
RMCA86-002-M-0066
RMCA86-002-M-0069
RMCA84-037-M-0176
USNM 477327
KUPRI 354
KUPRI 378
KUPRI 381
KUPRI 383
KUPRI 388
KUPRI 390
KUPRI 391
KUPRI 392
KUPRI 372
KUPRI 373
KUPRI 374
KUPRI 375
KUPRI 379
KUPRI 377
KUPRI 393
KUPRI 394
KUPRI 395

APPENDIX 2. — Raw data and result of the replicability study of the morphometric symphyseal protocol.

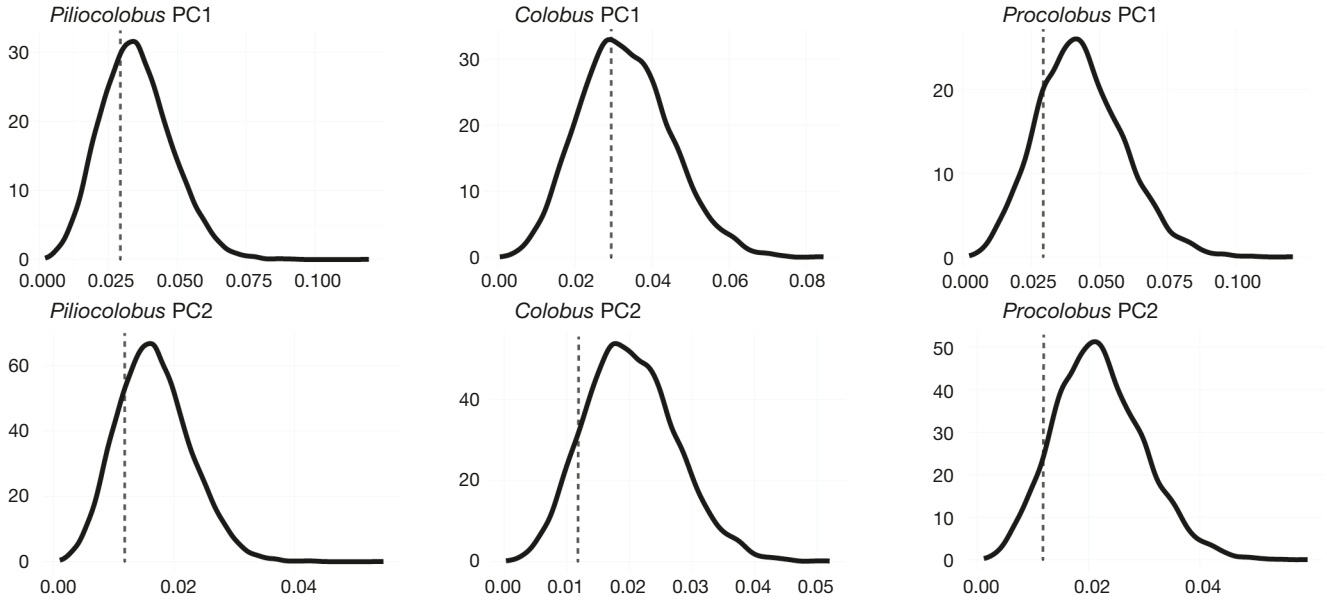
		SL	Diff (Abs-Mean val)	(Mean error-Mean)%	STT	Diff (Abs-Mean val)	(Mean error-Mean)%	ITT	Diff (Abs–Mean val)	(Mean error–Mean)%	PL	Diff (Abs–Mean val)	(Mean error–Mean)%	SA	Diff (Abs–Mean val)	(Mean error–Mean)%
Nasalis larvatus AMNH 103365	1	20.3	0.047		7.3	0.01		7.64	0.022		11.43	0.083		55.81	0.595	
	2	19.87	0.383		7.29	0		7.67	0.052		10.98	0.533		56.73	1.515	
	3	19.85	0.403		7.29	0		7.62	0.002		11.19	0.323		56.12	0.905	
	4	20.43	0.177		7.28	0.01		7.59	0.028		11.77	0.257		55.23	0.015	
	5	19.83	0.423		7.26	0.03		7.75	0.132		11.14	0.373		56.46	1.245	
	6	21.24	0.987		7.32	0.03		7.44	0.178		12.57	1.057		50.94	4.275	
	Mean	20.25	0.403	1.991441738	7.29	0.013	0.182899	7.618	0.069	0.904251	11.513	0.438	3.802355	55.215	1.425	2.580820429
Colobus satanas "MNHN 1914 263"	1	22.25	0.223		9.86	0.327		5.14	0.027		12.9	0.24		47.09	0.403	
	2	21.82	0.207		9.94	0.407		5.18	0.013		12.39	0.27		48.54	1.853	
	3	21.71	0.317		9.97	0.437		5.24	0.073		12.13	0.53		48.75	2.063	
	4	22.03	0.003		9.89	0.357		5.13	0.037		12.77	0.11		46.86	0.173	
	5	21.69	0.337		9.93	0.397		5.19	0.023		12.19	0.47		48.3	1.613	
	6	22.66	0.633		9.85	0.317		5.12	0.047		13.58	0.92		40.58	6.107	
	Mean	22.03	0.287	1.301452785	9.533	0.374	3.921275	5.167	0.037	0.709677	12.66	0.423	3.343865	46.687	2.362	5.059260317
Piliocolobus badius KUPRI 462	1	28.57	0.022		9.68	0.047		9.01	0.027		14.12	0.172		45.69	0.692	
	2	28.71	0.118		9.77	0.043		9.04	0.057		14.18	0.112		46.13	1.132	
	3	29.01	0.418		9.73	0.003		9	0.017		14.7	0.408		45.33	0.332	
	4	28.48	0.112		9.77	0.043		8.98	0.003		14.01	0.282		47.54	2.542	
	5	28.68	0.088		9.72	0.007		8.94	0.043		14.26	0.032		45.82	0.822	
	6	28.1	0.492		9.69	0.037		8.93	0.053		14.48	0.188		39.48	5.518	
	Mean	28.59	0.208	0.728650539	9.727	0.03	0.30843	8.983	0.033	0.371058	14.292	0.199	1.391642	44.998	1.839	4.087805721
Procolobus verus KUPRI 388	1	19.93	0.202		6.79	0.09		4.67	0.032		10.28	0.322		50.4	1.667	
	2	20.27	0.138		6.8	0.1		4.7	0.002		10.7	0.0982		48.02	0.713	
	3	20.07	0.062		6.75	0.05		4.69	0.012		10.46	0.147		50.56	1.827	
	4	20.12	0.012		6.78	0.08		4.65	0.052		10.57	0.037		49.81	1.077	
	5	20.18	0.048		6.78	0.08		4.82	0.118		10.58	0.022		48.27	0.463	
	6	20.22	0.088		6.7	0		4.68	0.022		11.02	0.418		45.34	3.393	
	Mean	20.13	0.092	0.455335707	6.767	0.067	0.985222	4.702	0.039	0.838946	10.602	0.172	1.624483	48.733	1.523	3.125854993

