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A window into the early evolutionary history of Cercopithecidae: Late Miocene evidence from Chad, Central Africa.

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Abstract

Central Africa is known as a major center of diversification for extant Old World Monkeys (OWM) and yet has a poorly documented fossil record of monkeys. Here we report a new colobine monkey (*Cercopithecoides bruneti* sp. nov.) from the Central African hominin-bearing fossiliferous area of Toros-Menalla, Chad at ca. 7 Ma. In addition to filling a gap in the spatial and temporal record of early OWM evolutionary history, we assess the ecomorphological diversity of early OWM by providing evidence on the onset of a folivorous diet and a partial reacquisition of terrestrial locomotor habits among Miocene colobines. We also support the phylogenetic affinities of the genus *Cercopithecoides* among the stem group of the extant African colobine monkeys.

Keywords: *Cercopithecoides*, Colobinae, stem Colobini, Adaptive Radiation, Ecomorphology

Introduction

With an extensive geographical distribution, a rich taxonomy and a marked ecomorphological diversity, extant Cercopithecidae (i.e., Colobinae and Cercopithecinae) represent one of the most successful adaptive radiations of Neogene primates on the African and Eurasian continents. Old World Monkeys (OWM) are known to diverge from an ancestral African stock (i.e., Victoriapithecidae) presenting dentognathic and postcranial morphologies adaptively linked to frugivory and terrestrial locomotion (Harrison, 1989; Benefit, 1993). Extant African (i.e., Colobini) and Asian (i.e., *Presbytini*) representatives of the subfamily Colobinae depart from this adaptive zone in exhibiting morphological and physiological adaptations associated with folivory and arboreal locomotion. While a rich Miocene OWM fossil record is documented in Eurasia at 8.5-6 Ma with the radiation of the putative stem colobine *Mesopithecus* spp. (Delson, 1973), the fossil record of Miocene OWM in Africa is sparse. Dating back as far as 12.5 Ma, the African cercopithecid fossil record is known from only a handful of localities mostly restricted to East (Benefit and Pickford, 1986; Leakey et al.,

2003; Hlusko, 2007; Frost et al., 2009; Gilbert et al., 2010; Nakatsukasa et al., 2010; Suwa et al., 2015) and North Africa (Delson, 1973; Benefit et al., 2008). In spite of being suggested as a cradle of diversity for extant Cercopithecidae (Böhm and Mayhew, 2005; Ting, 2008), Central Africa has provided little evidence of the early evolutionary history of OWM (Gundling and Hill, 2000). The Central African hominin-bearing fossiliferous area of Toros-Menalla (TM), Chad at ca. 7 ± 0.2 Ma (Brunet et al., 2002; Lebatard et al., 2010) has yielded colobine remains, giving us the unique opportunity to assess current hypotheses regarding the paleobiology and phylogenetic relationships of Late Miocene colobines in Africa. Particularly, the well-preserved dentognathic materials from TM fill a temporal gap between a primitive dental morphology related to frugivory (Benefit et al., 2008; Merceron et al., 2009; Rossie et al., 2013; Suwa et al., 2015; Thiery et al., 2017) and a derived dental morphology linked to a leaf-dominated diet (Gilbert et al., 2010). Moreover, the discovery of a nearly complete forelimb allows us to reconsider the emergence of terrestrial locomotor behavior among Miocene colobines (Leakey et al., 2003; Youlatos et al., 2012). In addition, the chronological setting of TM encompassed the estimated divergence times of extant crown Colobini taxa (Ting, 2008), permitting to assess hypotheses regarding the placement of the Chadian colobine among the stem or crown Colobini group (Jablonski and Frost, 2010; Frost et al., 2015). Here we describe *Cercopithecoides bruneti* sp. nov. from the Late Miocene of Central Africa, at ca. 7 Ma and provide new evidence for terrestrial locomotor habits and an increase in leaf consumption among Miocene colobines. We also provide insights into the phylogenetic affinities of the Chadian colobine, and discuss the contribution of TM to our understanding of cercopithecid evolution in light of the ecomorphological diversity of Late Miocene OWM in a previously unknown spatial and temporal setting.

Materials and methods

Material availability and imaging

All the materials described here have been collected between 2000 and 2003 by the Mission Paléoanthropologique Franco-Tchadienne (P.I. Michel Brunet) and are currently curated at the Service de Valorisation des Collections de Paléontologie (CNRD de N'Djamena). Apart from glue consolidation, the fossil material was not subjected to any modification. All the fossil material described here has been scanned at the Université de Poitiers, France. An Easy Tom XL duo μCT-scanner yielded virtual image stacks of the Chadian fossil material with resolutions ranging from 21.5µ to 45.6μ. Virtual reconstruction and visualization were obtained with the software Avizo Standard Edition.

Comparative sample

Qualitative and quantitative data for *Cercopithecoides williamsi* were gathered from µ-CT scan data provided by the Ditsong National Museum of Natural History (Plio-Pleistocene Section). Qualitative and quantitative date for all other early African colobines derived from the literature. Qualitative and quantitative data for the dentognathic fossil material of early Eurasian Colobinae (i.e., *Mesopithecus* ssp.*)* were gathered from µ-CT scans data of high quality dental casts provided by Dr. Gildas Merceron. *Mesopithecus pentelicus* postcranial data were taken directly from specimens of the Pikermian sample curated at the Museum National d'Histoire Naturelle (MNHN, France).

Postcranial and odontometric data for extant Cercopithecidae were gathered directly from specimens provided by PALEVOPRIM (Université de Poitiers, France); the Museum National d'Histoire Naturelle (MNHN, France); the Royal Museum of Central Africa (RMCA, Belgium); the Natural History Museum of Basel (NMB, Switzerland); the Anthropological Institute and

Museum, University of Zurich (AIM-UZH, Switzerland) and the Musée des Confluences, Lyon (MHNL, France). Additional odontometric data of extant Colobini were also gathered from high quality dental casts provided by Dr. Gildas Merceron.

Mandibular data of extant Colobinae were extracted from virtual specimens provided by the Smithsonian Institution (Division of Mammals, USA); Harvard University (Museum of Comparative Zoology (MCZ), USA)); the Digital Morphology Museum (Primate Research Institute, Kyoto University) and the American Museum of Natural History (Department of Anthropology, USA).

Humeral geometric cross-sectional properties were obtained on virtual specimens provided by the Harvard University (Museum of Comparative Zoology (MCZ), USA) and the Royal Museum of Central Africa (RMCA, Belgium).

Odontometric, morphological and biomechanical analyses

Odontometric

Odontometric data of the *C. bruneti* holotype and hypodigm were acquired using a Mitutoyo Digimatic caliper CD-8''CX on the original fossil material and on selected photographs obtained in Avizo Standard Edition and measured with ImageJ. Selected photographs of generated surfaces obtained in Avizo Standard Edition from µ-CT scans data of extant and extinct colobines (i.e., *C. bruneti*, *C. williamsi* and *M. pentelicus*) were used to calculate the NH/NR ratio (Benefit, 1993) as well as additional dental metrics. Odontometric data of extant Colobinae were acquired directly on specimens as well as on high quality dental casts using a Mitutoyo Digimatic caliper CD-8''CX.

Further information regarding odontometric measurement protocols, sample size, ratio formulas and references are presented in footnotes of Fig. 1, SOM Figure S2, Table 3-4 and SOM Table S2.

Mandibular

Mandibular morphometric data from *C. bruneti*, *C. williamsi* and the extant Colobinae comparative sample were obtained from selected symphyseal and corporeal cross-sections obtained via GeoMagic Studio and Avizo Standard Edition on virtual specimens. Measurements of the symphyseal and corporeal cross-sections were obtained via ImageJ.

Further information regarding mandibular morphometric measurement protocol, sample size and ratio formulas can be found in footnotes of Fig. 6 and Table 5 as well as in SOM Fig. S1.

Postcranial

Data of the *C. bruneti* postcranial specimen were acquired via a Mitutoyo Digimatic caliper CD-8''CX on the original fossil material as well as from selected photographs obtained in Avizo Standard Edition and measured in ImageJ. All data from extant Cercopithecidae were acquired directly on specimens using a Mitutoyo Digimatic caliper CD-8''CX and from digital photographs using Image J. Further information regarding samples size and measurement protocol can be found in footnotes of Figure 9 and Table 6 as well as in SOM Figure S1.

Humeral geometric cross-sectional properties were obtained via Image J's plugin Bone J on virtual specimens. In order to acquire humeral mid-diaphyseal cross-sectional properties, the virtual image stacks were first aligned at their moments of inertia and then subjected to the calculation of geometric properties. The zone of interest (*i.e.*, slice at mid-diaphysis) was subsequently obtained from the virtual image stack. Due to the lack of the humeral head of TM

266 03-034, the mid-diaphysis of the specimen was inferred at the midpoint of actual humeral length +5%.

Body mass estimation

All equationsfor estimating body mass were taken from Delson et al., 2000. Further details and extended interpretations of body mass can be found in footnotes of Table 2 and SOM Table S1.

Results

Systematic paleontology

Order **Primates** Linnaeus, 1758;

Suborder **Anthropoidea** Mivart, 1864;

Infraorder **Catarrhini** E. Geoffroy, 1812;

Superfamily **Cercopithecoidea** Gray, 1821;

Family **Cercopithecidae** Gray, 1821;

Subfamily **Colobinae** Blyth, 1863;

genus ***Cercopithecoides*** Mollet, 1947.

Type species: *Cercopithecoides williamsi* Mollet, 1947.

Generic diagnosis: As stated in Frost and Delson, 2002 "Medium to very large colobines with globular, rounded calvaria. The rostrum is short in comparison to neurocranial length, very different from *Paracolobus*, *Rhinocolobus*, *Dolichopithecus*, and *Nasalis*. It is not as short as that of *Rhinopithecus*, however. The frontal process of the zygomatic bone is narrow, unlike *Paracolobus* and *Rhinocolobus*. The inter- orbital region is broad, which is distinct from *Libypithecus*, *Rhinocolobus*, and *Nasalis*. The supraorbital tori are thick and separated from the calvaria by a deep ophryonic groove, which is distinct

from *Colobus*, and most species of *Presbytis* and *Trachypithecus*. The calvaria itself lacks a sagittal crest, at least anteriorly, which separates it from *Paracolobus* and *Procolobus*. The P^3 lacks a protocone, which is similar to modern African colobines, but different from *Libypithecus*, *Kuseracolobus*, *Paracolobus* and *Rhinocolobus*. The mandibular symphysis is steep, but shallow and pierced by a median mental foramen (except in *C. meaveae*), which is different from all colobines other than *Procolobus* (*Procolobus*) and *Rhinocolobus* from the Turkana Basin. The mandibular corpus is shallow and thick, which contrasts greatly with that of *Kuseracolobus*, *Rhinocolobus*, *Paracolobus* and to some degree *Colobus*, but is not unlike that of *Procolobus* (*Piliocolobus*). The gonial region is unexpanded or expanded only a small amount. This contrasts with mandibles of *Kuseracolobus*, *Rhinocolobus*, *Paracolobus mutiwa*, and *Colobus*. Associated postcrania are known for *C. williamsi* from an associated skeleton from Koobi Fora (the morphology of which may not be typical for the South African material, see remarks below). It is distinguished from all other known colobines, except *Dolichopithecus*, in the degree of its adaptations for terrestrial habitus (Birchette, 1981; 1982; Ting, 2001).”

On a taxonomic level, the combination of a faint P^3 protocone, a precocious and marked dental wear, an orthognathic subnasal region with short premaxillae and maxillary sinuses (MS), a buttressed corpus bulging below $M_{1\text{-}2}$ as well as a symphysis with a straight, smooth and vertical labial face align the Chadian cercopithecid with the East and South African genus *Cercopithecoides* (Freedman, 1957; Frost and Delson, 2002; McKee et al., 2011) (Table 1-2).

