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# New Early Pliocene Cercopithecidae (Mammalia: Primates) from Aramis, Middle Awash Valley, Ethiopia

STEPHEN R. FROST[1]

## ABSTRACT

The Middle Awash Research Project has collected a large sample of fossil cercopithecids from the Aramis, Kuseralee, and Sagantole drainages in the Middle Awash paleoanthropological study area of Ethiopia. These sites have been securely dated to 4.4 Ma. The craniodental material from this assemblage supports the diagnoses of two distinct new genera and species, which are described here. *Pliopapio alemui* is a mid-sized papionin represented by a complete cranium, several partial jaw fragments, and many isolated teeth. *Kuseracolobus aramisi* is a medium-sized colobine represented by several maxillae, mandibles, and other cranial fragments, as well as by isolated teeth. Stratigraphically associated postcranial remains will be discussed in a separate report.

*Pliopapio alemui* is distinctive from other known African papionins in the combination of its cranial, mandibular, and dental morphology. It lacks the diagnostic facial features of *Parapapio,* as well as the flattened muzzle dorsum, facial fossae, and maxillary ridges of *Papio.* Moreover, it does not possess any of the derived dental and cranial specializations of *Theropithecus. Kuseracolobus aramisi* is larger than all modern African colobines, but smaller than all known *Cercopithecoides, Paracolobus,* and *Rhinocolobus.* It is distinctive from *Cercopithecoides* and the colobine from Leadu in its symphyseal, corporal, and gonial morphology, and from *Libypithecus, Paracolobus,* and *Rhinocolobus* in its facial morphology.

This early Pliocene sample fills a temporal gap between the terminal Miocene and later Pliocene sites and documents the existence of two new cercopithecid taxa, increasing known diversity in the family.

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## INTRODUCTION

The Cercopithecidae are relatively common and diverse in most Pliocene and Pleistocene fossil assemblages from sub-Saharan Africa. During this period, the subfamily Cercopithecinae is represented by eight genera or subgenera while the Colobinae is represented by at least five (Szalay and Delson, 1979; Delson, 1984, 1988, 1994). Few of these taxa, however, are represented in the Early Pliocene. The locality of Aramis in the Awash River valley of Ethiopia has yielded the hominid *Ardipithecus ramidus* (White et al., 1994, 1995). The large cercopithecid sample from Aramis and sites of similar age in the Middle Awash adds considerably to our knowledge of cercopithecid evolution during this period. The craniodental anatomy and systematics of these cercopithecids are described here.

Between 1992 and 1999, the Middle Awash Research Project collected and catalogued 925 cercopithecid specimens from localities within the Aramis, Kuseralee, and Sagantole drainages. This sample comes from the Aramis Member of the Sagantole Formation between the Gàala Tuff Complex (GATC) and the Daam Aatu Basaltic Tuff (DABT). These tephra have been radiometrically dated to 4.39 ± 0.03 and 4.39 ± 0.05 Ma respectively (Renne et al., 1999). The size, precise stratigraphy, and dating of this sample make it one of the best documented in the African Pliocene.

From a limited initial sample, Wolde-Gabriel et al. (1994) listed three cercopithecid species at Aramis based on preliminary identifications by Delson: cf. *Paracolobus* sp., cf. Colobinae sp. ''A'' (sensu Eck, 1977) and cf. *Parapapio* sp. On the basis of the current, vastly expanded craniodental sample, two new genera and species are diagnosed here, one colobine and one cercopithecine. In the postcranial sample, two and possibly three morphs can be identified. None of the postcranial specimens are directly associated with any of the craniodental material, and their affinities and functional interpretations will be presented elsewhere.

This is one of the largest Early Pliocene samples of fossil cercopithecids; however, the diagnoses for the two taxa described in this paper are based on the limited number of relatively complete specimens. While the isolated teeth are only diagnosable to subfamily, they are assigned to the same two species as the more complete material based on size and a lack of evidence to the contrary.

**KNM** National Museums of Kenya, Nairobi, Kenya
**NME** National Museum of Ethiopia, Addis Ababa, Ethiopia
**NMT** National Museum of Tanzania, Dar es Salaam, Tanzania
**MB** Berlin Museum, Berlin, Germany

## SYSTEMATIC PALEONTOLOGY

CLASS MAMMALIA LINNAEUS, 1758

ORDER PRIMATES LINNAEUS, 1758

INFRAORDER CATARRHINI E. GEOFFROY, 1812

FAMILY CERCOPITHECIDAE GRAY, 1821

SUBFAMILY CERCOPITHECINAE GRAY, 1821

TRIBE PAPIONINI BURNETT, 1828

### *Pliopapio*, new genus

TYPE SPECIES: *Pliopapio alemui,* new species.

GENERIC DIAGNOSIS: A genus of African papionin, distinguished from *Parapapio, Lophocebus,* and *Cercocebus* by the presence of a clear anteorbital drop, although this is not as distinct as in most *Papio* and *Mandrillus.* In this aspect, its profile is most similar to that of *Macaca,* but *Pliopapio* has a relatively longer muzzle. It is different from *Papio* (*Papio*), *Gorgopithecus, Lophocebus, Cercocebus,* and *Mandrillus* in that the muzzle lacks postcanine and suborbital fossae. The absence of maxillary ridges distinguishes it from *Papio, Theropithecus* (*Omopithecus*) and *Mandrillus.* The muzzle dorsum is saddle-shaped and rounded in paracoronal section. In these aspects it is similar to *Theropithecus oswaldi* (sensu Leakey, 1993, as is used throughout this paper), but is unlike the flattened dorsum and squared paracoronal section found in *Papio* (including *Dinopithecus*) and *Mandrillus.* Relative to neurocranial breadth, the rostrum is narrow in comparison with those of all known African papionins, although it is in the lowest end of variation

for *Papio, Mandrillus,* and *Macaca.* Crushing in the anterior portion may contribute to this impression, but cannot account for it entirely.

Unlike those in *Parapapio, Cercocebus,* and *Lophocebus,* the cranial vault is separated from the brow ridges by a distinct ophryonic groove. The temporal lines in the holotype male remain widely separated and do not form a sagittal crest, as opposed to the situation in *Theropithecus, Gorgopithecus, Papio* (*Dinopithecus*), and *Paradolichopithecus.*

While the mandibular symphysis is shallower and more sloping in profile than that of most papionins, it is shorter and more rounded than that of *Parapapio ado* (from Laetoli and Kanapoi) or the papionin from Lothagam. In these latter taxa the symphysis is even longer and more sloping, with the incisive alveolar process projecting more anteriorly, producing a more procumbent incisor row. Corpus fossae are absent, distinguishing it from most *Papio* (*Papio*) (*P. h. kindae* females have very slight fossae, and some *P. izodi* lack them), *Gorgopithecus, Theropithecus* (*Omopithecus*), *Mandrillus,* and *Lophocebus.*

The molars are higher crowned, more straight-sided, and less flaring on average than those of *Papio, Macaca, Mandrillus,* and *Lophocebus,* and far less so than those of *Cercocebus.* As in most papionins, but unlike *Mandrillus* and *Cercocebus,* the premolars are not particularly large relative to the molars. The mandibular incisors are nearly vertically implanted, whereas those of *Parapapio ado* from Laetoli and Kanapoi are more procumbent.

ETYMOLOGY: The name refers to the Pliocene age of the taxon and its papionin status.

### *Pliopapio alemui,* new species

SPECIFIC DIAGNOSIS: As for genus.

ETYMOLOGY: Named in honor of Alemu Ademassu, Paleoanthropology Laboratory curator at the National Museum of Ethiopia responsible for assisting with preparation, molding, and study of all Middle Awash specimens.

HOLOTYPE: ARA-VP-6/933. A nearly complete male cranium and attached mandible with complete but damaged dentition, found by Awoke Amzaye in December 1995.

HYPODIGM: See appendix 1.

HORIZON: All specimens are derived from the Aramis Member of the Sagantole Formation, between the GATC and DABT, and are therefore dated to 4.4 Ma (Renne et al., 1999).

DESCRIPTION: The most complete specimen is the holotype male skull ARA-VP-6/933[2] (see fig. 1). The mandible is attached to the cranium by a thin layer of matrix that prevents the two from being safely separated. Therefore, the palate and much of the cranial base are not available for observation. Of the main cranial regions, only the left zygomatic is completely missing. The right orbit is damaged and lacks much of the right half, except for one triangular portion around the zygoma. The right zygomatic arch is mostly present, but crushed, missing only the region around the temporojugal suture. The right maxilla and mandible are weathered, revealing the roots of the teeth. The other cranial specimens are all considerably more fragmentary. ARA-VP-6/437 (see fig. 2) is a partial right male maxillary fragment with the dorsal surface up to the piriform aperture, the roots of the canine and fourth premolar, and complete central incisor and third premolar. ARA-VP-1/1723 (fig. 2) is a partial right female maxilla preserving the canine through third molar. ARA-VP-1/1007 (fig. 2) is a slightly crushed left female premaxillomaxillary fragment with the rostral surface preserved nearly to the lateral border of the piriform aperture, a damaged lateral incisor, and complete canine through first molar.

*Pliopapio alemui* is smaller in cranial size than all known *Theropithecus* and *Papio,* other than *P. hamadryas kindae, P. angusticeps,* and *P. izodi,* to which it is similar in size. It is sightly larger than all but the largest *Macaca,* such as *M. thibetana* and *M. nemestrina.* This cranial size estimate is confirmed by centroid sizes computed from a sample of 45 cranial landmarks (see fig. 3). In dental size, it is marginally smaller than *Parapapio ado* from Laetoli and Kanapoi,

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[2] Sex identifications throughout the text are based upon the highly dimorphic size and morphology of the upper and lower canines and the lower third premolar.
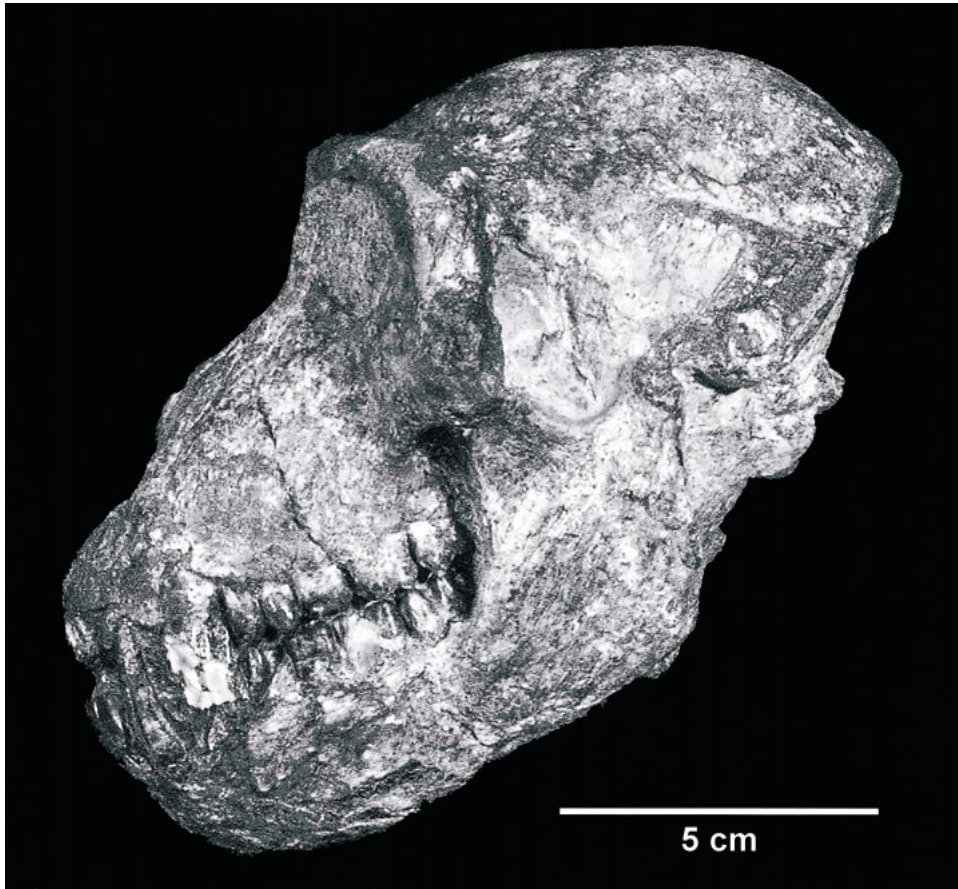
Fig. 1.   Holotype of *Pliopapio alemui* ARA-VP-6/933. All views are in Frankfurt orientation. Lateral view of the left side. Opposite page: dorsal view (above); lateral view of the right side (below).

and similar to specimens from Ekora, the Lomekwi Member of the Nachukui Formation, the Tulu Bor Member of the Koobi Fora Formation, and Unit 2 of the Chiwondo beds. Dental dimensions for *Pl. alemui* are listed in table 1.

*Rostrum.* The infraorbital foramina are only preserved on the left side of ARA-VP-6/933. The four foramina are arranged in a superolaterally concave arc, as in *Theropithecus* (Eck and Jablonski, 1987). Relative to the orbit they lie roughly in mid-mediolateral position and are placed more closely to its inferior rim than in *Theropithecus.*

In ARA-VP-6/933 and ARA-VP-6/437 there is little to no development of maxillary ridges, similar to *Parapapio* (Freedman, 1957), *Theropithecus* (*Theropithecus*) (sensu Delson, 1993), and most *Macaca,* but distinct from *Papio* and *Mandrillus.* The maxillary fossae are also extremely shallow. Once again, this is similar to the above genera and to *Papio* (*Dinopithecus*) (see Delson and Dean, 1993). From what is preserved in ARA-VP-1/1007 and ARA-VP-1/1723 the females seem to lack these structures as well.

The muzzle dorsum of ARA-VP-6/933 is largely smooth and saddle-shaped, as it is in *Theropithecus oswaldi.* It is concave in the sagittal plane and forms a convex arc in paracoronal cross section at the level of the second molar. This cross section is sharper, however, with the nasals forming a more acute angle than they do in *T. oswaldi.* This is closer to the cross section of *Macaca mulatta, M. nemestrina,* or *M. thibetana,* but with a relatively longer muzzle. When viewed laterally the muzzle profile is concave from gla-

