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ABSTRACT

Up to the mid-1990's, only a few remains of Cercopithecoidea were known from the Lukeino Formation (Tugen Hills, Kenya). Surveys from 1998 onwards by the Kenya Palaeontology Expedition led to the discovery of new material at Aragai, a site situated in the lower levels of the Lukeino Formation dated at *c.* 6-5.8 Ma. Most of the collection consists of craniodental specimens generally well-preserved in a hard matrix but there are three postcranial bones. A new taxon of fossil colobine monkey is described: *Sawecolobus lukeinoensis* n. gen., n. sp. It is a small to medium-sized, short-faced colobine. *Sawecolobus* n. gen. shares many features with *Cercopithecoides* Mollett, 1947, especially in the face and the calvarium, but differs from it by the less pronounced supraorbital tori. The two genera differ greatly in mandibular morphology. In *Sawecolobus* n. gen. the mandibular corpus is slender and not robust as in *Cercopithecoides* Mollett, 1947, and the anterior surface of its symphysis is inclined posteriorly and not vertical. The numerous new specimens from the Lukeino Formation contribute to our understanding of the local diversity of Miocene Cercopithecoidea and fill out the distribution of the superfamily in the continent for the same period.

KEY WORDS
Late Miocene,
Kenya,
Primates,
Cercopithecoidea,
Colobinae,
Sawecolobus,
new genus,
new species.

RÉSUMÉ

Les colobes du Miocène supérieur d'Aragai (Formation de Lukeino, Collines Tugen, Kenya).

Jusqu'au milieu des années 1990, on ne connaissait que peu de restes de Cercopithecoidea de la formation de Lukeino (Tugen Hills, Kenya). Des missions de terrain menées à partir de 1998 par la Kenya Palaeontology Expedition ont conduit à la découverte de nouveaux spécimens à Aragai, un site situé dans les niveaux inférieurs de la formation de Lukeino et datant d'environ 6-5,8 Ma. La plus grande partie de la collection est représentée par des restes cranio-dentaires, généralement bien conservés dans une matrice très dure, et trois os post-crâniens. Un nouveau taxon de colobe éteint est décrit : *Sawecolobus lukeinoensis* n. gen., n. sp. Il s'agit d'un colobe de petite à moyenne taille, à face courte. Le *Sawecolobus* n. gen. partage de nombreuses caractéristiques avec les *Cercopithecoides* Mollett, 1947, notamment au niveau de la face et la voute crânienne, mais certaines sont moins prononcées, comme le développement des torus supra-orbitaires. Les deux genres diffèrent largement dans la morphologie mandibulaire. Chez *Sawecolobus* n. gen., le corps mandibulaire est plus gracile et non robuste comme chez *Cercopithecoides* Mollett, 1947, la surface antérieure de la symphyse est inclinée postérieurement et non verticale. Les nombreux restes de Colobinae provenant de la Formation de Lukeino contribuent à une meilleure compréhension de la diversité locale des Cercopithecoidea du Miocène et complètent les données sur la répartition de la superfamille sur le continent pour la même période.

MOTS CLÉS
Miocène supérieur,
Kenya,
Primates,
Cercopithecoidea,
Colobinae,
Sawecolobus,
genre nouveau,
espèce nouvelle.

INTRODUCTION

In the Tugen Hills (County of Baringo, Kenya), the Late Miocene Lukeino Formation (*c.* 6-5.7 Ma) has yielded remains of the hominid *Orrorin tugenensis* (Pickford 1975a, b; Senut *et al.* 2001; Pickford *et al.* 2002; Gommery & Senut 2006) and isolated fossils of great apes (Senut & Pickford 2004; Senut 2007). Only a few remains of Cercopithecoidea have been described or mentioned from the formation (Pickford 1975a, b; Pickford *et al.* 2009; Gilbert *et al.* 2010). During the surveys of the KPE (Kenya Palaeontology Expedition) (1998 to 2005; 2010-2011), numerous cercopithecoid remains were discovered in the Lukeino Formation. The richest collection was made at Aragai (basal levels of the Lukeino Formation) where several exceptional remains of colobine monkeys were discovered in a small area. From this site, only a single well-preserved right astragalus has been described (KNM-LU 344) attributed to a Colobinae gen. et sp. indet. B by Gilbert *et al.* (2010).

Modern Colobinae are highly diversified in Africa and Asia (Oates *et al.* 1994; Disotell 2000; Groves 2001; Kingdon 2010). They diverged from Cercopithecinae probably during the Middle Miocene (Delson 1994; Pickford 1987a,b; Gundling & Hill 2000). The oldest fossil Cercopithecoidea are known perhaps from the terminal late Oligocene at Nsungwe in Tanzania (Stevens *et al.* 2013) or the basal early Miocene at Nakwai in Kenya (Rasmussen *et al.* 2019; Reynoso 2014). They are definitely represented in the Early Miocene at Napak in Uganda (Bishop 1964; Pilbeam & Walker 1968; Pickford *et al.* 1986, 2019), in Kenya at Buluk (Leakey 1985; Leakey & Walker 1985; Locke *et al.* 2020), Loperot (Szalay & Delson 1979; Benefit & McCrossin 2002; Grossman *et al.* 2014), and at Moghara in Egypt (Fourtau 1918; Simons 1969; Delson 1979; Miller *et al.* 2009). In the 1970's-1990's molecular biologists suggested that the Colobinae emerged in the basal Late Miocene (Cronin & Sarich 1976; Goodman *et al.* 1998), but more recent research concerning the dichotomy between the two subfamilies now propose a Middle Miocene divergence (Raaum *et al.* 2005; Sterner *et al.* 2006; Ting 2008; Perelman *et al.* 2011). The oldest African Colobinae are known from the late Middle Miocene at Kabarsero (Kenya) by two isolated teeth (species indet.) (Rossie *et al.* 2013), from the basal Late Miocene at Sheikh Abdallah (Egypt) by a fragmentary maxilla belonging to an indet. Colobinae (Mein & Pickford 2010), from Nakali (Kenya) by a skeleton and some isolated teeth of *Microcolobus* sp. (Nakatsukasa *et al.* 2010), and from Ngeringerowa (Tugen Hills, Kenya) by a mandible (the holotype of the species) of *Microcolobus tugenensis* (Benefit & Pickford 1986). In the middle of the late Miocene, they are recorded in the Chorora Formation (Ethiopia) (Suwa *et al.* 2015) and at Menacer in Algeria as "? *Colobus*" *flandrini* (Arambourg 1959; Szalay & Delson 1979; Thomas & Petter 1986). In the latest Miocene/basal Pliocene, they are known at Gar Maluk (Wadi Natrun, Egypt) by *Libypithecus markgrafi* (Delson 1973, 1975; Stromer 1913), at Sahabi (Libya) by Colobinae indet. (Benefit *et al.* 2008), in North-Central Africa at Toros-Menalla (Chad) by *Cercopithecoides bruneti* (Pallas *et al.* 2019), but also in East Africa from the Mpesida Formation in the Tugen Hills (Kenya) (Colobinae gen. and sp. indet B) (Pickford *et al.* 2009; Gilbert *et al.* 2010), at Nkondo (Uganda) by a few teeth assigned to cf. *Paracolobus* sp. (Senut 1994) and at Lemudong'o (Kenya) by *Paracolobus enkorikae* and two other Colobinae indet. (Hlusko 2007). In slightly more recent deposits, they are known from the Asa Koma Member of the Adu-Asa Formation in the Middle Awash (Ethiopia) cf. *Kuseracolobus aramisi* and a large indeterminate Colobinae (Frost *et al.* 2009), at Asa Issie (Ethiopia) by *Kuseracolobus hafu* (Hlusko 2006), at Gona from the Sagantole Formation (Ethiopia) by *Kuseracolobus aramisi* (Frost *et al.* 2020a), and in Kenya at Lothagam by *Cercopithecoides kerioensis* (Leakey *et al.* 2003) and Kanapoi by cf. *Kuseracolobus* sp. and Colobinae genus and species indeterminate (Frost *et al.* 2020b).

Fig. 1. — View of the site of Aragai, in the foreground, with the characteristic orange-red sediment of the Lukeino Formation, in the background are the Tugen Hills.

Colobines underwent a major radiation in the basal Pliocene of East Africa and during the Plio-Pleistocene diversification occurred in Eastern and Southern Africa (Freedman 1957; Jablonski *et al.* 2008; Jablonski & Frost 2010; Harrison 2011). During the Late Miocene and the Pliocene, colobines dispersed to Eurasia where they underwent another major diversification (*Dolichopithecus*, *Paradolichopithecus*, *Procynocephalus*, *Kanagawapithecus*, *Mesopithecus*, *Myanmarcolobus*, *Parapresbytis*, *Presbytis*, *Semnopithecus*, etc.) (Delson 1973, 1975; Szalay & Delson 1979; Zapfe 1991; Jablonski 2002; Delson *et al.* 2005; Koufos 2009; Costeur & Malvesy 2010; Nishimura *et al.* 2012; Takai *et al.* 2015).

In this paper, we describe new specimens of Colobinae collected by the KPE at Aragai (Upper Miocene of the Tugen Hills, Kenya). Numerous sites in Africa have yielded some primate remains from the Late Miocene and/or the beginning of the Early Pliocene, the specimens remain sparse and it is difficult to obtain precise taxonomic information. During this geological period, the geographical distribution of Colobinae in Africa was broad and different environments probably existed which promoted diversification of these primate.

STRATIGRAPHIC, CHRONOLOGICAL AND PALAEONTOLOGICAL CONTEXTS

The geology and stratigraphy of the Tugen Hills was studied by one of us (MP) in the 1970's who identified nine sedimentary formations spanning a long time period from the late early Miocene (around 17 Ma) to the Present (Pickford 1975a, b; Pickford *et al.* 2009). The fossil colobines studied herein came from the Lukeino Formation which accumulated *c.* 6 to 5.7 Ma (Pickford 1975a, b; Hill *et al.* 1985; Pickford & Senut 2001; Deino *et al.* 2002; Kingston *et al.* 2002; Sawada *et al.* 2002; Pickford *et al.* 2009; Dericquebourg 2016). The Lukeino Basin was predominantly a freshwater (and alkaline) lacustrine ecosystem for most of its existence. Near the base of the formation there is an intercalation of terrestrial and lacustrine deposits and as a result, the fossiliferous sites yield mixed assemblages of terrestrial and aquatic forms (Pickford *et al.* 2009).

Aragai (Locality 2/228 [grid reference 212805] [Fig. 1] from Pickford [1975a] and Pickford *et al.* [2009]) is the southernmost site in the Lukeino Formation (GPS location 00°34'45.1"N, 35°50'42.0"E with WGS 84 datum) (Pickford *et al.* 2009) but also corresponds to the oldest sedimentary

Fig. 2. — View of the site of Aragai, in the foreground, the small area (with orange-red sediment and around the big *Balanites* tree) which yielded the colobine material.

level within it, in the basal Lower Kapgoywa Member (aged probably *c.* 6 to 5.83-5.89 Ma) below a geomagnetic polarity event, the boundary between Chrons C3An.1n and C3r (Sawada *et al.* 2002; Dericquebourg 2016; Dericquebourg *et al.* 2019).

This site might correspond to a lake margin for the two fossiliferous levels in the basal part of the stratigraphic section (Dericquebourg 2016; Dericquebourg *et al.* 2019). The lower of the two is represented by red silts with hard ferruginised sand. Some footprints of large animals (Pickford *et al.* 2009) and phosphatic nodules (Dericquebourg *et al.* 2019) are present in this unit. Some of these nodules, discovered in a relatively small area (around 20 m^2) (Fig. 2), contained vertebrate remains such as colobines (Pickford & Senut 2001). This level is overlain by a pink fluvial sand and an intraformational conglomerate, where a femoral neck (BAR1215’00) of *Orrorin tugenensis* was found (Senut *et al.* 2001).

The lowest level yielded all the remains of colobines associated with parts of an impala (*Aepyceros* sp.), a hyracoid maxilla (the holotype of *Dendrohyrax samueli*, BAR 961’01 [Pickford 2005]), a juvenile suid mandible (*Nyanzachoerus tulotos*) and remains of rhinocerotids, equids and proboscideans (Pickford 2005; Pickford *et al.* 2009).

MATERIAL AND METHODS

All the studied material was collected at Aragai by the KPE. All specimens are curated by the Orrorin Community Organization (OCO) a Community Based Organisation in the Tugen Hills (see the list for the type specimen). The sample consists of 35 craniodental (including isolated teeth) and postcranial specimens, including three small numbered fragments which fit onto bigger specimens and are thus not included in the previous total of specimens. Most of the larger specimens are included in, or covered by a hard phosphatic matrix, which is difficult to clean and can only be removed mechanically (Fig. 3). Due to the fragility of the fossils, the cleaning had to be stopped on some specimens. The two skulls (BAR 757’00 and BAR 758’00) were prepared by Jane Chesang and David Chebor of the OCO. The smallest fossils, generally isolated teeth, were found on the surface of the red sediment or *in situ* with or without matrix.

Uppercase letters are used for upper teeth and lower case for lower teeth, followed by the meristic position except for the canine (see abbreviations). To prevent confusion due to the diversity of dental nomenclatures employed in the literature, a "/" is placed after the letter and the meristic for upper teeth and the "/" is placed between the letter and meristic position for lower teeth (e.g. p/3 lower third premolar, M1/, upper first molar), except for the canine where the unique letter is before the "/" for upper canine and after the "/" for the lower.

The anatomical nomenclature is based on and adapted from Delson (1975), Swindler (2002) and Szalay & Delson (1979) for the molars; for the premolars and the canines, it is based on Pickford *et al.* (2010). Dimensions of the teeth are given in millimetres and follow the method of Freedman (1957), in particular for the mesial (Mb) and distal (Bd) widths of the molars.

The wear stage system from Ingicco *et al.* (2012) is used here for assessing the ontogenetic age of the specimens.

The comparative material includes 252 specimens of African colobines from the Zoology Department – Afrika Museum in Tervuren in Belgium (*Piliocolobus tholloni* = 31; *Piliocolobus foai* = 32; *Piliocolobus badius* = 40; *Procolobus verus* = 50; *Colobus polykomos* = 30; *Colobus angolensis* = 43; *Colobus guereza* = 26) (Verheyen 1962), as well as of some Cercopithecinae in the same collection (*Cercocebus agilis* = 5, *Lophocebus albigena* = 5, *Cercopithecus* (*cephus*) *ascanius* = 3, *Cercopithecus lhoesti* = 3, *Cercopithecus neglectus* = 1, *Chlorocebus aethiops* = 3). Some Plio-Pleistocene fossils from South Africa are also included in the comparisons: The type specimen MP3 of *Cercopithecoides williamsi* from Makapansgat (M203/1326-3) (Mollett van der Spuy 1947) and BF 42 from Bolt's Farm (Freedman 1965) curated at the Medical School, University of Witwatersrand (Johannesburg, South Africa) and several specimens from Sterkfontein and Swartkrans curated at the Plio-Pleistocene Palaeontology Section in the Ditsong National Museum of Natural History (Pretoria, South Africa) (Freedman 1957). Some data concerning the type specimen of *Libypithecus markgrafi* (BSPG 1914 II 1) curated at the Bayerische Staatssammlung für Paläontologie und Geologie (München, Germany), are included.

CT Scan

BAR757 and BAR758 were CT-scanned separately using a high-resolution computed tomography (CT) scanner (GE Sensing and Inspection Technologies phoenix|x-ray v|tome|x L240-180) at the AST-RX platform of National Museum of Natural History, Paris, France. The scans were made with a tube voltage of 220 kV, a tube current of 215 µA, a filter of 0.5 mm Cu, a voxel of 0.0475mm for BAR757'00 and with a tube voltage of 230 kV, a tube current of 155 µA, a filter of 1 mm Cu, a voxel of 0.0357 mm for BAR758'00. The Scan method used for the two skulls was fastcan.

The nasal architecture was examined on various cross-sectional images reformatted from the serial CT images using Amira software (version 6.3; FEI Visualization Sciences Group, Burlington, MA, USA).

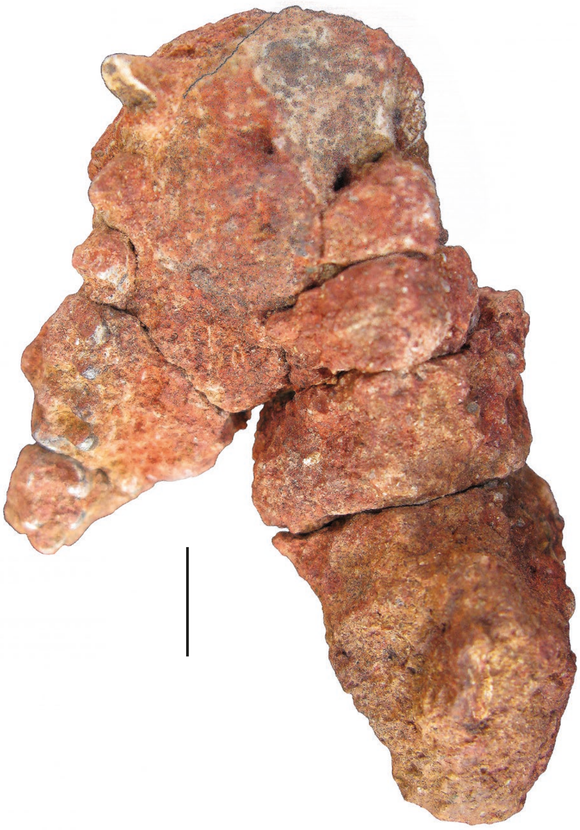

Fig. 3. — The mandible OCO 608'10 in hard phosphatic matrix before mechanical preparation. Scale bar: 1 cm.

Abbreviations

Collection references

BAR	Fossils collected by KPE at Aragai between 2000 and 2005;
OCO	Fossils collected by KPE at Aragai in 2010 and 2011.

Teeth

/c	lower canine;
C/	upper canine;
I1/	first upper incisor;
i/1	first lower incisor;
P3/	third upper premolar;
p/3	third lower premolar;
M1/	first upper molar;
m/1	first lower molar;
R	right;
L	left;
A1	wear stage 1 (Ingicco *et al.* 2012).

Measurements

MD	mesio-distal length ;
BL	bucco-lingual breadth of incisors, canines and premolars (Freedman 1957);
TH	total height of canine;
CrH	height of canine crown;
Mb	mesial breadth of molar (Freedman 1957);
Db	distal breadth of molar (Freedman 1957);
Hb	hypoconulid breadth of lower third molar (Freedman 1957);
LD	length of a dental segment.

SYSTEMATIC PALAEONTOLOGY

Order PRIMATES Linnaeus, 1758
Suborder ANTHROPOIDEA Mivart, 1864
Infraorder CATARRHINI E. Geoffroy, 1812
Superfamily CERCOPITHECOIDEA Gray, 1821
Family CERCOPITHECIDAE Gray, 1821
Subfamily COLOBINAE Jerdon, 1867

Genus *Sawecolobus* n. gen.

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TYPE SPECIES. — *Sawecolobus lukeinoensis* n. sp., by present designation.

GENERIC DIAGNOSIS. — A small-to-medium sized extinct genus of colobine monkey with a short muzzle and a general morphology with a *Cercopithecoides*-like aspect. The calvarium is large, especially in the frontal region, and rounded. The sagittal crest is absent in females and is probably weak when present in males. The frontal is prominent and convex, being close to *Cercopithecoides* but more expressed than in *Mesopithecus*. The face is broad. The inter-orbital pillar is broad typical of colobines but here moderately developed. The orbits are big, broad, and low. The supraorbital tori are moderately thick. The glabellar region is slightly proeminent, less than in *Cercopithecoides*, but more than in *Mesopithecus.* The ophryonic groove is broad and moderately deep, but not as deep as in *Cercopithecoides*. The post-orbital constriction is very weak with short prominent temporal lines. The skull presents a specific triangular coalescent area oriented latero-fronto-superiorly at the latero-superior corner of the orbits above the fronto-zygomatic suture at the junction of the temporal lines and the orbits. The frontal process of the zygomatic bone is narrow. The infraorbital part of the zygomatic bone, especially the area of the zygomatico-maxillary suture, is moderately low. The roots of the zygoma are located below the contact between M1/-M2/. The maxillary sinuses (MS) are present as in *Cercopithecoides* but *Sawecolobus* n. gen. differs from *Mesopithecus* in which they are absent. The palate is short, the usual morphology in many short-faced colobines, and the hard palate ends at the level of M3/. It is characterized by a staphylion located very anteriorly. The shape of the premaxilla imparts an ogival aspect of the anterior part of the muzzle and not a squared-off rostrum as seen in *Kurasocolobus* and *Cercopithecoides*.