Cercopithecoides bruneti sp. nov. Holotype: TM 266 03-100, left and right hemimaxillae preserving dI^1, dC^1, $dP^{3\text{-}4}$, C^1, $P^{3\text{-}4}$, $M^{1\text{-}2}$. Paratype: TM 266 03-034, a fragmented left and right maxilla with I^2, C^1-P^4; TM 266 03-099, partial mandible preserving left P_3-M_3 and associated right P_3-M_1; TM 112 00-093, partial mandible preserving left P_3; TM 219 01-102, partial mandible preserving left C_1 and right I_1-M_2; TM 266 03-036, a right

partial forelimb with sub-complete humerus, ulna and radius; TM 266 03-307, a sub-complete right femur. Type locality: Locality n°266 from the fossiliferous area of Toros-Menalla, western part of the Djurab desert, northern Chad basin. Type horizon: Anthracotherid Unit. Age*:* ca*.* 7 ± 0.2 Ma. Etymology: In honor of Pr. Michel Brunet for his significant contribution to paleoanthropology in Central Africa. Since 1994, he has initiated, led and directed the fieldwork of the Mission Paléoanthropologique Franco-Tchadienne (MPFT) in Chad.

Specific diagnosis: A colobine of moderate size, similar in overall dental dimensions and inferred body mass to *Paracolobus enkorikae* (Lemudong'o Formation (Fm.), Kenya)*, Mesopithecus pentelicus, Libypithecus markgrafi* (Wadi Natrun Fm., Egypt)*,* colobine gen. and sp. A from Mpesida (Mpesida Beds, Tugen Hillas, Kenya) and colobine sp. B from Lower (LN) and Upper Nawata (UN) (Nawata Fm., Lothagam, Kenya). Upper dentition with moderate cusp relief and molar flare, M^2 paraloph width enlarged relative to tooth length, P^3 protocone highly reduced relative to paracone, dP^4 paraloph width enlarged relative to tooth length and marked breadth differential between P^3 and P^4. Lower dentition with a narrow P_4 crown, a marked size differential between M_1 and M_2, M_3 lacking a tuberculum sextum and possessing a bucco-lingually narrow hypoconulid relative to hypolophid breadth. Craniofacial morphology characterized by maxillary sinuses and an orthognathic sub-nasal region. Mandibular morphology characterized by a prominent inferior transverse torus (ITT), a corpus of moderate robustness with marked prominentia lateralis and a deep mandibular symphysis with a flat and vertical labial face that lacks a median mental canal.

Differential diagnosis *Cercopithecoides bruneti* specimens are larger than *Microcolobus tugenensis* (Ngorora Fm., Tugen Hills, Kenya), *Microcolobus* sp*.* (Nakali Fm., Baringo, Kenya) and the indeterminate small colobines from Kabasero (Ngorora Fm., Tugen Hills, Kenya), Teso Tadecho (Chorora Fm., Ethiopia),

Beticha (Chorora Fm., Ethiopia), Lukeino (Lukeino Fm., Tugen Hills, Kenya), Lemudong'o (Lemudong'o Fm., Kenya) and colobine sp. A from LN-UN (Nawata Fm., Lothagam, Kenya). The Chadian colobine is smaller than the Miocene colobines from Menacer (Algeria) and Adu Asa (Adu Asa Fm., Ethiopia) as well as from the early Pliocene *Kuseracolobus hafu. C. bruneti* exhibits an enlarged paraloph relative to M^2 length with a crown shape ratio (CSR) matched by the small colobine from Lemudong'o (Fig. 1). *C. bruneti* further differs from *M. tugenensis* by the presence of an ITT, enlarged prominentia lateralis, a marked size differential between M_1 and M_2, a less developed talonid on P_3 and a narrow P_4 crown. *C. bruneti* is distinct from the Kabasero colobines in having a more developed hypoconulid and a narrow hypolophid relative to M_3 length. Forelimb morphology of *C. bruneti* is unlike the Nakali colobine in having a reduced and straight ulnar olecranon process and a short and retroflexed humeral medial epicondyle. *C. bruneti* is distinguished from the Teso Tadecho colobine, *Paracolobus enkorikae*, the small Lemudong'o colobine and *L. markgrafi* by having a reduced P^3 protocone. A marked breadth differential between P^3 and P^4 further differentiates *C. bruneti* from *P. enkorikae*, the small colobine from Lemudong'o and *L. markgrafi*. *C. bruneti* is also distinguished from the Teso Tadecho colobine by a broader P^4 crown. *C. bruneti* further differs from *P. enkorikae* by a narrow P_4 crown, maxillary sinuses and a flat symphyseal labial face with no break in slope. *C. bruneti* is morphologically distinct from *L. markgrafi* in having a narrow C^1. *C. bruneti* differs from the Mpesida Beds colobine gen. and sp. A in lacking a buccally curved hypoconulid and accessory cuspules between entoconid and hypoconulid and in exhibiting a broader hypolophid relative to tooth length. *C. bruneti* differs from *Kuseracolobus aramisi* by a reduced P^3 protocone (a feature described as variable in *K. aramisi*), an early eruption of molars relative to the anterior dentition, a marked dp^4 CSR, a moderate flare on M^2 with a marked M^2 CSR (i.e., with a value > 100), a marked $P^{3\text{-}4}$ breadth differential, a corpus with a sharp inferior margin, the presence of a double mental foramen and an absence of tuberculum sextum.

C. bruneti is one of the smallest species of the East and South African genus *Cercopithecoides*, with dental dimensions similar to *Cercopithecoides kerioensis, C. meavae*, *C. alemayehui* and *C. haasgati*. It differs from the large taxa *C. williamsi* and *C. kimeui* in lacking a median mental canal and in possessing a gracile corpus. It further differs from *C. williamsi* in possessing a shorter planum alveolare, a relatively smaller hypoconulid, a superiorly placed genioglossal fossa, a less marked size differential between ITT and STT (Superior Transverse Torus), a less developed humeral deltoid crest, a less developed humeral medial trochlear keel and a broader zona conoidea. *C. bruneti* is distinct from *C. meavae* in having a marked breadth differential between P^{3-4}, a broader dP^4, a less marked size differential between M_{1-2}, a shorter humeral medial epicondyle, a less developed humeral medial trochlear keel, a less rounded radial head and a gracile radial neck. *C. bruneti* also differs from *C. alemayehui* by a narrower P^3 crown and a broader M^2 paraloph relative to tooth length. *C. bruneti* displays an increased breadth differential between P^{3-4} relative to *C. kerioensis* (Fig. 1) and is distinguished from *C. haasgati* by a narrower P^3 crown, an elongated P_4 crown and a less marked size differential between M_1 and M_2.

Description of* C. bruneti *dentognathic morphology

<u>TM 266 03-100</u> The type specimen TM 266 03-100 is a right and left hemimaxilla belonging to a juvenile individual and preserving much of the upper postcanine dentition (Table 3, Fig. 2). Of the upper anterior dentition, the dI^1 are highly worn, a small portion of the left dC^1 root is preserved and a large portion of the C^1 crown remained intact in the dental crypt. The dI^1 exhibits a lingual rootward extension of enamel onto the cervix and a mesiodistally compressed root unfused at its apex. The upper canine displays the features characteristic of male cercopithecids (i.e., deep mesial sulcus, a sharp distal margin, a convex buccal face and a mesiodistal elongation of the canine crown relative to breadth). Deciduous premolars are severely worn, consistent with a J5 dental wear stage while the postcanine dentition already show an A2 wear stage

(Ingicco et al., 2012). This early and heavy wear of the dentition is unusual among extant colobines, especially when considering the ontogenetic status of the specimen. The deciduous upper premolars exhibit a large amount of flaring and a CSR consistent with a bucco-lingual enlargement of those teeth. The dP^3 is bilophodont and devoid of *crista obliqua*; the dP^4 possesses a paraloph broader than the metaloph and a mesial shelf longer than the distal one (SOM Table 2). M^{1-2} are in occlusion while dI^1 is still in place, confirming the presence of an early eruption of M^2 relative to the anterior dentition. The permanent premolars are preserved in their crypts and exhibit a characteristic colobine morphology. The P^3 crown is moderately broad and exhibits heteromorphic cusps with a faint protocone, a well-developed mesiobuccal flange, a paracone set distally relative to the protocone and a relatively narrow triangular mesial shelf compared to a squared-shape distal shelf. The P^4 crown is broad, displays a paracone higher than a distally set protocone, a high paracone relative to crown length, a high and sharp transverse loph, a marked mesiobuccal flange, a slight lingual cleft and a moderate length differential between mesial and distal shelves. In addition, there is a marked breadth differential between P^{3-4} (Fig. 1). The M^2s exhibit qualitatively thin enamel (Fig. 2) as well as a moderate amount of flare and crown relief relative to extant colobines. Note that the buccal parts of both M1 are missing as well as the hypocone of both M2 (Fig. 2). M^{1-2} present deep and marked median lingual clefts, a poor development of the mesiodistal developmental groove, widely spaced lophs and moderately developed shelves (SOM Table S2) that support the taxonomic status of TM 266 03-100 as a colobine (Benefit, 1993). A marked buccal cingular ridge is present on M^2 and a poorly developed interconulus is observed at the base of the M^1 lingual cleft. A body mass of ~16.5kg is inferred from M^{1-2} mesio-distal dimensions (SOM Table S1). Considering craniofacial morphology, TM 266 03-100 exhibits an orthognathic subnasal region with an anteriorly placed zygomatic process which originates low on the maxilla and above M^1. This morphological pattern is seen in

extant juvenile Colobinae and Cercopithecini of similar dental eruption stage (Fig. 3). The nasal aperture is straight in lateral view and tapers inferiorly to form an acute inferior margin in anterior view. The premaxilla is reduced and gives a square aspect to the premaxillo-maxillary complex. No maxillary or infraorbital fossae are observed. A large infraorbital foramen is present on the inferior portion of the orbital margin of the right hemimaxilla. The hard palate extends posteriorly at the level of M^2. Maxillary sinuses (MS) invade the lower portion of the maxilla, extend anteriorly at the level of M^1 and are pierced by the roots of M^{1-2}.

TM 266 03-034 is a fragmented anterior maxilla preserving most of the adult anterior dentition (Fig. 2). I^2 displays a parallelogram-shaped and mesially angled crown with a poorly developed basal cingulum, a faint lateral prong, a thin layer of enamel on the occlusal surface, a well-defined and horizontal cervix, a markedly convex labial face and no sulcus. C^1 presents a narrow crown with a long axis obliquely oriented relative to P^{3-4}, a low crown cusp with a raised cingulum on the mesial margin, a raised distal margin on the talonid and a mesial groove continuing from the crown onto the roots. TM 266 03-034 exhibits a female morphology with a low crowned C^1 relative to tooth length. Although fragmented, the P^3 bucco-lingual dimension is in the size range of TM 266 03-100 (SOM Table S2) and is morphologically consistent with the *C. bruneti* holotype in exhibiting a flange-like buccal margin and a raised paracone associated with a faint and mesially offset protocone. A slight portion of the lateral margin of the right nasal aperture is preserved and set vertically relative to the occlusal plane.

TM 266 03-099, TM 112 00-093 and TM 219 01-102 consist of adult mandibular remains allocated to the *C. bruneti* hypodigm (Fig. 4-5).