5 cm
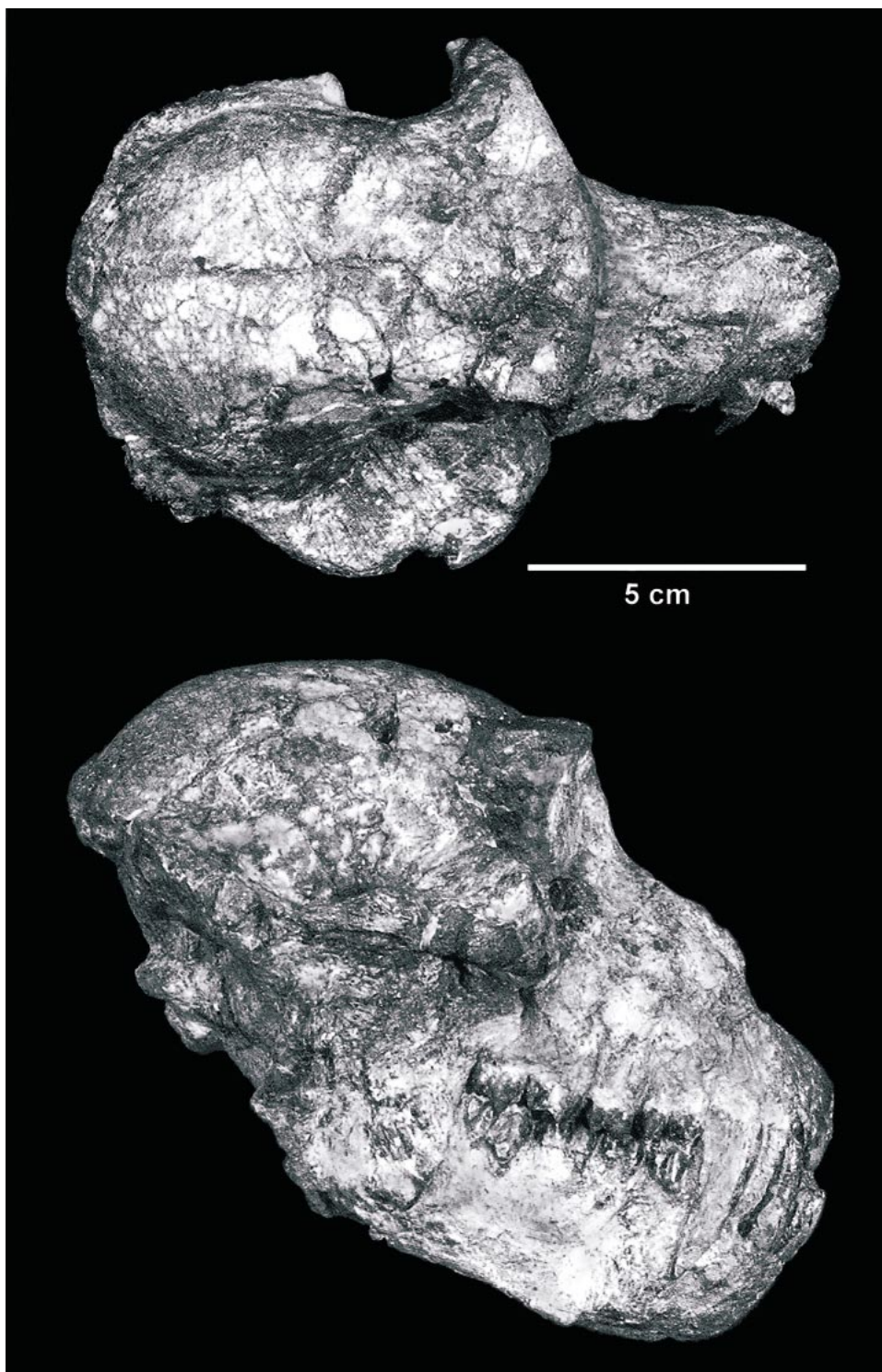
Fig. 1.   Continued.
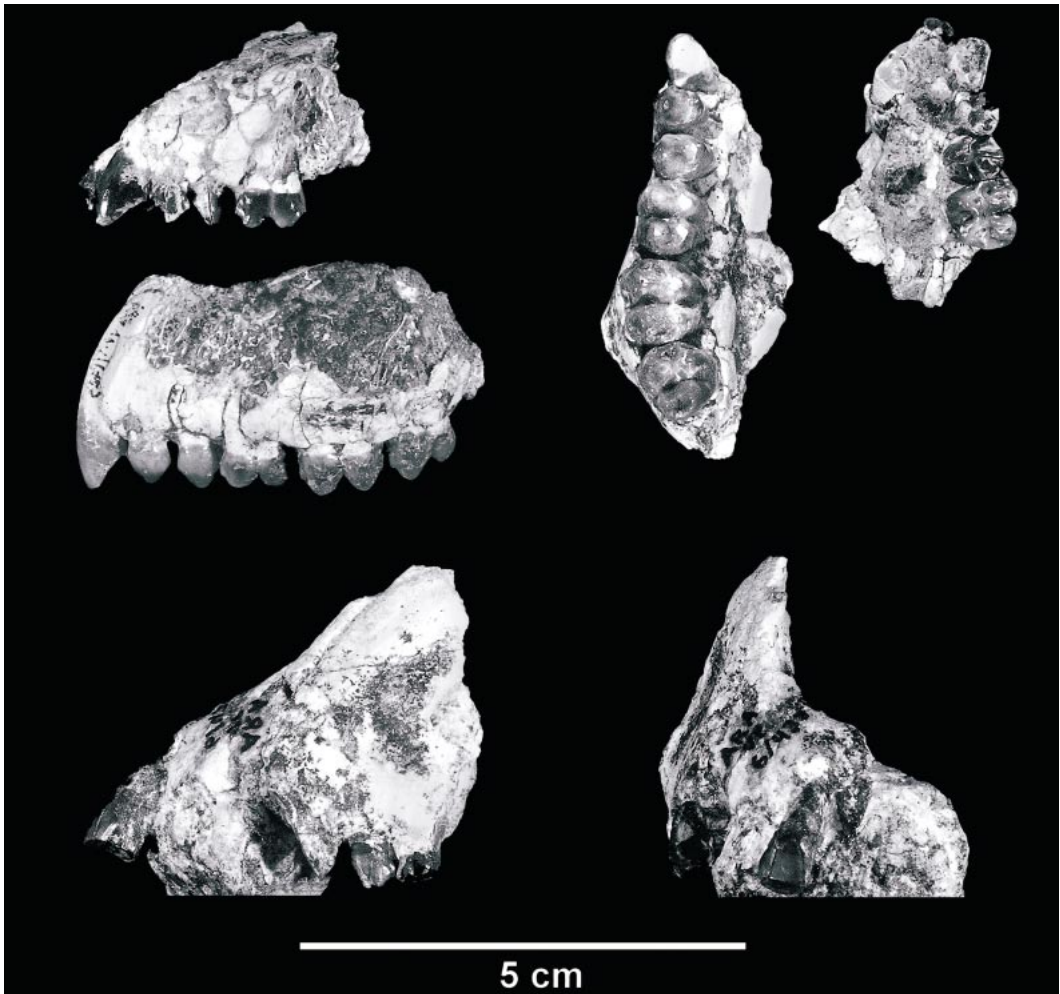
Fig. 2. Maxillae of *Pliopapio alemui.* Counterclockwise from top left: ARA-VP-1/1007 lateral view, ARA-VP-1/1723 (reversed), ARA-VP-6/437 lateral view (reversed), ARA-VP-6/437 frontal view, ARA-VP-1/1007 occlusal view, ARA-VP-1/1723 occlusal view.

bella to rhinion, displaying an antorbital drop, and is also concave from rhinion to nasospinale, and finally convex from nasospinale to prosthion. While the entire muzzle is quite long and not unlike that of *Papio,* the length of the segment from glabella to rhinion comprises less of the total muzzle length than it does in *Papio* (see fig. 4). Rhinion is also considerably more prominent than in *Papio* or *Theropithecus.*

The sutures of the muzzle are well preserved on the left side of ARA-VP-6/933 and on ARA-VP-6/437. The premaxillomaxillary suture follows the superior portion of the na-

sal aperture at a margin of approximately 4 mm, as it does in most larger papionins. Unlike in *T. gelada,* it does not enter the piriform aperture. The nasal process of the premaxilla projects further posteriorly than it does in *Papio,* approaching to within 1.5 cm of the orbits. The premaxillomaxillary suture is therefore largely an anterolaterally smoothly curving arc. The premaxillae project relatively far anteriorly beyond the canine, and there is a modest diastema separating the canine from the incisors (6.5 mm on the left side of ARA-VP-6/933).

When viewed superiorly, the muzzle is

Fig. 3. The *x*-axis represents different papionin genera or subgenera as follows: Ccb, *Cercocebus*; Din, *Papio* (*Dinopithecus*); Lop, *Lophocebus*; Mac, *Macaca*; Man, *Mandrillus*; Omo, *Theropithecus* (*Omopithecus*); Pap, *Papio* (*Papio*); Pdo, *Paradolichopithecus*; Ppa, *Parapapio*; Pli, *Pliopapio*; Smo, *Theropithecus oswaldi*; The, *T. gelada.* Sample size for each (sub)genus is given in parentheses below each label. The *y*-axis plots values of centroid size computed from 45 cranial landmarks. Centroid sizes were computed using Morpheus (Slice, 1998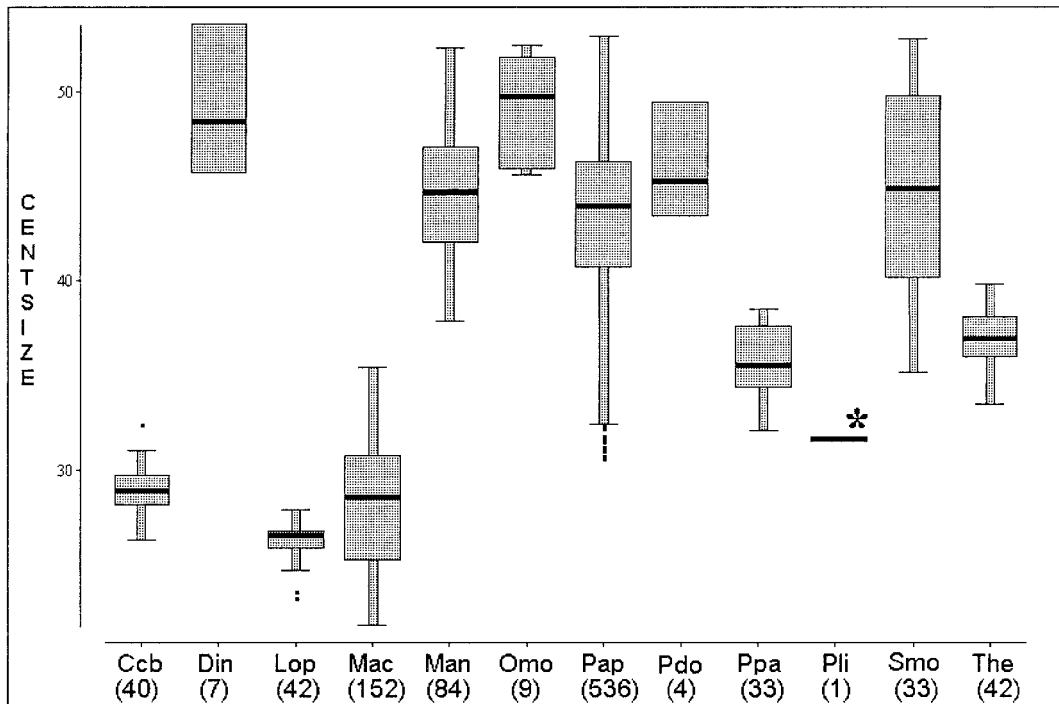). The central bar represents the median, or 50th percentile. The bottom and top of each box represent the value at the 25th and 75th percentiles, respectively, and the whiskers extend to the farthest observation that is less than 1.5 times the length of the box. Any individuals outside of the whisker range are marked separately.

much narrower than the neurocranium (see fig. 5). In comparison to the length of the neurocranium, the muzzle is longer than in most *Macaca* or *Parapapio* and shorter than in *Papio* (*Papio*) and *Mandrillus* (see fig. 6). The muzzle of the female ARA-VP-1/1007 is considerably shorter than that of the male ARA-VP-6/933. When they are lined up at the first molar, the mesial edge of the lateral incisor of ARA-VP-1/1007 is even with the middle of the canine of ARA-VP-6/933.

The piriform aperture is preserved in ARA-VP-6/933, partially preserved in ARA-VP-6/437, and only a small portion is preserved in the female ARA-VP-1/1007. The outline of the piriform aperture is typically papionin, being roughly ovoid but forming a V at its inferior pole. In breadth it is slightly

narrower than that of *Papio*. The nasals of ARA-VP-6/933 are distorted, but probably would have formed a straight superior margin. The premaxillae then bow gently laterally to the aperture's widest point just above the roots of the incisors, then curve convexly to meet at nasospinale in a relatively acute inferior angle. There is no evidence of anterior nasal tubercles.

The maxillary dental arcade is preserved in ARA-VP-6/933, and it is preserved from C to M3 in ARA-VP-1/1723 and from I2 to M1 in ARA-VP-1/1007. The dental arcade is somewhat distorted in ARA-VP-6/933, but appears to have been largely U-shaped, with the canines marking the bases of an anterior arc composed of the incisors. The alveolar margins appear to be gently bowed laterally,

TABLE 1
**Dental Measurements for *Pliopapio alemui* and *Kuseracolobus aramisi***

| | N | Width[a] | | | Other measures[b] | | | Length[c] | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max |
| *Pliopapio alemui* | | | | | | | | | | |
| I1 | 6 | 5.2 | 4.6 | 5.5 | 4.6 | 3.9 | 5.0 | 6.4 | 5.8 | 8.2 |
| I2 | 5 | 5.7 | 5.2 | 6.0 | 3.8 | 3.5 | 4.3 | 4.0 | 3.8 | 4.2 |
| C (♀) | 2 | 5.0 | 5.0 | 5.1 | — | — | — | 5.7 | 5.6 | 5.8 |
| C (♂) | 1 | | | | — | — | — | 11.1 | | |
| P3 | 3 | 6.0 | 5.6 | 6.5 | — | — | — | 5.1 | 4.7 | 5.8 |
| P4 | 3 | 6.2 | 5.9 | 6.5 | — | — | — | 5.1 | 4.9 | 5.3 |
| M1 | 3 | 7.6 | 7.4 | 7.8 | 7.0 | 6.9 | 7.2 | 8.2 | 7.8 | 8.6 |
| M2 | 2 | 9.0 | | | 7.9 | | | 9.7 | 9.2 | 10.2 |
| M3 | 3 | 8.6 | 8.0 | 9.1 | 6.7 | 6.1 | 7.4 | 9.0 | 8.1 | 9.5 |
| MX | 31 | 8.6 | 7.0 | 9.9 | 7.7 | 6.4 | 9.0 | 9.0 | 7.9 | 10.9 |
| dP4 | 4 | 6.4 | 6.1 | 6.7 | 5.8 | 5.4 | 6.3 | 7.1 | 6.7 | 7.3 |
| i1 | 5 | 4.5 | 3.5 | 5.2 | 3.2 | 2.2 | 4.4 | 4.5 | 3.3 | 5.8 |
| i2 | 6 | 4.8 | 3.8 | 5.5 | 3.2 | 2.2 | 4.3 | 5.6 | 3.4 | 11.1 |
| c (♀) | 2 | 5.8 | 5.7 | 6.0 | — | — | — | 3.9 | 3.4 | 4.3 |
| c (♂) | 3 | 9.3 | | | — | — | — | 5.4 | | |
| p3 (♀) | 2 | 3.7 | 3.6 | 3.8 | 7.2 | | | 6.4 | 5.5 | 7.4 |
| p3 (♂) | 1 | 3.7 | | | 15.6 | | | 9.2 | | |
| p4 | 12 | 5.5 | 4.6 | 6.7 | — | — | — | 6.3 | 4.8 | 7.2 |
| m1 | 9 | 5.9 | 5.3 | 6.5 | 6.2 | 5.7 | 6.6 | 7.8 | 7.2 | 8.6 |
| m2 | 7 | 7.2 | 6.4 | 7.9 | 7.3 | 6.7 | 7.8 | 9.4 | 8.7 | 10.4 |
| m3 | 32 | 7.6 | 6.5 | 8.7 | 6.9 | 6.0 | 8.0 | 11.5 | 9.7 | 13.2 |
| mX | 30 | 7.1 | 5.9 | 8.9 | 6.8 | 5.9 | 8.0 | 9.1 | 7.2 | 10.5 |
| dc | 1 | 4.6 | | | | | | 3.0 | | |
| dp3 | 1 | 4.0 | | | 4.4 | | | 6.8 | | |
| dp4 | 5 | 4.7 | 4.5 | 5.0 | 5.1 | 4.9 | 5.3 | 7.1 | 6.5 | 7.5 |
| *Kuseracolobus aramisi* | | | | | | | | | | |
| I1 | 7 | 5.1 | 4.6 | 5.8 | 4.7 | 3.9 | 5.5 | 5.7 | 4.8 | 6.1 |
| I2 | 13 | 4.9 | 4.3 | 6.1 | 4.9 | 3.9 | 6.3 | 3.9 | 1.9 | 5.4 |
| C (♀) | 2 | 5.0 | 4.8 | 5.1 | — | — | — | 6.7 | 6.4 | 6.9 |
| C (♂) | 2 | 7.3 | 7.1 | 7.5 | — | — | — | 10.4 | 10.2 | 10.6 |
| P3 | 9 | 6.4 | 5.9 | 7.4 | — | — | — | 5.7 | 4.9 | 6.7 |
| P4 | 5 | 6.5 | 6.2 | 7.1 | — | — | — | 5.5 | 5.1 | 5.8 |
| M1 | 10 | 7.1 | 6.4 | 7.9 | 6.9 | 6.4 | 7.4 | 7.9 | 7.3 | 9.0 |
| M2 | 7 | 8.0 | 7.6 | 8.7 | 7.3 | 7.0 | 7.9 | 8.7 | 8.2 | 9.0 |
| M3 | 6 | 8.2 | 7.8 | 8.7 | 6.8 | 6.7 | 6.9 | 9.0 | 8.6 | 9.5 |
| MX | 41 | 8.3 | 7.5 | 9.4 | 7.4 | 6.7 | 8.6 | 8.7 | 7.7 | 10.0 |
| dP4 | 4 | 5.7 | 5.7 | 5.7 | 5.6 | 5.5 | 5.7 | 6.7 | 6.5 | 7.0 |
| i1 | 3 | 4.4 | 4.2 | 4.6 | 2.7 | 2.5 | 3.1 | 3.7 | 3.5 | 3.8 |
| i2 | 9 | 4.6 | 3.8 | 5.5 | 3.3 | 2.2 | 4.4 | 3.1 | 2.3 | 3.9 |
| c (♀) | 1 | 5.7 | | | — | — | — | 3.7 | | |
| c (♂) | 3 | 8.4 | 7.8 | 8.8 | — | — | — | 5.5 | 5.3 | 5.7 |
| p3 (♀) | 2 | 4.8 | 4.5 | 5.1 | 8.2 | | | 5.9 | 5.6 | 6.3 |
| p3 (♂) | 4 | 4.7 | 4.5 | 5.0 | 11.6 | 11.0 | 12.8 | 7.3 | 7.0 | 7.4 |
| p4 | 16 | 5.1 | 4.7 | 5.7 | — | — | — | 6.7 | 6.0 | 7.5 |
| m1 | 14 | 6.1 | 5.8 | 6.6 | 6.3 | 5.5 | 6.9 | 7.9 | 6.9 | 8.7 |
| m2 | 11 | 7.2 | 6.5 | 7.6 | 7.2 | 6.4 | 8.0 | 8.7 | 7.9 | 9.9 |
| m3 | 35 | 7.2 | 6.4 | 7.9 | 7.1 | 6.3 | 7.7 | 11.8 | 10.5 | 13.5 |
| mX | 42 | 6.9 | 5.7 | 8.2 | 7.0 | 6.1 | 8.5 | 8.7 | 7.7 | 10.0 |
| dp4 | 4 | 4.5 | 4.3 | 4.7 | 4.8 | 4.4 | 5.0 | 6.7 | 6.3 | 7.0 |

[a] All widths are buccolingual. This measurement was taken across the mesial loph(id) for molars and deciduous premolars.