The mandibular symphysis is deep. The median mental foramen seems to be absent as is the case in most colobines except *Procolobus*, *Cercopithecoides* and *Rhinocolobus.* Unlike *Cercopithecoides*, in lateral view the contour is globally convex and inclined posteriorly with a lower break in the slope, and the anterior surface of the symphysis is convex transversally and not laterally compressed. The mandibular body is deep, gracile and vertical with a uniform height from m/1 to m/3. It does not present a strong lateral flare and the *prominentia laterales* are weak. The inferior border of the mandibular body is robust and tapers posteriorly near the gonial area, a morphology different from *Kuseracolobus*. There is no fossa on the lateral surface of the mandible and the lateral mental foramen is located below the p/4. The morphology of the base of the ascending ramus of the mandible suggests that it is almost vertical relative to the occlusal plane, less steep than in *Mesopithecus*, but not as inclined as it is in *Cercopithecoides*. It is situated near the rear of the m/3, more posteriorly than in *Cercopithecoides* and the extramolar sulcus is narrower medio-laterally.

In general, the dentition is typically colobine but presents some specificities. The canines reveal a strong dimorphism. On the mandible, the lower canine is labially curved as in *Mesopithecus* and *Colobus* but unlike *Paracolobus enkorikae*.

The presence of a protocone on P3/ is variable, and when present it is slightly developed. The M2/s are the largest molars. The p/3s are broader than the p/4s. The p/4s are very small in comparison with the other teeth. The protoconid and the metaconid in the p/4s are almost of the same height, the talonid is narrower than the anterior part of the tooth and bears a small entoconid. The breadth of the lower molars increases from m/1 to m/3, the distal width is broader that than the mesial width, except in the m/3s.

DIFFERENTIAL DIAGNOSIS. — The inter-orbital pillar is less broad than in typical Plio-Pleistocene *Cercopithecoides* (such as *C. meaveae*, *C. kimeui*, *C. williamsi*, *C. haasgati* and *C. alemayehui*), but also in *Paracolobus* and *Mesopithecus*. It is more moderately developed, as in *C. kerioensis* and *C. bruneti*, and also in *Libypithecus* and *Rhinocolobus*. The nasal aperture is located low down on the face, its top being situated below the inferior orbital margins, as in African fossil colobine genera (*Cercopithecoides*, *Libypithecus*, *Paracolobus* and *Rhinocolobus*) and *Mesopithecus* but different from extant African colobines (*Procolobus*, *Piliocolobus* and *Colobus*) and the majority of Asiatic extant colobines (*Presbytis*, *Rhinopithecus*, *Semnopithecus* and *Trachypithecus*), except *Nasalis* which has the top of the nasal aperture situated above the inferior orbital margins.

The specific triangular coalescent area above the fronto-zygomatic suture, the temporal lines and the orbits is not as infero-superiorly elongated as in some specimens of *Paracolobus*, and is not distinct, unlike *Cercopithecoides* (including *C. kerioensis*), *Libypithecus*, *Mesopithecus* and *Rhinocolobus*.

As in *Cercopithecoides* and *Mesopithecus*, in extant African colobines, and in extant Asian colobines (*Nasalis*, *Pygathrix*, *Rhinopithecus*, *Semnopithecus*), the frontal process of the zygomatic bone is narrow in *S. lukeinoensis* n. gen., n. sp. and not broad as in *Dolichopithecus*, *Libypithecus*, *Paracolobus* and *Rhinocolobus.* The infraorbital part of the zygomatic bone is moderately low as in *Cercopithecoides*, *Mesopithecus* and *Nasalis* but is higher than in *Piliocolobus*, *Procolobus*, some *Colobus*, *Pygathrix*, and *Rhinopithecus*, and lower than in *Dolichopithecus*, *Libypithecus*, *Paracolobus* and *Rhinocolobus*. In comparison with the different species of *Cercopithecoides*, the staphylion (or posterior nasal spine) is more anteriorly located, probably close to the line between the mesial parts of the M3/s.

ETYMOLOGY. — In recognition of the local people, the prefix 'Sawe' refers to the old age societal classes in the Tugen community (meaning wise). The other part of the name refers to its colobine status.

Sawecolobus lukeinoensis n. gen, n. sp.
(Figs 3-10; Tables 1-4)

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TYPE SPECIMENS. — **Holotype**: BAR 758'00 – Partial skull with the complete face and the palate including the complete post-canine dentition on both sides except for the left P3/. — **Paratypes**: BAR 756'00, maxilla with I1/ and P3/-M3/; BAR 757'00, partial skull with M2/-M3/ also with left P4/, right P3/-P4/ but damaged; BAR 759'00, left maxilla with P3/-M3/; BAR 760'00, left mandibular fragment with m/2-m/3 and broken m1/; BAR 761'00, back of calvarium; BAR 762A'00, the left maxilla with P4/-M3/, + BAR 762B'00/OCO 1049'11, right maxilla with P3/ and M1/-M3/; BAR 786'00/BAR 1368'00, left maxilla with M2/-M3/; BAR 1586'00, an edentulous mandibular symphysis; OCO 608'10, mandible with right p/3-m/3 and left i/2-m/3 and OCO 100'01, a fragment of edentulous mandible; 21 isolated teeth (BAR 784'00, BAR 785'00, BAR 1214'00, BAR 1369'00, BAR 1584'00, BAR 1585'00, BAR 470'01, BAR 1595'01, BAR 1597'01, BAR 250'03, BAR 1190'03, BAR 1381'03, BAR 1382'03, BAR 349'04, BAR 351'04, BAR 910'04, OCO 104'10, OCO 105'10, OCO 335'10, OCO 101'11 and OCO 305'11); and four post-cranial bones (BAR 757'00, an axis vertebra, BAR 914'04, a proximal extremity of a right metatarsal V, OCO 336'10, a distal extremity of a left humerus, and OCO 102'11, a distal extremity of a right humerus).

TABLE 1. — Measurements (in mm) of upper and lower teeth in specimens with more or less complete tooth rows. Symbol: *, indicates approximately (tooth partially damaged).

		C		P3/		P4/		M1/			M2/			M3/			P3/-M3/	P4/-M3/	M1/-M3/
N°	**Side**	**MD**	**BL**	**MD**	**BL**	**MD**	**BL**	**MD**	**Mb**	**Db**	**MD**	**Mb**	**Db**	**MD**	**Mb**	**Db**	**LD**	**LD**	**LD**
BAR 758’00	R	×	×	4.5	5.2	4.7	6.3	7	×	×	6.9	7.7	7	6.7	6.8	6.3	29.5	24.3	20.8
	L	×	×	×	×	4.8	6.5	7	6.5	7.3	7.3	7.6	6.9	6.5	6.7	6.1	×	26.5µ	21.3µ
BAR 756’00	R	7	5.6	4.2*	4.9*	4.3	5.7	5.4	5.7	5.5	6.5	7.1	6.3	6.2	6.3	5.2	29.5	24.8	19.6
	L	7.1	5.7	4.3	5*	4.2	5.5	5.1	5.8	5.6	6.5	7.2	6.6	6.3	6.4	5.3	29.7	25.4	20.6
BAR 757’00	R	×	×	×	×	5.3	×	×	×	×	7.7	7.8	7.4	7.2	6.7	6	×	×	×
	L	×	×	×	×	×	×	×	×	×	7.9	7.8	7.3	7.3	6.6	6	×	×	×
BAR 759’00	L	×	×	4	4.9	4.2	5.9	6.5	6.6	6.1	6.6	7.5	6.6	6.6	7	5.6	28.9	24.7	20.6
BAR 762A’00	L	×	×	×	×	4.8	6.3	7.1	6.9	6.7	7.7	7.8	7	7.5	7.3	6.1	×	26.7	22.6
BAR 762B’00+OCO1049’11	R	×	×	5.4	5.2	×	×	6.8	7	6.5	7.8	7.5	7.1	7.3	7.2	5.9	×	×	22.5
BAR 786’00+BAR 1368’00	L	×	×	×	×	×	×	×	×	×	7.2	7.3	6.7	7	6.7	5.9	×	×	×

		p/3		p/4		m/1			m/2			m/3				p/3-m/3	p/4-m/3	m/1-m/3
N°	**Side**	**MD**	**BL**	**MD**	**BL**	**MD**	**Mb**	**Db**	**MD**	**Mb**	**Db**	**MB**	**Mb**	**DB**	**Hb**	**LD**	**LD**	**LD**
BAR 760’00	L	×	×	×	×	×	×	5.3	7	6.4*	6.7*	8.7	6	5.7*	3.7*	×	×	×
OCO 607’10	R	7.2	5	5	4.1	6.3	5.2	5.5	6.5	5.6	5.6	8.7	5.9	5.6	3.5	34.6	28.3	22.9
	L	8.1	4.3	5	4.1	6.2	5.1	5.5	6.4	5.6	5.8	8.8	6	5.7	3.5	35.9	28.5	23.2

DIAGNOSIS. — As for the genus.

TYPE LOCALITY. — Aragai in the Tugen Hills (Baringo County, Kenya).

GEOLOGICAL AGE. — From the basal part of the Lukeino Formation, the Kapgoywa Member dated to the Late Miocene (*c.* 6-5.7 Ma). (Pickford & Senut 2001; Sawada *et al.* 2002).

ETYMOLOGY. — Named after the geological level, as well the geographical location, the Lukeino Formation (Tugen Hills, Baringo County, Kenya).

DESCRIPTION

BAR758’00 (Holotype) (Fig. 4A1-A6; Table 1)

General description and preservation. BAR 758’00 is a complete anterior part of a skull which suffered minor distortion during fossilization (maximum length: 60.3 mm; breadth: 61.5 mm; height: 46.5 mm). Of the calvarium only the frontal region is preserved which shows several cracks. The face is well-preserved including the orbits, the inter-orbital pillar, the nasal bones, the maxillae and the zygomatic bones (the right one being better preserved than the left one). The premaxilla is damaged and lacks all the anterior part. The same applies to the anterior/inferior part of the nasal aperture. The face is broad despite some distortion (maximal zygofrontal width: 59.8 mm (cf. Appendix 1: measurement MZM) and low (height between the prosthion and the upper part of the glabella: 38.7 mm).

The anterior part of the palate is missing and both canines and the incisors are absent (length from the anterior part to the distal part of the M3/s: 38.6 mm (see Appendix 1 for comparison with extant African colobine, PDL measurement). The right P3/ and P4/ are intact. The right M1/ is badly damaged; only the buccal side is preserved. The right M2/ is well preserved but lacks the metacone. The right M3/ is present but lacks the paracone and is partially hidden by matrix. The left P3/ is badly damaged and preserves only some lingual fragments. The left P4/ is well preserved. The left M1/ is intact but appears to have sunk into the alveolar process. The left M2/ is well preserved but lacks the mesiobuccal corner. The left M3/ is intact.

Orbital and frontal region. The inter-orbital pillar is broad (minimum: 7.5 mm) as is usual in colobine monkeys (cf. Appendix 1: measurement IW), but short (this is accentuated by the preservation, the pillar is displaced slightly under the nasal). It is broader superiorly (9.6 mm near the glabella). Most of the matrix inside the orbits was removed during mechanical preparation but not completely and it is impossible to describe the morphology of the bone inside the cavity. To preserve the fragile bone and avoid destroying some fragments, the matrix was partially extracted near the inferior margin of the orbit. It is especially true for the right orbit, near the nasal aperture, which leads to it having a deformed appearance. The mesio-lateral margins of the orbits present some cracks and moderate distortion. Despite the imperfect preservation, the orbits are rectangular, broad and low (right orbit: 13.5 mm high, 25.4 mm wide; left orbit: 15.5 mm high, 23.5 mm wide (cf. Appendix 1: measurement OH and OW). No *incisura supraorbitalis* can be seen.

The superior orbital margins are slightly thickened (right: 3.8 mm; left: about 3.5 mm). The glabellar region is moderately inflated anteriorly but prominent and slightly convex towards the supraorbital torus. The supraorbital torus is moderately developed. The ophryonic groove (or transverse supraglabellar groove [Mollett van der Spuy 1947; Freedman 1957]) is deep and broad antero-posteriorly. This groove is laterally deeper and broader resulting in the presence of a fossa on both sides. The latero-superior corner of the orbits above the fronto-zygomatic suture present a specific aspect. This area corresponds to the

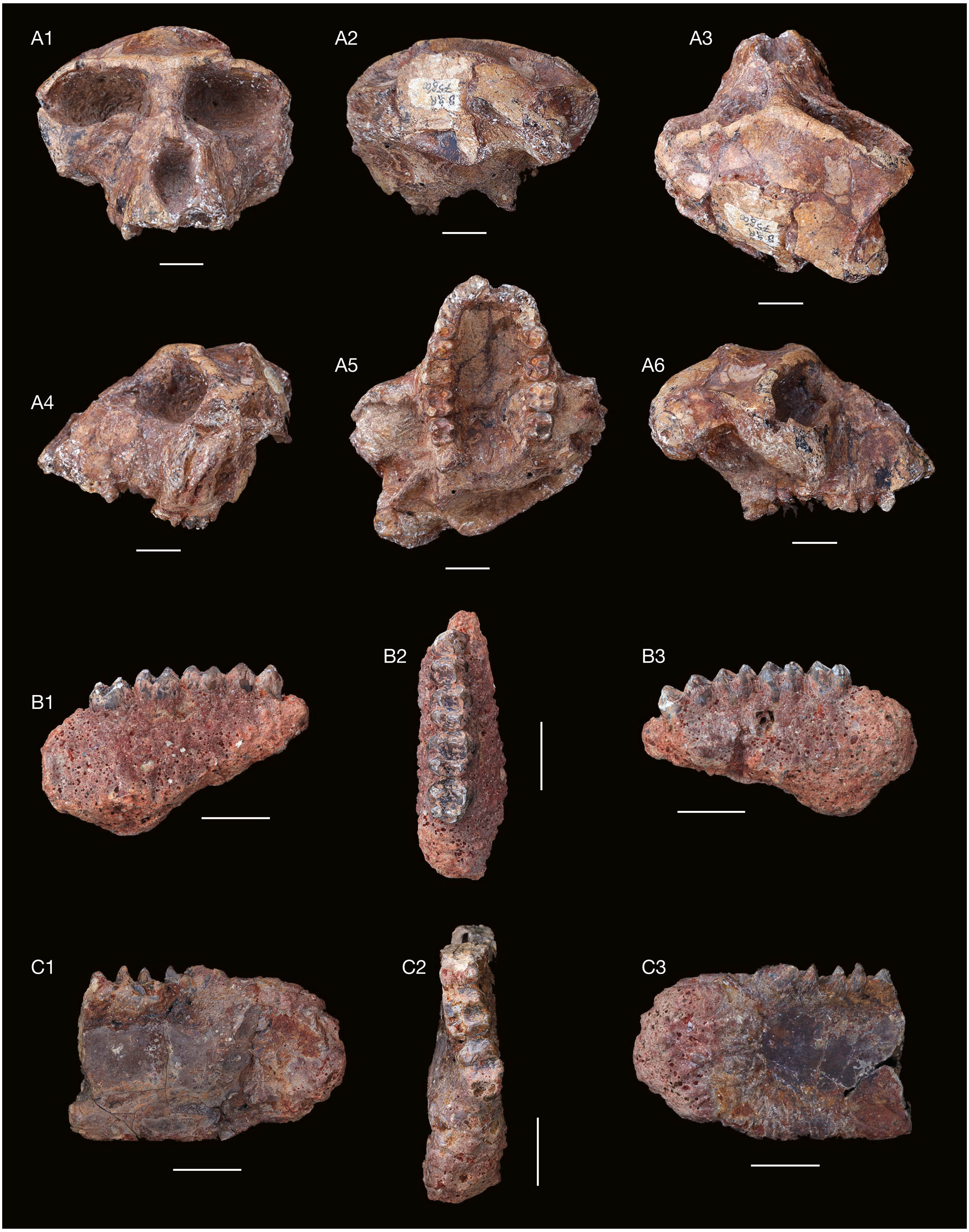

Fig. 4. — *Sawecolobus lukeinoensis* n. gen., n. sp.: **A**, holotype BAR 758'00, skull: **A1**, facial view; **A2**, posterior view; **A3**, superior view; **A4**, left lateral view; **A5**, palatal view; **A6**, right lateral view; **B**, BAR 759'00, left hemi-maxilla: **B1**, buccal view; **B2**, occlusal view; **B3**, lingual view; **C**, BAR 760'00, left hemi-mandible: **C1**, buccal view; **C2**, occlusal view; **C3**, lingual view. Scale bars: 1 cm.

junction of the temporal line with the orbit as in *Cercopithecoides* (including *C. kerioensis*), *Libypithecus*, *Mesopithecus*, and *Rhinocolobus* but unlike *Paracolobus*. This area is triangular in *Sawecolobus lukeinoensis* n. gen., n. sp. and is oriented latero-fronto-superiorly. The surface is antero-posteriorly flat and infero-superiorly slightly convex. The salient aspect of this area is reinforced by the presence of the broad fossa for the ophryonic groove. *Cercopithecoides*, *Mesopithecus*, *Libypithecus* and *Rhinocolobus*, are characterised by the proximity of the temporal lines and the frontal orientation of the orbits which appear as though stuck together. No other fossil colobines present the coalescent aspect seen in BAR 758'00. In some specimens of *Paracolobus*, a coalescent area occurs, but it is more infero-superiorly elongated than in BAR 758'00. The triangular aspect of the latero-superior corner of the orbits of BAR 758'00 is reminiscent of the same area in some *Parapapio* skulls such as BF 43.

The frontal is better preserved anteriorly than posteriorly. Behind the ophryonic groove, the skull vault is salient and strongly convex medially. The temporal lines are anteriorly salient. The postorbital constriction is weak. In morphology this region is similar to *Cercopithecoides.*

The right zygomatic is better preserved than the left one, but both are damaged, and the zygomatic arches are absent. It is long and almost frontally positioned with a nearly vertical and slightly convex surface. The infraorbital part of the zygomatic bone, especially the area of the zygomatico-maxillary suture is moderately low. The frontal process of the zygomatic bone is narrow as in *Cercopithecoides* and *Mesopithecus*, unlike *Paracolobus* and *Rhinocolobus*.

Muzzle and palate. The snout is well preserved, except for the anterior part of the premaxilla which is damaged. It is short. The root of the zygoma is located above the M1/-M2/ contact on both sides of the specimen despite minor distortion and are thus anteriorly positioned, similar to the position in *Rhinocolobus turkanensis* (Frost & Delson 2002) and *Kuseracolobus aramisi* where it is variable (above M1/ or M1/-M2/) (Frost 2001a, b) or at M1/ in *Kuseracolobus hafu* (Hlusko 2006). It is at M2/ for *Paracolobus enkorikae* and *Paracolobus chemeroni* which have more prognathic faces (Hlusko 2007), *Libypithecus*, but also for *Cercopithecoides kimeui* which differs from *Cercopithecoides williamsi* in which it is more anteriorly positioned (Frost & Delson 2002).

The nasal aperture is slightly inclined. It is narrow (9.1 mm wide), tall (about 17.1 mm high), showing an elongated oval outline (more or less as in BF 42A, *Cercopithecoides williamsi*). The left inferior border of the nasal aperture is damaged, but the right one is better preserved: the base of the aperture is V-shaped with sharp edges. The nasal processes are poorly preserved on both sides of the nasal aperture but they are easily distinguished from the maxilla by a clear suture. Due to the preservation, it is difficult to observe the edges of the nasal bone; it is present with some cracks. It forms a vertical, transversely convex rectangle. The superior suture on the inter-orbital pillar is not visible.