TM 266 03-099 displays a wear pattern consistent with an A6 dental wear stage (Ingicco et al., 2012). The P_3 crown is narrow and presents a large protoconid but no paraconid nor metaconid,

the mesiobuccal flange is developed, upright, and does not extend below the alveolar margin. The degree of development of the P_3 flange is consistent with a male morphology. The P_4 is bicuspid, lacks an entoconid and displays a protoconid broader than the distally offset metaconid and an elongated crown with a moderate mesiobuccal flange. Mesial and distal lophids are of nearly equal width on M_{1-2} but there is a marked size differential between M_1 and M_2 (SOM Fig. S2). The trigonid basin is reduced on all molars, and the M_3 lacks a tuberculum sextum but bears a buccally placed hypoconulid which is small relative to hypolophid breadth. The labial symphyseal face is flat and vertical with a minute symphyseosum foramen placed at its mid-height. It lacks rugosities, sub-incisal hollowing and a median mental canal (Fig. 4-5). The inferior margin of the symphysis is sharp with a rugose infero-lingual portion, a developed digastric spine and a poorly imprinted digastric fossa. The planum alveolare is straight and extends to the mesial part of P_3. The symphysis is robust (Fig. 4-5) and presents a bulbous and extensive ITT that reaches the mesial part of P_4. The infero-lingual margin of the corpus is sharp and inferiorly lacks an imprinted digastric fossa at M_1 level and superiorly an inter-toral sulcus. Prominentia laterales are prominent and extend anteriorly to the mesial portion of P_4. The corpus is deep and bulges below M_1, the linea obliqua merges with the corpus at the level of M_{1-2} contact and the extramolar sulcus is narrow.

<u>TM 112 00-093</u> morphology is consistent with that of TM 266 03-099 in exhibiting a similar symphyseal topography but with a less developed ITT extending only to the level of P_3 and a less acute symphyseal inferior margin. The planum alveolare is slightly concave and the STT overhangs a shallow genioglossal fossa. The corpus morphology is also consistent with TM 266 03-099 but exhibits a marked imprinting of the digastric fossa and submandibular fossa,

respectively below P_4-M_1 and M_{2-3}. Of the entire dental row, only the P_3 crown is preserved. The mesiobuccal flange is short and in accordance with a female morphology. The incisor row is narrow. The base of the M_3 crown tapers distally.

TM 219 01-102 is a fragmented mandible preserving the symphysis and hints of the superior portion of the right and left corpus. TM 219 01-102 exhibits peg-like incisors with poorly developed cingulum and a narrow incisal row. Canines are robust, labially recurved, and present an extensive talonid devoid of any tubercles. The canine root bears a faint mesial groove. The inferior margin of the symphysis is eroded but the toral morphology is clearly colobine-like with an extensive and bulbous ITT reaching the mesial part of M_1. The symphysis is vertical, and a slight hint of the linea obliqua is preserved on the upper part of the corpus at the level of M_2. Canine dimensions and morphology are consistent with identification as a male. In addition, dental and mandibular dimensions of TM 219 01-102 are congruent with those of TM 266 03-034 (Tables 4-5).

Body masses inferred from dental dimensions ranged from ~ 8.45kg for TM 112 00-093 to ~ 13.3kg and ~14.4kg (using equations from Delson et al., 2000), respectively for TM 219 01-102 and TM 266 03-099 (SOM Table S1).

Comparative aspect of* C. bruneti *dentognathic anatomy

The *C. bruneti* dP^4 possess a paraloph broader than the metaloph (SOM Table S2), a characteristic variable among Cercopithecoidea but mostly observed on Victoriapithecidae and Cercopithecinae (Benefit, 1994). Nevertheless, the absence of a crista obliqua, the bilophodont state of dP^{3-4} and the marked dP^4 mesial shelf length relative to the distal one clearly aligns *C.*

bruneti with crown cercopithecids (Benefit, 1994). The dP^4 CSR is consistent with an enlargement of the tooth, similar to victoriapithecids but also to the putative colobine dP^4 from Menacer (SOM Fig. S2). Furthermore, the early eruption of M^2 relative to the anterior dentition observed in *C. bruneti* is typical of Colobinae (Harvati and Frost, 2007). Although an early molar eruption relative to anterior dentition was previously documented in *M. pentelicus*, the extreme condition of the early eruption of M^2 relative to I^1 observed in *C. bruneti* was previously unknown among fossil colobines whereas it is documented either as a variant (e.g *Colobus angolensis*) or as a constant (*e.g Presbytis* spp.) among extant Colobinae (Harvati and Frost, 2007). *C. bruneti* upper molar morphology is similar to those of early Eurasian as well as North and East African colobines in exhibiting a basal flaring associated with a lack of sharp shearing crests (Benefit and Pickford, 1986; Rossie et al., 2013; Suwa et al., 2015). Even slightly worn, a quantification of *C. bruneti* left M^2 occlusal relief (i.e., NH/NR ratio, Fig. 1) yields a value higher than those observed among the penecontemporaneous Eurasian colobine *M. pentelicus* and the North African colobines from Menacer and As Sahabi (Delson, 1973; Benefit et al., 2008). *C. bruneti* subnasal morphology is consistent with the poor maxillary projection observed in *Cercopithecoides* spp. and *Kuseracolobus* spp. The deep and slender corpus as well as the deep symphysis of *C. bruneti* is similar to the early Pliocene *C. kerioensis* (Leakey et al., 2003). The Chadian *Cercopithecoides* further shares with *C. kerioensis* and *C. meavae* a moderate breadth of the M_3 hypolophid relative to tooth length and an absence of a median mental canal. *C. bruneti* is similar to the South African *C. williamsi* sample in exhibiting a marked P^{3-4} breadth differential (Fig. 1,3) and a marked M_{1-2} size differential (SOM Fig. S2). The enlargement and the square aspect of the *C. bruneti* upper second molar are also consistent with the South African

Cercopithecoides sample (i.e., *C. williamsi* and *C. haasgati*) (Fig. 1,3). Relative to extant colobines, *C. bruneti* dentognathic morphology is consistent with a Colobini morphology. Indeed, a narrow P^3 crown with heteromorphic cusps (Swindler and Orlosky, 1974), a height differential between lingual and buccal P^4 cusp (Gilbert et al., 2010), a distally offset P_4 metaconid (Swindler and Orlosky, 1974), a broad P_4 protoconid relative to metaconid (Swindler and Orlosky, 1974), a narrow P_4 crown, an elongated C^1 (Pan, 2006) and a poorly developed (i.e., *Colobus*-like) digastric fossa (Groves, 2007) aligns *C. bruneti* with the extant Colobini (Fig. 3). In spite of morphological affinities with the African colobine tribe, *C. bruneti* lacks the long and steeply inclined planum alveolare, the inferiorly placed genioglossal fossa and the diminutive ITT seen among several taxa of *Colobus* (Fig. 5-6). *C. bruneti* symphyseal topography is most consistent with the morphology exhibited by *Piliocolobus* but it does not exhibit the marked dental occlusal relief seen in the extant genus (Fig. 5-6).

Description of* C. bruneti *postcranial morphology

A sub-complete right forelimb (i.e., TM 266 03-036) composed of humerus, radius and ulna as well as a partial femur (i.e., TM 266 03-307) are here included in the *C. bruneti* hypodigm (Fig. 7). Collected from the same locality, it is parsimonious to assume that the fore- and hindlimbs come from the same taxon (i.e., *C. bruneti*). Joint congruency supports the hypothesis of the forelimb elements belonging to the same specimen.

<u>TM 266 03-036</u> The postero-distal portion of the humeral head is preserved and is flanked by well-defined distal margin of the greater and lesser tuberosities. In posterior view, the medial part of the surgical neck is markedly concave and accommodates the insertion of the

coracobrachialis profundus muscle. The humeral proximal diaphysis is fractured in its proximal and distal portion. It is surrounded by sharp crista tuberculi majoris and crista tuberculi minoris. Those crests are poorly developed and accommodate proximally set attachment sites for teres major and pectoralis major muscles. The posterior aspect of the proximal diaphysis is salient and bears moderate sites of attachment for the lateral head of the triceps brachii muscle. The deltoid tuberosity is flat, poorly developed, and does not extend below mid-diaphysis. The humeral diaphysis is gracile and elliptical in cross-section at mid-diaphysis, with a long-axis running anterolateral-to-posteromedially. The humeral shaft is straight in the anteroposterior plane but curved medially in the mediolateral plane. The posterior aspect of the distal portion of the diaphysis is flattened and exhibits a poorly developed lateral supracondylar ridge. The distal epiphysis is fractured and separated from the humeral shaft. Most of the humeral trochlea and zona conoidea are preserved (Fig. 7). The antero-proximal part and a slight hint of the proximo-lateral portion of the capitulum are preserved. The anterior aspect of the distal epiphysis is characterized by a wide and deep radial fossa, a shallow and poorly delineated coronoid fossa, a moderate-sized trochlea, a moderately developed medial trochlear keel compared to cercopithecins that is set obliquely relative to the long-axis of the shaft, a well-defined anterior margin of the medial trochlear keel, a faint lateral trochlear keel and a large zona conoidea (Fig. 7)**.** The posterior aspect of the distal epiphysis exhibits a deep and oval-shaped olecranon fossa that presents a septal aperture, a moderate breadth differential between its lateral and medial pillar, a short and retroflexed medial epicondyle and a salient posterior margin of the lateral pillar of the olecranon fossa.

The cresting of the proximal portion of the ulnar olecranon process is damaged (Fig. 7). The

olecranon process is short and aligned with the long axis of the diaphysis. The posterior margin of the proximal epiphysis is slightly convex. The anconeal process is short and does not project markedly anteriorly. Although eroded, the proximal margin of the anconeal process is asymmetric, with a proximal projection of its lateral margin. The ulnar sigmoid notch is fractured at its mid-height. The ulnar trochlear surface is poorly waisted and congruent with the moderate enlargement of the humeral trochlea. The postero-medial portion and the most anterior portion of the coronoid process is missing as is the postero-lateral portion of the radial notch. The anterior margin of the coronoid process is wide and is antero-distally slanted, consistent with a shallow humeral coronoid fossa. The radial notch is expanded, presents a waisting between its anterior and posterior facet and bears a lateral margin oriented posteriorly. The medial face of the proximal epiphysis is fractured longitudinally but exhibits a deep and wide insertion surface for the flexor digitorum profundus muscle that extends distally through the proximal part of the diaphysis. The ulnar diaphysis is fractured in its mid- and distal portion, resulting in separate fitting parts. The proximal portion of the diaphysis exhibits a raised supinator crest that borders a large insertion surface for the supinator muscle. The diaphysis is gracile and straight in lateral view. A raised pronator ridge is present on the distal portion of the diaphysis. The distal epiphysis is broken away.

The radius preserves the damaged proximal half. Only the antero-lateral portion of the radial head is missing (Fig. 7). The radial head is elliptical with the long-axis running antero-posteriorly. The articular fovea of the radial head is placed posteriorly and is bordered anteriorly by a wide peripheral articular surface and posteriorly by a proximally-raised margin. The radial head is strongly tilted in medio-lateral view. The neck is short, gracile, and bears a marked bicipital

tuberosity divided in two components by a deep sulcus. The medial margin of the proximal portion of the diaphysis is slightly concave and exhibits a faint interosseous crest whereas the lateral margin bears signs of rugosities for the supinator muscle.