[b] Other measures include: for incisors, alveolar length; for p3s, flange height taken from protoconid to inferior tip of mesio-buccal honing flange; for molars and deciduous premolars, width taken across distal loph(id).
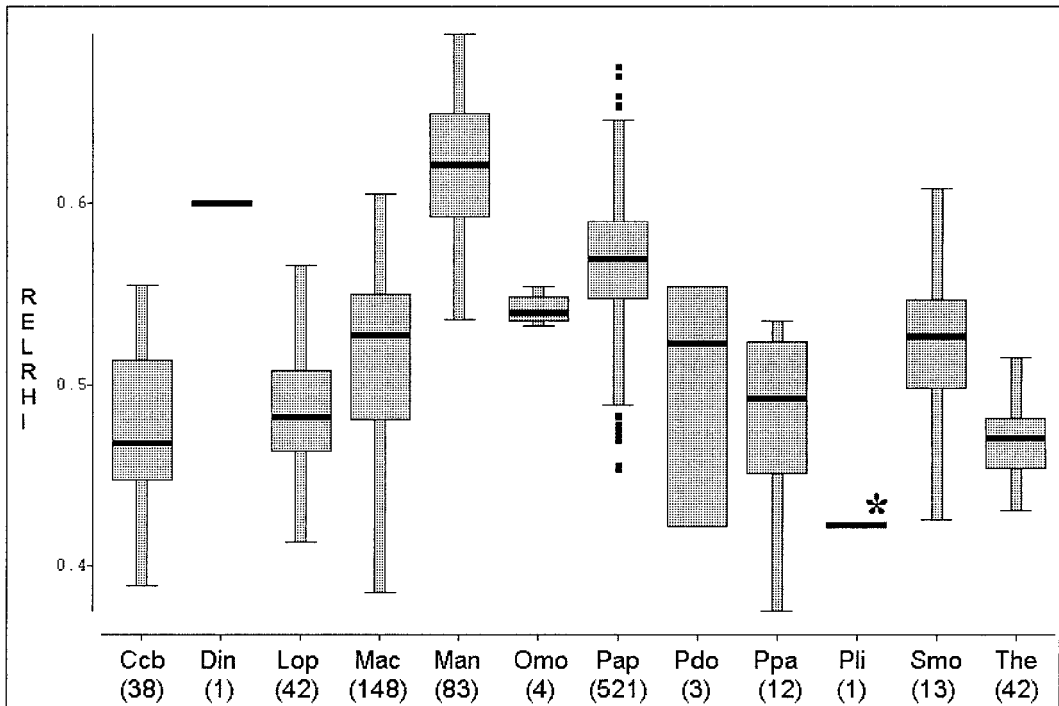
[c] All lengths are mesiodistal.

Fig. 4.  Box and whisker plot of the ratio: length nasion–rhinion/length nasion–prosthion. Labeling is the same as in fig. 3.

with their widest point at the mesial loph of M2 and narrowest at P3, bulging laterally again at the canine, although less so in the females ARA-VP-1/1007 and ARA-VP-1/1723. The molar series forms a short arc, with the M2 oriented slightly obliquely. The premolars are set in a straight line from M1 to C.

When viewed laterally, the maxillary dentition in ARA-VP-6/933 and ARA-VP-1/1723 is basically straight to very slightly concave, as in most cercopithecines. The palate is preserved in ARA-VP-6/933, but it is covered in matrix (which cannot be removed without causing damage to the specimen). ARA-VP-1/1723 preserves a small part of the palatal process, which is about 0.5 cm in depth anteriorly and deepens slightly posteriorly.

*Zygomatic Arch.* The maxillary root of the zygomatic arch arises from above the distal loph of M2 in the male ARA-VP-6/933 and above the mesial loph of M2 in the female ARA-VP-1/1723. This is farther anterior than in *Papio, Gorgopithecus,* and *Theropi-*

*thecus* (other than *T. gelada* and *T. oswaldi leakeyi*). ARA-VP-6/933 is the only specimen to preserve the zygomatic arches. The anterior surface of its zygoma curves gradually and smoothly superoposteriorly, with only a very slight depression in the region of the infraorbital foramina and maxillozygomatic suture. This depression is unrelated to any maxillary fossae and is the only feature to interrupt the otherwise smoothly curving surface. The inferior margin of the anterior portion of the zygomatic arch is a smooth semicircular curve interrupted by a small pyramidal process where the maxillozygomatic suture intersects. The superiormost point of the inferior margin lies below the lateral edge of the orbit, at which point the zygoma curves inferiorly again. The temporal surfaces do not appear strongly excavated as in *Theropithecus,* but there is some damage and distortion here.

In superior view, the zygomatic arches are no more laterally flared than in most *Macaca* or *Papio,* but are more smoothly curved. This is particularly notable anteriorly where
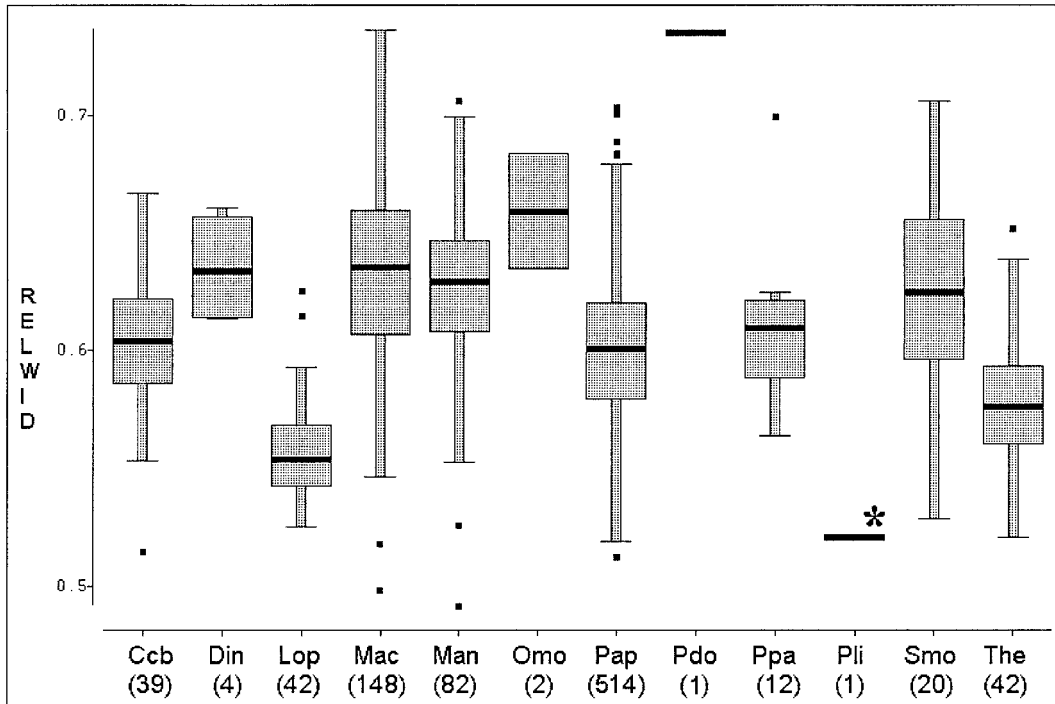
Fig. 5. Box and whisker plot of the ratio: width of muzzle at M1/M2 contact/biporionic width. Labeling is the same as in fig. 3.

they are more posteriorly angled than in *Papio.* The zygomata of the latter genus jut out more sharply, perhaps due to greater maxillary fossa development. The scar for the origin of the masseter muscle is visible in ARA-VP-6/933 and terminates anteriorly very close to the maxillozygomatic suture. The posterior termination is not preserved, but must have been anterior to the zygomaticotomporal suture as there is no scar on the zygomatic process of the temporal.

*Orbital Region.* The orbital region is only preserved in ARA-VP-6/933. Internally both orbits are occupied by matrix. The supraorbital torus is relatively prominent, but thin superoinferiorly. It is mildly V-shaped in superior view and separated from the neurocranium by a broad ophryonic groove. Unlike in *Papio, T. oswaldi,* and larger *Macaca,* there are no bulges above the torus at the midpoints of the orbits. In frontal view, the superior orbital rim and torus rise only very slightly lateral to the sagittal plane, then curve inferiorly, giving the torus a mildly superiorly bowed surface and the orbits a

slightly laterally ''drooping'' appearance. There are no supraorbital notches.

The interorbital breadth is narrow, and glabella is not prominent. There is some damage in this area, but nasion was probably the anteriormost point on the frontal. The orbits themselves are largely mediolaterally oval in outline, being relatively short and broad. The lacrimomaxillary suture seems to lie just at the orbital rim, and the lacrimal fossa was likely contained entirely in the lacrimal bone.

*Calvaria.* The calvaria is only preserved in ARA-VP-6/933. It is relatively globular in overall shape, with its greatest width at the external auditory meatus. It is generally lacking in superstructures and is considerably broader than the muzzle. When viewed in Frankfurt horizontal, the frontal bone rises above the supraorbital torus and achieves its maximum height about 1 cm anterior to bregma. The cranial vault remains at this height until about 2.5–3 cm posterior to bregma. The temporal lines are faint and widely separated, curving posteriorly less than 1 cm medial to the lateral orbital margins. Poste-
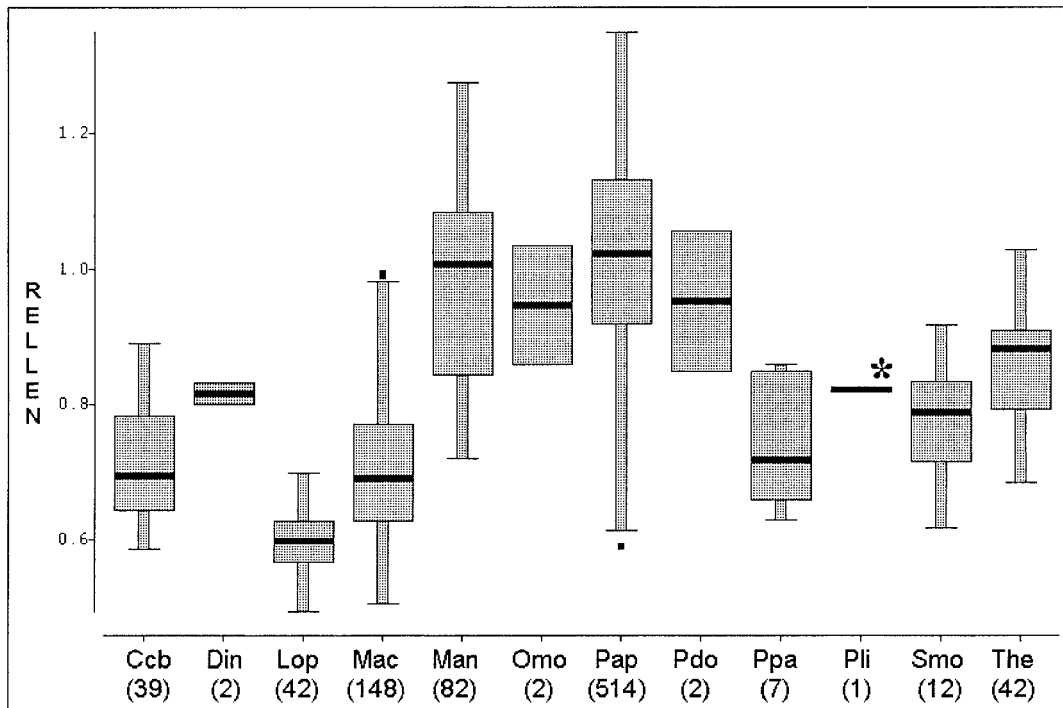
Fig. 6.   Box and whisker plot of the ratio: length inion–nasion/length nasion–prosthion. Labeling is the same as in Fig. 3.

rior to this, they remain subparallel, approximating only slightly posteriorly. In conjunction with the weak temporalis development, postorbital constriction is slight and the temporal fossae are narrow. The nuchal crests are slight to nonexistent at inion, but become rather large laterally, having their greatest width behind the external auditory meatus. Viewed posteriorly, the vault is taller than that of *Theropithecus,* which is broad and low, but is similar to that of *Papio* or *Macaca.*

*Basicranium.* The basicranium of ARA-VP-6/933 is largely covered in matrix, and the foramen magnum is obscured by an articulated atlas. The occipital plane is probably inclined at about 45° in Frankfurt orientation. The mastoid processes do not appear to be prominent. The postglenoid processes may be closely approximated to the glenoid fossae, but this is difficult to tell, and it is impossible to see whether they are separated by a sulcus, as in *T. oswaldi darti.* The external auditory meatus are basically normal

to the sagittal plane and appear nearly round in cross section.

