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### 4.3 Fossil Cercopithecidae from the Laetoli Beds

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#### INTRODUCTION

Most of the fossil Cercopithecidae from the Laetoli Beds are from two important collections. The first was recovered between 1934 and 1939 by the Kohl-Larsen expeditions and is presently housed in the Paläontologisches Museum der Humboldt-Universität, Berlin, German Democratic Republic. The second (which is the larger) was collected by Dr Mary Leakey and associates between 1974 and 1979 and is temporarily housed in the National Museum of Kenya, Nairobi. In addition, some specimens collected by Dr L. S. B. Leakey in the 1930s are housed in the British Museum (Natural History), London, and eight rather fragmentary specimens collected in 1959 and 1964 by Drs Louis and Mary Leakey are also housed in Nairobi.

The majority of the specimens reported here was carefully collected in the 1970s from localities in the Laetoli Beds, by expeditions led by Dr Mary Leakey. These localities have been dated between 3.46 and 3.76 Ma. (Drake and Curtis, this volume). At least four specimens from this collection derive from the overlying Ndolanya Beds of uncertain but younger age. The specimens recovered in the 1930s come from unknown localities in the Laetoli region of the Serengeti, but are treated together with the more precisely documented fossils which they match closely. The majority of the specimens in each collection is cranial and consists mainly of fragments of maxilla and mandible and isolated teeth. Some postcranial elements are included in the latest collection.

A fossil monkey from Laetoli was first reported by Hopwood (1936) on the basis of material collected by Dr L. S. B. Leakey in 1935. A partial female mandible was made the holotype of *Cercocebus ado* and distinguished from other species of this extant genus by its greater size, taller and more slender molar cusps and stronger M<sub>3</sub> talonid. 'Ado' means tall or big in the Masai language. Shortly afterwards, Reek and Kohl-Larsen (1936) reported on the latter's 1934-36

expedition to the Serengeti and included both *Cercocebus* sp. (Hopwood's species?) and *Papio* sp. ('cf. *Simopithecus oswaldi* Andrews, 1916') in their provisional faunal list.

The first detailed report of Kohl-Larsen's material appeared in Dietrich's (1942) analysis of the fauna and geology which also included specimens collected in 1938-39. Dietrich recognized a medium-sized papionin which he named *Papio* (*Simopithecus*) *serengetensis*. He distinguished this species from the living *Papio* 'neumanni' (= *P. hamadryas anubis*) by its smaller size and lack of a fossa on the lateral face of the mandible. Dietrich (1942, p. 53) also reported small isolated teeth of a 'short-snouted' (kurzschnauzigen) monkey in the Kohl-Larsen collection, which may represent the colobine recognized by Delson (1975) after he examined the collection in 1970. Delson recognized only one cercopithecine, ?*Parapapio ado* (Delson 1978; Szalay and Delson 1979), which had a large dental size-range. In 1976, M. G. and R. E. F. Leakey assigned the five best dental specimens collected in 1959 and 1964 to *Cercocebus ado*. The recovery by M. D. Leakey and associates of numerous additional monkey fossils, including jaws, teeth and postcranial elements, in the 1970s provided the opportunity for M. G. Leakey to clarify the taxonomic status of the Laetoli cercopithecids. This information is presented here in a joint report with E. Delson who had independently studied the Kohl-Larsen collection.

After much deliberation it was decided that, in the combined Kohl-Larsen/Leakey sample of 135 specimens, four species are present. The majority of the specimens are assigned to two taxa, *Parapapio ado* and cf. *Paracolobus* sp. while two other rarer taxa are also represented. Four isolated teeth (and perhaps a partial femur) appear to be sufficiently smaller than those assigned to cf. *Paracolobus* sp. to merit recognition as a separate, but currently indeterminate, colobine taxon. A large papionin, cf. *Papio* sp., is represented by a distal humerus and a dP<sup>4</sup>; these specimens may have

affinities with *Papio* (*Dinopithecus*) *ingens*, a large fossil papionin known from localities in South Africa. Sixteen specimens are too fragmentary to identify either to species or to genus.

Specimens with the prefix MB are housed in the Museum für Paläontologie, Humboldt Universität, Berlin, those with the prefix BM(NH) are in the British Museum (Natural History), London, and the remaining specimens are temporarily housed in the National Museum of Kenya, Nairobi. Measurements reported here were taken using Helios dial calipers with needle points, following the definitions given by Delson (1973), Freedman (1957) and others. All cheek teeth were scored for wear according to the system described by Delson (1973), but no subdivisions of measurements by wear classes is provided here. Measurement data were statistically summarized and plots and *t*-tests were produced using the Statistical Analysis System package on the central computer system of the City University of New York. Student's *t*-tests were run on the samples of *Parapapio ado* to compare specimens in the earlier collections from unknown localities with those in the later Mary Leakey collection from known localities. Since there were no cases of inconsistency we felt it was reasonable to run the statistical analysis on the larger combined samples rather than only on samples from the later collection. In Tables 4.4-4.11, L=length, B=anterior width, and B/L=anterior width divided by length.

## SYSTEMATIC DESCRIPTION

Order PRIMATES Linnaeus, 1758  
 Infraorder CATARRHINI E. Geoffroy, 1812  
 Family CERCOPITHECIDAE Gray, 1821  
 Subfamily CERCOPITHECINAE Gray, 1821  
 Tribe PAPIONINI Burnett, 1828

### Genus *Parapapio* Jones, 1937

*Diagnosis.* A medium to large fossil papionin known only from South and East Africa. Distinguished by the lateral profile of the muzzle dorsum which forms a straight line or a smooth, slightly concave curve from nasion to rhinion or beyond to nasospinale. The supraorbital tori are usually weakly developed and do not project forward in either sex, ophryonic groove absent. There are no strong maxillary ridges or deep maxillary fossae, although in the larger individuals there is some hollowing. Fossae on the lateral mandibular faces are weakly excavated or absent. Morphologically the cheek-teeth are indistinguishable from *Papio* (after Freedman, 1957).