TM 266 03-307 is a right femur with a damaged proximal epiphysis preserving the femoral neck, the postero-proximal aspect of the greater trochanter, a slight hint of the proximal portion of the intertrochanteric crest and the medial portion of the lesser trochanter. The distal third is broken away (Fig. 7). The neck is antero-posteriorly compressed, bears no grooving for the obturator externus tendon, forms an obtuse neck-shaft angle with the femoral shaft and is poorly anteverted. The cortical bone distribution of the femoral neck is asymmetric with a cortical bone distribution skewed toward the inferior margin of the neck, as in most extant cercopithecids (Rafferty, 1998). The trochanteric fossa is rounded, shallow and does not extend distally below the insertion for quadratus femoris. The shaft is robust and slightly bowed anteriorly. The medial margin of the lesser trochanter is salient and projects postero-medially. Inferiorly to the lesser trochanter is a rugose zone for the pectineal line and gluteal tuberosity. Although fragmented, TM 266 03-307 is here included in the *C. bruneti* hypodigm based both on its estimated body mass (SOM Table S1), which is consistent with values obtained from dental dimensions, and on its provenance from the *C. bruneti* type locality (i.e., locality n°266).

Comparative anatomy and functional morphology of* C. bruneti *postcranial anatomy

C. bruneti upper limb morphology presents clear colobine affinities in exhibiting a prominent zona conoidea (Frost and Delson, 2002), a marked breadth differential between the lateral and medial pillar of the olecranon fossa, an extensive ulnar insertion site for flexor

digitorum profundus (Krentz, 1993; DeSilva et al., 2013), a marked asymmetry of the peripheral articular surface of the radial head (Nakatsukasa et al., 2010) and a poorly defined interosseous crest on the radius (DeSilva et al., 2013). Considering humeral morphology, *C. bruneti* is similar to *C. williamsi*, *C. kimeui* and *C. meavae* in exhibiting a retroflexed medial epicondyle and a deep distal articular surface antero-posteriorly (i.e., *HDB* variable in Table 6) (Frost and Delson, 2002; Jablonski and Leakey, 2008). An abbreviated and retroflexed medial epicondyle has been linked to terrestrial locomotor behavior and particularly to stability enhancement of the humero-ulnar joint in pronated position (Jolly, 1967; Birchette, 1982). A moderate extension of the deltoid tuberosity and a proximal insertion of the teres major and pectoralis major illustrate an enhancement of rapid flexion/adduction of the *C. bruneti* elbow. The Chadian colobine exhibits an elliptical cross-section of the humeral mid-diaphysis, consistent with a structural adaptation related to stress dissipation of mechanical loadings engendered during terrestrial locomotor behavior (Fig. 9) (Carlson et al., 2011; Patel et al., 2013). Although structurally adapted to withstand mechanical stress and rapid flexion/extension in a terrestrial context, the functionally mosaic humeral morphology of *C. bruneti* exhibits characters reminiscent of arboreal locomotor habits. The enlargement of the humeral trochlea of *C. bruneti* is moderate, translating a weight-bearing function to the humero-ulnar joint as in extant arboreal Colobinae (Birchette, 1982). Although marked relative to extant Colobinae (Fig. 8), the development of the medial trochlear keel of *C. bruneti* is moderate relative to *C. williamsi* and *C. meavae* and reflects a humero-ulnar joint poorly adapted to restrict medial movement as occurred during leaping and/or terrestrial activities (Fig. 9) (Birchette, 1982; Harrison, 1989; Frost and Delson, 2002). The humeral shaft of *C. bruneti* is gracile and accords well with generating low reaction forces and an adaptation to

compliant substrate, as found in an arboreal context (Nakatsukasa, 1994). The insertion for the coracobrachialis profundus muscle is depressed and the insertion for the flexor digitorum profundus muscle on the ulna is marked and extensive, as in arboreal cercopithecids (Krentz, 1993). Relative to ulnar morphology, the olecranon process of *C. bruneti* is short and, coupled with a deep humeral olecranon fossa, reflects an important degree of elbow extension. The olecranon process is straight and not consistent with the anteflexed olecranon of arboreal colobines (Fig. 8) nor with the retroflexed olecranon of highly terrestrial Cercopithecinae (Birchette, 1982). In addition, the straight ulnar shaft contrasts with the posteriorly convex shaft of arboreal colobines (Fig.e 8) (Birchette, 1982). Consistent with the previously inferred weight-bearing function of the humero-ulnar joint*, C. bruneti* exhibits an enlarged humeral articular facet of the ulnar sigmoid notch (Table 6). A short anconeal process and a distally slanted coronoid process confirm the presence of a poorly stabilized humero-ulnar joint in *C. bruneti*. This flexibility of the elbow joint is consistent with an arboreal component in the locomotor behavior of the Chadian colobine. In accordance with the humeral morphology, the ulnar shaft is gracile. A marked elliptical radial head is observed in both extant *Colobus* and *C. bruneti* (Birchette, 1982). With a marked proximal projection of its posterior margin and a strong medial tilt, the radial head of *C. bruneti* is consistent with a reinforcement of the humero-radial joint in pronated position (Rose, 1988). The radial neck of *C. bruneti* is gracile and confirms the patterns of a poorly buttressed brachium and antebrachium. Considering femoral morphology, the neck-shaft angle of *C. bruneti* is obtuse, contrasting with the acute angle seen among hyper-terrestrial cercopithecids and reflecting an increase in hindlimb range of motion (Bacon, 2001; Frost).

Discussion

Cercopithecoides bruneti sp. nov. from the Late Miocene of Central Africa, Chad adds to the antiquity and to the extensive geographical range of the genus *Cercopithecoides*. The mandibular morphology of *C. bruneti* corroborates the presence of a relatively deep and slender corpus among early representatives of this genus (Fig. 4) (Leakey et al., 2003; Jablonski and Frost, 2010). It also documents a departure from the cercopithecine-like symphyseal topography documented in Miocene East African stem Colobinae (Benefit and Pickford, 1986) and brings evidence of a diversity in mandibular morphology among *Cercopithecoides*. Discrepancies in corporeal and symphyseal cross-sectional geometry and morphology further inform us on divergent structural adaptations to withstand at least different stress and loading regimes during feeding behavior (Ross et al., 2012). The relationships between diet, feeding behavior and mandibular morphology are not straightforward among primates (Daegling and McGraw, 2001; Daegling and Grine, 2017), blurring the ecomorphological signal inferred from corporeal and symphyseal morphology among early and late representatives of *Cercopithecoides* taxa. A frugivorous component was identified in the *C. williamsi* diet through Dental Microwear Textural Analysis (DMTA) (Williams and Geissler, 2014), and several proxies point to a fruit-dominated diet among Eurasian and several Late Miocene early colobines (Merceron et al., 2009; Rossie et al., 2013; Thiery et al., 2017). In contrast, the East African Miocene colobines from Lukeino Fm. and Mpesida Beds, respectively at ca. 5.7 and 6.37 Ma,

bear qualitative and quantitative (i.e., NH/NR) dental morphological hallmarks of adaptation to a leaf-dominated diet (Gilbert et al., 2010). *C. bruneti* occlusal relief is moderate relative to extant colobines but stands apart from the cercopithecine-like occlusal relief documented in North African (Benefit et al., 2008) and Eurasian Miocene colobines (Fig. 1). Accordingly, *C. bruneti* dental morphology provides evidence of an increase in occlusal relief and thus supports an increase in leaf consumption at ca. 7 Ma among African colobines relative to penecontemporaneous early African and Eurasian colobines. Subsequent adaptation to the consumption of abrasive food items had been postulated in regard to the severe degree of dental attrition wear stages observed among several *Cercopithecoides* taxa (Szalay and Delson, 1979; Jablonski and Frost, 2010). *C. bruneti* provides the earliest evidence of this peculiar dental wear pattern which may be linked to grit transport due to the onset of the Sahara Desert in Central Africa at ca. 7 Ma (Schuster, 2006).

The associated colobine postcranial remains from Nakali shed light on arboreal locomotor behavior among Late Miocene African stem Colobinae (Fig. 8) (Nakatsukasa et al., 2010). Further evidence of arboreality was inferred among several groups of early colobine postcranial remains from other Miocene East African localities (Hlusko, 2007; Gilbert et al., 2010). Contrasting with a plesiomorphic arboreal postcranial bauplan, the radiation of the Plio-Pleistocene *Cercopithecoides* taxa has been associated with locomotor behavior that includes moderate to marked terrestrial locomotor habits (Jablonski and Leakey, 2008). Morpho-functional adaptation to terrestrial locomotor behavior is inferred among Eurasian Miocene colobines (Fig. 8) (Youlatos et al., 2012; Youlatos and Koufos, 2010) but tenuous evidence of terrestriality was postulated from fragmentary and isolated Miocene colobine forelimb remains

from East Africa (Leakey et al., 2003). A nearly complete forelimb attributed here to *C. bruneti* firmly demonstrates a partial reacquisition of terrestrial locomotor behavior among colobines as early as the Late Miocene (Fig. 8-9) and confirms the autapomorphic condition of terrestrial habits in the locomotor behavior of the genus *Cercopithecoides*. Additionally, the Chadian colobine documents a morpho-functional trade-off typical of *Cercopithecoides*, with an elbow joint adapted to withstand stress engendered by terrestrial locomotor habits and to promote joint flexibility during foraging and frequent arboreal locomotor habits (Jablonski and Leakey, 2008). In addition to shedding light on the locomotor diversity of early African colobines, *C. bruneti* also establilshes the presence of an extreme variant of early molar eruption pattern among Late Miocene African colobines and confirms the diversity of dental eruption pattern inferred among early colobines (Harvati and Frost, 2007).

Toros-Menalla is similar to other East African Miocene cercopithecid-bearing localities in exhibiting an abundance of Colobinae relative to Cercopithecinae (Harrison, 2011). It also brings evidence for a substantial ecomorphological diversity among Miocene colobines, giving support to the hypothesis of a short-fused model of the adaptive radiation of Colobinae (Frost et al., 2009). The affinity of the East African *C. williamsi* with the tribe Colobini was recently reinforced by the demonstration of its marked pollical reduction (Frost et al., 2015). However, the affinity of the genus *Cercopithecoides* with crown or stem Colobini remains unclear. Fragmentary remains from an indeterminate colobine from the Lukeino Fm. demonstrates the presence of a synapomorphic Colobini astragalar morphology at ca. 6.1 Ma (Gilbert et al., 2010). Unlike the colobine gen. and sp. B from Lukeino Fm., no clear synapomorphic postcranial characters permit to assign *C. bruneti* within the Colobini crown group. However, the molecularly estimated

divergence times of extant Colobini taxa (i.e., 8-6 Ma) is clearly in the time range spanned by *C. bruneti* (Ting, 2008). On one hand, the Chadian colobine exhibits clear dental and mandibular morphological affinities with the African tribe (Fig. 3, 5). On the other hand, it retains plesiomorphic features observed among morphologically conservative Miocene colobines (i.e., square molars, moderate occlusal relief and MS) (Fig. 3). Additionally, the temporal setting of *C. bruneti* and its phenetic affinities with the early Pliocene *C. kerioensis* are in favor of its basal position in the *Cercopithecoides* lineage. Altogether, *C. bruneti* supports a placement of the genus *Cercopithecoides* among the stem (rather than crown) Colobini group.

Summary and conclusions

The newly described postcranial and dentognathic fossil cercopithecid material from the Late Miocene hominin-bearing fossiliferous area of Toros-Menalla sheds light on a previously unknown spatial setting during a poorly sampled, yet critical, period of the adaptive radiation of colobine monkeys in Africa.

We demonstrate the oldest occurrence of a speciose early colobine genus previously and securely known only from Plio-Pleistocene deposits of eastern and southern Africa. In addition to further documenting the morphological diversity of *Cercopithecoides*, *C. bruneti* supports the presence of gracile mandibular morphology as well as the autapomorphic condition of terrestrial locomotor habits among early representatives of its genus. While phenetic affinities of *Cercopithecoides* with the Colobini crown group are corroborated, in-depth analysis of the dentognathic morphology of *C. bruneti* underlined its basal position by revealing its morphological departure from the mandibular and dental anatomy of extant African colobines,

lending further support to a phylogenetic placement of *Cercopithecoides* into the stem Colobini group.