*Facial Hafting.* The only specimen where the relationship between the face and neurocranium can be assessed is ARA-VP-6/933. The glenoid fossa lies closely in line with the alveolar plane. The glenoid fossa is only slightly more elevated than in *Papio,* but less so than in *Theropithecus.* Its position is not unlike that in *Parapapio* cf. *jonesi* from Hadar (see Szalay and Delson, 1979: 345). The face is less klinorhynch than that of *Papio* (*Papio*), but also less airorhynch than that of *Theropithecus gelada.*

*Mandible.* ARA-VP-6/933 preserves most of the mandible, with considerable damage to the right side. ARA-VP-1/73 (see fig. 7) is a male mandible with most of the corpora and symphysis intact. The inferior margin is missing posterior to the symphysis. The complete dentition is present other than the left canine through right i1. ARA-VP-1/133 (see fig. 7) is a considerably distorted and crushed female mandible lacking the left ramus, but
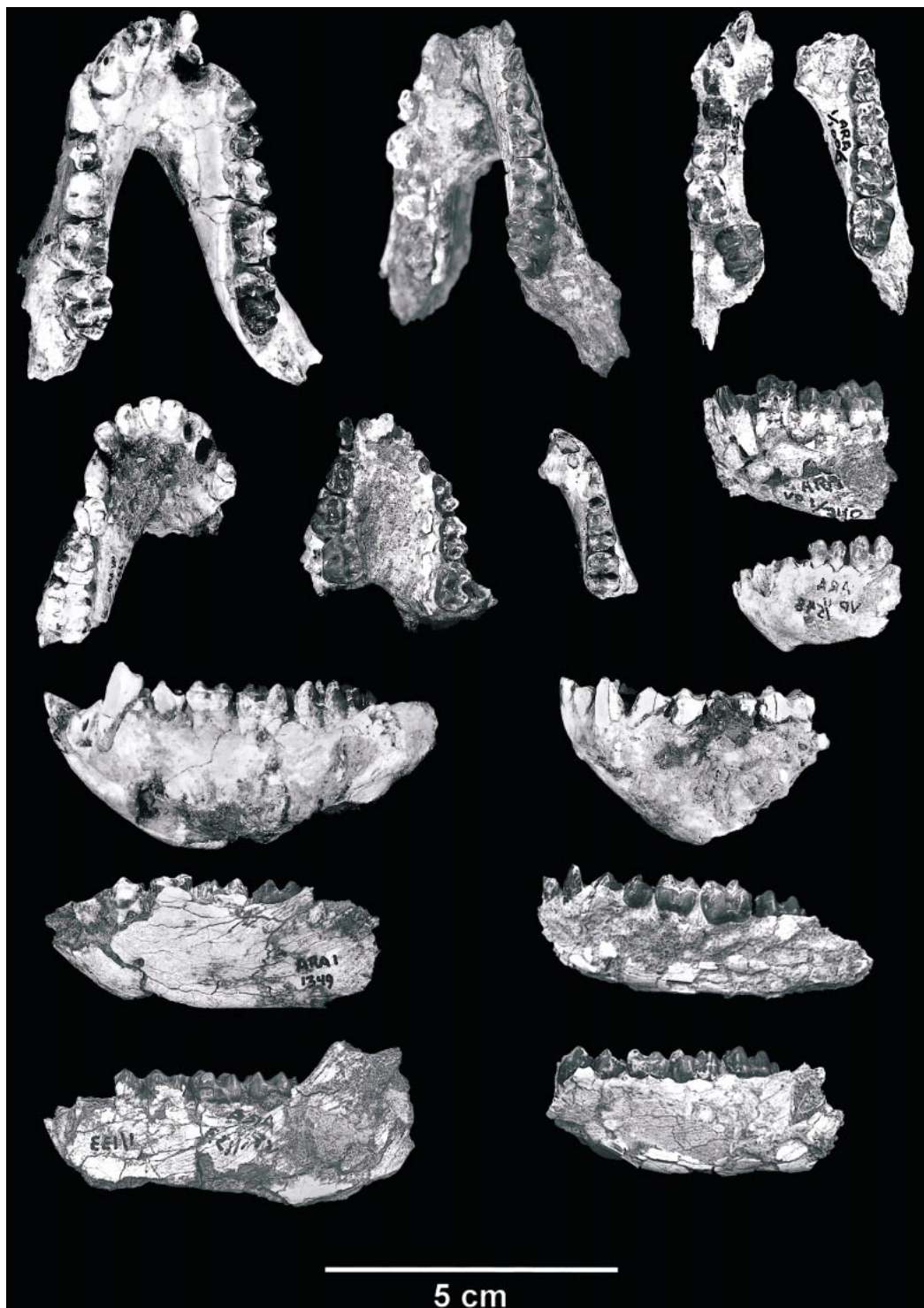
Fig. 7.    Mandibles of *Pliopapio alemui*. **Top row** left to right: ARA-VP-1/73, ARA-VP-1/133, ARA-VP-1/1006 (two pieces). **2nd row**: ARA-VP-1/563, ARA-VP-1/740, ARA-VP-1/548, ARA-VP-1/740,
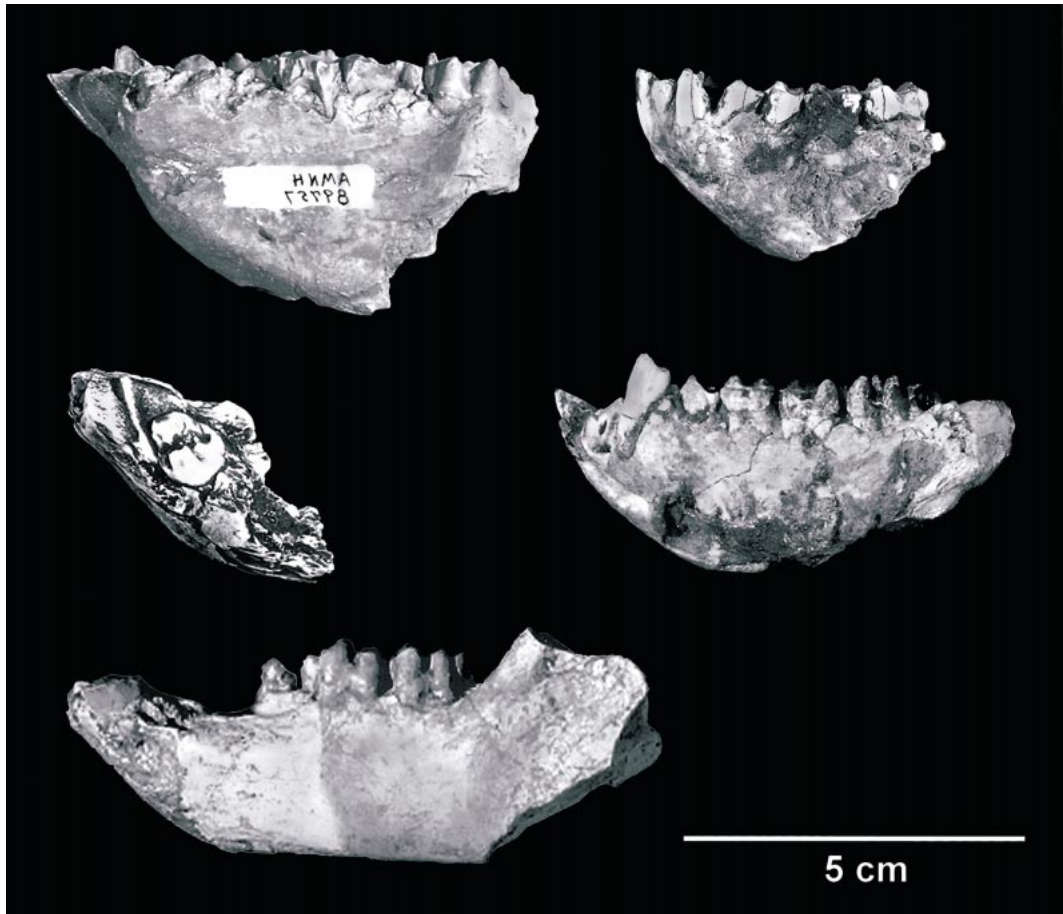
Fig. 8. Profile views of symphyses of *Pliopapio alemui, Parapapio ado* from Laetoli, and *P. ado* from Kanapoi. **Top**: MB 1938–1 (cast, reversed), ARA-VP-1/563. **Middle**: NMT-LAET 74/322b (cast), ARA-VP-1/73. **Bottom**: KNM-KP-286 (reversed).

preserving most of the right. The inferior margins are largely intact, and the left and right p4-m3 are present. ARA-VP-1/1006 (see fig. 7) preserves separate and partially crushed female right and left corpora with all of the dentition other than the right central incisor through the left canine. ARA-VP-1/563 (see fig. 7) is a female symphysis with some of the left corpus and the dentition from the right i1 through the left m2, and the right p3. ARA-VP-1/740 (see fig. 7) is a ju-

venile mandible with most of the corpus and the right dp3-m1 and the left dc-m1. ARA-VP-1/548 (see fig. 7) is a right juvenile corpus with dp4 and m1 in place, and the tips of the crowns of i1-c just beginning to emerge from their crypts.

The symphysis slopes at an angle similar to that of *Macaca fascicularis.* This is more sloping than in many papionins when viewed in profile, but less so than the symphysis of *Parapapio ado* from Laetoli (Leakey and

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←

ARA-VP-1/548 (reversed). **3rd row**: ARA-VP-1/73, ARA-VP-1/563. **4th row**: ARA-VP-1/133 left corpus (1349 is an old number), ARA-VP-1/1006 left corpus. **Bottom row**: ARA-VP-1/133 right corpus, ARA-VP-1/1006 right corpus.

Delson, 1987) and Kanapoi (Patterson, 1968), and considerably less so than in the papionin from Lothagam (Leakey et al., in press). The incisive alveolar plane is oriented nearly vertically, whereas it projects more anteriorly in the above-mentioned taxa. The incisor row is thus nearly vertical in *Pliopapio alemui,* whereas the incisors of the others are more procumbent, with the central incisor projecting well beyond the lateral. The projecting alveolar process of *P. ado* produces a symphysis that is quite different in profile from that of *Pl. alemui* (see fig. 8). The symphysis is pierced by a median mental foramen. There appear to have been very faint, triangular mental ridges. The superior transverse tori in ARA-VP-1/73 and ARA-VP-1/133 extend posteriorly to the middle of P4 in superior view. Both superior and inferior transverse tori are well developed.

The Middle Awash mandibles show only slight or no development of corpus fossae. Although there is some damage to the inferior margin in ARA-VP-6/933, it appears that the deepest point was relatively anterior, perhaps under p4, and that the inferior margin curved gently convex down. The inferior margin is thus anteriorly divergent. The oblique line emerges near the level of the mesial lophid of m3 or the distal lophid of m2. The extramolar sulcus is smooth and weakly developed. The gonial region is unexpanded. If present at all, the mylohyoid line is poorly developed.

Viewed superiorly, the tooth rows are nearly parallel along their lingual surfaces, from M3 to P3, with the canine slightly medial and the incisors curving sharply medially. In lateral view there is a normal curve of Spee (i.e., the tooth row is concave upward).

The ramus is well preserved only in ARA-VP-6/933. It is back-tilted, although less so than in *Papio* but more so than in *Macaca* or *Theropithecus* (*Theropithecus*). The coronoid process is even with or slightly higher than the condyle, from which it is separated by a shallow semicircular mandibular notch. There is a deep triangular fossa below the coronoid process on an otherwise relatively smooth lateral surface. The masseteric tuberosity is faint, and the whole area of its attachment is not heavily scarred.

*Dentition.* The incisors are fairly large relative to the molars, which is typical for most papionins. The I1 is broad, flaring, and spatulate in anterior view. The I2 is more asymmetrical and not as broad, with a small lateral tubercle. The lower incisors have straight mesial and distal borders in anterior view, so that they are less flaring than the uppers. The lateral border of the i2 is more laterally curved than that of the i1. As is typical of cercopithecines, they lack lingual enamel and the labial surface stands out, yielding a somewhat chisel-like occlusal surface. The labial surface is often "squared" in occlusal view. The canines are typical of cercopithecoids, being highly sexually dimorphic and having a mesial groove on the uppers that extends onto the surface of the root.

The upper premolars are typical bicuspid papionin teeth. The p3 is a highly sexually dimorphic tooth. The paraconid is less well developed than in the colobine, and the male mesiobuccal flange is significantly longer than that of the females. The p4 develops a small mesiobuccal flange in some males (e.g., ARA-VP-6/933), has more of a talonid than the p3, and has a fairly high lingual notch.

The molars in general are high-crowned for a papionin, with relatively little flare, especially in comparison to the Kanapoi sample. Cusp relief above the lower lingual/upper buccal notch is high for a papionin, but lower than in colobines. Accessory cuspules are often present in the lingual notch. In the upper molars, the lingual cusps are elevated relative to the central basin and seem to be connected by continuous, well-developed postproto- and prehypocristae. The mesial loph is wider than the distal. The M2 is often the largest of the upper molars. The lower molars have normal low relief and higher lingual notch. The buccal cusps tend to be fairly columnar, with the mesial and distal foveae being pinched, although not to the extent of those of *Theropithecus.* The floor of the median buccal notch seems to slope downward distally. On the m1–2, the distal cingula develop a very small hypoconulid 6–10% of the time depending on scoring. In the m3, the hypoconulid is generally tightly pressed against the hypoconid, so that the distal buccal notch is very constricted compared to the

mesial. Additionally, the distal buccal notch rarely preserves any ''shelf'' at the base.

The dI2 has a crown that is basically spatulate, low in height, broad, and angles mesially. The root is broad and labiolingually flattened. The dC is a mesiodistally elongate tooth, with a crown that is approximately triangular in labial view. The dc crown has a prominent central cusp that is labiolingually compressed and a crest that extends mesially from its apex. Distally there is a small accessory cuspule. In general, the deciduous premolars are similar to adult molars, but narrower, with more lateral flare, and loph(id)s that are more weakly developed than the adult teeth. In addition, the upper dPs have relatively larger mesial and distal foveae. The mesial fovea is particularly large and elongate on the dP3. The dp3 protolophid is much narrower than the hypolophid. There is also a well-developed preprotocristid, and what may be a paraconid, yielding a mesial fovea that is triangular in shape. The dp4 is more similar to an adult m1, but narrower with a relatively longer mesial fovea.

## SUBFAMILY COLOBINAE JERDON, 1867

### *Kuseracolobus*, new genus

TYPE SPECIES: *Kuseracolobus aramisi,* new species.

GENERIC DIAGNOSIS: A genus of colobine monkey with a broad interorbital area, as is typical for colobines, but distinguishing it from *Libypithecus, Nasalis,* and *Rhinocolobus* (especially considering size). The projection of the lower face anterior to the zygomatic arches in *K. aramisi* is generally similar, in proportion to overall cranial size, to that of *Cercopithecoides, Mesopithecus, Trachypithecus,* and the undescribed colobine from Leadu (NME AL2–34, which is associated with a partial skeleton; see Delson, 1994: 40). In comparison to *Colobus,* the lower face of *K. aramisi* is less projecting, and it is distinctly less so than in the long-faced genera *Paracolobus, Rhinocolobus, Dolichopithecus,* and *Nasalis.* In profile, the maxillary alveolar margin completely lacks the airorhynchous shape of *Semnopithecus.*

As is typical for most colobines, the mandibular symphysis lacks a median mental foramen. This distinguishes the genus from both *Rhinocolobus* (at least as known from the Shungura and Koobi Fora Formations) and *Cercopithecoides,* which possess one. In lateral view, the symphysis is deep with a vertical profile. The corpus is quite deep and robust overall and it deepens posteriorly. In its depth and robusticity, the corpus is very different from the Leadu colobine, *Procolobus, Cercopithecoides, Semnopithecus, Pygathrix,* and *Presbytis.* It is more like *Colobus, Paracolobus,* and *Rhinocolobus,* but is not as deep as the corpora of the last two genera. It is further differentiated from *Paracolobus* and *Rhinocolobus* by the presence of larger *prominentia laterales,* similar to *Nasalis* (including *N.* (*Simias*)). The gonial region is expanded, separating it from the Leadu colobine, *Cercopithecoides,* and *Procolobus,* but far less so than in *Paracolobus mutiwa.*

In the dentition, the I1 crown does not flare in anterior view, so that the apex is not significantly wider than the base. This is distinct from the flaring I1 in *Procolobus.* The P3 protocone is not reduced, as in *Cercopithecoides, Colobus,* and *Rhinocolobus.* The distal lophid of the m3 is typically narrower than the mesial, as is typical for the Presbytina and likely primitive for the Colobinae (Szalay and Delson, 1979). Three individuals out of 30 in the *K. aramisi* sample show hypolophids that are wider than their protolophids, and most are near to even. Most of the m3 hypolophids are wider relative to their protolophids than those of *Mesopithecus.*

ETYMOLOGY: Named after the Middle Awash locality of Kuseralee Dora (''Place of the Kusera tree'' in the Afar language).

### *Kuseracolobus aramisi*, new species

SPECIFIC DIAGNOSIS: As for genus.

ETYMOLOGY: Named after the type site of Aramis.

HOLOTYPE: ARA-VP-1/87. A nearly complete male mandibular corpus with the entire postcanine dentition except the right m1, associated with left and right C, left c, and a left maxillary fragment with M1–3 found by A. Asfaw on December 18, 1992 (see fig. 9).

HYPODIGM: See appendix 2.

HORIZON: All specimens are derived from

Fig. 9.   Holotype of *Kuseracolobus aramisi* ARA-VP-1/87. Occlusal view. Opposite page: lateral views, left side above, right (reversed) below.

the Aramis Member of the Sagantole Formation, between the GATC and DABT, and are therefore dated to 4.4 Ma (Renne et al., 1999).