The nasal aperture is low on the face in comparison with extant African colobines and some Asiatic colobines but is close to the position observed in *Cercopithecoides* and *Mesopithecus*. In BAR 758'00, the superior margin of the nasal aperture is located below the line joining the inferior margins of the orbits. In extant African colobines, the superior margin of the nasal aperture is located above this line.

The preserved portion of the right premaxilla suggests that it is conical, different from the squared-off shape seen in *Kuseracolobus* and *Cercopithecoides*. The same morphology is observed in BAR 756'00 and BAR 757'00. The right portion of the premaxilla is more laterally positioned than anteriorly as in BF 42A. It is more convex than flattened like BF 42A. No maxillary ridge and maxillary fossa are visible, the lateral surface of the muzzle being more or less convex.

The palate appears to be deep, especially posteriorly. Despite the distortion of the anterior part, the palate looks concave and suggests that this part is deep too. The dental arcade is preserved only in the post-canine area, although there is some alteration due to post-mortem distortion. Both postcanine tooth rows are curved; the palate is broadest close to the contact between M1/-M2/ (external width between M1/-M2/: 32.7 mm; see Appendix 1: measurement EPW). Most of the palate is covered with matrix but the bone is apparent near the right M2/ and the left M3/. On the left side, a smooth cavity occurs below the contact between M2/ and M3/ which corresponds to the groove of the posterior palatine foramen (about 4.6 mm long). The posterior edge of the palatine with the choanae is preserved in the left side (although it is difficult to distinguish from the matrix). It is oriented more strongly anteriorly than medially. This suggests that the staphylion (or posterior nasal spine) would have been anteriorly positioned, probably close to the line between the mesial parts of the M3/s.

Paranasal sinus. The maxillary region is severely damaged and distorted, preventing detailed examination of the maxillary sinus in the specimen (Fig. 5A, B). However, the frontal and sphenoid regions are well preserved and show that there is no sinus (Fig. 5A, B).

Dentition. The canines and incisors are not preserved in this specimen, but the sections of the roots are visible on the right side. The size of the roots suggest that the canine was small, indicating that this specimen belonged to a female. The gap between the canine and I2/ is small, but there is no diastema between these two teeth (unlike BF 42A and the well-preserved specimens from Makapansgat, both of which are attributed to *Cercopithecoides williamsi*). The I2/ root is oval in section. It is probably the same for the I1/ but it is difficult to confirm. The other teeth are slightly worn and correspond to wear stages A3 (fully adult). The P3/ is the smaller of the two premolars (Table 1) and the protocone is worn but present. The protocone is well developed in the P4/ as is usually the case in colobines (Swindler 2002). The paracone and protocone are located mesially and aligned bucco-lingually in P3/ and P4/. The mesial fovea is much reduced in both premolars and the trigon basin is spacious, especially on P4/.

The crowns of the molars have a mesio-distally long and moderately deep trigon basin as is typical in colobine upper

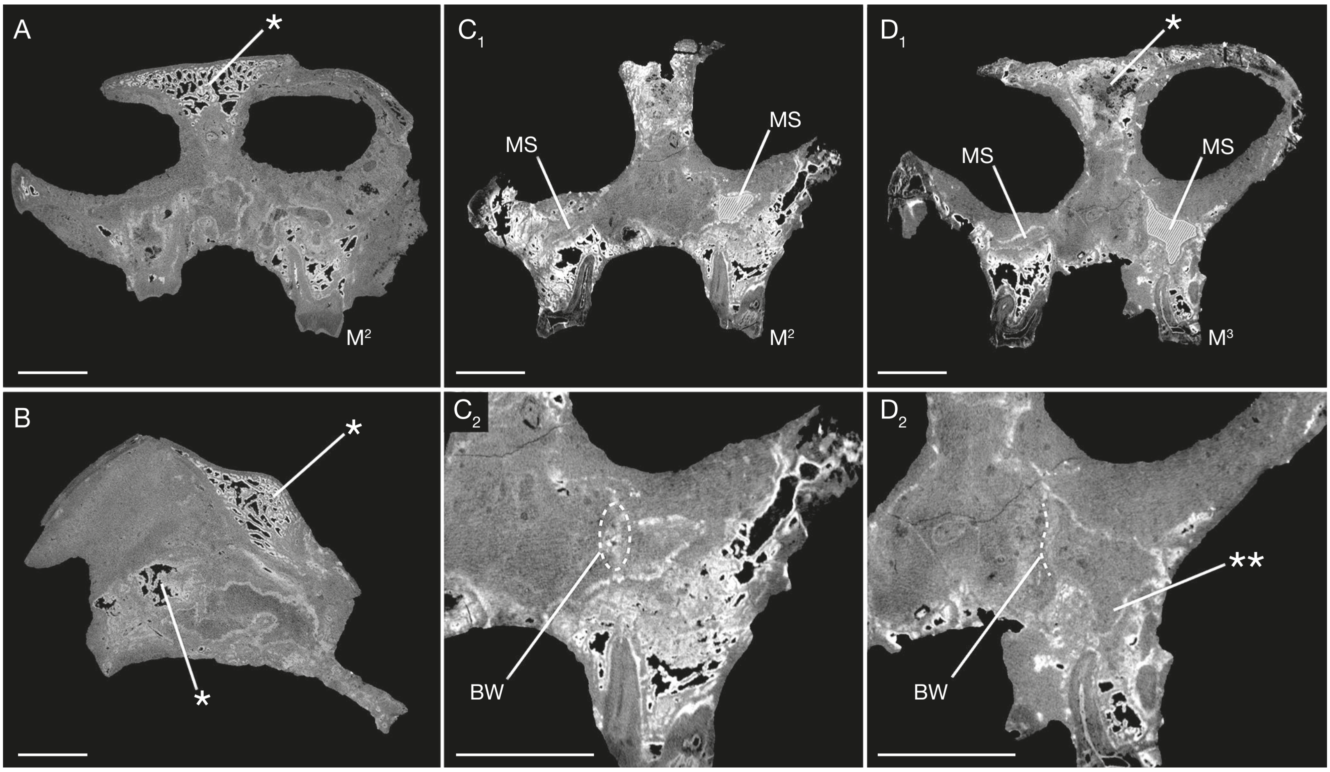

FIG. 5. — CT scans of *Sawecolobus lukeinoensis* n. gen., n. sp., crania: **A**, **B**, frontal and mid-sagittal scans of BAR 758'00; **C**, **D**, frontal scans of BAR 757'00, respectively; **C₂**, **D₂**, are expanded images of **C₁** and **D₁**, respectively. The bony region has rather low CT values and is coloured in dark grey on the CT scans. The frontal and sphenoid bones are fully occupied by cancellous bone in both specimens (*). The maxillary sinus (**MS**) is separated by the thin bony wall (**dotted line**, **BW**) that, in part, includes cancellous bone (**dotted circle**) on the left side in BAR 757'00, but its trace is detected on the right. The left M3/ alveolus is excavated by the maxillary sinus in BAR 757'00 (**). Scale bars: 1 cm.

molars (Delson 1975). The crowns are low. In the left M1/ the two lophs are almost equal in size. In the M2/s the mesial loph is broader than the distal one (Table 1). The same occurs in the M3/s (as in BAR 756'00). The molars are bucco-lingually broad (Table 1) compared to those of extant African colobines (Appendix 2) and relative to the face (Appendix 1: measurement MZW) (Verheyen 1962; Swindler 2002). The M3/ has a mesial fovea that is longer mesio-distally than in the M1/ and M2/. The left M3/s have no distal fovea/talon basin but a central cusplet distally, in the left one some matrix covers this area.

Sex and age. The canine is small (as indicated by the section of the root) and there is no swelling of the maxilla in this area, suggesting that it is probably a female. The jugal teeth are worn but the M3/s weakly, which corresponds probably to A3 wear stages, indicating that the specimen belongs to a middle-aged adult.

BAR 756'00 (Fig. 6B1-B3; Table 1)

General description and preservation. This specimen represents an almost complete palate partially covered by matrix (maximum length: 50.5 mm, breadth: 32.7 mm and height: 23.9 mm). The dental rows bearing the postcanine teeth, the base of the two canines and part of the left I2/ are preserved. At the surface of the right maxilla, a fragment of a tooth root is present included in the matrix. The palate suffered from an antero-posterior distortion. The left side has slipped (the tooth row C/-M3/ is located posteriorly to the rest of the palate). The right side is laterally compressed. The root of the left zygomatic process of the maxilla is preserved and is located above the contact between M1/ and M2/, and is thus, very anteriorly positioned. The muzzle was short.

Dentition. The I2/s are not preserved. The I1/s are fragmentary, the left one being better preserved. The apex of the crown of the left I1/ is broken and the tooth is partially embedded in matrix. The crown is triangular and seems large compared to the postcanine teeth. The crowns of the canines are broken showing heart-shaped sections. The large size of the preserved part of the canines indicate that the fossil was a male individual. A short diastema (clearly marked on the right side) is present between the I2/ and C/.

The P3/s are the smaller of the premolars and possess a small protocone. The occlusal outline of the P3/s is subtriangular. The right P3/ has lost some enamel bucco-mesially. The protocone is more developed on P4/ as is usually the case in colobines (Swindler 2002). As for BAR 758'00, the paracone and protocone are located mesially and aligned bucco-lingually in both premolars except in the right P4/ which has moved during fossilization. The mesial fovea is tiny and the distal one is spacious. The P4/s are wider bucco-lingually than the P3/s as in BAR 758'00.

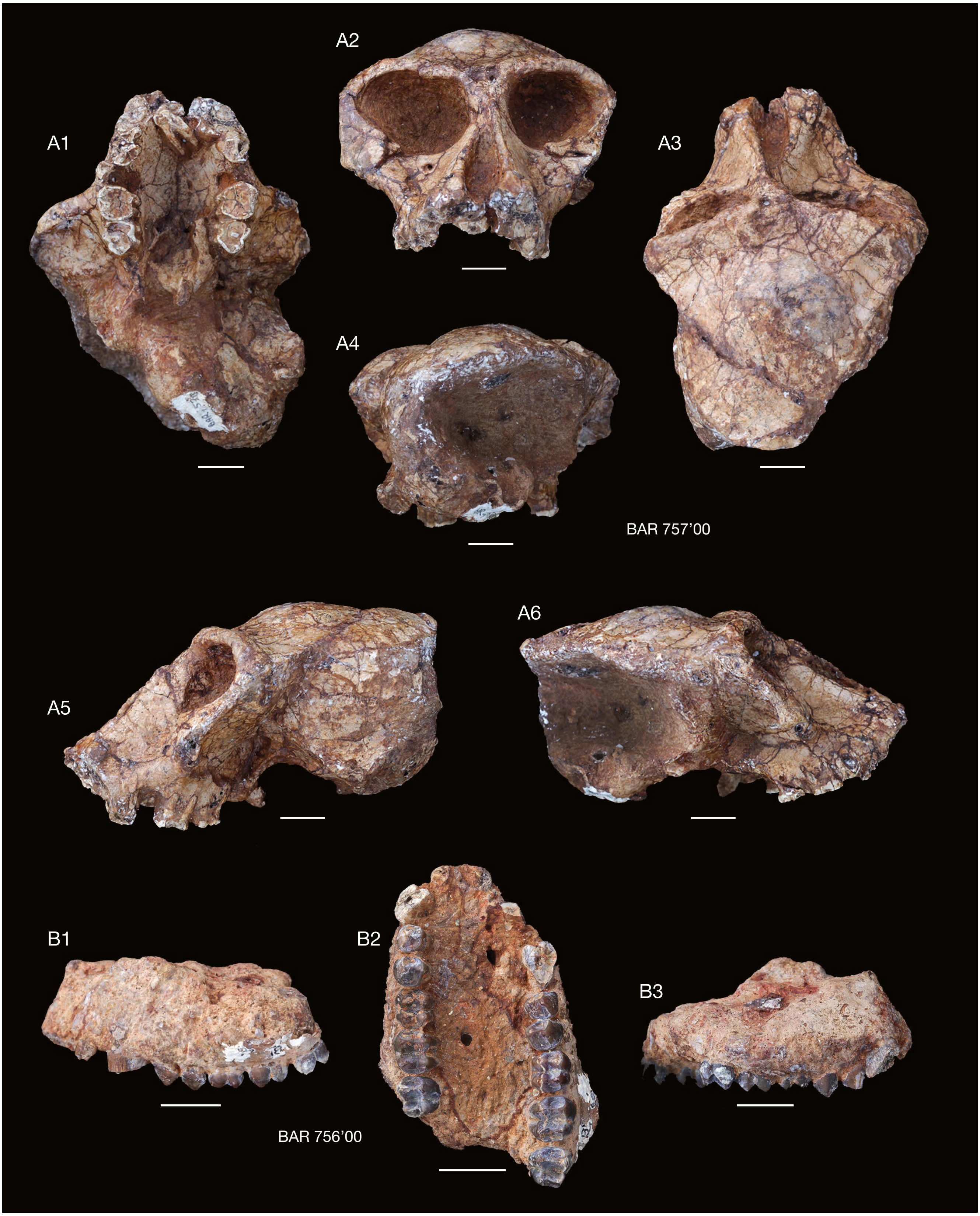

FIG. 6. — *Sawecolobus lukeinoensis* n. gen., n. sp.: **A**, skull BAR 757'00: **A1**, palatal view; **A2**, facial view; **A3**, superior view; **A4**, posterior view; **A5**, left lateral view; **A6**, right lateral view; **B**, Maxilla BAR 756'00: **B1**, left lateral view; **B2**, palatal view; **B3**, right lateral view. Scale bars: 1 cm.

The molars are well preserved except for longitudinal cracking on the left M1/ and M2/. The left M3/ has lost some enamel from the paracone. The molars are broader than long (Table 1). The M2/ is the largest molar. The mesial and distal lophs of the M1/s are almost equal in size. The distal loph is narrower than the mesial one in the M2/s, and more so in the M3/s. The teeth are almost unworn, just the apex of the paracone and the hypocone on the M1/ which correspond to wear stage A1, which suggests that the individual was a young adult when it died. The mesial fovea is shorter mesio-distally and broader bucco-lingually in the M1/s and M2/s than the distal fovea. In the M3/s, the distal fovea is present and more buccal than central. Buccally, there are distal and mesial clefts in the M1/s and M2/s, only a mesial cleft on M3/s. They present the same morphological features concerning the trigon basin as in BAR 758'00.

BAR 757'00 (Fig. 6A1-A6; Table 1)

General description and preservation. BAR 757'00 preserves three quarters of a fragmentary skull (the posterior part is missing) associated with an axis vertebra (described in this part and not in the section on postcranial bones) (maximum length: 87.6 mm, breadth: 64.2 mm and height: 50.1 mm). It suffered distortion and cracking during fossilization, but the calvarium is better preserved than in BAR 758'00, especially the left side comprising the frontal, the parietal and the temporal. The left part of the basicranium is preserved. The face preserves the orbits, the inter-orbital pillar, the maxillae and the zygomatic bones but they show strong distortion due to lateral compression during fossilisation. The face is broad (maximal zygofrontal width: 64.2 mm (cf. Appendix 1: measurement MZM) and low (height between the preserved anterior part of the palate and the upper part of the glabella: 42.2 mm).

The premaxillae are broken and are represented only by some fragments near the pyramidal aperture and the posterior part of the palate is present. Only the left and right M2/ and M3/ are present but they are deeply worn. The M1/s are absent. The left P4/, the right P3/ and the right P4/ are severely damaged. A tooth fragment observed on the anterior part of the palate could represent the left P3/.

Calvarium. The bone is pervasively cracked, and a major crack extends backwards from the left side posterior to the ophryonic groove to the middle of the rear of the skull. This alters the shape of the calvarium which would have been more rounded and shorter. The frontal is very convex and tall anteriorly, the postorbital constriction is weak (width: 47.5 mm). As for BAR 758'00, BAR 757'00, it exhibits a deep and broad antero-posteriorly oriented ophryonic groove which ends in a fossa on both sides. The temporal lines are well developed anteriorly but abraded by erosion. The temporal lines extend backwards, are quickly blurred and do not converge on the top of the calvarium. The morphology of this region is similar to that of BAR 757'00 and *Cercopithecoides*, *Rhinocolobus* and *Mesopithecus* and unlike *Paracolobus* and *Libypithecus*. The parieto-temporal area is high and rounded. Even though the right side is broken, it seems that the maximum width of the calvarium is in a high position as in BF 42A, which confirms its rounded morphology.

Basicranium. Matrix covers most of the preserved portion of the basicranium. An anterior fragment, above the pterygo-maxillary fissure of the lateral pterygoid plate is present on both sides but the left one is better preserved and deep. Some matrix obscures the pterygo-maxillary fissure on the right side. The origin of the zygomatic process is preserved. On the left side, the poorly preserved *fossa mandibularis* seems to be reduced and shallow. The postglenoid process is salient and robust. Some matrix covers the external auditory meatus. A portion of the tympanic plate is visible as is the petrosal, which is well developed. The petrosal is elongated antero-posteriorly and slightly laterally oblique (as observed in some *Piliocolobus badius*). In BF 42A, this bone is shorter antero-posteriorly and more elongated laterally. A large mastoid process is present but is slightly eroded.

Orbital region. The face of BAR 757'00 is more damaged than that of BAR 758'00 and the orbits are more affected. However, some features are visible: the inter-orbital pillar is broad (8.8 mm wide) as is usual in colobine monkeys (cf. Appendix 1: measurement IW) and short as in BAR 758'00. It is also broader superiorly than inferiorly. The orbits are filled with matrix, more than in the holotype. The upper parts of the orbits show some cracking, but the shape is not seriously affected. The infero-lateral corner of both sides is more affected by distortion and they are thus slightly displaced inside the orbit. Despite all these distortions, the orbits are broad and low showing a rectangular outline (more marked in the right orbit) (right orbit: 18.1 mm high and 26.2 mm wide; left orbit: 18.2 mm high and 22.7 mm wide (cf. Appendix 1: measurements OH and OW).

As for BAR 758'00, the superior orbital margins are slightly thickened (about 3.5 mm on the right side and 3.6 mm on the left one). The glabellar region is damaged but the convexity of the supero-median orbital margin and the aspect of the inter-orbital pillar suggests that it is moderately inflated and weakly incurved to the level of the supraorbital torus as in BAR 758'00. The supraorbital torus is slightly more developed than in BAR 758'00 (sexual dimorphism?) but it is different from that of *Cercopithecoides* in which it is strongly salient. The superficial bone is missing on the lateral margin of the left orbit. No *incisura supraorbitalis* is observable.

Below the orbits, two infra-orbital foramina are preserved on the left side and only one on the right side.

On the right side, at the latero-superior corner of the orbits above the fronto-zygomatic suture, the temporal lines and the orbits form at their junction a specific triangular coalescent area latero-fronto-superiorly broad, antero-posteriorly flat and slightly convex infero-superiorly as seen in BAR 758'00 but better expressed. On the left side, this area is more eroded and is not as well preserved but presents the same morphology.

The infraorbital part of the zygomatic bones presents many cracks and is distorted; they have suffered compression during fossilization. The infero-lateral part is missing on the left. The right one is long, frontally positioned, despite the distortion, and low. The infraorbital parts of the zygomatic bone are moderately low and the frontal processes of the zygomatic bone are narrow as in BAR 758'00.

Muzzle and palate. The snout is more distorted than that of BAR 758'00. Most of the premaxilla is missing. The maxilla is strongly distorted. The roots of the zygomatic bones are located above the contact between M1/-M2/, and are thus very anteriorly positioned. The muzzle is short. The nasal aperture is damaged, and the nasal is absent. The nasal processes, long and narrow, are well preserved on both sides of the aperture. The general morphology of the nasal aperture indicates that it was tall, narrow and oval as in BAR 758'00. However, probably due to the distortion during fossilisation, the aperture appears to be more inclined.