As an anatomical hallmark of extant colobines, the emergence of a folivorous dental morphology is of prime interest in the understanding of the colobine adaptive radiation. On this aspect, *C. bruneti* departs from the cercopithecine-like occlusal relief and the subsequently inferred frugivory documented among penecontemporaneous colobines, bringing evidence of an increase in leaf consumption among African Miocene colobines. Similarly, we demonstrate the presence of a terrestrial signal in the *C. bruneti* postcranial morphology, confirming the alteration of the colobine postcranial arboreal bauplan as early as 7 Ma in Africa.

By providing evidence of substantial ecomorphological diversity among Miocene colobines, we highlight the role of Central Africa not only in the radiation of extant cercopithecids but also in the early evolutionary history of those widespread primates.

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Figure captions

Figure 1. Dental indices of *C. bruneti* holotype (TM 266 03-100) and extinct African colobines. Morphologies of extant cercopithecids associated with the maximum and minimum ratio value

are figured on the right of the graphs. Violin plots of extant Colobini on the right. Boxplots of early colobines on the left. Miocene colobines in underlined brown font and boxplot in brown background. Plio-Pleistocene colobine boxplots in grey background. Boxplots with mean (red circle), median (black square), first quartile, third quartile, minimum and maximal values as well as outliers (red diamonds). *C. bruneti* values identified by a black arrow. ASBI: As Sahabi; LMDG'O: Lemudong'o; MNCR: Menacer; KF: Koobi Fora; EA: East Africa; SA: South Africa. Dental indices calculated from value provided in Freedman, 1957; Delson, 1973; Frost, 2001; Frost et al., 2003, 2014; Leakey et al., 2003; Leakey, 1987; Hlusko, 2006, 2007; Benefit et al., 2008; Gilbert and Frost, 2008; Jablonski and Leakey, 2008; Suwa et al., 2015.

(*A.*) M^2 crown shape ratio (CSR) as M^2 PBL*100/MD with *Colobus* sspp. (*n*=50), *Piliocolobus* sspp. (*n*=16), *Procolobus verus* (*n*=12) and African fossil colobines. **(*B.*)** P^{3-4} breadth differential (BD) as P^3BL*100/P^4BL with *Colobus* sspp. (*n*=45), *Piliocolobus* sspp. (*n*=16), *Procolobus verus* (*n*=12) and African fossil colobines **(*C.*)** Boxplot of the upper molars NH/NR ratio of *C. bruneti* (*n*=1; M^2 from TM 266 03-100), *C. williamsi* (*n*=1; M^1 from KB5277), *M. pentelicus* (*n*=3; M^2 from NHMW 1863, NHMW 1998, PK25), M^2s from extant Cercopithecinae (*n*=8) and extant Colobinae (*n*=18).

Figure 2. Digital photographs of *C. bruneti* maxillary remains. ***A.-N.*** TM 266 03-100 (***A.-F.***) left side, (***G.-L.***) right side, (***B.&G.***) mesial view, (***A.&H.***) distal view, (***C.&J.***) buccal view, (***D.&I.***) lingual view, (***E.&L.***) superior view, (***F.&K.***) occlusal view, (***M.***) section at the mesial loph of right M^2, (***N.***) section at the mesial loph of left M^2 (***N.***). ***O.-Z.*** TM 266 03-034 (***Q.&Z.***) lingual view, (***O.&V.***) mesial view, (***P.&Q.***) buccal view, (***R.&Y.***) occlusal view, (***S.&X.***) labial view, (***T.&W.***) lingual view.

Abbreviations: A= Anterior; Ap= Apical; M= Medial, P= Posterior, L= Lateral, B= Buccal, M= Medial, S= Superior.

Figure 3. ***(A.)*** Comparative anatomy of *Cercopithecoides spp.* (i.e., *C. bruneti* and *C. williamsi*) dental morphology relative to extant Colobini (i.e., *Colobus spp.*, *Piliocolobus spp.* and *Procolobus verus*). ***(B.)*** Comparative anatomy of juvenile *Cercopithecoides* spp. (i.e., *C. bruneti* and *C. williamsi*) cranial morphology relative to extant juvenile Colobini (i.e., *Colobus guereza* sspp. indet.) with photographs courtesy of the Mammalian Crania Photographic Archive Second Edition (MCPA2) of the Dokkyo Medial University (http://1kai.dokkyomed.ac.jp/mammal/en/mammal.html).
Abbreviations: Mes=Mesial, Lng=Lingual, Sup=: Superior, Lat=Lateral, Post=Posterior, Ant=Anterior.

Figure 4. Digital photographs of C*. bruneti* mandibular remains. ***A.-I.*** TM 219 01-102 ***(A.)*** occlusal view, ***(B.)*** inferior view, ***(C.)*** right side view, ***(D.)*** left side view, ***(E.)*** labial view, ***(F.)*** posterior view, (***G.***) sagittal cross-section at symphysis, (***H.***) coronal cross-section at mid-P_3 a, ***(I.)***. coronal cross-section mid-M_2. ***J.-R.*** TM 266 03-099 ***(J.)*** occlusal view, ***(L.)*** inferior view, ***(M.)*** right side view, ***(N.)*** labial view, ***(E.)*** labial view, ***(O.)*** posterior view (***P.***) sagittal cross-section at symphysis (***Q.***) coronal cross-section at mid-P_3, (***R.***) coronal cross sectionsand mid-M_1. ***S.-A3.*** TM 112 00-093 (***Y.***) sagittal cross-section at symphysis, (***Z.***) coronal cross-sections at mid-P_3, (***A1.***) coronal cross-section at mid-M_1, (***A2.***) coronal cross-section at mid-M_2 , (***A3.***) coronal cross-section at mid-M_3.

Abbreviations: S= Superior; A=Anterior; M=Medial, P=Posterior, L=Lateral.

Figure 5. Comparative anatomy of *Cercopithecoides spp.* (i.e., *C. bruneti* and *C. williamsi*) mandibular morphology relative to extant Colobini (i.e., *Colobus guereza occidentalis*, *Piliocolobus badius badius* and *Procolobus verus*). ***A.1-3*** anterior view, ***B.1-3*** lateral view, ***C.1-3*** superior view, ***D.1-3*** saggital cross-section at symphysis, ***E.1-3*** coronal cross-section at mid-M_1. Abbreviations: Sup=Superior, Lat=Lateral, Post= Posterior, Ant= Anterior.

Figure 6. Mandibular morphometric indices of *C. bruneti* paratypes (i.e., TM 266 03-099, TM 219 01-102, TM 112 00-093), *C. williamsi* (i.e., KB680, STS 394) and extant African (*n*=37) and Asian colobines (*n*=66). Morphologies of extant Colobinae associated with the maximum and minimum ratio value are figured on the right of the graphs. Violin plots of extant Colobini and Presbytini on the right. Boxplots of early colobines on the left. Miocene colobines in underlined brown font and boxplot in brown background. Plio-Pleistocene colobine boxplots in grey background. Boxplots with mean (red circle), median (black line), first quartile, third quartile, minimum and maximal values as well as outliers (red diamonds). *C. bruneti* values identified by a black arrow. For extended measurement protocol, refer to SOM Figure S1. **(*A.*)** STT/ITT ratio of *C. bruneti* (*n*=3), *C. williamsi* (*n*=1; KB680) and extant African and Asian Colobinae with STT/ITT as [(SBSTT/SBITT)*100]. **(*B.*)** Symphyseal angle of *C. bruneti* (*n*=3), *C. williamsi* (*n*=1; KB680) and extant African and Asian Colobinae. ***(C.)*** Relative position of the genioglossal fossa (GFP) of *C. bruneti* (*n*=2; TM 219 01-102, TM 112 00-093), *C. williamsi* (*n*=1; KB680) and extant African and Asian Colobinae with GFP as [(GFH/SL)*100]. **(*D.*)** Symphyseal robustness (SR) in *C. bruneti* (*n*=3;

TM 266 03-099, TM 219 01-102, TM 112 00-093), *C. williamsi* (*n*=1; KB680) and extant African and Asian Colobinae with SR as [(SB/SL)*100]. ***(E.)*** Planum alveolare extension (PAE) in *C. bruneti* (*n*=3), *C. williamsi* (n=1; KB 680) and extant African and Asian Colobinae with PAE as [(PAL/SL)*100]. ***(F.)*** Corpus robustness (CR) at M_1 in *C. bruneti* (*n*=2; TM 266 03-099, TM 112 00-093), *C. williamsi* (*n*=2; KB 680, STS 394) and extant African and Asian Colobinae with CR as [(CWM1/CLM1)*100].

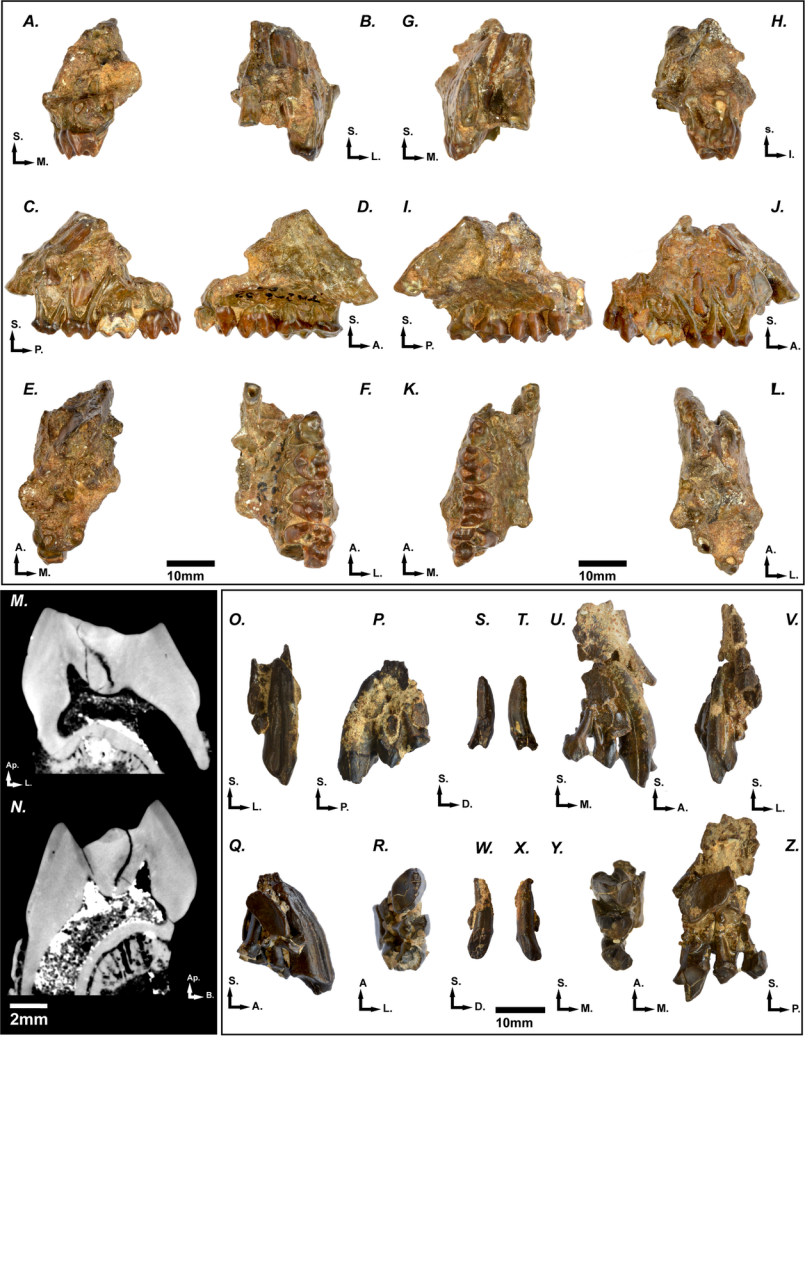
Figure 7. Digital photographs of *C. bruneti* postcranial remains (i.e., TM 266 03-100 and TM 266 03-307) with *C. bruneti* ulna ***(A.-D.)***, radius ***(E.-H.)***, humerus ***(I.-L.)*** and femur ***(M.-P.)***. Abbreviations: Px=Proximal; A= Anterior; M= Medial, P= Posterior, L= Lateral.