DESCRIPTION: The best cranial specimens, ARA-VP-6/1686 and KUS-VP-2/70 (see fig. 10), are both females. ARA-VP-6/1686 preserves both maxillae and premaxillae below the middle of the zygomatic process of the maxilla, but little of the palate. The entire dentition is preserved other than the right I2 and M2. KUS-VP-2/70 preserves a left premaxillomaxillary fragment with C-M1, most

of the root of the zygoma, part of the lateral aspect of the face and piriform aperture, and most of the palatal process. A small fragment of the right maxilla with M1–2 and some of the palatal process is also preserved, along with the glabellar portion of the frontal and an isolated left I1. The holotype, ARA-VP-1/87, preserves a left maxillary fragment with M1–3 and the roots of P4, a small part of the palatine process, and the very base of the zygomatic process (see fig. 10). ARA-VP-1/6 is a male left maxilla preserving P3-M3 and the root of C (see fig. 10). It is highly
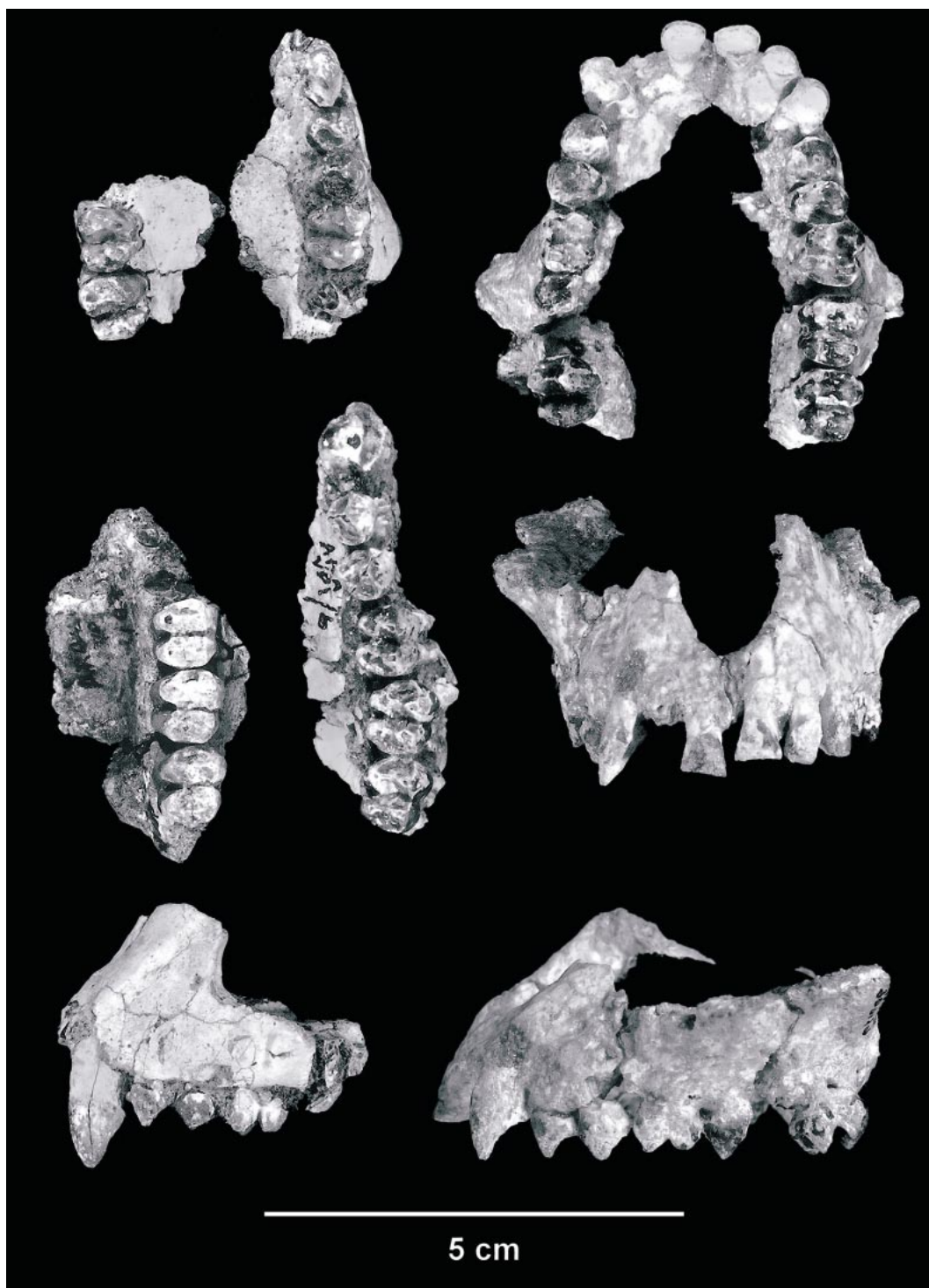
Fig. 9.   Continued.

Fig. 10.   Maxillae of *Kuseracolobus aramisi.* **Top row**: KUS-VP-2/70, ARA-VP-6/1686. **Middle row**: ARA-VP-1/87, ARA-VP-1/6, ARA-VP-1/1686. **Bottom row**: KUS-VP-2/70, ARA-VP-1/1686 (reversed).

damaged, however, revealing the roots of the teeth.

*Kuseracolobus aramisi* is larger in craniodental size than *Colobus, Libypithecus,* and *Mesopithecus,* but smaller than *Cercopithecoides* (other than a new species from Lothagam to be described by Leakey et al., in press), *Paracolobus, Rhinocolobus,* and *Dolichopithecus.* It is similar in size to *Nasalis,* the colobine from Leadu, the smaller colobine at Hadar, and larger subspecies of *Semnopithecus.* Colobines of similar dental size also occur in the Omo Shungura Formation in Members B, C, D, and G, from the Tulu Bor Member at Koobi Fora, and from the Upper Laetolil beds. It is also similar in dental size to *Pl. alemui.* The dental dimensions of *K. aramisi* are given in table 1.

*Frontal.* A small part of the glabellar area is preserved in KUS-VP-2/70 and ARA-VP-1/13. Both are similar in overall morphology to the Leadu colobine. The first specimen is a female and has an interorbital breadth of 12.1 mm; the second is of unknown sex and has an interorbital breadth of 10.8 mm, compared with 13.8 mm in the male Leadu specimen. Both Aramis specimens preserve nasals that are slightly pointed anterosuperiorly.

*Maxilla.* The most complete specimens are ARA-VP-6/1686 and KUS-VP-2/70, but the male ARA-VP-1/87 also preserves a left maxillary fragment. The root of the zygoma appears to be positioned above M1, or the M1/M2 contact in both male and female specimens. This placement of the zygoma is slightly more anterior than that found in *C. williamsi* from Koobi Fora and in most *C. williamsi* from South Africa. The piriform aperture is more vertically inclined and the rostrum shorter than in the male cercopithecines ARA-VP-6/437 and ARA-VP-6/933. The piriform aperture is quite narrow and tall, and the plane of its outline forms an angle slightly more than 60° with the alveolar margin in the subadult KUS-VP-2/70 and approximately 45° in ARA-VP-6/1686. The inferior portion of the piriform aperture is sharply V-shaped. In superior view, the premaxillae form a squared-off rostrum. The premaxillae would have been relatively short overall and generally similar in outline to those of the Leadu colobine and KNM-ER 4420.

The maxillary dental arcade is best preserved in ARA-VP-6/1686, and although distorted bilaterally, it is reasonably intact on the left. KUS-VP-2/70 and ARA-VP-1/87 also preserve partial tooth rows. The dental arcade forms a gentle arc from M3 to C, being widest around the M1/M2 contact, with no tooth deviating from this line. There is a sharp angle at the canines, and the incisors form a relatively straight, flat arc between the canines. The palate is partially preserved in KUS-VP-2/70 and appears to have been fairly shallow and flat. It is slightly deeper in the male ARA-VP-1/87, which preserves a small part of the palatal process.

*Mandible.* The mandible is best preserved in the male specimen ARA-VP-1/87, which retains much of the corpus and most of the rami, although the margins and gonion are damaged and the condyles are lacking. Except for the right m1, the entire postcanine dentition is preserved. ARA-VP-1/5 (see fig. 11) is the symphysis of a male with the left c-m1 and right p3-m1. ARA-VP-1/290 (see fig. 11) is probably a subadult male symphysis with the left i1–2 and p4-m1 and the crowns of the canines and p3s erupting. ARA-VP-6/796 (see fig. 11) is the symphysis of a female with the left m1 through right p4. ARA-VP-1/1774 (see fig. 11) preserves the right corpus down the inferior margin under the m1–3. ARA-VP-1/564 (see fig. 11) preserves part of the corpus below the molars, but none of the margin. Other specimens preserve more fragmentary portions.

The symphysis is quite steeply sloping, rather deep overall, and has a vertical profile. Both transverse tori are robust. The superior transverse torus extends posteriorly to the distal portion of p3, and is fairly steeply sloping. Anteriorly, the symphysis lacks a median mental foramen.

A shallow fossa is present on the lateral surface of the corpus. This is largely due to the presence of lateral bulging near the inferior margin, which is the widest part of the corpus. This can be most clearly seen in the female ARA-VP-6/796, but also in ARA-VP-1/290. This morphology is unlike that of the Leadu colobine, AL231–1a (a specimen from Hadar most likely to be the same taxon as the Leadu colobine), and *Cercopithecoides* (particularly KNM-ER 4420), where the

Fig. 11.   Mandibles of *Kuseracolobus aramisi*. **Top row**: ARA-VP-1/7, ARA-VP-1/70, ARA-VP-1/564, ARA-VP-1/1774, **2nd row**: ARA-VP-6/796, ARA-VP-1/5, ARA-VP-1/290. **3rd row**: ARA-VP-6/796, ARA-VP-1/5, ARA-VP-1/290. **Bottom row**: ARA-VP-6/796, ARA-VP-1/1774 (reversed).
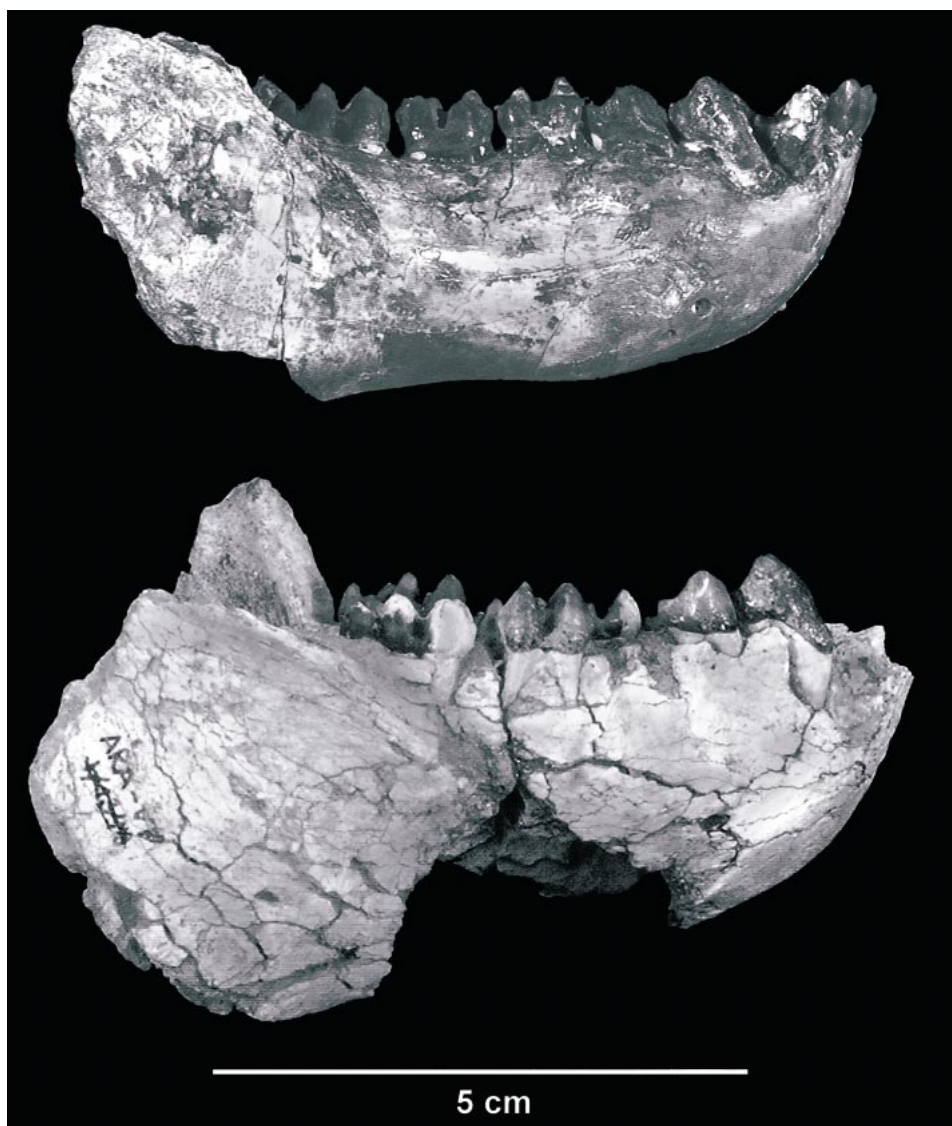
Fig. 12.   Lateral views of mandibles from the Leadu colobine AL2–34 (above) and *Kuseracolobus aramisi* ARA-VP-1/87 (below).

corpus is the widest at mid-height. The mental foramen seems to be single in all of the mandibles recovered, and its position varies from the below the m1/p4 contact in ARA-VP-1/1774 to the p3/p4 contact in the juvenile ARA-VP-1/290. The corpus is fairly deep overall, especially compared with the Leadu colobine (see fig. 12), AL231–1a, or *Cercopithecoides* from both East and South Africa. It is shallower but thicker than mandibles of *Paracolobus mutiwa* and *Rhinoco-*

*lobus.* In ARA-VP-1/87 the right corpus deepens posteriorly from p3 to m3, although there is damage below the m1 through mesial m3. ARA-VP-1/1774 deepens from m1 to m3 and preserves a bulge below the m2. The gonial area is partially preserved in ARA-VP-1/87 and is expanded, although not to the extent seen in *Paracolobus mutiwa.* This is quite distinct from the comparatively unexpanded gonial area seen in the Leadu colobine and *Cercopithecoides.*

Viewed superiorly, there is a wide extra-molar sulcus, and the oblique line blends into the corpus at mesial m2 or distal m1, comparable to that in the Leadu colobine and AL231–1a. There is no strongly marked ridge at the anterior limit of the masseter scar. The mandibular dental arcade, although slightly distorted, is best preserved in ARA-VP-1/87. It forms a parabolic arch, except that the area across the incisors is flattened.

*Dentition.* The dentition overall is typical for colobines. The upper incisors are smaller and far less flaring than in papionins. The mesial and distal margins of the I1 crown are roughly parallel and slant mesially, and the widest part of the crown is approximately at mid-height. Lingually, there is a cingulum around the base. The I2 is caniniform in crown shape and also has a lingual cingulum. The lower incisors possess lingual enamel and are small, peglike teeth compared with those of papionins. The i1 lingual surface is shoveled, and the crown is slightly flaring in anterior view. The i2 has a crown that is narrower overall, is more of a parallelogram in outline, and possesses a distal cuspule, or "lateral prong" (Delson, 1975). The canines are typical of cercopithecids, being comparatively large teeth and highly sexually dimorphic.

The upper premolars are typical bicuspid teeth. The protocone of the P3 is usually present and often large, but is sometimes reduced. The P3 is generally more triangular in occlusal outline, and the P4 often has a bit more of a talon. The p3 is sexually dimorphic as for most cercopithecids, particularly in the development of the mesiobuccal flange. It is also typical of colobines in that the paraconid is generally more pronounced than in cercopithecines. The male mesiobuccal flange is shorter than those of male cercopithecines (although longer than female cercopithecines), is more inferiorly directed, and the talonid extends more lingually. The p4 is a more molariform tooth, but may develop a mesiobuccal flange in males. There is also a greater amount of cusp relief (i.e., the difference between the height of the cusps and the lowest points of the crown between them) than is the case in cercopithecines.

The molar crowns are only slightly flaring with tall, widely spaced cusps that are connected by sharp cross-lophs. On the upper molars, the paraloph is broader than the hypoloph, but less so than in cercopithecines. The buccal notch has a "crease" reaching toward the cervix from the buccal notch. A distal fifth cuspule is variably present on the M3. The upper molars are all roughly similar in overall size and generally arranged in a straight line. The lower molars have very deep lingual notches with high cusps. The distal cingulum of m1–2 forms a distal cuspule 6–8% of the time, depending on scoring. On the m3, the hypoconulid is well developed, and there is typically (62–92%, depending on scoring) a tuberculum sextum as well. This contributes to the presence of a well-developed distal lingual notch between the hypoconulid and the entoconid. There is also a well-developed distal buccal cleft. The metalophid is usually wider than the protolophid on m1–2 but generally not on m3 (although it is occasionally). These lophid proportions for *K. aramisi* are typical of Asian colobines (which may be the primitive state for the subfamily; see Szalay and Delson, 1979) but different from extant African colobines.