It is difficult to describe the anterior view of the muzzle because the premaxillae are not preserved. No maxillary ridge is observed. On the lateral aspect of the muzzle, a deep depression is present but it is not a maxillary fossa and is probably due to lateral compression during fossilisation.

The preserved portion of the anterior part of the palate is slightly distorted and the palate is deeper than in BAR 758'00. In comparison, the palate of BF 42A is shallower than in BAR 757'00 and BAR 758'00. The postcanine tooth row (only the M2/s and M3/s are preserved) is curved and the palate seems broadest near the contact of the M1/-M2/ (M1/s are not preserved) (external width between M1/-M2/: 34.1 mm (cf. Appendix 1: measurement EPW). The palate is partly obscured by matrix and is moderately deep. The hard palate ends at M3/. In the posterior part of the hard palate, on the right side, the groove of the posterior palatine foramen is visible below the distal end of the M2/ and the mesial two thirds of the M3/, but it is filled with matrix. This groove is short (5.8 mm long). In BF 42A, this groove extends more posteriorly behind the M3/. The hard palate ends distally beyond the M3/ in *Paracolobus enkorikae* and even farther back in *Paracolobus chemeroni* (Hlusko 2007). In *Cercopithecoides bruneti*, it extends posteriorly to M2/ (Pallas *et al.* 2019). The posterior edge of the palatine with the choanae is well preserved in the right side (better preserved than in BAR 758'00). It is also oriented more strongly anteriorly than medially. It is not possible to observe the exact position of the staphylion, but the preserved morphology suggest strongly that it has an anterior position probably close to the line between the mesial ends of the M3/s. In BF 42A, the staphylion is situated slightly posteriorly to the M3/s, as in *C. williamsi* (Szalay & Delson 1979: figs 197-198), and in the holotypes of *C. meaveae* (Frost & Delson 2002: figs 20, 23) and of *C. kimeui* (Leakey 1982: fig. 2). Despite sexual differences, the staphylion is posterior to well posterior to the M3/ in *Colobus* (Verheyen 1962: pls 1-2 ; Pallas *et al.* 2019: fig. 3), posterior in *Piliocolobus* (Verheyen 1962: pl. 6 ; Pallas *et al.* 2019: fig. 3) and at the level of the distal loph of the M3/ in *Procolobus* (Verheyen 1962: pl. 7 ; Pallas *et al.* 2019: fig. 3)

Paranasal sinus. The left maxilla is well preserved, whereas the right one is severely damaged and distorted. The maxillary sinus (MS) is present at the level of M2/-M3/ on the left side (Fig. 5C, D). The right MS was also detected while it is distorted in the ventro-dorsal direction. The left MS region is separated from the nasal cavity by a thin bony wall that in part involves cancellous bone. The left MS excavates the alveolar region at the level of the M2/, whereas the right one has no trait for such an excavation (Fig. 5C). Unfortunately, the nasal conchae and ostium were destroyed or severely distorted. The frontal sinus is not formed in this specimen, and the frontal and sphenoid bones are occupied by cancellous bone.

Dentition. As in BAR 758'00, the incisors and the canines are missing but the section of the canine roots are visible, better on the left side. The size of the section suggests that the canine was small (Left C/: MD = 3.7 mm, BL = 4.5 mm) indicating that the specimen was a female. When present, the teeth are worn and correspond to wear stage A6 suggesting an old individual. The premolars are poorly preserved; the only possible observation is that the P3/s are smaller than the P4/s. The M1/s are absent. The M2/s and the M3/s are heavily worn. The mesial lophs of the molars are broader than the distal ones. Two roots are visible buccally and lingually, but they are separate buccally and coalescent lingually.

Axis. This vertebra is stuck at the back of the palate partially embedded in matrix. Only the anterior part is preserved showing the vertebral body associated with the odontoid process, the superior articular facets, and part of the neural arch on the left side. Its general shape is conical as is usually the case in cercopithecoids.

Sex and age. The proportions of the face are greater than in BAR 758'00. The size of the preserved section of the canine root suggests a small canine which indicates a female. The preserved teeth are deeply worn typical of an old adult (wear stage A6).

BAR 759'00 (Fig. 4B1-B3; Table 1)

General description and preservation. BAR 759'00 is a left hemi-maxilla embedded in matrix, of which only the P3/-M3/ are visible.

Dentition. All the teeth are well preserved. The P3/s are sub-triangular and have no protocone. The protocone is well developed on P4/ and the two cuspids are aligned bucco-lingually. This premolar is relatively wide bucco-lingually. The morphology is similar to that in BAR 758'00. The mesial and distal lophs of the M1/ are almost equal in width. The distal loph is narrower than the mesial one in the M2/s, and more so in the M3/s. The morphology of the molars is the same as in the previously described fossils. The distal fovea is small and buccally positioned in M3/. Only the distal buccal cleft is visible, matrix covers most of the buccal surface of the molars. Only the linguo-mesial cusp of the M1/ is worn (wear stage A1). This hemi-maxilla belongs probably to a young adult.

BAR 760'00 (Fig. 4C1-C3; Table 1)

General description and preservation. BAR 760'00 is a portion of a left mandible broken mesially at the middle of m/1. The m/2 and m/3 are present. The posterior part of the mandible is fragmentary and partly embedded in the matrix.

Mandibular corpus. It is well preserved; the discrete cracking does not affect the body. It is deep compared to the size of the molars (height between m/1 and m/2: 21.3 mm; width between m/1 and m/2: 7.9 mm (see Appendix 1: respective measurements MH and NW)). The lateral surface is almost flat and vertical. The buccal surface is convex below the m/2. The *corpus mandibularis* is broader in its middle part, but the inferior edge is robust and broad. Its depth is equal from m/1 to m/3 up to the gonial area and not increasing as in *Kuseracolobus*. A *prominentia lateralis* exists under the m/3 partly obscured by matrix but it is weak. The beginning of the mesial edge of the ascending ramus is present under the matrix and the extramolar sulcus is narrow medio-laterally, unlike *Cercopithecoides williamsi*, *Cercopithecoides bruneti*, *Kuseracolobus aramisi*, *Kuseracolobus hafu*, *Mesopithecus pentelici*, *Paracolobus chemeroni* and *Rhinocolobus turkanensis* in which it is large (Szalay & Delson 1979; Leakey 1982; Frost 2001a, b; Pallas *et al.* 2019) and as well as in *Paracolobus enkorikae* where it is intermediate (Hlusko 2007).

Dentition. Some matrix covers the buccal side of the molars. The protoconid of the m/2 is broken. The distal lophid is broader than the mesial one and the distal fovea is spacious. The m/3 is well preserved with the mesial lophid broader than the distal one. The buccal parts of the lophids of the m/2 and m/3 are moderately worn but the lingual ones are salient and unworn. The specimen represents a medium-aged adult individual (wear stage A3 or A4).

BAR 761'00 (Fig. 7A1-A2)
General description and preservation. This is a portion of the back of a skull (central and right side) (maximum length: 37.1 mm; width: 46.2 mm). In size, it is close to the skulls BAR 758'00 and BAR 757'00. The parietal is convex and has a smooth surface which indicates that there was no sagittal crest. The nuchal plane is flat and seems tall and short. There is no sign of a sagittal crest or of a nuchal crest. Part of the right mastoid process is present but is not well preserved. These observations indicate that this fragment was a part of a rounded and short calvarium.

BAR 762A'00 + BAR 762B'00/OCO 1049'11 (Fig. 7B1-B3; C1-C3; Table 1)
General description and preservation. This composite specimen is comprised of two hemi-maxillae: the right one (BAR 762B'00: a maxillary portion with the three molars found in 2000 (maximum length: 30.4 mm; breadth: 11.4 mm; height: 16.3 mm) + OCO 1049'11: a fragment with a piece of the root of the canine and the P3/ found in 2011) and the left one (BAR 762A'00: a portion of maxilla with P4/-M3/) (maximum length: 39.3 mm; breadth: 16.3 mm; height: 21.2 mm). A fragment of the root of the zygomatic is preserved on each side of the maxilla and is located very anteriorly above the contact between M1/-M2/. The muzzle was probably short. Some matrix covers the median part of the palate.

Dentition. The right P3/, sub-triangular in occlusal view is preserved and shows a weak protocone. A tiny fragment of enamel is missing bucco-distally from the apex. The protocone is well developed in the P4/ and is slightly worn. As for the previous fossils, the two cuspids are mesially positioned and aligned bucco-lingually. The P4/s are relatively broad bucco-lingually. The molars are well preserved, the M2/s being the largest of the molars. On the buccal aspect, a tiny accessory cusp (mesostyle) is present in the M2/s in the middle of median cleft. The mesial and distal lophs of the M1/s are almost equal in breadth. The distal loph is narrower than the mesial one in the M2/s, and more so in the M3/s. The lophs are so well preserved that it is possible to see a central slit which separates the endocrista of the opposite cusplets. On the buccal side of the M1/s and M2/s the mesial and distal clefts are visible, and only the mesial one on the M3/s. The M3/s have a reduced distal fovea. The left M3/ has a cusplet between the distal cingulum and the postmetacrista. The right one shows the same cusplet but extremely small and another bigger one in the middle of the distal cingulum. The M3/s are unworn, the protocone of the M2/s is slightly worn. The M1/s are lingually more worn than the other molars; this corresponds to wear stage A2 and suggests that the individual was probably a young adult.

BAR 786'00/BAR 1368'00 (Fig. 7D1-D3; Table 1)
General description and preservation. This fossil consists of two fragments which fit together: BAR 1368'00, a left M2/ and BAR 786'00 a portion of the left hemi-maxilla with the M3/ (maximum length: 21.4 mm; breadth: 14.2 mm; height: 21.2 mm). A fragment of hard palate is preserved in BAR 786'00. The groove of the posterior palatine foramen is present opposite the M3/. The hard palate seems to end at the M3/ level.

Dentition. Only the left M2/ and M3/ are preserved and are quite worn. M2/ is the bigger of the teeth. The distal loph is narrower than the mesial one in the M2/, and more so in the M3/. The M2/ presents an eroded tiny accessory cusp (mesostyle) in the middle of median buccal cleft. The distal fovea in the M3/ is small and worn. On the buccal side, the mesial and distal cleft are visible on M1/ and M2/. The wear stage could correspond to A3, the specimen is a medium-aged adult individual.

OCO 100'01 (Fig. 8A1-A3)
This specimen is 20.2 mm long comprising a fragment of right mandible partly covered with matrix and associated with other small fragments of bone. The *corpus mandibularis* is as narrow as in BAR 760'00 and OCO 608'10. The preserved parts of the two surfaces are vertical. In occlusal view, sections of four tooth roots are seen, but are difficult to identify. Not much can be said about the fragment.

BAR 1586'00 (Fig. 8B1-B3)
General description and preservation. This fragment (15.7 mm height; 12.5 mm width) is a part of a mandibular symphysis, well preserved in its occlusal and labial parts (despite a

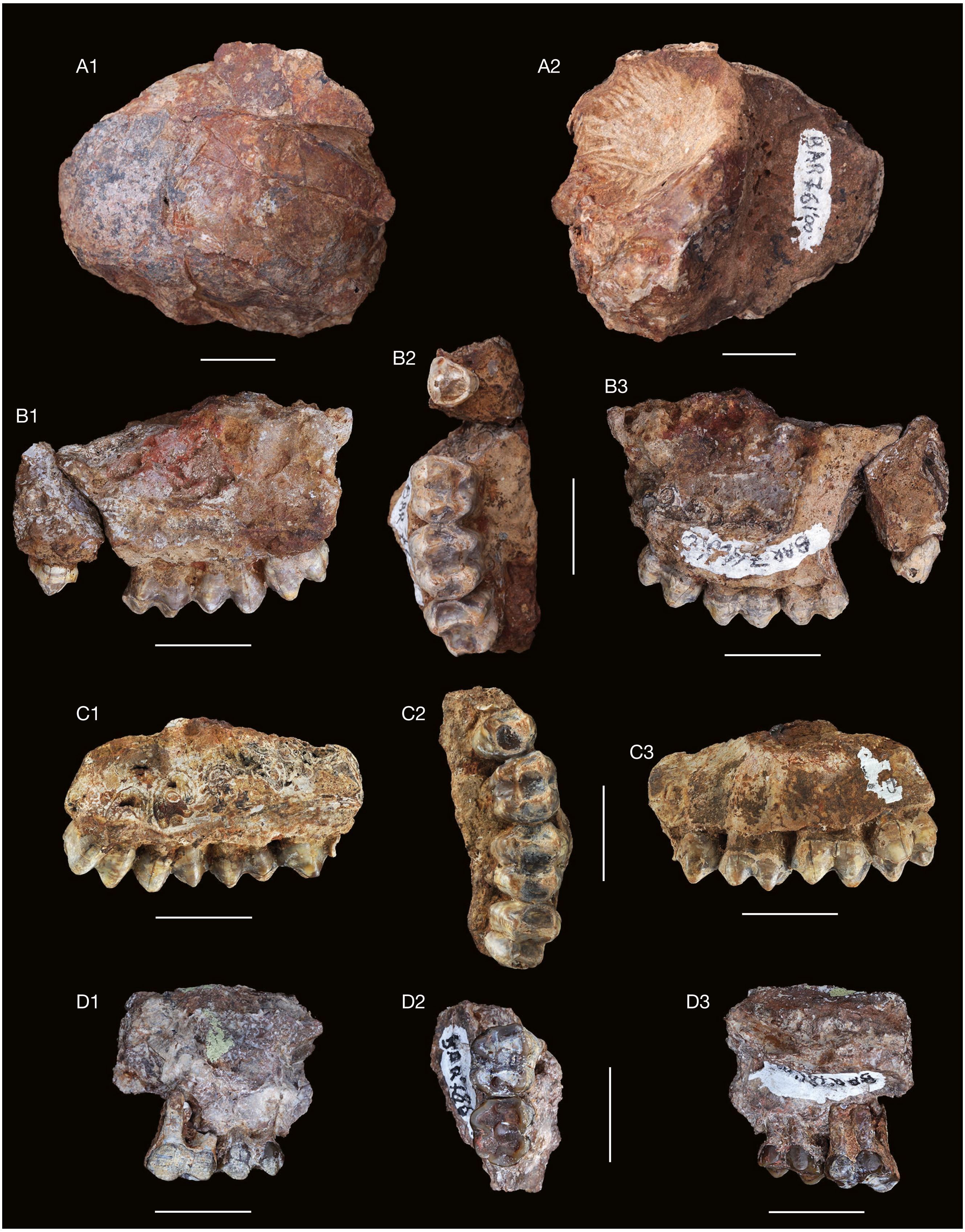

FIG. 7. — *Sawecolobus lukeinoensis* n. gen., n. sp.: **A**, skull fragment BAR 761'00: **A1**, nucho-lateral view; **A2**, internal view; **B**, right maxilla fragment BAR 762B'00 (maxilla fragment with M1/ to M3/) + OCO 1049'11 (P3/) associated with BAR 762A'00: **B1**, lingual view; **B2**, occlusal view; **B3**, buccal view; **C**, left maxilla fragment BAR 762A'00 (maxilla fragment with P4/ to M3/) associated with BAR 762B'00: **C1**, lingual view; **C2**, occlusal view; **C3**, buccal view; **D**, left maxilla fragment BAR 786'00 (partial maxilla with M3/) + BAR 1368'00 (left M2/): **D1**, buccal view; **D2**, occlusal view; **D3**, lingual view. Scale bars: 1 cm.

median vertical crack). The medial mental foramen is not visible. The beginning of the *planum alveolare* is preserved. It is almost vertically inclined and concave. The symphysis is vertical and gracile, differing from the broad symphysis seen in *Cercopithecoides*.

Only the roots of the left i/1, i/2, /c and of the right i/1 and i/2 are preserved. The mesial part of the right canine alveolus is preserved. The roots of the incisors have a compressed ovoid outline. The incisors would have been small and close together as suggested by the morphology of the roots, typical of colobine monkeys. The roots of i/1 are slightly bigger than those of i/2. There is no diastema between the incisors and the canines as in *Cercopithecoides*, *Kuseracolobus*, *Mesopithecus* and unlike *Libypithecus* and *Paracolobus.*

Sex and age. The left canine root and the socket of the right one are small. The left canine root has a compressed and ovoid outline. These features and the relatively small size suggest that this specimen probably represents a female individual.

OCO 608'10 (Fig. 8C1-C3; Table 1)

General description and preservation. The mandible OCO 608'10 is composed of nine isolated fragments of the same fossil embedded in a hard matrix (maximum length: 56.6 mm; breadth: 45.4 mm; height: 34.7 mm). An extensive mechanical preparation was done to extract the specimen from the matrix but it could not be completed because of the fragility of the fossil. The right side, the most complete, comprises the *corpus mandibularis*, the base of the ascending ramus and all the post-canine teeth. Most of the inferior border of the left mandibular corpus is absent but the post-canine teeth are better preserved and prepared than on the opposite side. On the symphysis, vertical cracks and a slight lateral distortion between the left i/2 and /c are visible. Some matrix remains inside the mandible and covers the posterior surface of the symphysis.

Symphysis. The symphysis is damaged inferiorly; it is deep but also seems long (only 20.2 mm preserved (see Appendix 1: measurement SL) compared to the total the length of the dental arch of 42 mm (see Appendix 1: measurement NW). Despite the damage, the inferior edge of symphysis seems to extend at least as far posteriorly as the p/4. Laterally, the contour of the anterior surface is inclined globally posteriorly but presents a break in the slope, the upper third is less inclined than the lower part. However, the contour appears to be convex. In *Cercopithecoides williamsi*, this anterior surface appears slightly inclined and straighter despite a lower third that is more inclined posteriorly (below the medial mental foramen). Furthermore, the inferior edge of the symphysis extends less posteriorly, to the p/3 (especially in BF 42B). In *Cercopithecoides bruneti*, the external part doesn't present a break in slope with a straight and inclined contour (Pallas *et al.* 2019) and neither does *C. kerioensis* (Leakey *et al.* 2003). In *Paracolobus enkorikae*, the symphysis presents a rounded slope with a slight break for the lower half (Hlusko 2007). In *Rhinocolobus*, the symphysis extends posteriorly at a shallow angle but a break in the slope exists below the alveoli (Frost & Delson 2002). In anterior view, the symphysis of OCO 608'10 is narrow, convex transversely and not laterally compressed in the middle of each side, unlike *Cercopithecoides williamsi.* No medial mental foramen is visible as is the case in most colobines except in *Procolobus*, *Cercopithecoides* and *Rhinocolobus*.

Mandibular corpus. The left mandibular corpus is broken. The right one is deep and vertical as is the case in BAR 1586'00. The buccal surface is slightly convex and the lateral fossa is absent. The inferior edge is broken on the right side, but it does not present a strong lateral flare as in *Cercopithecoides* (in *C. kerioensis*, the lateral flare is more important than in *C. williamsi* (Leakey *et al.* 2003). A lateral mental foramen is present under the p/4. The area of the *prominentia laterales* is too eroded to confirm or not its presence. A narrow extramolar sulcus is present between the m/3 and the ramus.

Dentition. The right and left post-canine teeth are well preserved. Only the right m/1 presents a transverse crack on its mesial lophid. The right teeth being slightly more covered by matrix than those of the left side, the latter are used for the descriptions.