Figure 8. Comparative anatomy of extant and extinct Colobinae forelimbs. ***(A.)*** *C. guereza guereza.* ***(B.)*** *P. rufomitratus langi*. ***(C.)*** *M. pentelicus*. ***(D.)*** *Microcolobus.* sp. with photographs reproduced from (Nakatsukasa et al., 2010)). ***(E.)*** Forelimb anatomy of *C. bruneti*. Abbreviations: Prox= Proximal; Med= Medial, Post= Posterior, Lat=Lateral.

Figure 9. Postcranial indices of extant cercopithecids, *C. bruneti* and early colobines (i.e., *Mesopithecus pentelicus*). Morphologies of extant cercopithecids associated with the maximum and minimum ratio value are figured on the right of the graphs. Violin plots of extant cercopithecids on the right. Boxplots of early colobines on the left. Miocene colobines in underlined brown font and boxplot in brown background. Boxplots with mean (red circle), median (black square), first quartile, third quartile, minimum and maximal values as well as

outliers (red diamonds). *C. bruneti* values identified by a black arrow. For extended measurement protocol of medial epicondyle angulation, refer to SOM Figure S1. **(*A.*)** Boxplot of the medial epicondyle angulation of *C. bruneti* (n=1; TM 266 03-036), *M. pentelicus* (*n*=6; PIK 244, 245, 355, 356, 1429, 1727), extant *Papio* ssp. (*n*=26), extant Colobini (*n*=44) and extant Presbytini (*n*=38). **(*B.*)** Boxplot of the medial trochlear keel relative development of *C. bruneti* (*n*=1; TM 266 03-036), *C. williamsi* (*n*=1; KNM-ER 4420 with data from Frost and Delson, 2002), *C. meavae* (*n*=1; AL2-64 with data from Frost and Delson, 2002), *M. pentelicus* (*n*=7; PIK 244, 245, 355, 356,1727,1728,1729), extant *Papio* ssp. (*n*=17), extant Colobini (*n*=34) and extant Presbytini (*n*=22). Medial trochlear keel development calculated and measured as in (Frost and Delson, 2002). **(*C.*)** Boxplot of the Imax/Imin ratio of *C. bruneti* (*n*=1; TM 266 03-034), extant cercopithecines (*n*=6) and extant colobines (*n*=17).

A.
M2 CSR
120
110
100
90
80
C. brunetti
C. alemayehui
C. kimeui
C. cf. meavae
C. meavae
C. williamsi EA
Colobus cf. angolensis
Colobus freedmani
Colobus sp. Asbole
K. aramisi
K. hafu
LMDG/O small colobine
L. markgrafi
MNGR putative colobine
Nawata colobine sp. B
P. enkorikae
P. chemeroni
P. mutiwa KF
R. turkanensis KF
WM colobine sp. B
Colobus sspp.
Piliocolobus sspp.
Procolobus verus sp.
B.
P3-4 BD
110
100
90
80
70
C. alemayehui
C. brunetti
C. kerionensis
C. kimeui
C. meavae
C. williamsi EA
Colobus cf. angolensis
Colobus freedmani
Colobus sp. Asbole
K. aramisi
K. hafu
LMDG/O small colobine
L. markgrafi
P. chemeroni
P. enkorikae
P. mutiwa KF
R. turkanensis Omo
WM colobine sp. B
Colobus sspp.
Piliocolobus sspp.
Procolobus sp.
C.
NH/NR
160
120
80
40
C. brunetti
C. williamsi
M. pentelicus
Extant Cercopithecinae
Extant Colobinae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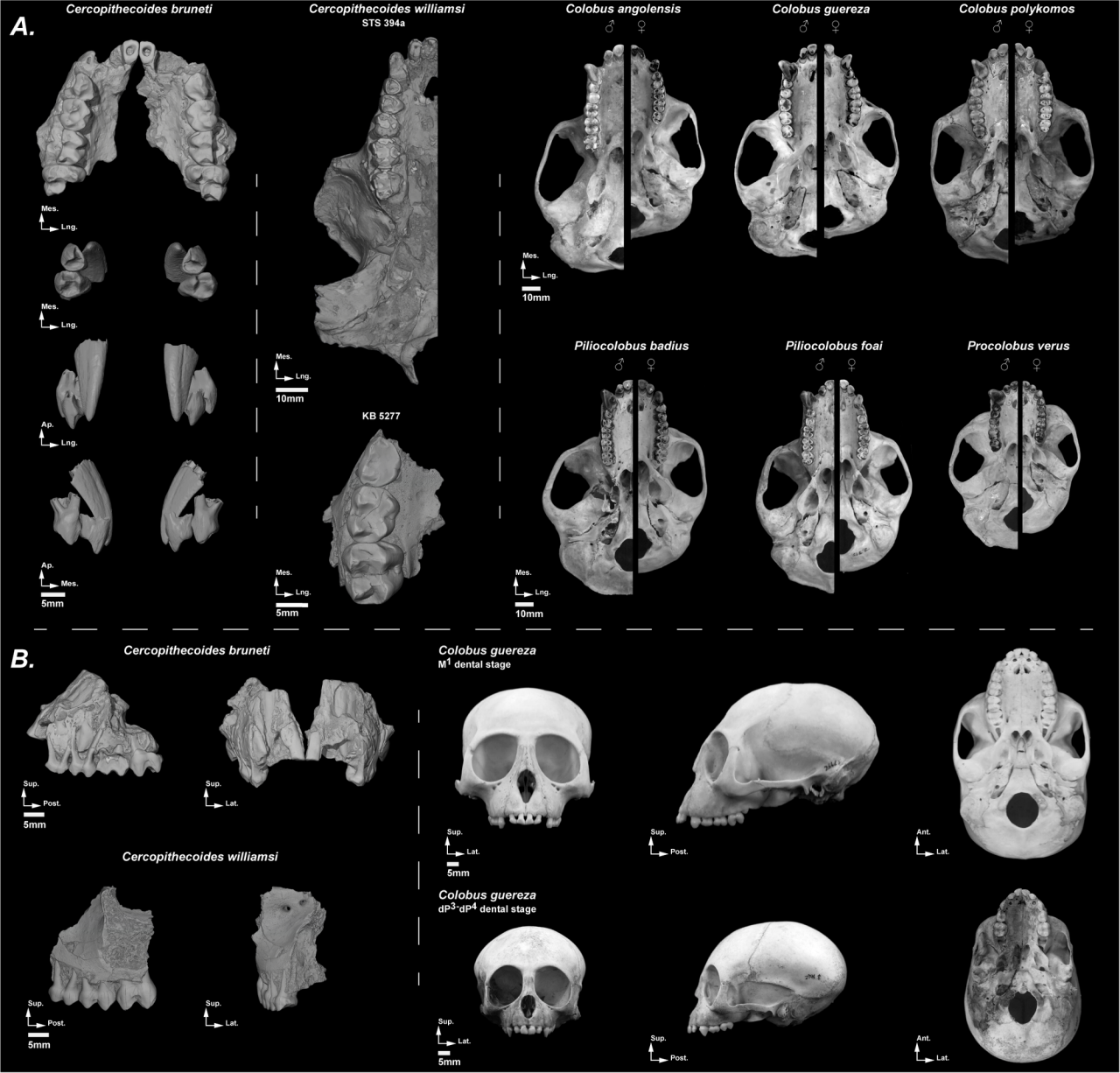
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Ap.
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Cercopithecoides williamsi
STS 394a
Mes.
Lng.
10mm
KB 5277
Mes.
Lng.
5mm
Colobus angolensis
♂ ♀
Mes.
Lng.
10mm
Colobus guereza
♂ ♀
Colobus polykomos
♂ ♀
Piliocolobus badius
♂ ♀
Mes.
Lng.
10mm
Piliocolobus foai
♂ ♀
Procolobus verus
♂ ♀
B.
Cercopithecoides bruneti
Sup.
Post.
5mm
Sup.
Lat.
Cercopithecoides williamsi
Sup.
Post.
5mm
Sup.
Lat.
Colobus guereza
M1 dental stage
Sup.
Lat.
5mm
Sup.
Post.
Ant.
Lat.
Colobus guereza
dP3-dP4 dental stage
Sup.
Lat.
5mm
Sup.
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Ant.
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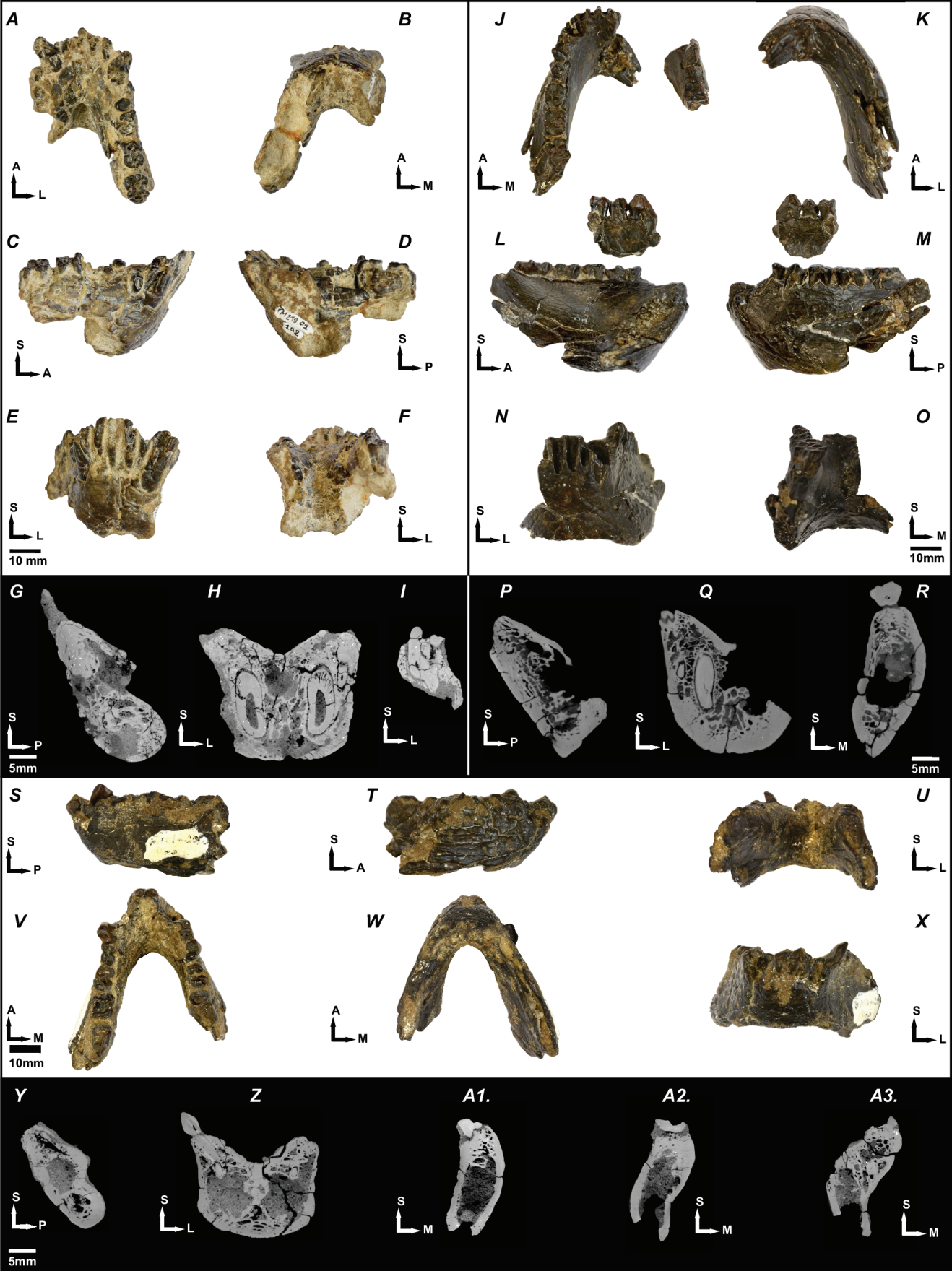
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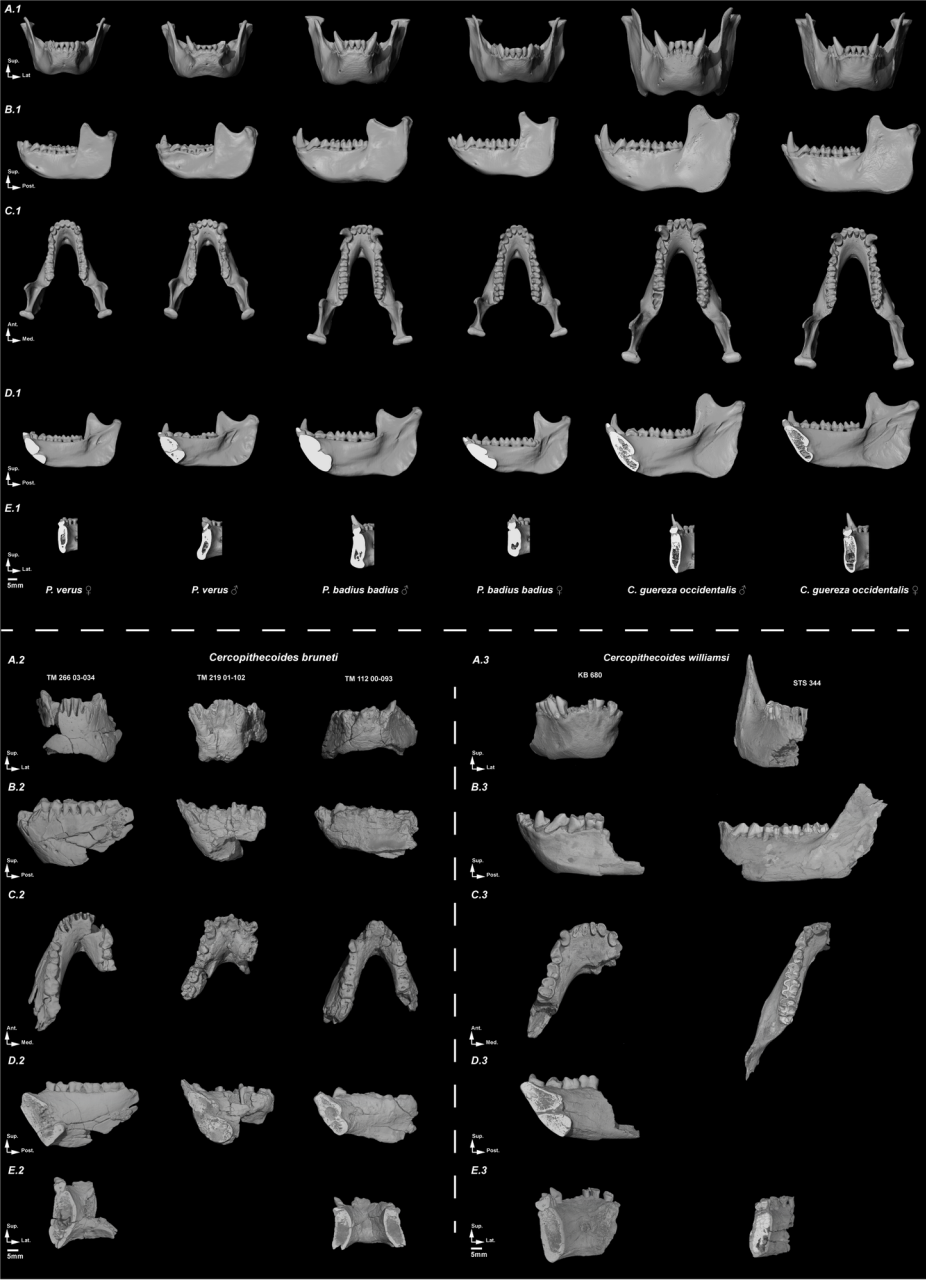
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C.1
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P. verus ♀
P. verus ♂
P. badius badius ♂
P. badius badius ♀
C. guereza occidentalis ♂
C. guereza occidentalis ♀
A.2
Cercopithecoides bruneti
TM 266 03-034
TM 219 01-102
TM 112 00-093
B.2
C.2
D.2
E.2
A.3
Cercopithecoides williamsi
KB 680
STS 344
B.3
C.3
D.3
E.3