Of the deciduous dentition, the di2 is possibly known in ARA-VP-1/2092. It looks like a miniature of the permanent i2, with a relatively narrow crown and a distal prong. This is distinct from normal papionin morphology, where the lower dIs are rather broad. Of the deciduous premolars, upper and lower dP4s are known. The dP4 is much like the M1, but far more flaring, with more approximated cusps. The mesial and distal foveae are relatively longer than in the molars. The dp4 is similar to the m1, but is narrower relative to its length, with a metalophid that is wider in comparison to the protolophid than in m1. The lophids are not quite as well developed as those of the molars, but are better developed than those of the deciduous premolars of cercopithecines.

### BODY WEIGHT AND SEXUAL DIMORPHISM

Based on the available dental material that is assignable to sex, body weight has been estimated here for the Aramis cercopithecids utilizing the methods and prediction equations of Delson et al. (2000). In their study,

TABLE 2
**Distribution of Characters in Various Cercopithecid Genera[a]**

| | *Pliopapio* | *Parapapio* | *Lophocebus* | *Cercocebus* | *Mandrillus* | *Papio (Papio)* | *P. (Dinopithecus)* | *Gorgopithecus* | *T. (Theropithecus)* | *T. (Omopithecus)* | *Macaca* | *Paradolichopithecus* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ophryonic groove | X | — | — | — | X | X | X | X | — | X | V | X |
| Sagittal crest in males | — | — | — | — | V | — | X | X | X | X | V | X |
| Maxillary fossae | — | — | X | X | X | X | — | X | V¹ | X | V² | — |
| Maxillary ridges in males | — | — | X | V | X | X | X | — | — | X | V² | — |
| Muzzle dorsum flat | — | — | X | — | X | X | X | — | — | X | V² | — |
| Anteorbital drop | X | — | — | — | X | X | X | X | X | X | V | X |
| Deep corpus fossae | — | — | X | — | X | X | — | X | V¹ | X | — | — |
| Symphysis sloping | X | V³ | V | V | — | — | — | — | — | — | V | — |
| High molar flare | — | — | X | X | X | — | — | — | — | — | — | — |

| | *Kuseracolobus* | *Libypithecus* | *Leadu* | *Cercopithecoides* | *Paracolobus* | *Rhinocolobus* | *Colobus* | *Procolobus* |
|---|---|---|---|---|---|---|---|---|
| Interorbital narrow | — | X | — | — | — | X | — | — |
| Lower face projecting | — | X | — | — | X | X | X | — |
| Median mental foramen | — | — | — | X | — | X | — | V |
| Mandible deep | X | ? | — | — | X | X | X | — |
| Large prominentia | X | ? | — | — | — | — | — | X |
| Corpus broadest at mid-height | — | ? | X | X | — | — | — | — |
| Corpus deepens posteriorly | X | ? | — | — | X | X | X | — |
| Gonial expansion | X | ? | — | — | V⁴ | X | X | — |
| P3 protocone reduced | — | — | — | — | — | — | X | X |
| m3 broader distal lophid | — | ? | — | — | — | — | X | — |

[a] Symbols: X = present; — = absent; V = variably expressed; V¹ = present in *T. gelada,* absent in *T. oswaldi*; V² = present only in Sulawesi species; V³ = extreme in *P. ado* and Lothagam papionin; V⁴ = absent in *P. chemeroni,* present in *P. mutiwa*; ? = unknown.

subfamily-specific equations for each sex were derived based on a large cercopithecid sample with associated or literature-compiled body weights. These equations were used here on the Aramis dental material that is assignable to sex and subfamily. The results are based on the means of several estimates based on equations for dental measurements found to be most accurate at predicting body weights of known samples (for a thorough discussion, see Delson et al., 2000). Males and females of *Pliopapio alemui* are estimated to have had a mean body weight of

12 kg (range 10–15 kg) and 8.5 kg (7–10 kg), respectively. These estimates yield a ratio of male-to-female body mass of 1.4:1. This value is similar to that seen in such extant species as *Lophocebus albigena, Macaca sylvanus, M. nemestrina leonina,* and *Cercopithecus aethiops pygerythrus. M. sylvanus* is similar in body weight to *Pl. alemui,* whereas the others are smaller.

Body weight estimates have been made for *Kuseracolobus aramisi* in the same manner. Males and females of this population are estimated to have had mean body weights of

approximately 18 kg (range 14–22 kg) and 12 kg (10–14 kg), respectively. This yields a ratio of 1.5:1 for male-to-female body weight. This level of dimorphism is similar to that of most subspecies of *Semnopithecus entellus, Pygathrix* (*Rhinopithecus*) *roxellana,* and *Procolobus badius oustaleti.* Of these taxa, only *S. entellus* approaches *K. aramisi* in weight (Delson et al., 2000).

## DISCUSSION

The Middle Awash sample described here fills a temporal gap between the latest Miocene and oldest known Pliocene localities. Sites of broadly similar age to Aramis with fossil cercopithecids are relatively few in sub-Saharan Africa, and none of them contains specimens that can be unambiguously allocated to either of the Aramis taxa. The Early Pliocene (3.7–3.5 Ma) Upper Laetolil beds in Northern Tanzania have produced a sizable sample in which four species of cercopithecids are represented. Included in this collection is a small papionin larger in dental size than *Pl. alemui.* This sample includes the type specimen of *Cercocebus ado* (Hopwood, 1936). Leakey and Delson (1987) reassigned it to the genus *Parapapio* (which is best diagnosed on facial morphology, absent at Laetoli), as *P. ado,* largely based on an absence of mandibular corpus fossae. There are two specimens of a larger papionin also present. A colobine tentatively assigned to an unnamed species of *Paracolobus* is the most abundant colobine at Laetoli. A smaller colobine, similar in size to *K. aramisi,* is present but represented by only a few isolated teeth.

The site of Kanapoi is closer in age to Aramis at approximately 4.1 Ma and has produced a papionin mandible, KNM-KP 286, collected in 1966 and described as *Parapapio jonesi* on the basis of molar dimensions by Patterson (1968). Leakey and Leakey (1976) reassigned this specimen to the same species as the small papionin from Laetoli, *Cercocebus ado,* based on the mandibular morphology. This specimen was tentatively moved to the genus *Parapapio* along with the Laetoli material by Leakey and Delson (1987) and was thus designated cf. *Parapapio* aff. *ado.* Leakey et al. (1995) listed cf. *Parapapio* aff. *ado* and an unnamed colobine in their faunal list based on more extensive recent collections. The Kanapoi mandible fits well into the variation seen at Laetoli. KNM-KP 286 possesses the distinctive symphyseal morphology of the Laetoli material, and the molars show an even greater level of flare than does the Laetoli material. There are also two specimens of a small colobine of unknown affinity (Leakey et al., 1995). The site of Ekora is probably similar in age to Kanapoi and has produced a single broken cercopithecine lower molar, KNM-KP 287, similar to the papionin from Kanapoi in size and morphology (Leakey and Leakey, 1976).

From farther north in the Turkana basin there is a small papionin mandible, KNM-WT 16752, from the Nachukui Formation west of Lake Turkana. It has been assigned to cf. *Parapapio* aff. *ado* by Harris et al. (1988). This mandible is from just above the Tulu Bor tuff, and thus dates to ca. 3.4 Ma. It seems to lack the symphyseal morphology of *P. ado.* Fragmentary remains of a larger papionin, allocated to *Parapapio whitei* based on size and a lack of mandibular corpus fossae, have also been recovered from this level, but they are substantially larger than *Pl. alemui.* At Koobi Fora there is a small mandibular fragment with the second and third molars, KNM-ER 3122, from the Tulu Bor Member near the Toroto Tuff dated to about 3.3 Ma. It is from a papionin of similar size to those from Aramis and Kanapoi (personal obs.). Also from the Tulu Bor Member, and thus between 3.4 and 2.68 Ma, is KNM-ER 3041, a colobine mandibular fragment with m1–3 that is similar in dental size to *K. aramisi* (personal obs.).

The Hadar Formation is downstream from Aramis in the Awash Valley. In the Middle Pliocene portion of the formation (spanning 3.4–2.9 Ma) four species of Cercopithecidae are known. *Theropithecus oswaldi darti* is the most common species (Eck, 1993). A species of *Parapapio* is also present, termed *P.* cf. *jonesi* by Delson (Szalay and Delson, 1979; Delson, 1984). This taxon is near in size to *Pliopapio alemui,* but it possesses the distinctive cranial features of *Parapapio.* Two colobines are also present. One is a large colobine, tentatively assigned to *Rhinocolobus turkanaensis* (Delson, 1994) and

clearly different from *K. aramisi*. A smaller colobine, similar in size to *K. aramisi,* is also present. Based on a nearly complete mandible (AL231–1a) and a partial humerus (AL222–14), this taxon is likely to be the same species as the Leadu colobine (AL2–34 and the associated partial skeleton). This taxon is quite different from *K. aramisi* in its mandibular morphology, as discussed above. Additionally, the Leadu colobine was probably fairly terrestrial in its locomotor behavior (see Delson, 1994), much more so than is tentatively suggested by any of the postcrania found at Aramis.

There is an isolated lower third molar from Unit 2 of the Chiwondo Formation, which has been biostratigraphically dated to between 3.5 and 4.5 Ma (Kaufulu et al., 1981). This tooth is from a papionin similar in size to *Pl. alemui* and the Kanapoi papionin (Frost and Kullmer, in prep.). In South Africa, there is only the earliest Pliocene or Late Miocene Quarry E at Langebaanweg, from which only two isolated cercopithecine premolars have been recovered (Grine and Hendey, 1981).

North of the Sahara, the Mio-Pliocene sites of Sahabi and Wadi Natrun have each produced a single species of colobine and cercopithecine (Szalay and Delson, 1979; Meikle, 1987). The cercopithecines at both sites are represented by isolated teeth placed in the genus *Macaca* largely based on geography (Delson, 1975). The colobine, *Libypithecus markgrafi,* is represented by the relatively complete holotype cranium at the latter site and a few teeth and postcrania at the former (Delson, 1994). *Libypithecus* has also been listed from the Middle Awash, but from lower in section (Kalb et al., 1982). This diagnosis was based on a mandible from the Kuseralee Member (older than Aramis and currently under analysis by Y. Haile-Selassie), which probably represents a taxon other than *Libypithecus.*

Neither of the taxa described in this paper can be positively recognized outside of the Middle Awash. *P. ado* is recognized at Laetoli and Kanapoi, but this species is quite distinct from *Pl. alemui.* The fossils from the Chiwondo beds in Malawi and from Koobi Fora are clearly small papionins, but they are too fragmentary to be diagnosed as either *Pliopapio alemui, Parapapio ado, Parapapio jonesi* (all of which are broadly similar in size and molar morphology), or any other well represented taxon. The mandible from the Nachukui Formation lacks the diagnostic symphyseal morphology of *P. ado* but is too fragmentary to allocate to *Pliopapio* based on anything other than size.

Colobines similar in size to *K. aramisi* also occur at Hadar in the Sidi Hakoma Member, Leadu, the Omo Shungura Formation in Members B, C, D, and G, the Tulu Bor Member at Koobi Fora, and the Upper Laetolil beds (Delson, 1994; Leakey, 1987; Leakey and Delson, 1987). The colobine from Leadu and Hadar is clearly different from *K. aramisi.* All of the others are essentially represented by isolated dental remains and thus lack the morphological features that distinguish among *K. aramisi,* the Leadu colobine, and other colobine taxa.

One possible explanation for the absence of the Aramis taxa at other sites is that these taxa were endemic to northern Ethiopia. Given the lack of sites of similar age to Aramis, let alone sites that sample a similar habitat, a more likely hypothesis for their absence in the fossil record outside Aramis is sampling. WoldeGabriel et al. (1994) discussed the environment at Aramis and found that faunally it was most consistent with a closed habitat. They noted the high abundance of primates, particularly colobines. Other East African Pliocene sites have high proportions of cercopithecids, such as the Shungura Formation (Bobé, 1997). Aramis, however, is different from all other East African Pliocene sights in the very high abundance of colobines relative to cercopithecines (56% colobines at Aramis vs., e.g., 2–11% for different members of the Shungura Formation; see Eck, 1976). The cercopithecid sample at Kanapoi, which is most similar in age to Aramis, is dominated by papionins, with very few colobines present (Leakey et al., 1995). The only African site that approaches Aramis in this respect is Laetoli, where colobines represent 36% of the identifiable cercopithecids. At Laetoli, however, cercopithecids make up only a small proportion of the total fauna (Leakey and Delson, 1987). Thus, in its combination of abundant cercopithecids, and most of those cercopithecids being colobines,

Aramis is unique, which may suggest a habitat different from other known localities.

## PHYLOGENETIC RELATIONSHIPS

The phylogenetic positions of the taxa described here have not yet been completely analyzed, as this task requires an extensive analysis of the family. However, it is possible to offer hypotheses based on the evidence presented above. The Asian and North African genus *Macaca* is recognized by most modern studies as the sister taxon to a monophyletic sub-Saharan African papionin clade (Szalay and Delson, 1979; Harris and Disotell, 1998; Tosi, et al., 2000). Among the extant genera, there appear to be two main clades, one consisting of *Mandrillus* and *Cercocebus* and the other of *Papio, Theropithecus,* and *Lophocebus* (Harris and Disotell, 1998; Fleagle and McGraw, 1999). The suprageneric relationship of the fossil forms, however, remains controversial (Delson, 2000). Within the sub-Saharan African papionins there are four main groups, which may represent clades. The first group, *Parapapio,* is often regarded as the most primitive genus and as a potential ancestral form from which the other genera radiated (Szalay and Delson, 1979). No fossils known to date can be unambiguously identified as belonging to the second group, the *Mandrillus/Cercocebus* clade. The third group consists of *Papio, Theropithecus,* and possibly *Gorgopithecus. Lophocebus* forms the fourth group, as its position relative to *Papio, Theropithecus,* and *Gorgopithecus* is ambiguous.

In relation to these groups, two possible phylogenetic positions seem likely for *Pliopapio alemui.* One option is that anteorbital drop may be a synapomorphy uniting *Pliopapio* with the *Papio/Theropithecus* clade to the exclusion of *Parapapio.* Within this group, however, *Pliopapio* is clearly distinct from the former genera, as each possesses derived features it lacks. A second, although less likely option, is that *Pl. alemui* may be a primitive member of its tribe, either an ancestor to or sister taxon of the remaining genera. This position requires that the rostral profile and facial hafting of *Parapapio* be autapomorphies, derived relative to the primitive African papionin morphotype. The Af-

rican ancestral morphotype would then be more *Macaca*-like, but with a longer rostrum, as in *Pl. alemui.* Thus, the anteorbital drop present in *Papio, Theropithecus, Mandrillus, Pliopapio,* and possibly *Gorgopithecus* would be primitive for the subtribe. Since *Parapapio* has been identified based on facial material at the late Miocene site of Lothagam (Leakey et al., in press), this alternative would require that the *Pliopapio* lineage extend back at least as far.

The Colobinae are generally divided into two subtribes, the Colobina in Africa and the Presbytina in Asia (Szalay and Delson, 1979). The only cranial features typically used to diagnose the two subtribes are that the P3 has a reduced protocone and that the m3 has a distal lophid that is wider than the mesial lophid in the Colobina, whereas the Presbytina possess a larger P3 protocone and narrower m3 distal lophid. For both of these features, the derived state is that of the African forms. How the many extinct African forms fit into this framework is difficult to discern. As stated above, these features are both intermediate in *Kuseracolobus aramisi,* with the P3 protocone being variably reduced and the m3 distal lophid being approximately equal in width to the mesial. This may indicate that *K. aramisi* is partially evolved toward the derived state for these features and therefore may indicate some affinity with the African clade. This is a hypothesis that clearly needs more thorough analysis.

Within the larger fossil colobines from Africa there appear to be two groups. One of these is a long-faced group composed of *Paracolobus* and *Rhinocolobus* (but not necessarily *Libypithecus*). In addition to large size and long faces, this group is further diagnosed by having mandibular corpora that are deep and narrow in breadth, that deepen posteriorly, that are flared at gonion (except less in *P. chemeroni,* but greatly in *P. mutiwa*), and that have tall rami. This group is further distinguished from the second group by being generally more arboreal. The second group is a short-faced and terrestrial group composed of East African *Cercopithecoides* and possibly the Leadu colobine. This second group, along with South African *Cercopithecoides,* shares a mandibular morphology that includes a shallow but very broad

corpus, a shallow and vertical symphysis, and a short but deep ramus with a relatively unexpanded gonion. Unfortunately, *K. aramisi* does not fit well into either group. The diagnostic features and geographic distributions of all Afar and Turkana Basin taxa are discussed in more detail in Frost (2001).