The incisors are broken or embedded in matrix but the enamel is visible on the left i/2. The right canine is broken. The big left canine has lost the supero-distal portion of the crown. It is labially curved and tilted as in *Mesopithecus* and *Colobus* but unlike *Paracolobus enkorikae* (Hlusko 2007). The premolars are heteromorphic as in all Cercopithecidae (Swindler 2002). The p/3s are longer and broader than the p/4s; they are sectorial and monocuspidate (developed protoconid). There is a developed mesio-buccal flange as is usual in Cercopithecoidea, but they were not yet honed by the upper canine (Zingeser 1969). The preprotocristid is very salient and the mesial cingulum forms a swelling which continues lingually. The trigonid is small and shallow. The postprotocristid is less salient and shorter than the preprotocristid. The lingual surface is complex with two vertical crests. The disto-lingual part of the teeth is covered by matrix. The p/4s are more tricuspid than bicuspid (Hornbeck & Swindler 1967). The metaconid is opposite the protoconid (Swindler & Orlosky 1974) and the two cusps are almost of equal height but the protoconid is more massive than the metaconid. A small but salient entoconid is present disto-lingually. They have a mesio-buccal flange, less than for the p/3s, typical of colobine in which flare is more prominent than in cercopithecines (Swindler 2002). It is well preserved and not yet worn by contact with the P3/ (Zingeser 1969). The preprotocristid is very salient and together with the mesial cingulum, it forms a tall, curved mesio-buccal wall to the trigonid basin which is small and shallow. The postprotocristid is less salient than the preprotocristid. The endoprotocristid is longer than the endometacristid and the two cristids are separated by a discrete slit. The distal cingulum is short and bucco-distally positioned. The talonid basin is narrow and larger than the trigonid basin. A short endoentocristid is present (some matrix

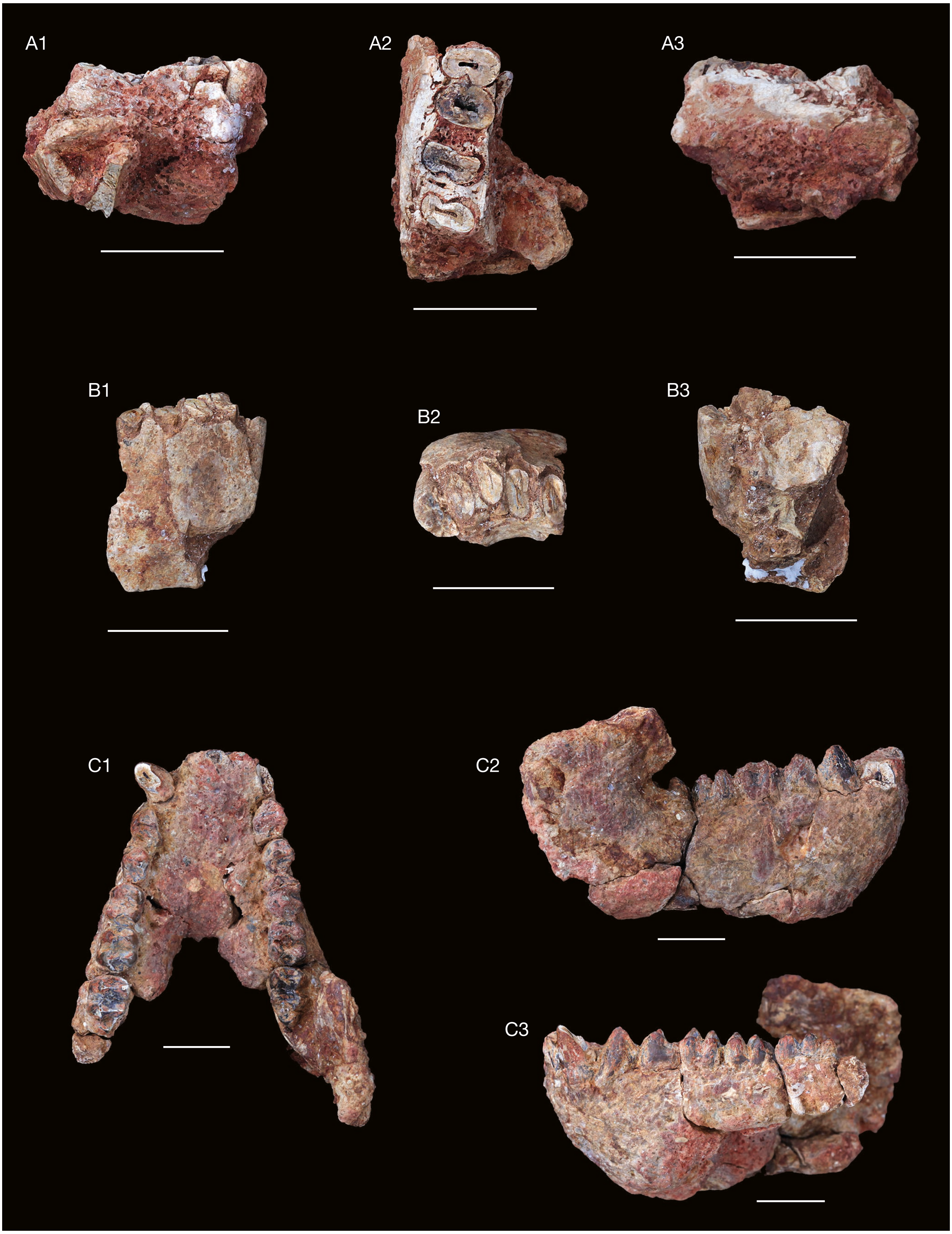

Fig. 8. — *Sawecolobus lukeinoensis* n. gen., n. sp.: **A**, right mandibular fragment OCO 100'11: **A1**, buccal view; **A2**, occlusal view; **A3**, lingual view; **B**, mandibular symphysis BAR 1586'00: **B1**, labial view; **B2**, occlusal view; **B3**, lingual view; **C**, mandible OCO 608'10: **C1**, occlusal view; **C2**, right lateral view; **C3**, left lateral view. Scale bars: 1 cm.

TABLE 2. — List of the isolated teeth from Aragai with measurements (in mm). Symbols: **µ**, hypoplasia mark; *****, worn or broken.

INCISORS

Collection number	Identification	Side	MD	BL
BAR 1214’00	I1/	R	4.5	5
BAR 910’04	I2/*	R	3	4.1

CANINES

Collection number	Identification	Side	MD	BL	TH	CrH
BAR 784’00	C/	L	11	6.5	28.2*	16.8*
BAR 1585’00	C/ (root)	L	9.7	6.3	×	×
BAR 1595’01	C/	L	11.2	7.4	24.9*	11.8*
OCO 105’10	C/	R	9.7	6.9	×	11.1*
BAR 785’00	/c	L	9.3	5.5	×	×
BAR 1369’00	/c	R	5	3.2	15.9*	4.9*
BAR 1584’00	/c	L	8.6	6.3	31.7	15.8
BAR 1381’03	/c$^{\mu}$	R	5.7	3.3	13.2*	7.7
BAR 1382’03	/c	L	4.9	3.8	8.6*	4.8*
BAR 351’04	/c	L	4.3	3.6	×	5.7*
OCO 104’10	/c$^{\mu}$	L	5.5	3.7	×	7.5

PREMOLARS

Collection number	Identification	Side	MD	BL
OCO 305’11	P3/	L	6	6
OCO 101’11	p/3$^{\mu}$	R	7.5	3.5

MOLARS

Collection number	Identification	Side	MD	Mb	Db	Hb
BAR 470’01	M2/	L	7	6.8	6.5	–
BAR 1597’01	M2/ (half)$^{\mu}$	L	7.5*	×	×	–
BAR 1190’03	m/2	L	6.8	5.7	5.6	–
BAR 349’04	m/2	R	7.7	6.4	×	–
BAR 1190’03	m/2	L	6.8	5.7	5.6	–
OCO 335’10	m/2	R	6.9	5.5	5.3	–
BAR 250’03	m/3 (distal part)	R	×	×	6.1	4.1

covers this in the right p/4). The distal part of the p/4 is low and narrower than the rest of the premolar, it looks like a long distal heel (like a platform). This is not so marked in *Colobus*, *Piliocolobus*, *Cercopithecoides williamsi*, *Kuseracolobus*, *Libypithecus* and *Paracolobus* but a bit more in *Procolobus*. The p/4s do not have a lingual notch separating the talonid basin from the metaconid unlike *Kuseracolobus* sp. from Kanapoi (Frost *et al.* 2020b) and *Libypithecus* which do.

The molars increase in size from m/1 to m/3 as is usual in colobines (Table 1; Appendix 2). The m/1s are small compared to the m/2s and m/3s. The width strongly increases from m/1 to m/3 (the same but to a lesser degree occurs in *Cercopithecoides*, *Kuseracolobus* and extant African colobines but not in *Paracolobus*.). The distal lophid of the m/1s is broader than the mesial one; the same applies to the m/2s. In m/3s, the mesial lophid is the broadest. The hypoconulid is present in the m/3s as is usual in colobines, but it is buccally positioned, prominent and very salient.

Sex and age. The post-canine teeth are unworn which suggests that the specimen represents a young adult individual. The canine is big, and the p/3 is tall mesially, a morphology typical of male individuals.

ISOLATED TEETH

The collection includes 21 isolated teeth which are briefly presented in Table 2. They are attributed to *Sawecolobus lukeinoensis* n. gen., n. sp. on the basis of their morphology and dimensions.

Incisors

Apart from the damaged left I1/ of BAR 756’00, the collection from Aragai is represented by only two isolated incisors, BAR 910’04 and BAR 1214’00. These teeth are small as is usual in colobines.

BAR 1214’00 (Fig. 9B1-B5), a right I1/, presents many colobine features (Swindler 2002) such as a deep central groove on the lingual surface and a strong lingual cingulum, and the mesial and distal marginal ridges are present but, in this specimen, salient with a stronger mesial marginal ridge. Mesially, there is a clear interstitial contact facet caused by contact with the left I1/. The worn occlusal surface corresponds to wear stage A2 and could belong to a young adult.

BAR 910’04 (Fig. 9A1-A5), a right I2/, is caniniform and reduced, a morphology seen in colobines. The labial cingulum is strong. Buccally, several hypoplastic lines are visible, but a strong line occurs at mid-crown. The occlusal surface is slightly worn distally and could represent wear stage A2 or the beginning of A3, suggesting that the specimen also belongs to a young adult.

Lower canines

Of the seven lower canines known from Aragai, two belong to males (BAR 785’00 and BAR 1584’00) and four to females (BAR 1369’00, BAR 1381’03, BAR 1382’03, BAR 351’04 and OCO 104’10). The morphology and size of these canines indicate the presence of strong sexual dimorphism in *Sawecolobus lukeinoensis* n. gen., n. sp. For a better understanding of the morphology of the tooth category, the description of each sex will start with the best-preserved specimen. For interpreting the canine honing mechanism, Zingeser (1969) was consulted.

Male. BAR 1584’00 (Fig. 9L1-L4) is a complete and well preserved left lower canine. The crown is tapered and sharp and slightly inclined buccally. On the disto-lingual part of the crown, the extensive honing facet with the upper canine

FIG. 9. — *Sawecolobus lukeinoensis* n. gen., n. sp.: **A**, **B**, incisors: **A**, right I2/ BAR 910’04: **A1**, lingual view; **A2**, labial view; **A3**, mesial view; **A4**, distal view; **A5**, occlusal view; **B**, right I1/ BAR 1214’00: **B1**, occlusal view; **B2**, lingual view; **B3**, labial view; **B4**, mesial view; **B5**, distal view; **C**-**L**, canines: **C**, left upper canine BAR 784’00: **C1**, mesial view; **C2**, distal view; **C3**, lingual view; **C4**, buccal view; **D**, left upper canine BAR 1595’01: **D1**, distal view; **D2**, mesial view; **D3**, lingual view; **D4**, buccal view; **E**, right upper canine OCO 105’10: **E1**, distal view; **E2**, mesial view; **E3**, buccal view; **E4**, lingual view; **F**, left lower canine BAR 785’00: **F1**, lingual view; **F2**, labial view; **F3**, mesial view; **F4**, distal view; **G**, right lower canine BAR 1369’00: **G1**, lingual view; **G2**, labial view; **G3**, mesial view; **G4**, distal view; **H**, right lower canine BAR 1381’03: **H1**, lingual view; **H2**, labial view; **H3**, mesial view; **H4**, distal view; **I**, left lower canine BAR 1382’03: **I1**, lin-

gual view; **I2**, labial view; **I3**, distal view; **I4**, mesial view; **J**, left lower canine BAR 351’04: **J1**, lingual view; **J2**, labial view; **J3**, distal view; **J4**, mesial view; **K**, left lower canine OCO 104’10: **K1**, distal view; **K2**, lingual view; **K3**, mesial view; **L**, left lower canine BAR 1584’00: **L1**, lingual view; **L2**, labial view; **L3**, distal view; **L4**, mesial view. Scale bars: 1 cm.

suggests wear stage A4 (adult). Distally, a strong doubled distal tubercle forms a distal heel and occurs at the base of the crown at the top of a shallow disto-lingual groove (sulcus) which extends along the root. The distal heel was considered by Lucas & Teaford (1994) to be common in colobines and it becomes more noticeable with wear. Mesially, a relatively deep mesial groove is worn apically by a honing facet for the I2/. The "V"-shaped mesial cervix rises weakly apically and is bordered by a weak cingulum. A broad shallow groove rises along the mesial face of the root but is less marked than in BAR 785'00.

In BAR 785'00 (Fig. 9F1-F4) only the root and the lower part of the lower canine crown are preserved. A small honing facet is present on the disto-lingual part of the crown on which basis this canine is inferred to belong probably to a young adult. The honing facet is located just above a strong disto-lingual tubercle at the base of the crown which corresponds to the distal heel, under which a shallow sulcus extends along the root disto-lingually. The "V"-shaped mesial cervix is developed and rises apically, bordered by a cingulum. A broad and shallow groove runs along mesial surface of the root.

Female. The right lower canine BAR 1381'03 (Fig. 9H1-H4), is the best-preserved female lower canine. It lacks only the apical part of the root which is slightly compressed mesio-distally, probably during fossilization. The apex of the crown is slightly worn. There is no honing facet indicating wear stage A1. The canine belongs to a young adult. Hypoplastic lines are well marked on the labial and distal faces, but the most prominent one occurs at the base of the crown, just above the cervix and may have resulted from stresses related to weaning. The crown is straight. In distal view, there is a salient cingulum which forms a discrete disto-lingual tubercle. Two narrow and shallow grooves run down the root disto-lingually but could be due to fossilization. In mesial view, a small and salient crest runs from the apex of the crown to a well-marked distal cingulum. The "V"-shaped mesial cervix extends weakly apically, as well as the cingulum. A narrow shallow groove runs down the root. In mesial and distal views, the lingual part of the crown is low and forms a pronounced overhang or a platform (distal heel of Lucas & Teaford (1994)). In labial view, the crown is moderately high and narrow. The surface is strongly convex. The mesial face of the root presents two shallow grooves, the one closer to the lingual edge of the root is more pronounced and is probably the only natural one (cf. BAR 1369'00 and BAR 1382'03).

BAR 1369'00 (Fig. 9G1-G4) is an entire right lower canine with a worn apex. A honing facet is visible at the junction between crown and root in distal and lingual views. The wear stage can be A4 or A5. The "V"-shaped mesial cervix is developed apically, as well as the cingulum. A narrow and flat groove runs along the mesial surface of the root. In distal view, the surface of the root is convex labio-lingually. The root is elongated contrasting with a low crown.

BAR 1382'03 (Fig. 9I1-I4) is a small left lower canine preserving the crown with a worn apex and part of the root compressed mesio-distally but less so than in BAR 1381'03 and OCO 104'10. A developed honing facet has damaged the distal part of the crown (area of the distal overhang or platform) and part of the root. The wear stage is A4 or A5. BAR 1382'03 resembles BAR 1381'03 in the morphology of the "V"-shaped mesial cervix, small and salient mesial crest on the crown and the associated cingulum, and a mesial groove on the root. In lingual and distal views, the distal overhang or platform is almost completely gashed by the honing facet. The distal surface of the root is convex labio-distally.

BAR 351'04 (Fig. 9J1-J4) is a damaged left lower canine crown. The apex of the crown is broken off. The discrete disto-lingual tubercle is almost smooth. The "V"-shaped mesial cervix, the lower part of the mesial crest on the crown and neighbouring strong cingulum have the same characteristics as the other female canines described above. In mesial and distal views, the lingual overhang or platform is clearly defined.

OCO 104'10 (Fig. 9K1-K3) is a well-preserved left lower canine. This tooth is morphologically identical to the right canine BAR 1381'03 with the same worn aspect of the apex and hypoplastic lines, especially the biggest one at the base of the crown above the cervix. OCO 104'10 and BAR 1381'03 could belong to the same individual. The root is compressed mesio-distally but less so than BAR 1381'03, the root also seems to be affected by fossilisation. The distal and mesial surfaces present two shallow grooves, both of which are pronounced.

Upper canines

The upper canines are represented by three partial canines (BAR 784'00, BAR 1595'01 and OCO 105'10) and a fragment of root (BAR 1585'00), all of them belong to male individuals. The upper canines are morphologically similar to those of large extant African colobines and are of the same size or slightly larger than the biggest male of *Colobus guereza* (Appendix 3).

BAR 784'00 (Fig. 9C1-C4) is a left upper canine which preserves the crown with a broken apex and part of the root. The mesial groove is deep, curved rootwards and runs along the root. The buccal slit is well marked. The disto-lingual part of the cervix of the crown was compressed during fossilization. The canine is bucco-lingually flattened and resembles a dagger.

The upper and lower apices of the left upper canine BAR 1595'01 (Fig. 9D1-D4) are broken off, but the crown did not suffer compression during fossilization. The mesial groove is deeper than in BAR 784'00. The lingual surface of the distal crest presents a honing facet for the p/3 (wear stage A4 which suggests an adult individual).

BAR 1585'00 is the upper part of an upper canine root with part of honing facet on its distal side.

OCO 105'10 (Fig. 9E1-E4) is a right upper canine represented by a crown missing the apex and part of the root. The mesial sulcus is well preserved on the root and is as deep as in BAR 784'00. There is a huge honing facet on the distal side of the tooth and a moderate honing facet cut off by the mesial groove on the apex. The wear stage could be A5.

Premolars

Aragai yielded two isolated premolars.

OCO 101'11 (Fig. 10B1-B4) is a well-preserved right p/3 with a lightly worn protoconid (wear stage A2; young adult). There is no honing facet despite a relatively well-developed mesio-buccal flange which is however less extended than in OCO 608'10 suggesting that it could be a female as in *Colobus* and *Piliocolobus*. It also presents some hypoplastic lines. An acerate lingual ridge descends from the protoconid towards the small metaconid. The metaconid is distally positioned and not opposite the protoconid. The shallow mesial fovea (or trigonid basin) is smaller than the distal fovea which is deep. The mesial cingulum is slightly developed. Strong pre- and postprotocristids are salient and descend from the protoconid mesially and distally respectively. Distally a contact facet with the p/4 is weak. The postprotocristid is separated from the distal cingulum by a cusplet. A short postmetacristid has a cusplet in its median part and is separated by a small slit from the distal cingulum. There is another cusplet lingually in the distal cingulum. There are two straight coalescent roots, the mesial of which is the stronger and the apices are curved gently distally.

OCO 305'11 (Fig. 10A1-A4) is a well-preserved crown of P3/. The apex of the paracone is slightly worn (wear stage A1 of a very young adult). The protocone forms more of a salient smooth curved crest rather than a typical cusp but it nevertheless exists. The preparacrista is more salient than the postparacrista. The low endoparacrista joins the developed salient endoprotocrista. The mesial fovea (trigon basin) is small and shallow and the distal basin (talon basin) is large and deep. The distal cingulum is salient and long.

Molars

Five isolated molars were discovered at Aragai, three lowers (BAR 1190'03, BAR 394'04 and OCO 335'10) and two uppers (BAR 470'01 and BAR 1597'01).

BAR 1190'03 (Fig. 10E1-E5) is a left m/2 The specimen is complete comprising the crown, the roots and some mandibular bone. The morphology of the occlusal surface corresponds to wear stage A4 indicating that this tooth belongs to an adult.

BAR 349'04 (Fig. 10G1-G5) is a right m/2. The crown is well preserved except for the disto-buccal part which is missing. Only the cervical part of the roots is preserved. The crown is slightly worn suggesting wear stage A2 which corresponds to a young adult. Its large size indicates that it could belong to a male individual.