A.
STT/ITT
175
150
125
100
75
Presbytini
Colobini
Trachypithecus ssp.
Simias concolor
Semnopithecus ssp.
Semnopithecus roxellana
Rhinopithecus ssp.
Pygathrix verus
Procolobus ssp.
Presbytis ssp.
Piliocolobus ssp.
Nasalis larvatus
Colobus ssp.
C.williamsi
C.brunneii
B.
SA (°)
60
55
50
45
Presbytini
Colobini
Trachypithecus ssp.
Simias concolor
Semnopithecus ssp.
Semnopithecus roxellana
Rhinopithecus ssp.
Pygathrix verus
Procolobus ssp.
Presbytis ssp.
Piliocolobus ssp.
Nasalis larvatus
Colobus ssp.
C.williamsi
C.brunneii
C.
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Presbytini
Colobini
Trachypithecus ssp.
Simias concolor
Semnopithecus ssp.
Semnopithecus roxellana
Rhinopithecus ssp.
Pygathrix verus
Procolobus ssp.
Presbytis ssp.
Piliocolobus ssp.
Nasalis larvatus
Colobus ssp.
C.williamsi
C.brunneii
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Simias concolor
Semnopithecus ssp.
Semnopithecus roxellana
Rhinopithecus ssp.
Pygathrix verus
Procolobus ssp.
Presbytis ssp.
Piliocolobus ssp.
Nasalis larvatus
Colobus ssp.
C.williamsi
C.brunneii
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Colobini
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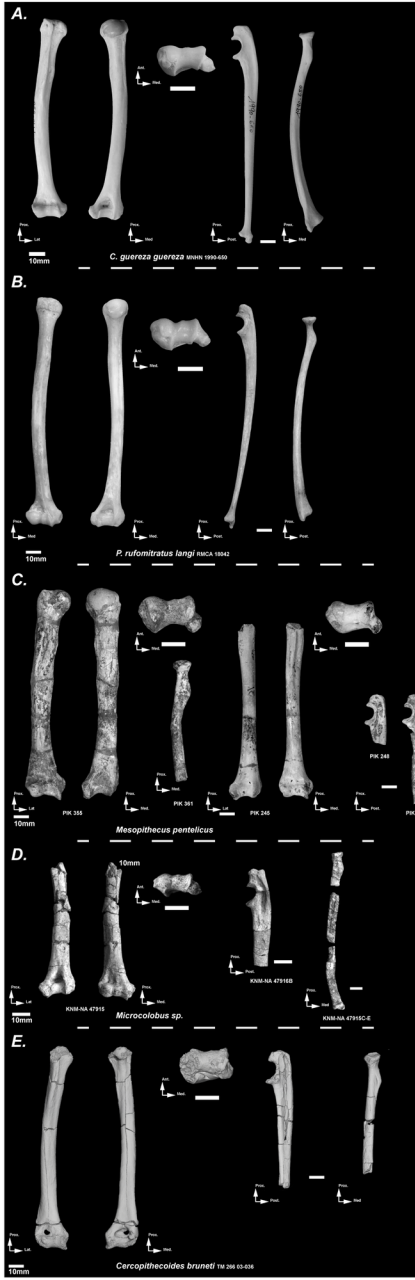
Simias concolor
Semnopithecus ssp.
Semnopithecus roxellana
Rhinopithecus ssp.
Pygathrix verus
Procolobus ssp.
Presbytis ssp.
Piliocolobus ssp.
Nasalis larvatus
Colobus ssp.
C.williamsi
C.brunneii
F.
CR
60
50
40
30
Presbytini
Colobini
Trachypithecus ssp.
Simias concolor
Semnopithecus ssp.
Semnopithecus roxellana
Rhinopithecus ssp.
Pygathrix verus
Procolobus ssp.
Presbytis ssp.
Piliocolobus ssp.
Nasalis larvatus
Colobus ssp.
C.williamsi
C.brunneii

A.
B.
C.
D.
E.
F.
G.
H.
I.
J.
K.
L.
M.
N.
O.
P.
Px.
P.
A.
L.
M.
20mm
20mm
20mm


A.
Ant.
Med.
Prox.
Lat.
Med.
Prox.
Med.
Prox.
Post.
Prox.
Med.
10mm
C. guereza guereza MNHN 1990-650
B.
Ant.
Med.
Prox.
Med.
Prox.
Post.
Prox.
Post.
10mm
P. rufomitratus langi NMCA 18942
C.
Ant.
Med.
Ant.
Med.
Prox.
Med.
Prox.
Lat.
Prox.
Med.
Prox.
Post.
PIK 248
10mm
PIK 355
PIK 361
PIK 245
PIK 249
Mesopithecus pentelicus
D.
10mm
Ant.
Med.
Prox.
Post.
Prox.
Lat.
Prox.
Med.
10mm
KNM-NA 47915
KNM-NA 47916D
KNM-NA 47915C-E
Microcolobus sp.
E.
Ant.
Med.
Prox.
Lat.
Prox.
Med.
Prox.
Post.
Prox.
Med.
10mm
Cercopithecoides bruneti TM 266 03-038

A.
Medial epicondyle angulation (°)
70
60
50
40
30
20
Cercopithecoides bruneti
Mesopithecus pentelicus
Colobini
Presbytini
Papio sp.
B.
Medial trochlear keel relative development
80
70
60
50
40
Cercopithecoides meavae
Cercopithecoides williamsi
Cercopithecoides bruneti
Mesopithecus pentelicus
Colobini
Papio sp.
Presbytini
C.
Imax/Imin
2.0
1.5
1.0
Cercopithecoides bruneti
Cercopithecinae
Colobinae

Table 1: Spatial and temporal setting of the *Cercopithecoides* representatives

	Type locality	***Temporal record***	***Spatial record***
C. bruneti	Toros-Menalla, Chad, **Central Africa**.	ca. 7 Ma.	Only known from its type locality.
C. kerioensis	Lothagam, Kenya, **East Africa**.	ca. 5-4.2 Ma.[1]	Only known from its type locality.
C. meavae	Leadu, Ethiopia, **East Africa**.	3.8 - 3.28 Ma.[2]	Hadar, Leadu, Woranso-Mille[2].
C. kimeui	Olduvai Gorge, Tanzania, **East Africa**	2.5-1.2 Ma.	Olduvai Gorge, Rawi, Koobi Fora, Hadar.
C. haasgati	Haasgat, **South Africa**.	?Pleistocene.[3]	Only known from its type locality.
C. williamsi	Makapansgat, **South Africa**.	3.5-1.5 Ma.	Makapansgat, Sterkfontein, Swarktrans, Cooper's A, Bolt's Farm, Kromdraai, Drimolen, Koobi Fora, ?Shungura, Leba (Angola).
C. alemayehui	Daka, Ethiopia, **East Africa**.	1.0 Ma.	Only known from its type locality.
C. sp. indet. Laetoli	Laetoli, Tanzania, **East Africa**.	3.81-3.63 Ma.	Uncertain taxonomy and known only from Laetoli.
cf. *C. sp. indet.* Koobi Fora	Koobi Fora, Ethiopia, **East Africa**.	3.95-3.45 Ma.	Uncertain taxonomy and known only from Allia Bay[4].
i C. sp. indet. Kanapoi	Kanapoi, Kenya, **East Africa**	4.19-4.11 Ma.	Uncertain taxonomy and known only from Kanapoi.