## SUMMARY

A sample of 925 fossil cercopithecids has been collected from the GATC–DABT interval of the Sagantole Formation of Ethiopia. This is the largest collection from the Early Pliocene of Africa described to date, and contains two new species, each in a new genus. *Pliopapio alemui* is distinct from other known papionin genera in its cranial morphology. This species is similar in dental size to *Parapapio ado* from Laetoli and Kanapoi, but is distinct from these samples in its mandibular morphology. *Kuseracolobus aramisi* is similar in overall size to a medium-sized colobine from Leadu, near Hadar. *K. aramisi* is different in its mandibular morphology from this latter species. Other colobine teeth of similar size occur across East Africa, but their affinity is impossible to determine given the existence of at least two similarly sized species. None of the available morphology aligns this species with any other known colobines. Neither of these species can be definitively identified outside of the Middle Awash. This is probably due to a lack of sites of similar age and environment to Aramis. The phylogenetic placements of both species are currently unresolved, but *Pl. alemui* may be more closely related to *Papio* and *Theropithecus* than to *Parapapio*. *K. aramisi* does not clearly fit within the Colobina or Presbytina. It is also not clearly allied with either the long-faced fossil genera or with the shorter-faced (semi-)terrestrial forms.

## ACKNOWLEDGMENTS

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APPENDIX 1

## List of All Specimens Assigned to *Pl. alemui*

For each specimen, the catalog number, sex (if diagnosable), side, and element are listed. The catalog number includes the collection locality ahead of the slash; thus, ARA-VP-1/73 is from locality Aramis 1. The abbreviations KUS and SAG stand for Kuseralee Dora and Sagantole, respectively. Associated elements share a catalog number.

| Catalog No. | Sex | Side | Element | Comments |
|---|---|---|---|---|
| ARA-VP-1/8 | | Left | Mandible | m3 |
| ARA-VP-1/9 | | Left | m3 | |
| ARA-VP-1/12 | | Left | m3 | |
| ARA-VP-1/19 | | Right | M1 or 2 | |
| ARA-VP-1/20 | | Right | M1 or 2 | |
| ARA-VP-1/23 | | Left | M1 or 2 | |
| ARA-VP-1/24 | | Left | m3 | |
| ARA-VP-1/45 | | Right | Mandible | |
| ARA-VP-1/73 | ♂ | Right | Mandible | m3 |
| ARA-VP-1/132 | | Left | M1 or 2 | Right i2–m3; left p3–m3 |
| ARA-VP-1/133 | ♀? | | Mandible | Left + right p4–m3 |
| ARA-VP-1/135 | | Right | m1 or 2 | |
| ARA-VP-1/139 | ♂ | Right | Maxilla | M1 |
| ARA-VP-1/185 | | Right | m3 | |
| ARA-VP-1/190 | | Right | m3 | |
| ARA-VP-1/191 | | Left | i1 | |
| ARA-VP-1/239 | | Right | m3 | Fragment |
| ARA-VP-1/289 | | Left | m3 | |
| ARA-VP-1/309 | | Left | i1 | |
| ARA-VP-1/330 | | Right | M1 or 2 | |
| ARA-VP-1/333 | | Left | M1 or 2 | |
| ARA-VP-1/339 | | Left | M1 or 2 | |
| ARA-VP-1/359 | | Left | M | |
| ARA-VP-1/362 | | Left | m2 | |
| ARA-VP-1/390 | | Left | m3 | |
| ARA-VP-1/403 | | Right | M | |
| ARA-VP-1/404 | | Right | m1 or 2 | |
| ARA-VP-1/405 | | | M | Fragment |
| ARA-VP-1/406 | | Left | I1 | |
| ARA-VP-1/427 | ♂ | | Dentition | P, C, M, m, right m3 |
| ARA-VP-1/485 | | Left | I1 | |
| ARA-VP-1/486 | | Right | i1 | |
| ARA-VP-1/487 | | Left | i1 | |
| ARA-VP-1/489 | | Right | Mandible | dp4–erupt. m1 |
| ARA-VP-1/491 | | Right | m1 or 2 | |
| ARA-VP-1/492 | | Left | m3 | |
| ARA-VP-1/494 | | Right | dP4 | |
| ARA-VP-1/496 | | Right | m1 or 2 | |
| ARA-VP-1/499 | | Left | M3 | |
| ARA-VP-1/505 | | Right | M1 or 2 | |
| ARA-VP-1/545 | | Left | m1 or 2 | |
| ARA-VP-1/548 | | Right | Mandible | dp4–m1 |
| ARA-VP-1/563 | ♀ | | Mandible | Right i1–left m2, right p3 |
| ARA-VP-1/695 | | Right | I1 | |
| ARA-VP-1/740 | | | Mandible | Left dc–m1; right dp3–m1; left i1–2 roots |
| ARA-VP-1/743 | | Right | Mandible | i2?, dc–m1 |
| ARA-VP-1/744 | ♂ | | Cranial | Fragments, left i1–c; right i2, m3 |
| ARA-VP-1/791 | | Right | M | Fragment |
| ARA-VP-1/820 | | Right | I1 | |
| ARA-VP-1/831 | | Left | m3 | Fragment |
| ARA-VP-1/852 | | Right | M3 | |
| ARA-VP-1/884 | | Right | M | |
| ARA-VP-1/885 | | Right | dP4 | |
| ARA-VP-1/890 | | Left | I1 | |
| ARA-VP-1/893 | | Right | p4 | |
| ARA-VP-1/936 | | Left | Maxilla | M1 |
| ARA-VP-1/938 | | Left | Maxilla | I2 |
| ARA-VP-1/944 | | Left | M1 or 2 | |
| ARA-VP-1/948 | | Left | m1 or 2 | |
| ARA-VP-1/949 | | Left | I2 | |
| ARA-VP-1/953 | ♀ | Left | p3 | |
| ARA-VP-1/953 | ♀ | Left | m1 | |
| ARA-VP-1/953 | ♀ | Left | m2 | |
| ARA-VP-1/953 | ♀ | Left | m3 | |
| ARA-VP-1/1006 | ♀ | | Mandible | Left i2–m3; right p3–m3 |
| ARA-VP-1/1007 | | Left | Maxilla | I2–M1 |
| ARA-VP-1/1008 | | Right | i1 | |
| ARA-VP-1/1008 | | | Indet. | Fragment |
| ARA-VP-1/1097 | | Right | m1 or 2 | |

APPENDIX 1—(Continued)

| Catalog No. | Sex | Side | Element | Comments |
|---|---|---|---|---|
| ARA-VP-1/1132 | | Left | I1 | |
| ARA-VP-1/1236 | | Right | I2 | |
| ARA-VP-1/1237 | | Left | I1 | |
| ARA-VP-1/1262 | | Right | i1 | |
| ARA-VP-1/1266 | | Left | m1 or 2 | |
| ARA-VP-1/1347 | | Right | M | |
| ARA-VP-1/1377 | | Left | m3 | |
| ARA-VP-1/1408 | | Right | p4 | |
| ARA-VP-1/1483 | | Left | I | Fragment |
| ARA-VP-1/1539 | | Right | I2 | |
| ARA-VP-1/1542 | | Right | I2 | |
| ARA-VP-1/1553 | | Right | m1 or 2 | |
| ARA-VP-1/1554 | | Right | m2 | |
| ARA-VP-1/1555 | | Left | m2 | |
| ARA-VP-1/1556 | | Right | m1 or 2 | |
| ARA-VP-1/1558 | | Right | m1 | |
| ARA-VP-1/1559 | | Right | m1 or 2 | |
| ARA-VP-1/1560 | | Right | m1 or 2 | |
| ARA-VP-1/1568 | | | M or m | Fragment |
| ARA-VP-1/1569 | | Right | m3 | |
| ARA-VP-1/1571 | | Right | m3 | |
| ARA-VP-1/1573 | | Left | m3 | |
| ARA-VP-1/1574 | | Left | m3 | |
| ARA-VP-1/1575 | | Left | m3 | |
| ARA-VP-1/1596 | | Right | I1 | |
| ARA-VP-1/1615 | | Left | m3 | |
| ARA-VP-1/1639 | | Right | i1 | |
| ARA-VP-1/1662 | | Left | dp4 | |
| ARA-VP-1/1675 | | | M or m | |
| ARA-VP-1/1723 | ♀ | Right | Maxilla | C–M3 |
| ARA-VP-1/1917 | | Left | m1 or 2 | |
| ARA-VP-1/1922 | | Left | I1 | |
| ARA-VP-1/1948 | | Left | m3 | |
| ARA-VP-1/1951 | | Right | m1 or 2 | |
| ARA-VP-1/1954 | | Left | I2 | |
| ARA-VP-1/1983 | | Left | dP4 | |
| ARA-VP-1/2045 | | Right | M | |
| ARA-VP-1/2057 | | Left | M | |

| Catalog No. | Sex | Side | Element | Comments |
|---|---|---|---|---|
| ARA-VP-1/2059 | | Left | m1 or 2 | Fragment |
| ARA-VP-1/2061 | ♂ | Left | p3 | |
| ARA-VP-1/2075 | | Right | I1 | |
| ARA-VP-1/2076 | | Right | I1 | |
| ARA-VP-1/2078 | | Right | M | |
| ARA-VP-1/2079 | | Left | M3 | |
| ARA-VP-1/2080 | | Left | p4 | |
| ARA-VP-1/2082 | | Left | m1 | Fragment |
| ARA-VP-1/2085 | | Left | m3 | |
| ARA-VP-1/2086 | | Left | m1 or 2 | |
| ARA-VP-1/2090 | | Left | m1 or 2 | |
| ARA-VP-1/2098 | ♂ | Left | i2 | |
| ARA-VP-1/2098 | ♂ | Left | c | |
| ARA-VP-1/2098 | ♂ | Left | P3 | |
| ARA-VP-1/2098 | ♂ | Left | P4 | |
| ARA-VP-1/2099 | | Left | M | Fragment |
| ARA-VP-1/2168 | ♀ | Right | i2 | |
| ARA-VP-1/2353 | ♀ | Right | i1 | |
| ARA-VP-1/2353 | ♀ | Right | i2 | |
| ARA-VP-1/2353 | ♀ | Right | c | |
| ARA-VP-1/2353 | ♀ | Right | P3 | |
| ARA-VP-1/2353 | ♀ | Right | p4 | |
| ARA-VP-1/2353 | ♀ | Right | m1 | |
| ARA-VP-1/2354 | ♀ | Left | I2 | |
| ARA-VP-1/2354 | ♀ | Left | C | |
| ARA-VP-1/2354 | ♀ | Left | P3 | |
| ARA-VP-1/2354 | ♀ | Left | M3 | |
| ARA-VP-1/2354 | ♀ | Right | I1 | |
| ARA-VP-1/2354 | ♀ | Right | M1 or 2 | |
| ARA-VP-1/2431 | | Left | p4 | |
| ARA-VP-1/2441 | | Right | M | M2 or 3 |
| ARA-VP-1/2470 | ♂? | Left | I1 | Crown, root forming |
| ARA-VP-1/2470 | ♂? | Left | dI2 | |
| ARA-VP-1/2470 | ♂? | Left | dC | |
| ARA-VP-1/2470 | ♂? | Left | dP3 | |
| ARA-VP-1/2470 | ♂? | Left | dP4 | |
| ARA-VP-1/2470 | ♂? | Left | C | Tip, crown still forming |
| ARA-VP-1/2470 | ♂? | Left | P4 | Crown still forming |

APPENDIX 1—(*Continued*)

| Catalog No. | Sex | Side | Element | Comments |
|---|---|---|---|---|
| ARA-VP-1/2470 | ♂? | Right | I1 | |
| ARA-VP-1/2470 | ♂? | Right | dC | Crown |
| ARA-VP-1/2470 | ♂? | Right | M1 | |
| ARA-VP-1/2494 | | Right | m1 or 2 | |
| ARA-VP-6/8 | | Right | Mandible | m2–3 |
| ARA-VP-6/9 | | Right | M3 | |
| ARA-VP-6/52 | | Right | I1 | |
| ARA-VP-6/52 | | Left | I1 | |
| ARA-VP-6/57 | | Left | M1 or 2 | |
| ARA-VP-6/61 | | Right | m | |
| ARA-VP-6/62 | | Left | m1 or 2 | |
| ARA-VP-6/63 | | Right | M | |
| ARA-VP-6/83 | | Left | M | |
| ARA-VP-6/95 | | Right | m3 | Fragment |
| ARA-VP-6/96 | | Right | I1 | |
| ARA-VP-6/437 | ♂ | Right | Maxilla | C–P4 roots, I1, P3 |
| ARA-VP-6/576 | | Left | m1 or 2 | In tiny mandible fragment |
| ARA-VP-6/577 | | Left | M | |
| ARA-VP-6/586 | | Right | m3 | |
| ARA-VP-6/597 | | Left | i1 | |
| ARA-VP-6/599 | | Left | m3 | |
| ARA-VP-6/600 | | Right | m3 | |
| ARA-VP-6/602 | | Right | m1 or 2 | |
| ARA-VP-6/623 | | Left | p4 | |
| ARA-VP-6/625 | | Left | p4 | |
| ARA-VP-6/627 | | Left | p4 | |
| ARA-VP-6/628 | | Left | M2 | |
| ARA-VP-6/629 | | Right | M2 | |
| ARA-VP-6/632 | | Right | M1 | |
| ARA-VP-6/643 | | Left | dP4 | |
| ARA-VP-6/647 | | Left | dp4 | |
| ARA-VP-6/656 | | Right | I2 | |
| ARA-VP-6/659 | | Right | m3 | |
| ARA-VP-6/771 | | Right | m | |
| ARA-VP-6/797 | | | Mandible | m1 erupting, juvenile |
| ARA-VP-6/799 | | Right | m3 | |
| ARA-VP-6/809 | | Left | i1 | |
| ARA-VP-6/810 | | Left | i2 | |
| ARA-VP-6/933 | | | Skull | |
| ARA-VP-6/1277 | | Right | I2 | |
| ARA-VP-6/1281 | | Right | m1 or 2 | |
| ARA-VP-6/1283 | | Right | dp4 or m1 | |
| ARA-VP-6/1284 | | | M | Fragment |
| ARA-VP-6/1289 | | Right | M1 or 2 | |
| ARA-VP-6/1292 | | Right | I1 | |
| ARA-VP-6/1296 | | Right | M1 or 2 | |
| ARA-VP-6/1307 | | Left | i2 | |
| ARA-VP-6/1562 | | Right | M1 or 2 | |
| ARA-VP-17/004 | ♀ | | Mandible | Roots left p3–right P3 |
| KUS-VP-2/085 | | Right | M1 or 2 | |
| KUS-VP-2/092 | | Left | i1 | |
| KUS-VP-2/098 | | Right | m3 | |
| KUS-VP-2/104 | | Right | I2 | |
| KUS-VP-2/115 | | Right | i1 | |
| KUS-VP-2/118 | | Left | I1 | |
| KUS-VP-2/118 | | Left | I | Fragment |
| KUS-VP-2/139 | | Left | M | M2 or 3 |
| KUS-VP-2/142 | | Right | m1 or 2 | |
| SAG-VP-7/103 | | Left | m3 | |
| SAG-VP-7/106 | | Left | m3 | |
| SAG-VP-7/133 | | Right | M | M2 or 3 |
| SAG-VP-7/155 | | Left | M1 or 2 | |

APPENDIX 2
**List of All Specimens Assigned to *K. aramisi***
Fields are as described for Appendix 1.