OCO 335'10 (Fig. 10H1-H5) is a right m/2. The crown and the two roots are well preserved, and is smaller than BAR 1190'03. The crown is slightly worn and suggests wear stage A2. The two specimens show similarities: square occlusal outline, the talonid equal to the trigonid, well-marked lophids, a reduced mesial fovea and a wider distal one which is bordered by a strong cingulum. The lingual cusps are much higher than the buccal ones, a feature characteristic of colobines. The metaconid is well developed, higher than the entoconid. The protoconid and hypoconid are almost equal in height. The buccal cuspids are horizontal. The hypoconulid is absent at least in BAR 1190'03 and OCO 335'10.

BAR 250'03 (Fig. 10F1-F5) is the distal fragment of a right m/3, the three cuspids (entoconid, hypoconid and hypoconulid) are slightly eroded and not deeply worn suggesting wear stage A1 or A2. The molar belongs to a young adult. Lingually to the hypoconulid, two discrete cuspids are present but neither could be recognized as the *tuberculum sextum* (Saheki 1966; Swindler & Orlosky 1974). The hypoconid is as high as the hypoconulid but the hypoconulid is bigger.

BAR 470'01 (Fig. 10C1-C5) and BAR 1597'01 (Fig. 10D1-D2) are two left M2/s. BAR 470'01 preserves the crown and the cervical parts of the lingual and the distal roots. The contour of the crown is moderately trapezoidal (the buccal surface is mesio-distally longer than the lingual one, the protocone is more salient lingually than the hypocone and they are isolated by a deep groove) as are M2/s of BAR 756'00, BAR 758'00, BAR 762A'00 and BAR 762B'00, and as well as those of *Colobus* and *Piliocolobus*, different from M1/ in which the contour is more square. The morphology of the occlusal surface corresponds to wear stage A3, typical of adults. Only the lingual side of BAR 1597'01 is preserved and the cusps are slightly worn as in wear stage A2 (young adult) and present a well-marked hypoplastic line close to the cervix. BAR 470'01 has contact facets mesially and distally for the M1/ and M3/ respectively. The trigon basin is deep and short. There is a small and clear mesostyle in the median buccal cleft between the paracone and the metacone. The mesial and distal cingula are well developed in BAR 1597'01 but worn in BAR 470'01. In both teeth, the fovea are clearly visible, but poorly developed.

Postcranial bones

Aragai yielded four cercopithecoid post-cranial bones: BAR 757'00, an axis vertebra (which is described above), BAR 914'04, a proximal right metatarsal V and two distal humeri (OCO 102'11, a right distal humerus, OCO 336'10, a left distal humerus). They were found in the same restricted area as the craniodental material.

BAR 914'04 (Fig. 11A1-A5) comprises two fragments which fit together (maximum length: 22.2 mm; maximum width: 7.7 mm, proximal height (measurement n°3 in Gommery *et al.* 2009: 5.6 mm). The proximal end is slightly eroded, but the shaft is well preserved. The morphology of the superior and medial views of the proximal extremity are similar to those of the extant African colobines in the morphology of the articular facet for the cuboid which does not occupy all the surface in proximal view but is located more laterally (height: 7.1 mm, width: 3.6 mm). This differs from *Parapapio* from Waypoint 160 at Bolt's Farm, WP 19 (Gommery *et al.* 2009), from Laetoli, LAET 76-3870 (Harrison 2011) and from Hadar, A.L.363-1f/1 (Frost & Delson 2002), in which the articular facet occupies all the surface or is supero-medial. In

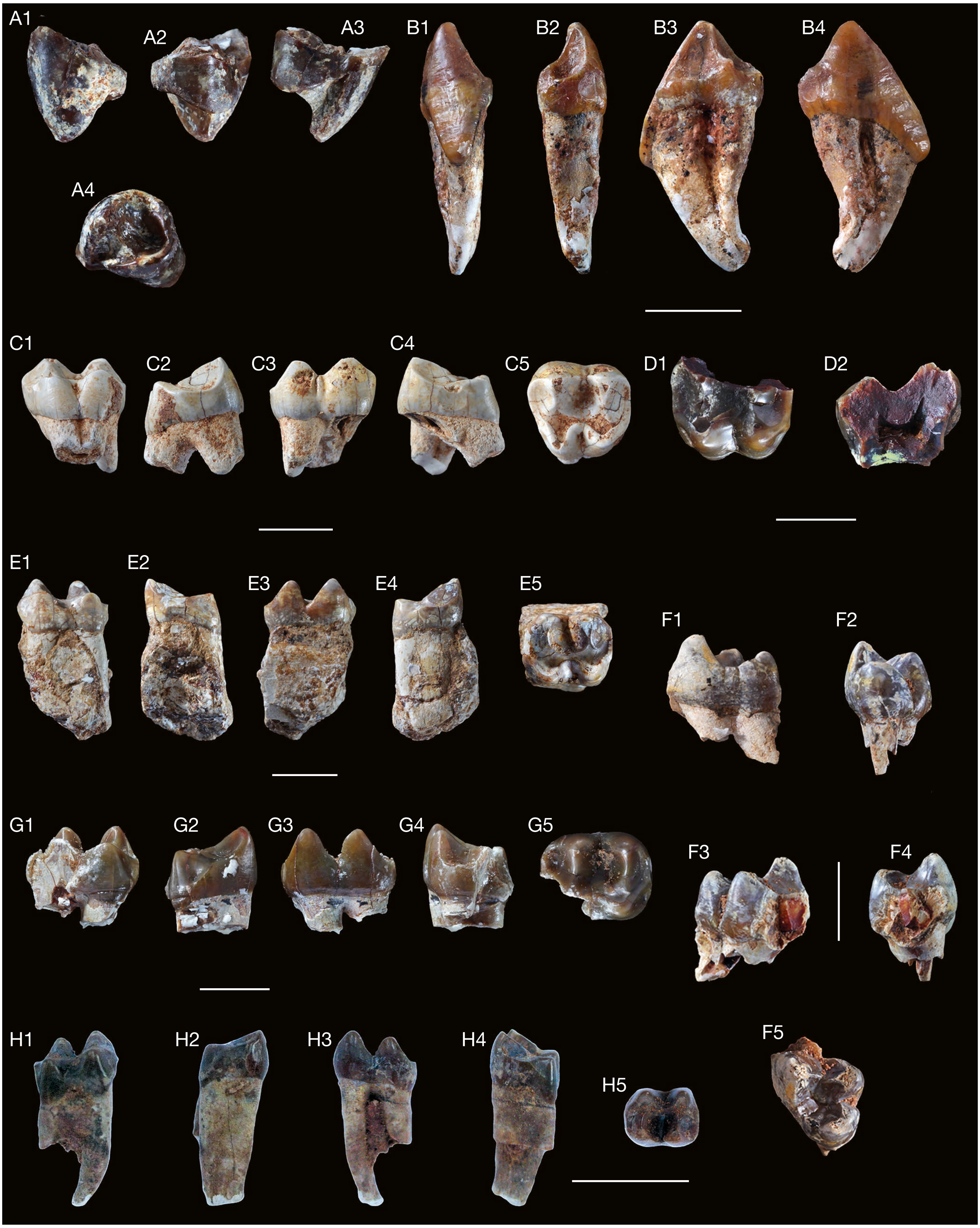

Fig. 10. — *Sawecolobus lukeinoensis* n. gen., n. sp., post-canine teeth: **A**, left P/3 OCO 305’11: **A1**, buccal view; **A2**, lingual view; **A3**, mesial view; **A4**, occlusal view; **B**, right p/3 OCO 101’11: **B1**, mesial view; **B2**, distal view; **B3**, lingual view; **B4**, buccal view; **C**, left M2/ BAR 470’00: **C1**, lingual view; **C2**, distal view; **C3**, buccal view; **C4**, mesial view; **C5**, occlusal view; **D**, left: M2/ BAR 1597’01: **D1**, occlusal view; **D2**, buccal view of interior of tooth; **E**, left m/2 BAR 1190’03: **E1**, buccal view; **E2**, mesial view; **E3**, lingual view; **E4**, distal view; **E5**, occlusal view; **F**, half right m/3 BAR 250’03: **F1**, lingual view; **F2**, distal view; **F3**, mesio-buccal view; **F4**, mesial view; **F5**, occlusal view; **G**, right m/2 BAR 349’04: **G1**, lingual view; **G2**, distal view; **G3**, buccal view; **G4**, mesial view; **G5**, occlusal view; **H**, right m/2 OCO 335’10: **H1**, buccal view; **H2**, mesial view; **H3**, lingual view; **H4**, distal view; **H5**, occlusal view. Scale bars: 5 mm except for H, 1 cm.

Fig. 11. — *Sawecolobus lukeinoensis* n. gen., n. sp., postcranial bones: **A**, proximal right metatarsal V, BAR 914'04: **A1**, plantar view; **A2**, lateral view; **A3**, superior view; **A4**, medial view; **A5**, distal view; **B**, right distal humerus OCO102'11: **B1**, anterior view; **B2**, posterior view; **B3**, distal view; **C**, left distal humerus OCO 336'10: **C1**, anterior view; **C2**, posterior view; **C3**, distal view. Scale bars: 1 cm.

median view, the articular facet for the metatarsal IV is important (height: 6.3 mm, width: 3.1 mm). In plantar view, as usual, there are two facets for the sesamoid bones. Laterally, there is a moderately developed bony bulge as is the case in extant African colobines. The distal part of the shaft appears robust relative to the proximal part of the metatarsal and is flattened medio-laterally in comparison to those of extant African colobines. The aspect of the shaft is very similar to WP 19 from Bolt's Farm but differs from that of *Paracolobus chemeroni* from the Tugen Hills, KNM BC 3 AA (Birchette 1982). The size of BAR 914'04 is intermediate between *Piliocolobus* and *Procolobus*, so it can be attributed with confidence to *Sawecolobus lukeinoensis* n. gen., n. sp.

OCO 102'11 (Fig. 11B1-B3) is a well-preserved right distal humeral articulation with a broken lateral epicondyle (maximum length: 13.1 mm; maximum width: 21.2 mm, maximum height: 11.8 mm). OCO 102'11 is smaller than the specimens of the *Piliocolobus* sample. In distal view, the trochlear surface is narrow relative to the total articular width. The rounded *capitulum humeri* is distally salient and separated from the *trochlea humeri* by a low and smooth crest. The *zona conoidea* appears short and low. The disto-lateral edge of the capitulum is damaged but the lateral edge of the radial fossa is preserved and marks the end of the capitulum which appears cylindrical as in African colobines. The preserved distal part of the medial epicondyle indicates that it is strong, short and projects strongly posteriorly. The angle of the medial epicondyle is approximately 50° and falls within the range of variation of African colobines as well as that of many other Cercopithecoidea (Frost & Delson 2002). In anterior view, the trochlea is short proximodistally and wide. The preserved part of the radial fossa is deeper and larger than the coronoid fossa, as is typical in colobines (Olivier & Caix 1959; Szalay & Delson 1979; Frost & Delson 2002). The *zona conoidea* is narrow and moderately-to-slightly shallow, differing from those of *Colobus* and *Piliocolobus*. The surface of the lateral edge of the trochlea, which separates it from the *zona conoidea*, forms a smooth ridge elongated antero-posteriorly and is not as prominent as in *Cercopithecus lhoesti* (Gebo & Sargis 1994). It is somewhat similar to those of *Colobus*, *Piliocolobus* and *Lophocebus*, and more pronounced than that of *Chlorocebus* (Senut 1989; this study). It is more pronounced than in *Cercopithecoides* and in *Rhinopithecus* from Hadar (Frost & Delson 2002) or *cf. Paracolobus* from Nkondo (NK 322'88) (Senut 1994) and *Kuseracolobus aramisi* (DID-VP-1/78) (Frost *et al.* 2009). The medial trochlear flange projects disto-medially. It is straighter than in *Colobus* and *Piliocobus* where it projects more medially and less distally, but is less straight than in *Lophocebus* and especially in *Cercocebus* (Senut 1989; this study). It is less straight than in *Cercopithecoides* and unlike that of *Rhinopithecus* from Hadar (Frost & Delson 2002) or *cf. Paracolobus* from Nkondo (NK 322'88) (Senut 1994) and *Kuseracolobus aramisi* (DID-VP-1/78) (Frost *et al.* 2009) in which it is straight. In posterior view, the articular surface is oblique latero-proximally to disto-medially as evidenced by the inclination of the medial trochlear rim, as in *Cercopithecus mitis* (Gebo & Sargis 1994) but also in *Colobus*, *Piliocolobus*, *Lophocebus* and *Cercocebus*.

OCO 336'10 (Fig. 11C1-C3) is a left distal humerus. It is smaller (maximum length: 14 mm; maximum width: 18.3 mm; maximum height: 10.8 mm) and is more gracile than OCO 102'11 (some anatomical features are less pronounced). In distal view, as for OCO 102'11, the trochlear surface is narrow relative to the total articular width. The capitulum is cylindrical. The well-preserved medial epicondyle confirms the observation made on the right humerus. The angle of the median epicondyle is approximately 52°. In anterior view, the trochlea is short proximo-distally and narrow. The radial fossa is deep and large. The coronoid fossa is reduced. The *zona conoidea* is also narrow and shallow. The smooth and low ridge which separates the *capitulum humeri* from the *trochlea humeri* is less pronounced than in OCO 102'11. The surface of the ridge corresponding to the lateral edge of the trochlea is slightly eroded but is very similar to that of OCO 102'11. In posterior view, only the distal part of the *fossa olecrani* is preserved and is deep and narrow as in the vervet monkey (*Chlorocebus aethiops*) and some *Cercopithecus* (*C.* (*Cephus*) *ascanius*, *C. lhoesti*, *C. neglectus*). There is no groove between the trochlea and the medial epicondyle. The medial trochlear rim projects distally, but less than in OCO 102'11.

DISCUSSION AND CONCLUSION

The Aragai colobine collection is represented by a minimum of six individuals. This quantity is estimated on the basis of the skulls and the partial palate (BAR 756'00, BAR 757'00 and BAR 758'00) but also from the isolated left upper canines (BAR784'00, BAR 1585'00 and BAR 1595'01). All the specimens were found in a small area. The specimens are not rolled. All these observations could suggest that the specimens might belong to the same monkey troop which died during a specific event (as for example a flood or a mudslide) or that they were attracted to something and got trapped in the mud. But a more likely hypothesis would be that the specimens represent remains of the diet of a large raptor (Jenkins 2018) such as the Crowned Eagle or the Martial Eagle which are known to feed on small and medium-size mammals including bushbuck, impala calves or monkeys. The bones would have accumulated at the base of the tree where the raptors were eating or nesting; a hypothesis which is reinforced by the fact that the material was found in a restricted area (20 m^2). However, it is not possible to observe the marks left by potential raptors as some specimens are covered with matrix and the long bones are fragmentary. Apart from Aragai, only one other site of the Lukeino Formation (Kapsomin) has yielded a rich collection of primate remains, not only isolated teeth but also mandibles. They were also found on a limited surface which would also support the hypothesis.

A high diversity of colobine taxa is now recognized from the African late Miocene to the middle Pliocene: *Cercopithecoides – C. bruneti*, *C. kerioensis*, *C. meaveae* and *C. williamsi*; *Kuseracolobus – K. aramisi* and *K. hafu*; *Libypithecus – L. markgrafi*; *Paracolobus – P. enkorikae* and *P. mutiwa*; *Rhinocolobus – R. turkanensis*. They are all medium-sized to large colobines, most of them being bigger than *Sawecolobus lukeinoensis* n. gen., n. sp. (Tables 3; 4). It is especially true for the size of the teeth of the oldest ones such as *K. aramisi* (Frost 2001a, b; Frost *et al.* 2009) and *P. enkorikae* (Hlusko 2007) and it also differs from these species by some anatomical features (morphology of mandibular body and the splanchnocranium for example). The teeth of *S. lukeinoensis* n. gen., n. sp. fall within the range of metric variation of the small colobine from Lemudong'o (Hlusko 2007) but there are some differences such as the hard palate ending at M2/ in the Lemudong'o species and at M3/ in the Aragai one. If the two sites are close in age, it is impossible to reject the possibility that the small taxon from Lemudong'o could belong to *S. lukeinoensis* n. gen., n. sp. But, we need more material to confirm or reject this hypothesis. Colobine remains from other sites in the Lukeino Formation are under study and may perhaps throw light on this question.

Sawecolobus n. gen. is a short-faced colobine and it shares many similarities with the genus *Cercopithecoides* such as the morphology of the frontal and facial region but it differs from this genus by a less broad inter-orbital pillar (narrower than *C. kerioensis*, the oldest species of the genus) and is more similar, in this respect, to *Libypithecus* and *Rhinocolobus*, and the deep mandibular corpus.

TABLE 3. — Measurements (in mm) of the upper post-canine teeth of fossil colobines in the literature.