Appendix 3. — Biplots of PC scores of the replicability study of the corpus shape 2D GM analysis.

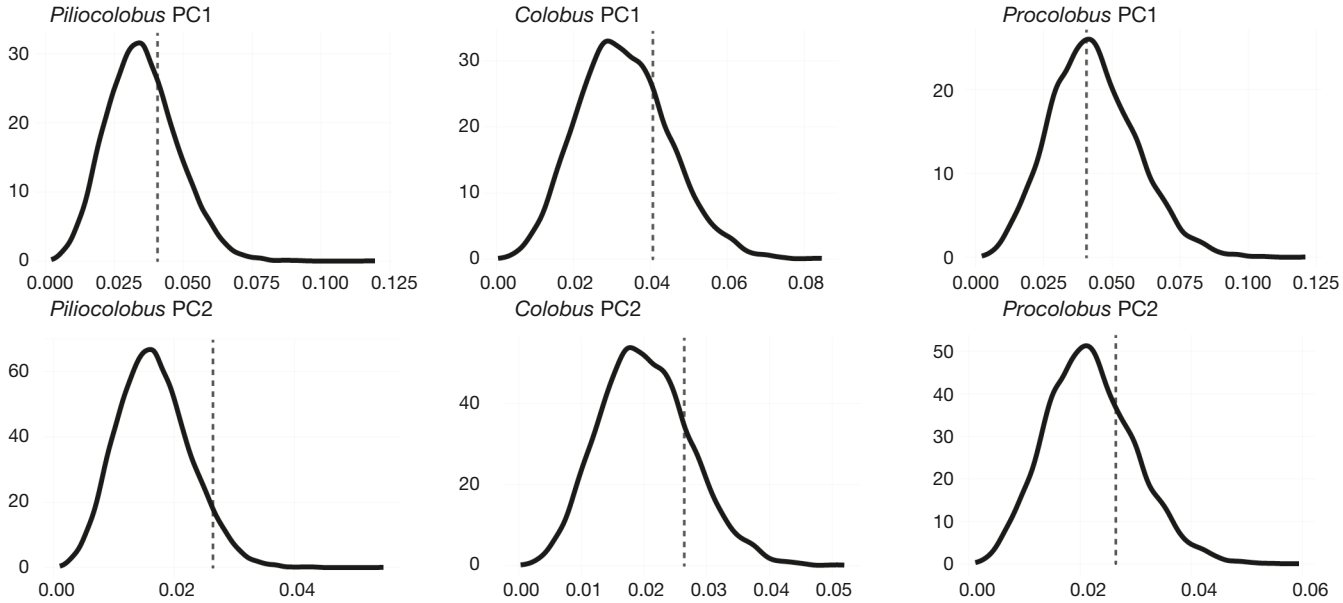


APPENDIX 4. — Distribution of coefficient of variation of extant Colobini species compared with that of the Asbole sample for PC scores of corpus shape

Distribution of coefficient of variation of extant Colobini species compared with that of the Asbole sample



Distribution of coefficient of variation of extant Colobini species compared with that of the Asbole and Koobi Fora sample



Appendix 5. — Distribution of coefficient of variation of extant Colobini species compared with that of the Asbole sample for PC scores of corpus depth at mid-M_1