[1] According to Leakey et al., 2003, there is no secure stratigraphic context relative to *C. kerioensis*.
[2] It includes here specimens from Woranso-Mille and allocated to *C. cf. meavae*.
[3] According to McKee et al., 2011, there is uncertainty relative to the exact temporal setting of the *Cercopithecoides* sample from Haasgat
[4] According to Jablonski et al., 2008, a partial mandible, KNM-ER 36985, exhibit phenetic affinities with *C. kerioensis* but the authors referred to this specimen as *C. sp. indet.*
[5] Uncertain age estimation based on faunal assemblage (Jablonski, 1994)

Table 2: Comparative morphology of the cranio-dental anatomy of *Cercopithecoides spp.*

	BM (kg)[1]	M^2 CSR	P^3-P^4 BD	P^3 protocone	M_3 RHD	M_{1-2} SD	P_4 CSR	MS	STT/ITT	CW
C. bruneti	16.6 - 8.4	111.5	77.2	Faint	63.2	75.4	73	Present	127.6 - 104.3	39.9 - 39.3
C. kerioensis	9.8[2]	NA	93.9	Faint	62.5	NA	NA	NA	NA	NA
C. meavae	17.7 – 15.0[3]	100.0 - 98.9	89.5	Faint	69.5 – 58.2	87.5 - 75.3	74.2 - 61.2	NA	NA	NA
C. kimeui	51.0 - 25.0[4]	106.4 - 89.4	89.2 – 84.0	Faint	89.2 - 84	88.7	76.1	Present	NA	NA
C. williamsi	23.0 – 16.0[4]	107.4 - 87.5	84.8 - 73.1	Faint	84.8 – 73.1	87.6 - 70.9	101.6 - 78.6	Present	142.4	53.2 - 41.1
C. alemayehui	16.3[5]	100.0	82.6	Faint	NA	NA	NA	?Present[8]	NA	NA
C. haasgati	18.2 - 12.3[6]	107.2[7]	82.4[7]	Faint	69.4[7]	71.7[7]	96.6[7]	NA	NA	NA

Range values of odontometric indices and qualitative assessment of several morphological characteristics of *Cercopithecoides spp*. With Body Mass (BM); Crown Shape Ratio (CSR); Breadth Differential (BD); Relative Hypolophid Development (RHD); Maxillary Sinuses (MS); Superior Transverse Torus (STT); Inferior Transverse Torus (ITT); Corpus Width (CW); Not Available (NA).

[1] Based on the equation provided by Delson et al., 2000.

[2] Calculated from M^1 MD dimension with *"All-colobine*" model parameters.

[3] Range value calculated from M^2 MD dimension with *"All-colobine*" model parameters.

[4] Values given in Delson et al., 2000 for the *"Estimated mass"* value.

[5] Calculated from M^2 MD dimension with *"All-colobine*" model parameters.

[6] Range value alculated from M^2 MD dimension with *"All-colobine*" model parameters on minimum and maximum dental dimensions provided in McKee et al., 2011.

[7] Ratio calculated from mean dental dimensions provided in McKee et al., 2011.

[8] The presence of MS is not clearly asserted (Frost et al., 2008).

Table 3 : *C. bruneti* holotype (i.e TM 266 03-100) dental metrics

Measurements

dP³ MD[1]	**5.6 (5.5)**	*P³ MD*[2]	**6.0 (5.9)**
dP³ BL[1]	**5.4 (5.3)**	*P³ BL*[2]	**6.1 (6.1)**
dP⁴ MD[1]	**7.1 (6.8)**	*P⁴ MD*[2]	**6.0 (6.1)**
dP⁴ PBL[1]	**6.8 (6.8)**	*P⁴ BL*[2]	**7.8 (7.9)**
dP⁴ MBL[1]	**6.6 (6.3)**	*M¹ MD*[1]	**7.5 (7.8)**
C¹ MD[2]	**8.4 (8.6)**	*M² MD*[1]	**8.3**
C¹ BL[2]	**5.2 (5.3)**	*M² MBL*[1]	**9.4**

Dental metrics in mm and dental metrics of right teeth given in brackets. *MD*: mesio-distal dimension; *BL*: bucco-lingual dimension; *MBL:* bucco-lingual dimension at the paraloph. Measurement protocol from (Benefit, 1993).
Extended dental metrics in Table S2.
[1] Measurements acquired using a *Mitutoyo* Digital Calliper CD-8''CX on original specimens
[2] Measurements acquired on ImageJ through selected photographs of the segmented model obtained in Avizo Standard Edition

Table 4: Dental metrics and dental indices of *C. bruneti* lower dentition (i.e TM 266 03-099; TM 112 00-093; TM 219 01-102)

Measurement	TM 266 03-099	TM 112 00-093	TM 219 01-102
C_1 *MD*	~5.4	~4.3 (~4.4)	6.7
C_1 *BL*	~8.5	~5.2 (~5.3)	8.9 (9.1)
P_3 *OL*	(7.6)	4.8	
P_3 *TL*	(10.2)	6.8	9.4
P_3 *FL*	(7.7)	6.3	
P_3 *BL*	(4.2)	3.2	
P_4 *MD*	6.1	5.5	6.3
P_4 *BL*	4.4		
M_1 *MD*	6.9	6.6	7.5
M_1 *MBL*	5.7		
M_1 *HBL*	5.6		
M_2 *MD*	7.7	7.1	7.9
M_2 *MBL*	6.8		
M_2 *HBL*	6.4		
M_3 *MD*	10.3	8.8	
M_3 *HBL*	6.5		
M_3 *HYPOB*	3.1		
M_3 *HYPOB/HBL*	47.9		
M_3 *HBL/MD*	63.4		
P_4 *BL/MD*	73.0		
M_{1-2} *SD*	75.5		
P_3 *BL/OL*	55.2	65.8	

Dental metrics in mm and right teeth metrics given in brackets. Dental indices and measurement protocols from (Benefit, 1993; Harrison and Harris, 1996). All measurements acquired using a *Mitutoyo* Digital Calliper CD-8''CX on original specimens. *MD*: mesio-distal dimension; *BL*: bucco-lingual dimension; *OL:* Occlusal length; *TL:* Total length; *FL*: Flange length as in (Benefit, 1993); *MBL:* bucco-lingual dimension at the metalophid; *HBL:* bucco-lingual dimension at the hypolophid; *HYPOB:* bucco-lingual dimension at the hypoconulid.

Table 5: Mandibular morphometry of *C. bruneti* hypodigm

	TM 266 03-099	TM 112 00-093	TM 219 01-102
SL	26.7	20.8	27.5
SA	63.4	62	62.6
GFH		7.9	27.5
PAL	11.3	11.3	27.5
SB	12.3	9.7	27.5
SBSTT	11.3	9.7	27.5
SBITT	12.3	7.6	27.5
CWM1	26.7	18.8	27.5
CLM1	10.5	7.5	27.5

Morphometric data in mm. All measurements taken on selected photographs of symphyseal and corporeal cross section obtained through Avizo and Geomagic and measured through ImageJ. *SL*: symphyseal length; *SA*: symphyseal angle; *GFH:* genioglossal fossa height; *PAL*: planum alveolare length; *SB*: maximum breadth of the symphysis; *SBSTT*: breadth of the symphysis at the STT (superior transverse torus) level; *SBITT*: breadth of the symphysis at the ITT (inferior transverse torus) level; *CWM*1: corpus width at mid-M_1; *CLM1*: corpus length at mid-M_1. For an extended description of the morphometric protocol, refers to SOM Figure S1.

Table 6: *C. bruneti* postcranial morphometric data

Measurements	
HTL	151.7
HML	10.6
HAP	11.7
HAW	19.7
MEPP	2.3
TW	7.0
HAH	11.0
MKPD	12.1
HCW	12.0
HDW	25.3
HDB	15.3
MEA[1]	50.1°
OPH	11.9
TNH	15.9
CPH[1]	7.5
TWMH	8.0
RHAP	14.4
RHML	11.0
RNAP	9.4
RNML	6.2
RTP	8.5
*FAP**	~14.1
*FML**	~14.8
*FNAP**	~10.0
*FNSI**	~11.8
*FNSA**[1]	124°

All measurements in mm and acquired using a *Mitutoyo* Digital Calliper CD-8''CX. *HTL*: Humeral total length; *HML*: Humeral medio-lateral diameter at mid-diaphysis (HTL+5%); *HAP*: Humeral antero-posterior diameter at mid-diaphysis (HTL+5%); *HAW*: Humeral articular width measured as in (Birchette, 1982); *MEPP*: Medial epicondyle posterior projection measured as in (Birchette, 1982); *TW*: Humeral trochlear width measured as in (Birchette, 1982); *HAH*: Humeral distal articular height measured as in (Birchette, 1982); *MKPD*: Humeral medial keel distal projection measured as in (Frost and Delson, 2002); *HCW*: Humeral capitulum and zona conoidea width measured as in (Birchette, 1982); *HDW*: Humeral distal epiphysis width measured as in (Harrison, 1989); *HDB*: Humeral distal epiphysis breadth measured as in (Rose, 1988); *MEA*: Medial epicondyle angulation as in the protocol presented in ;*OPH*: Ulnar olecranon process height measured as in (Ciochon, 1986); *TNH*=Ulnar trochlear notch height measured as in (Birchette, 1982); *CPH*: Ulnar coronoid process height measured as in (Birchette, 1982); *TWMH*: Ulnar trochlear width at mid-height measured as in (Birchette, 1982); *RHAP*: Radial head antero-posterior diameter measured as the long axis of the radial head; *RHML*: Radial head medio-lateral diameter measured as the short axis of the radial head; *RNAP*: Radial neck antero-posterior diameter measured as the long axis of the radial neck; *RNML*: Radial neck medio-lateral diameter as the short axis of the radial neck; *RTP*: Radial tuberosity projection measured as in (Birchette, 1982); *Due to conservation state, the measurement of TM 266 03-307 are given here as estimated value. *FAP*: Femoral mid-diaphysis antero-posterior diameter (taken as a rough estimate of the mid-diaphyseal point and diaphysis subject to distortion); *FML*: Femoral mid-diaphysis medio-lateral diameter (taken as a rough estimate of the mid-diaphyseal point and diaphysis subject to distortion); *FNAP*: Femoral neck antero-posterior diameter; *FNSI*: Femoral neck medio-lateral diameter (femoral neck superior portion abraded); *FNSA*: Femur neck-shaft angle.

[1] Measurements taken from selected photographs.