	P3/		P4/		M1/				M2/				M3/				
Taxon	**MD**	**BL**	**MD**	**BL**	**MD**	**BL**	**Mb**	**Db**	**Mb**	**BL**	**Mb**	**Db**	**MD**	**BL**	**Mb**	**Db**	**Reference**
Sawecolobus lukeinoensis n. gen., n. sp.	4-6 (6)	4.9-6 (6)	4.2-5.3 (7)	5.5-6.5 (6)	5.1-7.1 (7)	×	5.7-7 (6)	5.5-7.3 (6)	6.5-7.9 (12)	×	6.8-7.8 (11)	6.3-7.4 (11)	6.2-7.5 (10)	×	6.3-7.3 (10)	5.6-6.3 (10)	This article
Colobinae (Lemudong'o)	3.82-4.58 (2)	5.23-5.88 (2)	4.77-5.06 (2)	6.81-6.93 (2)	5.85-7.3 (3)	6.06-7.42 (3)	×	×	6.05-7.89 (3)	6.61-8.14 (3)	×	×	6.19-7.06 (3)	6.35-7.48 (3)	×	×	Hlusko 2007
Cercopithecoides bruneti	5.9-6 (2)	6.1-6.16 (3)	6-6.1 (2)	7.8-7.9 (2)	7.5-7.8 (2)	×	×	×	8.3 (1)	×	9.4 (1)	×	×	×	×	×	Pallas *et al.* 2019
Cercopithecoides kerioensis	×	6.2 (1)	5.2-5.3 (2)	6.6-6.7 (2)	6.6 (2)	×	7-7.1 (2)	6.5-6.6 (2)	×	×	×	×	×	×	×	×	Leakey *et al.* 2003
Cercopithecoides kimeui	6.5-7.3 (2)	7.4-8.4 (2)	7-7.3 (5)	8.3-10 (5)	9-10.9 (5)	×	9.6-10.9 (4)	9.5-10.4 (3)	10.9-12 (7)	×	10.1-12.1 (7)	8.9-11.8 (7)	8.9-12.5 (4)	×	10.4-11.7 (4)	8.2-10.4 (4)	Frost *et al.* 2003
Cercopithecoides meaveae	4.9-5.5 (2)	6.8 (1)	5.6 (1)	7.6 (1)	8-8.8 (2)	×	7.5-7.8 (2)	7.3-7.4 (2)	8.6-9.2 (2)	×	8.6 (1)	7.5-7.8 (2)	9.2-9.5 (2)	×	7.4-8.8 (2)	7.5-7.6 (2)	Frost 2001b; Frost & Delson 2002
Cercopithecoides williamsi	4.5-5.7 (6)	5.7-7.1 (8)	5-6 (11)	7.1-9.38 (9)	7-9.7 (14)	×	7.7-9.61 (12)	7.4-9 (12)	8.2-11.4 (17)	×	7.8-11.6 (13)	7.7-10.3 (13)	8.6-11 (18)	×	9-11 (16)	7.3-9.8 (17)	McKee *et al.* 2011
Cercopithecoides haasgati	4.42-5.13 (4)	5.59-6.4 (4)	4.81-6.02 (6)	6.76-7.34 (5)	7.42-8.4 (6)	×	7.72-8.45 (5)	7.37-8.06 (5)	7.9-9.31 (6)	×	8.48-9.93 (6)	8.32-9.62 (6)	9.38-10.1 (6)	×	8.38-9.8 (6)	7.7-8.74 (5)	McKee *et al.* 2011
Libypithecus markgrafi	5.5-5.6 (2)	6.3-6.5 (2)	5.2-5.6 (2)	6.5-6.6 (2)	7.2-7.5 (2)	×	6.5-6.8 (2)	6-6.2 (2)	7.5-7.6 (2)	×	7.5-8 (2)	6.3-7 (2)	8.2-8.5 (2)	×	7.8-8 (2)	6.2-6.8 (2)	Delson 1973
Kuseracolobus aramisi	4.9-6.7 (9)	5.9-7.4 (9)	5.1-5.8 (5)	6.2-7.1 (5)	7.3-9.0 (10)	6.4-7.9 (10)	×	×	7.9-9.9 (11)	6.5-7.6 (11)	×	×	10.5-13.5 (35)	6.4-7.9 (35)	×	×	Frost 2001a
Kuseracolobus hafu	6.7-8.2 (3)	7.4-8.2 (2)	6.3-7.1 (4)	8.5-8.8 (4)	8.8-10.2 (3)	×	8.6-9.4 (2)	9.3 (1)	11 (2)	×	9.4 (1)	8.8 (1)	11.8 (1)	×	×	×	Hlusko 2006
Paracolobus chemeroni	9	9.5	8	10.6	11	×	10.8	10.5	12	×	12.2	11.5	13.5	×	12.1	10.6	Leakey 1982
Paracolobus mutiwa	7.8 ? (1)	9.5 (1)	7.7 (1)	10.2 (1)	10.4 (1)	10.8 (1)	×	×	12.2 (1)	13 (1)	×	×	14 (1)	11.4 (1)	×	×	Leakey 1982; Hlusko 2007
Paracolobus enkorikae	4.55-6.0 (3)	5.95-7.28 (3)	5.29-6.19 (3)	7.09-7.95 (3)	8.27 (1)	7.27-7.43 (2)	×	×	8.28-9.04 (2)	8.63-9.0 (2)	×	×	7.75-9.4 (2)	7.7-8.43 (2)	×	×	Hlusko 2007
Rhinocolobus turkanensis	7.5-8.3 (4)	7.7-8.5 (2)	7.5-8.8 (3)	8.6-8.9 (2)	10.0-10.5 (5)	×	9.0-9.1 (4)	8.0-9.0 (4)	10.7-11.2 (5)	×	10.0-10.5 (3)	7.8-9.8 (3)	10.8-12.5 (4)	×	10.0-11.0 (4)	8.1-9.0 (3)	Leakey 1982
Rhinocolobus sp. (Laetoli)	6.8-7.7 (5)	7.5-9.1 (5)	6.9-8.1 (6)	8.2-9.7 (7)	9-10.2 (9)	×	8.6-9.4 (4)	8.5-9 (5)	9.7-11.6 (8)	×	9.9-11.4 (7)	8.7-10.7 (5)	10-13 (5)	×	9.8-11.2 (4)	8.7-10 (4)	Harrison 2011
Mesopithecus pentelici	4.2-5.8 (15)	4.9-6.5 (15)	4.5-5.2 (13)	5.7-7.3 (13)	6.4-7.4 (14)	×	6.2-7.5 (14)	6-7.3 (14)	6.7-8.2 (15)	×	6.8-8.3 (15)	6.9-7.8 (15)	6.5-8 (14)	×	6.7-7.6 (13)	5.7-6.9 (12)	Delson 1973
Dolichopithecus ruscinensis	6.8-8 (7)	6.4-8.9 (7)	5.8-8.8 (9)	6.7-9.3 (9)	8.1-9.8 (13)	×	7.4-9.4 (12)	6.8-9 (11)	9.6-12.1 (11)	×	9.2-10.4 (11)	8.2-10.2 (10)	8.4-10.6 (9)	×	8.6-9.7 (9)	6.9-9.3 (9)	Delson 1973

The nasal aperture of *S. lukeinoensis* n. gen., n. sp. is located low on the face resembling *Cercopithecoides*, *Libypithecus*, *Paracolobus* and *Rhinocolobus* and probably also *Kuseracolobus*. It is different from all African and Asian extant colobines, with the exception of *Nasalis*, which presents a lower position of the nasal aperture, probably related to the specific nasal

TABLE 4. — Measurements (in mm) of the lower post-canine teeth of fossil colobines in the literature.

	p/3		p/4		m/1				m/2				m/3				
Taxon	**MD**	**BL**	**MD**	**BL**	**MD**	**BL**	**Mb**	**Bd**	**MD**	**BL**	**Mb**	**Bd**	**MD**	**BL**	**Mb**	**Bd**	**Reference**
Sawecolobus lukeinoensis n. gen., n. sp.	7.2-8.1 (3)	3.5-5 (3)	5 (2)	4.1 (2)	6.2-6.3 (2)	×	5.1-5.2 (2)	5.5 (1)	6.5-7.7 (6)	×	5.5-6.4 (6)	5.3-6.7 (5)	8.7-8.8 (3)	×	5.8-6 (3)	5.5-6.1 (4)	This article
Colobinae (Lemudong'o)	5.25 (1)	4.63 (1)	5.03 (1)	4.5 (1)	6.01-6.14 (2)	5.13-5.24 (2)	×	×	6.46-6.86 (2)	6.06 (1)	×	×	8.5-8.72 (2)	5.27 (1)	×	×	Hlusko 2007
Microcolobus tugenensis	4.65-5.1	2.65-2.70	3.7-3.8	3.15-3.25	5.5	×	4.4	4.4	5.6	×	4.7	4.9	6.5	×	4.6	4.4	Benefit & Pickford 1986
Cercopithecoides bruneti	×	×	5.5-6.3 (3)	4.4 (1)	6.6-7.5 (3)	×	5.7 (1)	5.6 (1)	7.1-7.9 (3)	×	6.8 (1)	6.4 (1)	8.8-10.3 (2)	×	6.5 (1)	×	Pallas *et al.* 2019
Cercopithecoides kerioensis	×	×	6.5 (1)	4.6 (1)	×	×	×	×	7.9 (1)	×	6.6 (1)	6.7 (1)	9.6 (1)	×	6.3 (1)	6 (1)	Leakey *et al.* 2003
Cercopithecoides kimeui	11.2-12.4 (2)	×	8.8-9.7 (2)	6.7 (1)	10.7 (1)	×	×	×	11.7-13.4 (3)	×	9.5-10.7 (2)	9.8-10.8 (2)	12.5-16.9 (5)	×	8.5-10.7 (3)	8.5-10.7 (3)	Frost *et al.* 2003
Cercopithecoides meaveae	7.2-8.5 (2)	4.3-4.6 (2)	6.6-8 (2)	4.9 (2)	8.3-8.8 (2)	×	6.5-6.6 (2)	6.6-6.8 (2)	8.6-9.2 (2)	×	7-7.4 (2)	7.4-7.5 (2)	10.5-12.2 (2)	×	7-7.8 (2)	7.3-7.9 (2)	Frost 2001b; Frost & Delson 2002
Cercopithecoides williamsi	×	×	5.6-7.5 (16)	5.1-6.9 (12)	7.4-10.1 (15)	×	6.5-8.2 (13)	7.1-8.3 (13)	8.4-10.7 (23)	×	7.5-8.7 (16)	7.6-9.7 (17)	10-12.6 (19)	×	7.6-8.9 (18)	7-8.9 (17)	McKee *et al.* 2011
Cercopithecoides haasgati	×	×	5.07-6.45 (5)	5.37-6.19 (4)	6.47-8.42 (7)	×	5.92-7.38 (5)	6.25-7.56 (5)	8.25-10.37 (6)	×	7.29-8.76 (7)	7.55-8.37 (4)	9.84-12.73 (4)	×	7.58-8.73 (4)	7.44-8.13 (3)	McKee *et al.* 2011
Libypithecus markgrafi	×	×	×	×	7.3 (1)	×	5.6 (1)	5.4 (1)	×	×	×	×	×	×	×	×	Delson 1973
Kuseracolobus aramisi	5.6-7.4 (6)	4.5-5.1 (6)	6.0-7.5 (16)	4.7-5.7 (16)	6.9-8.7 (14)	5.8-6.6 (14)	×	×	7.9-9.9 (11)	6.5-7.6 (11)	×	×	10.5-13.5 (35)	6.4-7.9 (35)	×	×	Frost 2001a
Kuseracolobus hafu	9.9-13.3 (5)	5.3-6.9 (5)	8.2-9.4 (3)	6.8-7.1 (2)	9-10.2 (2)	×	7.5 (1)	7.2 (1)	9.9-10.9 (2)	×	8.1-8.7 (2)	8.4-8.9 (2)	13.4-14.8 (6)	×	7.9-8.4 (6)	7.6-8.5 (6)	Hlusko 2006
Paracolobus chemeroni	×	×	×	×	11.3	×	7.8	8.4	12.5	×	9.3	10	16	×	9.9	9.9	Leakey 1982
Paracolobus mutiwa	×	×	×	×	11-11.9 (6)	×	7.4-8.6 (4)	7.7-8.5 (5)	12.1-14 (8)	×	8.2-9.7 (8)	9-10 (6)	16-19 (7)	×	9-11 (7)	9-10.8 (6)	Leakey 1982; Hlusko 2007
Paracolobus enkorikae	5.87-9.72 (4)	3.8-4.78 (4)	5.92-6.92 (3)	4.97-5.44 (2)	7.07-7.58 (4)	5.93-6.04 (2)	×	×	7.93-8.53 (6)	6.83-7.2 (4)	×	×	9.47-11.84 (6)	6.71-7.57 (5)	×	×	Hlusko 2007
Rhinocolobus turkanensis	×	×	×	×	9.2-10.3 (18)	×	6.6-8.8 (16)	6.6-7.8 (16)	9.6-11.5 (23)	×	7.1-8.6 (20)	7.2-8.9 (19)	12.2-16 (29)	×	7.9-9.3 (29)	7.3-9.5 (28)	Leakey 1982
Rhinocolobus sp. (Laetoli)	9.4-12.6 (3)	6-6.3 (2)	7.6-10.1 (3)	5.9-6.9 (3)	9-10.7 (10)	×	6.4-8 (5)	6.9-8.3 (6)	10.3-11.9 (8)	×	7.7-9.5 (6)	8.1-9.1 (7)	13.4-15.8 (8)	×	7.8-10.5 (6)	8.1-9.6 (5)	Harrison 2011
Mesopithecus monspessulanus	5.2-6.9 (6)	3.3-4.3 (6)	4.8-6.1 (7)	4-4.4 (6)	6-8 (10)	×	4.5-5.8 (10)	6.1-4.7 (10)	6.3-7.7 (11)	×	4.9-6.5 (11)	5.3-6.5 (11)	8-9.6 (14)	×	5.1-6.3 (13)	5.4-6.5 (11)	Delson 1973
Mesopithecus pentelici	6.1-8.2 (8)	3.3-4.6 (8)	4.8-6.8 (9)	4.2-4.9 (8)	6.5-7.5 (11)	×	5-6 (11)	5.4-6.2 (11)	7-8.1 (14)	×	5.9-6.9 (14)	6.1-7.5 (14)	8.5-9.9 (11)	×	6-7.3 (11)	5.6-7.3 (11)	Delson 1973
Dolichopithecus ruscinensis	7.2-12.5 (19)	5-9 (23)	7.1-9.4 (20)	5.2-6.5 (20)	8.8-10.3 (19)	×	6-7.7 (18)	6.2-8 (18)	9.5-12.1 (18)	×	7-9.3 (18)	7.1-9 (17)	11.9-14.7 (17)	×	7.6-9.3 (14)	7.2-8.8 (18)	Delson 1973

morphology of this monkey. The lower location of the nasal aperture in the fossil African colobines is more similar to that of the cercopithecines. In *Mesopithecus*, it is intermediate.

The paranasal sinuses, including the maxillary sinus and the frontal sinus, are absent in most extant genera of Old World monkeys, Cercopithecoidea, while the maxillary sinus is always present in the genus *Macaca* and sometimes in *Papio* and *Theropithecus* (Koppe & Ohkawa 1999; Ito *et al.* 2009, 2014a; Nishimura *et al.* 2014). Among the Cercopithecine fossils, the maxillary sinus is also found in extinct species of *Macaca* (Rae *et al.* 2007; Ito *et al.* 2009, 2014b) and in *Paradolichopithecus sushkini* from the Pleistocene of central Asia (Nishimura *et al.* 2007), but not in *Pa. arvernensis* from Europe and *Procynocephalus wimani* from China, and probably not in *Pa. gansuensis* (Nishimura *et al.* 2009, 2010, 2014). The paranasal sinuses are absent in all extant colobines from Africa and Asia so far studied (Koppe & Ohkawa 1999) and in the fossil European *Mesopithecus* and *Dolichopithecus* (Rae *et al.* 2007; Nishimura *et al.* 2012). The maxillary sinus is found in *Cercopithecoides* and *Libypithecus* from Africa (Rae *et al.* 2007; Rae 2008; Kuykendall & Rae 2008) and *Kanagawapithecus* from east Asia (Nishimura *et al.* 2012). Based on the evolutionary hypothesis that the maxillary sinus was absent in the common ancestor of extant Old World Monkeys (OWM) (Rae *et al.* 2002), the observed distribution of this feature suggests that it was acquired independently in the lineages of *Sawecolobus lukeinoensis* n. gen., n. sp., *Cercopithecoides* and *Libypithecus* (Rae *et al.* 2007; Rae 2008), and if so it is not an apomorphy. More data are required to test the hypothesis.

The two tribes of Colobinae, which are considered to have split around 12-9 Ma are distinguished by some anatomical features in the P3/ and m/3 (Simons & Delson 1978; Szalay & Delson 1979). In African Colobinae, the protocone of the P3/ is reduced and the distal lophid of m/3 is wider than the mesial one. *S. lukeinoensis* n. gen., n. sp. presents a protocone on the P3/ which is variable as in *K. aramisi* (Frost 2001a, b) but it seems (the m/3 sample is limited at Aragai) that the mesial lophid on the m/3 is the broadest. In this respect it is probably better to consider *S. lukeinoensis* n. gen., n. sp. as Colobinae tribe *incertae sedis.*

Sawecolobus lukeinoensis n. gen., n. sp. presents a strong sexual dimorphism regarding the size of the canines as is usually the case in African colobine monkeys (Table 2; Appendix 3). It is especially evident when we observe the female lower canines (BAR 1369'00, BAR 1381'03, BAR 1382'03, BAR 351'04 and OCO 104'10) and the male ones (BAR 785'00 and BAR 1584'00). In BAR 1369'00, BAR 1381'03, BAR 1382'03, BAR 351'04 and OCO 104'10, the crowns are morphologically similar; they show a straight and smooth lingual ridge and the base elongated distally forming a platform (more pronounced than in *Procolobus*, *Piliocolobus* and *Colobus*) terminating in a strong cingulum. BAR 1584'00 is better preserved than BAR 785'00: the crown presents a strong distal tubercle, the lingual ridge is long and slightly curved, the lingual cingulum is short and forms a bulge, the disto-buccal part of the crown bears a honing facet, and the mesial groove is long and deep. Only upper canines of males are preserved in the collection from Aragai. The crown presents the shape of a dagger.

Aragai yielded a few postcranial bones but the distal humerus shows a morphology, especially for the trochlear flange, not so different from that of extant African colobines and *Lophocebus.* They differ more in the morphology of the *capitulum humeri* and the *zona conoidea* from the corresponding bones of *Paracolobus* and *Cercopithecoides*. The few slight morphological differences between the two fossils can be explained by sexual dimorphism. Terrestrial tendencies are generally associated with an adaptation for elbow stability produced by a well-developed trochlear flange but a lesser projection of this may be related to an «active» arboreal quadruped behaviour (Birchette 1982; Fleagle & Simons 1978; Senut 1981). OCO 336'10 and OCO 102'11 differ from *Cercopithecoides* by the more cylindrical aspect of the capitulum as in *Colobus* and *Piliocolobus*. The *zona conoidea* is narrow as in *Cercopithecoides* but the ridge (between the trochlea and the capitulum) is more pronounced. For Gebo & Sargis (1994), the presence or absence of the *zona conoidea* in different species of *Cercopithecus* is correlated with different behavioural and ecological distinctions. The *zona conoidea* (very prominent and moderately large) is present only in the arboreal species which has a vertical alignment of the medial trochlear rim. Furthermore, it is not much inclined, but neither is it vertical. In distal view, the general aspect of the distal humerus from Aragai shows some similarities with those of *Victoriapithecus macinnesi*, especially the posterior orientation of the medial condyle which is characteristic of semi-terrestrial behaviour (Senut 1987a, b; Harrison 1989; Benefit & McCrossin 2002). The shaft of the metatarsal V in BAR 914'04 is robust as in *Parapapio* from Bolt's Farm and as is generally the case in terrestrial or semi-terrestrial forms. These three postcranial bones probably belong to *S. lukeinoensis* n. gen., n. sp. This primate probably had a degree of semi-terrestriality but could practice «active» arboreal quadrupedalism as well. Gilbert *et al.* (2010) described a right astragalus from Aragai (KNM-LU 344) the size of which could correspond to *S. lukeinoensis* n. gen., n. sp. For these authors, this astragalus belongs to an arboreal animal by the lack of the facet for the lateral calcaneo-navicular ligament and the presence of a narrow groove for the tendon of the *m. flexor tibialis*. This groove is present in *Semnopithecus* (Olivier & Fontaine 1957) and in *Mesopithecus* (De Bonis *et al.* 1990); these two colobines are considered to be essentially semi-terrestrial or terrestrial (Youlatos & Koufos 2010). Considering the absence of the facet for the lateral calcaneo-navicular ligament, the astragalus of *Dolichopithecus* illustrated in Delson (1973) and Szalay & Delson (1979) shows this morphology but there is debate concerning its locomotion. It is considered to be a terrestrial colobine by the latter authors whilst Ingicco (2008) demonstrated that the long bones of *Dolichopithecus* present some anatomical adaptations suggestive of a semi-terrestrial colobine. The collection of the cercopithecid postcranial bones for the late Miocene and early Pliocene is scanty so it is difficult to solve the problems concerning the locomotor behaviour of the colobine from Aragai. Locomotor diversity was probably important for these extinct colobines and was not limited to terrestrial or semi-terrestrial repertoires as suggested by

Hlusko (2007). The two humeri from Aragai present some morphological features associated with arboreality (Senut 1989; Gebo & Sargis 1994).

Body weight is usually estimated by reference to the size of the teeth (Delson *et al.* 2000), especially the molars. The molars of *S. lukeinoensis* n. gen., n. sp. plot within the sample of African Colobines (Tables 1-4; Appendix 2). The two most complete fossil skulls are smaller than the biggest *Piliocolobus badius* (5.5 to 10 kg) and are bigger than *Procolobus verus* (3 to 5.7 kg) (Kingdon 2010). The body weight of *S. lukeinoensis* n. gen., n. sp. can be estimated to have been between 5 to 9 kg. The dimensions of the molars of *S. lukeinoensis* n. gen., n. sp. are smaller or plot within the range of variation of *C. bruneti* and *C. kerioensis*. The most recent body estimate for the two species are respectively 8.4-16.6 kg and 9.8 kg (Pallas *et al.* 2019: table 2). However, the method used is that of Delson *et al.* (2000) which over-estimates the weight probably due to the fact that the study was realized on zoo specimens. The size of two fragmentary humeri also seems to suggest a body weight of between 5 to 9 kg. This could be confirmed with the discovery of more complete postcrania.