| Catalog No. | Sex | Side | Element | Comments |
|---|---|---|---|---|
| ARA-VP 1/5 | ♂ | | Mandible | Symphysis, left i1–m1; right i1, p3–m1 |
| ARA-VP 1/6 | ♂ | Left | Maxilla | C–M3 |
| ARA-VP 1/7 | | Left | Mandible | m2–3 |
| ARA-VP 1/10 | | Left | m3 | |
| ARA-VP 1/11 | | Left | m3 | |
| ARA-VP 1/13 | | Left | Frontal | Glabella with small bit of nasals |
| ARA-VP 1/14 | | Left | m1 or 2 | |
| ARA-VP 1/15 | | Left | m1 or 2 | |
| ARA-VP 1/16 | | Left | dp4 | |
| ARA-VP 1/17 | | Left | M or m | Fragment |
| ARA-VP 1/18 | | Right | M3 | |
| ARA-VP 1/21 | | Right | M | |
| ARA-VP 1/22 | | Right | M | |
| ARA-VP 1/46 | | Right | m1 or 2 | Fragment |
| ARA-VP 1/48 | | Left | dp4 | |
| ARA-VP 1/49 | | Left | M1 or 2 | |
| ARA-VP 1/50 | | Right | M1 or 2 | |
| ARA-VP 1/70 | | Left | Mandible | m2–3 |
| ARA-VP 1/87 | ♂ | Left | Mandible | Left p3–4, m2–3; right p3–m3 |
| ARA-VP 1/87 | ♂ | Left | Maxilla | M1–3 |
| ARA-VP 1/87 | ♂ | Left | c | |
| ARA-VP 1/87 | ♂ | Right | C | |
| ARA-VP 1/87 | ♂ | Left | C | |
| ARA-VP 1/116 | | Right | m3 | |
| ARA-VP 1/121 | | Left | M | |
| ARA-VP 1/130 | | Right | m3 | |
| ARA-VP 1/134 | | Left | M3 | |
| ARA-VP 1/169 | | Left | p4 | |
| ARA-VP 1/170 | | Right | m3 | |
| ARA-VP 1/177 | | Left | Maxilla | dP4–M1 |
| ARA-VP 1/178 | | Right | Maxilla | dP4–M1 |
| ARA-VP 1/179 | | Right | M | |
| ARA-VP 1/180 | | Left | p4 | |
| ARA-VP 1/186 | | Right | M3 | |
| ARA-VP 1/189 | | Left | m | Fragment |
| ARA-VP 1/192 | | Right | dP or M | Fragment |
| ARA-VP 1/196 | | Right | i2 | |
| ARA-VP 1/197 | | Left | Maxilla | Damaged, P3, M1–3 |
| ARA-VP 1/197 | | Right | Cranial | Fragment, right P4 |
| ARA-VP 1/197 | | | Temporal | Ectotympanic and mastoid |
| ARA-VP 1/198 | | Left | Mandible | m1–3 |
| ARA-VP 1/205 | | Right | M | |
| ARA-VP 1/238 | | Left | m3 | |
| ARA-VP 1/286 | | Right | m1 or 2 | |
| ARA-VP 1/290 | | Right | Mandible | Left i1–2, p4–m1, left + right p3 erupting |
| ARA-VP 1/306 | ♂ | Left | p3 | |
| ARA-VP 1/306 | ♂ | Left | m1 | |
| ARA-VP 1/306 | ♂ | Left | m3 | |
| ARA-VP 1/306 | ♂ | Right | c | |
| ARA-VP 1/306 | ♂ | Right | p3 | |
| ARA-VP 1/306 | ♂ | Right | m2 | |
| ARA-VP 1/306 | ♂ | Right | m3 | |
| ARA-VP 1/308 | | Right | m3 | |
| ARA-VP 1/324 | | Right | m1 or 2 | |
| ARA-VP 1/329 | | Left | m3 | |
| ARA-VP 1/331 | | Left | m3 | |
| ARA-VP 1/336 | | Left | p4 | |
| ARA-VP 1/337 | | Left | m3 | |
| ARA-VP 1/338 | | Right | m1 or 2 | |
| ARA-VP 1/351 | | Right | m3 | |
| ARA-VP 1/379 | | Left | M1 or 2 | |
| ARA-VP 1/383 | ♂ | Right | Mandible | p3–m1 |
| ARA-VP 1/389 | | Right | Maxilla | P3–4 |
| ARA-VP 1/483 | | Right | I1 | |
| ARA-VP 1/484 | | Left | I1 | |
| ARA-VP 1/490 | | Right | I1 | |
| ARA-VP 1/497 | | Right | M1 or 2 | |
| ARA-VP 1/549 | | Left | m1 or 2 | |
| ARA-VP 1/550 | | Left | m3 | |
| ARA-VP 1/551 | | Right | M | |
| ARA-VP 1/559 | | Right | Mandible | m3 |
| ARA-VP 1/564 | | Right | Mandible | m1–3 |

APPENDIX 2—(Continued)

| Catalog No. | Sex | Side | Element | Comments |
|---|---|---|---|---|
| ARA-VP 1/566 | | Left | Mandible | p4–m2 |
| ARA-VP 1/694 | | Left | M1 or 2 | |
| ARA-VP 1/742 | | Right | M | |
| ARA-VP 1/747 | | Right | m | Fragment |
| ARA-VP 1/748 | | Right | m1 or 2 | Fragment |
| ARA-VP 1/785 | | Right | Mandible | m1–3 |
| ARA-VP 1/788 | | Right | Maxilla | Fragment, M3 |
| ARA-VP 1/790 | | Right | m1 or 2 | Fragment |
| ARA-VP 1/793 | | Left | M3 | |
| ARA-VP 1/794 | | Left | M | |
| ARA-VP 1/795 | | Left | I1 | |
| ARA-VP 1/795 | | Left | I2 | |
| ARA-VP 1/850 | | Right | M1 or 2 | |
| ARA-VP 1/853 | | Left | i2 | |
| ARA-VP 1/872 | | Right | I1 | |
| ARA-VP 1/879 | | Left | m1 or 2 | |
| ARA-VP 1/887 | | Left | m1 or 2 | |
| ARA-VP 1/889 | | Left | M | |
| ARA-VP 1/892 | | Right | M | |
| ARA-VP 1/894 | | Right | p4 | |
| ARA-VP 1/896 | | Right | M | |
| ARA-VP 1/900 | | Right | Maxilla | M1–2 |
| ARA-VP 1/939 | | Left | m1 or 2 | Fragment |
| ARA-VP 1/943 | | Right | M3 | |
| ARA-VP 1/950 | | Right | m1 or 2 | |
| ARA-VP 1/1168 | | Right | I1 | Fragment |
| ARA-VP 1/1168 | | Right | i2 | Fragment |
| ARA-VP 1/1238 | | Left | M | |
| ARA-VP 1/1241 | | Left | dp4 | |
| ARA-VP 1/1255 | | Right | M | |
| ARA-VP 1/1256 | | Left | M | |
| ARA-VP 1/1258 | | Right | M | |
| ARA-VP 1/1259 | | Right | i1 | |
| ARA-VP 1/1267 | | Right | m1 or 2 | |
| ARA-VP 1/1268 | | Right | dp4 | Fragment |
| ARA-VP 1/1271 | | Right | dp4 | |
| ARA-VP 1/1483 | | Left | I2 | Fragment |
| ARA-VP 1/1483 | | Left | i2 | Fragment |
| ARA-VP 1/1537 | | Right | I1 | |
| ARA-VP 1/1540 | | Left | i2 | |
| ARA-VP 1/1546 | | Right | p4 | |
| ARA-VP 1/1548 | | Right | M | |
| ARA-VP 1/1549 | | Right | m1 or 2 | |
| ARA-VP 1/1550 | | Left | m1 or 2 | |
| ARA-VP 1/1551 | | Left | m1 or 2 | |
| ARA-VP 1/1557 | | Right | m1 or 2 | |
| ARA-VP 1/1561 | | | M or m | Fragment |
| ARA-VP 1/1562 | | Left | M | |
| ARA-VP 1/1563 | | Right | M | |
| ARA-VP 1/1565 | | Right | M1 or 2 | |
| ARA-VP 1/1566 | | Left | M | |
| ARA-VP 1/1570 | | Right | m3 | Fragment |
| ARA-VP 1/1572 | | Left | m3 | |
| ARA-VP 1/1592 | | Left | I1 | |
| ARA-VP 1/1593 | | Left | P3 | |
| ARA-VP 1/1601 | | Left | m1 or 2 | |
| ARA-VP 1/1661 | | Right | I1 | |
| ARA-VP 1/1713 | | Right | m1 or 2 | Fragment |
| ARA-VP 1/1715 | | Left | m3 | |
| ARA-VP 1/1720 | | Left | m1 or 2 | |
| ARA-VP 1/1721 | | Left | p4 | |
| ARA-VP 1/1774 | | Right | Mandible | m1–3 |
| ARA-VP 1/1781 | | Left | M | Fragment |
| ARA-VP 1/1783 | | Left | M | |
| ARA-VP 1/1807 | | Left | m2 | |
| ARA-VP 1/1808 | ♂ | Left | p4 | |
| ARA-VP 1/1809 | | Right | m1 or 2 | |
| ARA-VP 1/1840 | ♀ | Right | Mandible | i2–p4 |
| ARA-VP 1/1841 | | Right | I1 | |
| ARA-VP 1/1863 | | Right | I1 | |
| ARA-VP 1/1867 | | Left | M1 or 2 | |
| ARA-VP 1/1869 | | Right | m3 | |
| ARA-VP 1/1888 | | Left | M3 | |
| ARA-VP 1/1891 | | Left | I2 | |
| ARA-VP 1/1918 | | Right | M | M2 or 3 |
| ARA-VP 1/1919 | | Left | M | |

APPENDIX 2—(Continued)

| Catalog No. | Sex | Side | Element | Comments |
|---|---|---|---|---|
| ARA-VP 1/1924 | | Left | i1 | |
| ARA-VP 1/1950 | | Left | I2 | |
| ARA-VP 1/1984 | | Left | M | |
| ARA-VP 1/1986 | | Right | M1 or 2 | |
| ARA-VP 1/2046 | | Right | m1 or 2 | |
| ARA-VP 1/2047 | | Right | I2 | |
| ARA-VP 1/2060 | | Left | P3 | |
| ARA-VP 1/2064 | | Left | m1 or 2 | |
| ARA-VP 1/2065 | | Right | I2 | |
| ARA-VP 1/2068 | | Left | M | |
| ARA-VP 1/2069 | | Right | m1 or 2 | |
| ARA-VP 1/2070 | | Left | dP4 | |
| ARA-VP 1/2072 | | Left | M3 | |
| ARA-VP 1/2073 | | Right | m1 or 2 | |
| ARA-VP 1/2074 | | Left | m1 or 2 | |
| ARA-VP 1/2083 | | Right | M | |
| ARA-VP 1/2087 | | Left | m1 | |
| ARA-VP 1/2091 | | Right | m3 | |
| ARA-VP 1/2095 | | Left | P3 | |
| ARA-VP 1/2159 | | Left | m3 | |
| ARA-VP 1/2164 | | Right | M3 | Fragment |
| ARA-VP 1/2167 | | Right | I1 | |
| ARA-VP 1/2175 | | Right | Maxilla | dP4–M1 |
| ARA-VP 1/2440 | | Left | I1 | |
| ARA-VP 1/2451 | | Right | P4 | |
| ARA-VP 1/2451 | | Right | M1 | |
| ARA-VP 1/2451 | | Right | M2 | |
| ARA-VP 1/2451 | | Right | M3 | |
| ARA-VP 1/2473 | | Left | p4 | |
| ARA-VP 6/25 | | Right | I1 | |
| ARA-VP 6/56 | | Right | m1 or 2 | |
| ARA-VP 6/60 | | Left | m1 or 2 | |
| ARA-VP 6/87 | | Right | m3 | |
| ARA-VP 6/88 | | Left | I1 | |
| ARA-VP 6/97 | | Left | i2 | |
| ARA-VP 6/286 | | Right | m1 or 2 | |
| ARA-VP 6/570 | | Right | Mandible | m3 |
| ARA-VP 6/575 | | Left | M1 or 2 | In tiny maxillary fragment |
| ARA-VP 6/578 | | Right | m1 or 2 | In tiny maxillary fragment |
| ARA-VP 6/579 | | Left | M1 or 2 | |
| ARA-VP 6/580 | | Right | M1 or 2 | |
| ARA-VP 6/583 | | Right | m3 | |
| ARA-VP 6/584 | | Left | m3 | |
| ARA-VP 6/585 | | Right | m3 | Fragment |
| ARA-VP 6/593 | | Right | m | |
| ARA-VP 6/595 | | Left | I1 | |
| ARA-VP 6/598 | | Right | I1 | |
| ARA-VP 6/605 | | Right | m1 or 2 | |
| ARA-VP 6/606 | | Right | m | |
| ARA-VP 6/607 | | Left | m | |
| ARA-VP 6/608 | | Left | m1 or 2 | |
| ARA-VP 6/610 | | Left | m3 | Fragment |
| ARA-VP 6/626 | | Left | p4 | |
| ARA-VP 6/630 | | Left | M1 or 2 | |
| ARA-VP 6/635 | | Left | dP4 | |
| ARA-VP 6/637 | | Right | M1 or 2 | |
| ARA-VP 6/639 | | Right | M | Fragment |
| ARA-VP 6/640 | | Left | dp4 | |
| ARA-VP 6/641 | | Left | m1 or 2 | |
| ARA-VP 6/644 | | Left | dp or m | |
| ARA-VP 6/650 | | Left | dp | Fragment |
| ARA-VP 6/654 | ♀ | Left | Mandible | p3–4 |
| ARA-VP 6/796 | ♀ | Left | Mandible | Symphysis, left i1–m1, right i1–p2 |
| ARA-VP 6/798 | | Left | m1 or 2 | |
| ARA-VP 6/800 | | Left | I2 | |
| ARA-VP 6/931 | | Right | M1 or 2 | |
| ARA-VP 6/1282 | | Right | dp | Fragment |
| ARA-VP 6/1285 | | Right | i2 | |
| ARA-VP 6/1287 | | Left | i1 | |
| ARA-VP 6/1294 | | Right | m3 | |
| ARA-VP 6/1295 | | Right | m1 or 2 | |
| ARA-VP 6/1619 | | Left | m1 or 2 | |
| ARA-VP 6/1620 | | Right | m1 or 2 | |
| ARA-VP 6/1686 | | Right | Face | Inferior part, left I1–M3, right I1, C–M3 |

APPENDIX 2—(Continued)

| Catalog No. | Sex | Side | Element | Comments |
|---|---|---|---|---|
| ARA-VP 17/3 | | Right | Mandible | m1 |
| ARA-VP 17/5 | | Left | i2 | |
| KUS-VP 2/2 | ♂ | Right | c | |
| KUS-VP 2/2 | ♂ | Right | p3 | |
| KUS-VP 2/2 | ♂ | Right | p4 | |
| KUS-VP 2/2 | ♂ | Right | m1 | |
| KUS-VP 2/2 | ♂ | Left | c | |
| KUS-VP 2/2 | ♂ | Left | p3 | |
| KUS-VP 2/5 | | Right | p4 | |
| KUS-VP 2/5 | | Right | m1 | |
| KUS-VP 2/5 | | Right | m2 | |
| KUS-VP 2/5 | | Left | m2 | |
| KUS-VP 2/20 | | Right | m3 | |
| KUS-VP 2/70 | ♀ | Left | Maxilla | C–M1 |
| KUS-VP 2/70 | ♀ | Right | Maxilla | M1–2 |
| KUS-VP 2/70 | ♀ | Left | I1 | |
| KUS-VP 2/70 | ♀ | | Frontal | Glabella |
| KUS-VP 2/89 | | Left | m1 or 2 | |
| KUS-VP 2/90 | | Left | I2 | |

| Catalog No. | Sex | Side | Element | Comments |
|---|---|---|---|---|
| KUS-VP 2/91 | | Right | dp4 | |
| KUS-VP 2/93 | | Left | M | |
| KUS-VP 2/94 | | Left | M3 | |
| KUS-VP 2/96 | | Right | M1 or 2 | |
| KUS-VP 2/97 | | Right | m1 or 2 | |
| KUS-VP 2/116 | | Left | i2 | |
| KUS-VP 2/118 | | Left | p4 | Fragment |
| KUS-VP 2/118 | | Left | m1 or 2 | Fragment |
| KUS-VP 2/140 | | Left | i2 | |
| KUS-VP 2/145 | | Right | I2 | |
| KUS-VP 2/146 | | Right | P3 | |
| SAG-VP 7/1 | ♂ | Left | I2 | |
| SAG-VP 7/1 | ♂ | Left | C | |
| SAG-VP 7/1 | ♂ | Right | I2 | |
| SAG-VP 7/1 | ♂ | Right | C | |
| SAG-VP 7/1 | ♂ | | M | |
| SAG-VP 7/57 | | Left | I2 | |
| SAG-VP 7/101 | | Right | m1 or 2 | |
| SAG-VP 7/107 | | Left | M | |