To conclude, the fossil remains from Aragai belong to what we can call a *Cercopithecoides*-like primate. The genus *Cercopithecoides* was created in 1947 by Mollett van der Spuy on the basis of terminal late Pliocene specimens discovered at Makapansgat Limeworks in South Africa. The collection increased greatly since 1947, both in South Africa and East Africa. Since the first description established by Mollett van der Spuy (1947), the diagnosis of the genus *Cercopithecoides* was continually modified (Freedman 1957; Leakey 1982; Frost & Delson 2002; Leakey *et al.* 2003; Jablonski & Frost 2010). The generic diagnosis is perfectly adapted to the different species dated from the middle Pliocene to the terminal early Pleistocene (*C. meaveae*, *C. kimeui*, *C. williamsi*, *C. haasgati* and *C. alemayehui*). *C. meaveae* is the oldest species and represents the smallest species (except *C. alemayehui* which is the last occurrence of the genus (Jablonski & Frost 2010)). All these specimens from the Plio-Pleistocene represent typical *Cercopithecoides*. After 2000, some older colobine monkey remains from the late Miocene and early Pliocene with anatomical features found in *Cercopithecoides*, but with some important differences, were attributed to this genus. This explains why in the different diagnoses (Leakey *et al.* 2003; Jablonski & Frost 2010; Pallas *et al.* 2019) introduced important variations such as a smaller size, a narrow interorbital width, the thin superior orbital margins, a mandible with a different morphology (deeper, sloping symphysis). This resulted in some confusion the systematic definition of *Cercopithecoides*. It seems more appropriate to attribute the oldest remains to *Cercopithecoides*-like until more diagnostic fossils are discovered which may permit clarification of the systematic status of these species. The phylogenetic relationship between *Sawecolobus* n. gen. and *Cercopithecoides* remains uncertain due to limitations of the fossil record. *C. bruneti* and *C. kerioensis*, but not *S. lukeinoensis* n. gen., n. sp., present a squared-off rostrum of the premaxilla and a mandible with strong *prominentia laterales* and a flared inferior margin of the anterior part of the mandible similar (or more developed) to that of the typical *Cercopithecoides*. For the moment, in the absence of a more informative collection, these two species seem to be closer to typical *Cercopithecoides*.

An interesting anatomical feature in *Sawecolobus* n. gen. is the anterior position of the staphylion. In extant African colobines, only *Procolobus verus* presents a similar feature. Is it related to a shorter or a different morphology of the face? To answer this question, new researches must be done. It is interesting to observe that in some species of *Cercopithecus* and of *Erythrocebus*, the staphylion is in an anterior position (Verheyen 1962).

The Lukeino Formation yielded other remains of colobine monkeys from younger geological levels (but also of late Miocene age), which are currently under study. It seems that some present the same morphology as the specimens from Aragai. The study could yield additional information, and this will allow the characterisation of this species to be refined.

The present paper, with diagnosis of a new genus and species, *Sawecolobus lukeinoensis* n. gen., n. sp., confirms that the diversity of Colobinae was important during the late Miocene in Africa. Future research needs to investigate the palaeoenvironments of the different taxa of these primates to determine whether some ecological specificity existed.

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Appendix 1. — Measurements (in mm) of skulls and mandibles of extant African Colobines in the Afrika Museum (Tervuren, Belgium). On the skull: **MLS**, Maximum Length of the skull between the Prosthion and the Inion; **MZW**, Maximum zygofrontal width; **IW**, Interorbital Width; **PDL**, Palate Dental Length from the Prosthion to the distal part of M3/s; **EPW**, External Palate Width between M1/ and M2/; **OH**, Orbit Height; **OW**, Orbit Width. On the mandible: **MLM**, Maximum Length of the Mandible between the infradental of symphysis and the posterior edge of the mandibular branch; **SL**, Symphyseal length between the infradental and the gnathion; **MH**, Mandibular Height of the mandible body between m/1 and m/2; **MW**, Mandibular Width measurement in the middle of mandibular body below m/1 and m/2; **MDL**, Mandible Dental Length from infradental of symphysis to the distal part of the m/3s; **EMW**, External Mandible Width between m/1 and m/2.

SKULL	MLS	MZW	IW	PDL	EPW	OH	OW
Procolobus verus	78.7-92.1 (30)	51.4-61.4 (30)	5.7-9.9 (30)	31.7-37.5 (30)	26.3-32.1 (30)	17.7-21.1 (30)	18.6-21.5 (30)
Piliocolobus tholloni	99.6-119.6 (28)	60.1-74.4 (28)	8.3-12.2 (28)	42.5-50.5 (28)	31.8-37.1 (28)	21-24.7 (28)	21.9-25.4 (28)
Piliocolobus foai	93.8-122.8 (18)	54-74.3 (18)	7.9-11.9 (18)	40-49.2 (18)	29-38.8 (18)	20.5-23.8 (18)	19.5-24.1 (18)
Piliocolobus badius	92.3-103.9 (19)	58.3-71.6 (18)	7.9-10.7 (19)	38.5-46.5 (19)	29.8-34.5 (19)	20.4-23.9 (19)	21.5-24.2 (19)
Colobus polykomos	102.3-120.8 (17)	65.8-78.4 (17)	9.4-13.8 (17)	43.5-50.8 (17)	33.6-40.5 (17)	21.6-24.1 (17)	21.3-26 (17)
Colobus angolensis	105.3-119.9 (18)	62.6-75.3 (19)	8.6-11.6 (19)	42.4-49.1 (19)	33.9-39 (19)	20.9-25.7 (18)	22.4-25.9 (18)
Colobus guereza	106.1-123.9 (17)	62.9-70.3 (17)	9.7-12.6 (17)	42.5-52.6 (17)	34.2-41.5 (17)	21-25.5 (17)	21.3-27.6 (17)

MANDIBLE	MLM	SL	HM	MW	MDL	EML
Procolobus verus	50.9-63.3 (30)	16.9-22.1 (30)	11.6-16.4 (30)	4.6-6.5 (30)	31.6-37.5 (30)	20.1-24.8 (30)
Piliocolobus tholloni	64.8-82.3 (28)	22-32.5 (28)	13.4-22.2 (28)	6.2-7.6 (28)	44.8-51.1 (28)	26.1-30.7 (28)
Piliocolobus foai	61.8-83.8 (18)	19.2-32.4 (18)	13.8-21.3 (18)	6-8 (18)	41.5-49.4 (18)	24.8-31.5 (18)
Piliocolobus badius	63.4-75 (19)	20.8-29.4 (19)	14.8-20.9 (19)	5.8-7.8 (19)	40.6-46.5 (19)	23.8-29.4 (19)
Colobus polykomos	74.2-90.5 (17)	19.5-30.3 (17)	16.7-21.7 (17)	6.5-9.5 (17)	44.3-51.4 (17)	26.7-33.1 (17)
Colobus angolensis	70.5-85.5 (19)	23.9-28.6 (19)	16.9-21.9 (19)	6.2-7.9 (19)	41.2-48.1 (19)	27.2-31.5 (19)
Colobus guereza	75.5-88.7 (18)	23.1-32.5 (18)	19.1-23.7 (18)	5.3-7.9 (18)	43.3-52.9 (18)	26.5-33.6 (18)

Appendix 2. — Measurements (in mm) of the post-canine teeth of extant African Colobines in the Afrika Museum (Tervuren, Belgium).

	P3/		P4/		M1/			M2/			M3/		
	MD	**BL**	**MD**	**BL**	**MD**	**Mb**	**Db**	**MD**	**Mb**	**Db**	**MD**	**Mb**	**Db**
Procolobus verus	3.2-3.9 (50)	3.6-5 (50)	3.1-4 (50)	3.8-5.4 (50)	4.4-5.4 (50)	4.3-5.1 (50)	4-4.8 (50)	4.8-5.7 (50)	4.6-5.8 (50)	4.3-5.4 (50)	4.6-5.7 (50)	4.8-6.4 (50)	3.9-5.4 (50)
Piliocolobus tholloni	4.2-5.2 (31)	4.1-5.4 (31)	4.2-5.3 (31)	5.1-6.1 (31)	6.3-7.2 (31)	5.5-6.3 (31)	5-6.1 (31)	6.5-7.7 (31)	5.6-6.9 (31)	5.3-6.4 (31)	6.1-7.6 (31)	5.7-7 (31)	4.7-6.1 (31)
Piliocolobus foai	4.1-5.2 (32)	4-5.3 (32)	4.1-5.1 (32)	4.9-6 (32)	5.9-7.1 (32)	5.3-6.3 (32)	5.1-6 (32)	6-7.4 (32)	5.4-6.9 (32)	4.9-6.3 (32)	5.7-7 (32)	5.3-6+.7 (32)	4.6-5.6 (32)
Piliocolobus badius	3.8-5 (40)	4.1-5.5 (40)	4.2-5 (40)	4.6-6.4 (40)	5.6-7.2 (40)	5-6.5 (40)	4.8-6.3 (40)	5.9-7.3 (40)	5.4-7 (40)	5-6.8 (40)	5.7-7.1 (40)	5.3-6.7 (40)	4.6-5.9 (40)
Colobus polykomos	4.4-6 (30)	4.7-6.2 (30)	4.6-5.4 (30)	5.9-7.2 (30)	6.1-7.2 (30)	5.9-7.1 (30)	5.5-6.7 (30)	6.1-7.9 (30)	6.2-7.8 (30)	4.8-7.3 (30)	5.7-7.6 (30)	5.9-7.4 (30)	3.9-7 (30)
Colobus angolensis	3.8-5.7 (43)	4.5-5.9 (43)	4.1-5.3 (43)	5.2-6.6 (43)	5.9-7.1 (43)	5.4-6.3 (43)	5.1-6.2 (43)	6.2-7.4 (43)	5.8-7.2 (43)	5.5-6.8 (43)	5.5-7.8 (43)	5.7-7 (43)	4.4-6 (43)
Colobus guereza	4.8-8.3 (35)	4.6-6.7 (35)	4.3-5.6 (35)	5.7-7.1 (35)	6.1-7.2 (35)	5.5-6.6 (35)	5.1-6.5 (35)	6.3-7.8 (35)	6-7.8 (35)	5.5-7 (35)	6.6-8.3 (35)	6.1-7.5 (35)	5.5-6.8 (35)

	p/3		p/4		m/1			m/2			m/3		
	MD	**BL**	**MD**	**M**	**MD**	**Mb**	**Db**	**MD**	**Mb**	**Db**	**MD**	**Mb**	**Db**
Procolobus verus	4.7-8.4 (50)	2.6-3.4 (50)	3.7-4.7 (50)	2.7-3.6 (50)	4.7-5.5 (50)	3.3-4 (48)	3.3-4.4 (50)	4.9-5.5 (50)	3.8-4.8 (50)	4.1-5.1 (50)	5.6-7.8 (50)	3.9-5.2 (50)	3.8-5 (50)
Piliocolobus tholloni	6.7-11.3 (31)	3.4-4.3 (31)	4.7-5.9 (31)	4-4.7 (31)	6.3-7.3 (31)	4.3-5.5 (31)	4.5-5.4 (31)	6.5-7.3 (31)	4.9-5.9 (31)	5.1-5.9 (31)	8.1-9.6 (31)	5-9.6 (31)	4.9-5.7 (31)
Piliocolobus foai	6.7-11.3 (32)	3-4.3 (32)	4.4-5.5 (32)	3.7-4.7 (32)	5.8-7.3 (32)	4.2-5.1 (32)	4.4-5.3 (32)	6.1-7 (32)	4.8-5.9 (32)	4.7-6.1 (32)	7.4-9.6 (32)	4.6-6 (32)	4.3-5.7 (32)
Piliocolobus badius	6.1-10.2 (40)	3-4.4 (40)	4.2-5.4 (40)	3.6-4.2 (40)	5.6-7.2 (40)	4.2-4.9 (40)	4.2-5.3 (40)	6.1-7.5 40)	4.6-5.7 (40)	5-6 (40)	7.5-9.2 (40)	4.9-6 (40)	4.8-5.8 (40)
Colobus polykomos	6.9-10.2 (30)	3.6-4.4 (30)	4.9-6.7 (30)	4-4.8 (30)	6.3-7.1 (30)	4.8-5.6 (30)	5.1-5.9 (30)	6-7.5 (30)	5.3-6.5 (30)	5.7-6.7 (30)	6.9-9.6 (30)	5.1-6.4 (30)	5.2-6.3 (30)
Colobus angolensis	6.8-10.4 (43)	3.3-4.7 (43)	4.6-6.8 (43)	3.9-4.8 (43)	5.9-7.1 (43)	4.4-5.3 (43)	4.6-5.6 (43)	6.1-7.8 (43)	5.1-6.3 (43)	5.1-6.4 (43)	7.7-10.1 (43)	5.2-6.5 (43)	4.4-6.6 (43)
Colobus guereza	7.3-10.7 (35)	3.5-4.9 (35)	5.6-8.8 (35)	3.8-4.8 (35)	6.3-7.4 (35)	4.8-5.7 (35)	5-6 (35)	6.2-7.9 (35)	5.3-6.4 (35)	5.4-6.8 (35)	8-10.3 (35)	5.3-6.7 (35)	5.1-6.4 (35)

	P/3-M/3 LD	P/4-M/3 LD	M/1-M/3 LD	p/3-m/3 LD	p/4-m/3 LD	m/1-m/3 LD
Procolobus verus	20.6-24.1 (30)	17.5-21.1 (30)	14.5-17.6 (30)	24.9-29.8 (30)	19.3-23.1 (30)	15.5-18.9 (30)
Piliocolobus tholloni	28.6-33 (11)	23.9-28.1 (11)	19.8-23.3 (11)	34.9-40 (11)	26.9-31.5 (11)	21.3-24.9 (11)
Piliocolobus foai	26.6-32.7 (18)	22-27.3 (18)	18.3-21.3 (18)	31.6-39.2 (18)	24.2-30.2 (18)	19.5-24.1 (18)
Piliocolobus badius	25.1-30.5 (19)	20.7-25.5 (19)	17.3-20.9 (19)	32.4-37.7 (19)	25-28.6 (19)	20.3-23.5 (19)
Colobus polykomos	27.1-33.8 (17)	23.1-27.8 (17)	19.1-22.5 (17)	34.7-40.5 (17)	27.5-32.4 (17)	21.2-24.9 (17)
Colobus angolensis	26.6-32.9 (19)	22-27.3 (19)	18.3-22.2 (19)	32.3-39.4 (19)	24.7-31.3 (19)	20.5-24.5 (19)
Colobus guereza	29.7-34.9 (18)	24.7-28.9 (18)	20-23.5 (18)	35.3-42.9 (18)	27.7-42.9 (18)	21.6-26.8 (18)

Appendix 3. — Measurements (in mm) of the canines of extant African Colobines in the Afrika Museum (Tervuren, Belgium). Abbreviations: **M**, Male; **F**, Female.

		C/MD	**C/ BL**	**/c MD**	**/c BL**
Procolobus verus	M	5.5-8 (20)	4.1-6.3 (20)	5.7-7.3 (19)	3.7-5 (19)
	F	4.3-5.5 (14)	3.1-4.8 (14)	4.2-5.1 (14)	3-3.9 (14)
Piliocolus tholloni	M	8.6-10.8 (9)	6-7.1 (9)	7.8-9.3 (10)	5.1-6 (10)
	F	6.4-7.3 (10)	5-6.1 (10)	5.8-7 (10)	4-4.6 (10)
Piliocolus foai	M	7.4-8.9 (9)	5-6.2 (9)	6.7-7.7 (10)	4.6-5.7 (10)
	F	5.9-6.5 (10)	4.1-4.9 (10)	5.5-5.8 (10)	3.3-4 (10)
Piliocolus badius	M	6.8-9.3 (20)	5.2-6.6 (20)	6.7-8 (20)	4.3-5.3 (20)
	F	5.7-6.8 (20)	3.9-5.1 (20)	5.2-5.9 (20)	3.4-4.3 (20)
Colobus polykomos	M	8.1-9 (8)	6-6.4 (8)	6.9-8.7 (8)	5.1-5.9 (8)
	F	6.7-8 (9)	5.1-6.6 (9)	6-6.5 (9)	4.2-5 (9)
Colobus angolensis	M	7.1-9.1 (16)	5.6-6.4 (16)	6.5-8 (16)	4.6-5.4 (16)
	F	6.7-8.1 (13)	4.5-5.9 (13)	5.6-6.8 (13)	3.8-5.2 (13)
Colobus guereza	M	7.2-10.8 (13)	5.4-7.1 (13)	6.3-8.8 (14)	4.7-6 (14)
	F	6.9-9.1 (13)	5.2-6.3 (13)	6-7.1 (13)	3.8-5.3 (13)

Appendix 4. — Authorships of the taxon cited in the article (species and genera).

Aepyceros Sundevall, 1847
Colobus Illiger, 1811
Colobus angolensis P. Sclater, 1860
Colobus flandrini (Arambourg, 1959)
Colobus guereza Rüppell, 1835
Colobus polykomos (Zimmermann, 1780)
Cercocebus agilis Milne-Edwards, 1886
Cercopithecus Linnaeus, 1758
Cercopithecus ascanius (Audebert, 1799)
Cercopithecus lhoesti P. Sclater, 1899
Cercopithecus neglectus Schlegel, 1876
Cercopithecoides Mollett, 1947
Cercopithecoides bruneti Pallas, Daver, Mackaye, Likius, Vignaud & Guy, 2019
Cercopithecoides alemayehui Gilbert & Frost, 2008
Cercopithecoides haasgati McKee, von Mayer & Kuykendall, 2011
Cercopithecoides kerioensis M. G. Leakey, Teaford & Ward, 2003
Cercopithecoides kimeui M. G. Leakey, 1982
Cercopithecoides meaveae Frost & Delson, 2002
Cercopithecoides williamsi Mollett, 1947
Chlorocebus aethiops (Linnaeus, 1758)
Dendrohyrax samueli Pickford, 2005
Dolichopithecus Depéret, 1889
Dolichopithecus ruscinensis Depéret, 1889
Erythrocebus Trouessart, 1775
Kanagawapithecus Iwamoto, Hasegawa & Koizumi, 2005
Kuseracolobus Frost, 2001
Kuseracolobus aramisi Frost, 2001
Kuseracolobus hafu Hlusko, 2006
Lophocebus Palmer, 1903
Lophocebus albigena (Gray, 1850)
Libypithecus Stromer, 1913
Libypithecus markgrafi Stromer, 1913
Macaca Lacépède, 1799
Mesopithecus Wagner, 1839
Mesopithecus monspessulanus (Gervais, 1849)
Mesopithecus pentelici Wagner, 1839
Microcolobus Benefit & Pickford, 1986
Microcolobus tugenensis Benefit & Pickford, 1986
Myanmarcolobus Takai, Thaung-Htike, Zin-Maung-Maung-Thein, Soe, Maung, Tsubamoto, Egi, Nishimura & Nishioka, 2015
Nasalis E. Geoffroy Saint-Hilaire, 1812
Nyanzachoerus tulotos Cooke & Ewer, 1972
Papio Müller, 1773
Parapresbytis Kalmykov & Maschenko, 1992
Paracolobus R. E. F. Leakey, 1969
Paracolobus chemeroni R. E. F. Leakey, 1969
Paracolobus enkorikae Hlusko, 2007
Paracolobus mutiwa M. G. Leakey, 1982
Paradolichopithecus Necrasov, Samson & Radulesco, 1961
Paradolichopithecus arvernensis (Depéret, 1929)
Paradolichopithecus gansuensis Qiu, Deng & Wang, 2004
Paradolichopithecus sushkini Trofimov, 1877
Parapapio Jones, 1937
Piliocolobus Rochebrune, 1877
Piliocolobus badius (Kerr, 1792)
Piliocolobus foai de Pousargues, 1899
Piliocolobus tholloni (Milne-Edwards, 1886)
Presbytis Eschscholtz, 1821
Procolobus Rochebrune, 1877
Procolobus verus (van Beneden, 1838)
Procynocephalus Schlosser, 1924
Procynocephalus wimani Schlosser, 1924
Pygathrix E. Geoffroy Saint-Hilaire, 1812
Orrorin tugenensis Senut, Pickford, Gommery, Mein, Cheboi & Coppens, 2001
Rhinocolobus M. G. Leakey, 1982
Rhinocolobus turkanensis M. G. Leakey, 1982
Rhinopithecus E. Geoffroy Saint-Hilaire, 1812
Semnopithecus Desmarest, 1822
Theropithecus I. Geoffroy Saint-Hilaire, 1843
Trachypithecus Reichenbach, 1862
Victoriapithecus von Koenigswald, 1969
Victoriapithecus macinnesi von Koenigswald, 1969