*Type species.* *P. broomi* Jones, 1937

### *Parapapio ado* (Hopwood, 1936)

- 1936 *Cercocebus ado* Hopwood: 638  
 1936 *Papio* sp.; Reck and Kohl-Larsen: 421  
 1942 *Papio* (*Simopithecus*) *serengetensis* Dietrich: 52, figs. 1-4  
 1976 *Cercocebus ado*; M. G. and R. E. F. Leakey: 131  
 1978 ?*Parapapio ado*; Delson: 389  
 1979 ?*Parapapio ado*; Szalay and Delson: 343

*Holotype.* BM(NH) M14940, right half female mandibular body, weathered but undistorted, with alveoli for I<sub>1</sub>-C̄, partial crowns P<sub>3</sub>-M<sub>3</sub>. The specimen was collected by L. S. B. Leakey in 1935 in the Vogel River (Laetolil) Beds (approximately 35°10'E, 3°10'S).

### Material

- (a) Early collections, locality uncertain;  
 MB 1938.1, female mandible, lacking rami and base below M<sub>2</sub>s. Lt. I<sub>1</sub>-M<sub>3</sub> and rt. M<sub>1-3</sub>.  
 MB 1938.2, rt. male mand. frag. P<sub>4</sub>, M<sub>2-3</sub>, broken M<sub>1</sub>, base C̄-P<sub>3</sub>.  
 MB 1939.16.1, lt. juvenile mand. dP<sub>3</sub>-M<sub>1</sub>.  
 MB 1939.16.2, male mand. frag., crushed symphysis, damaged lt. P<sub>4</sub>-M<sub>2</sub>, rt. I<sub>2</sub>-P<sub>3</sub>, roots rt. I<sub>1</sub>, lt. I<sub>1</sub>, C̄, P<sub>3</sub>.  
 MB 1939.16.3, rt. mand. frag., rt. M<sub>2-3</sub>.  
 MB 1939.16.7, lt. M<sub>1-3</sub>.  
 MB 1939.16.8, rt. M<sub>1</sub> or 2.  
 MB 1939.16.11, rt. max. frag., P<sup>4</sup>-M<sup>1</sup>.  
 MB 1939.16.13, rt. M<sup>22</sup>.  
 MB 1939.16.14, rt. M<sup>23</sup>.  
 MB 1939.16.15, mand. frag., P<sub>4</sub>-M<sub>2</sub>.  
 MB 1939.16.16, male mand. frag., damaged M<sub>1-2</sub>.  
 MB 1939.16.18, lt. mand. frag., M<sub>2</sub>, base P<sub>4</sub>-M<sub>1</sub>.  
 MB 1939.16.22, lt. P<sub>4</sub>.  
 MB 1939.16.24, rt. M<sup>22</sup>.  
 LIT '59-197, female rt. mand. frag., P<sub>3-4</sub>, damaged M<sub>1</sub>.  
 LIT '59-363, lt. P<sub>4</sub>.  
 LIT '59-463, female lt. edentulous max., alveoli I<sup>1-2</sup>, roots C̄-P<sup>4</sup>.  
 LIT '59-464, lt. M<sup>22</sup>.  
 LAET '64, lt. mand. frag., M<sub>3</sub>.

### (b) Mary Leakey collection, localities known;

- Loc. 1* LAET 4667, lt. dP<sup>3</sup>.  
*Loc. 2* LAET 3904, lt. unworn P<sup>24</sup>, lt. cuboid, lt. capitae, lt. m/c I, prox. lt. m/c V, proximal phalanx, phalanx shaft.  
 LAET 5442, unworn lt. P<sub>4</sub>.  
 LAET 5469, male rt. max. frag. C̄ root, P<sup>3-4</sup>.  
*Loc. 3* LAET 2727, mand. frag., broken lt. I<sub>1</sub>, dC̄ root, dP<sub>3-4</sub>, rt. I<sub>1-2</sub> in crypt, roots dP<sub>3-4</sub>, isolated lt. M<sub>1</sub>.  
 LAET 3614, rt. male C̄.

- LAET 3829, mand. frag., damaged  $M_{1-3}$ .  
*Loc. 6* LAET 453, broken rt.  $M^2$  or  $M^3$ .  
 LAET 4602, rt.  $P^{23}$ .  
 LAET 5441, lt. mand. frag.,  $M_{2-3}$ .  
 LAET 5510, ? female mand. frag., rt.  $P_4$ - $M_1$ , roots  $P_3$  and  $M_2$ .  
*Loc. 7* LAET 315, lt. male  $\bar{C}$ .  
 LAET 316, lt. mand. frag.,  $d\bar{C}$ - $dP_4$  and root  $dI_2$ .  
 LAET 319, rt. female  $\bar{C}$ .  
 LAET 320, weathered lt.  $dP^3$ .  
 LAET 322, male max. frags., lt.  $\bar{C}$  root,  $P^4$ ,  $M^{2-3}$ , rt.  $P^{3-4}$ ,  $M^{2-3}$ , edentulous mand. symph., roots lt. and rt.  $I_1$  and  $\bar{C}$ , and rt.  $P_4$ .  
 LAET 812, mand. frags., lt.  $M_{1-2}$ , rt.  $M_2$ .  
 LAET 1390, lt. unerupted  $M_3$ .  
*Loc. 8* LAET 223, female mand. lacking rami, broken through symphysis, body cracked, both sides crushed together, lt.  $P_3$ - $M_3$ , rt.  $\bar{C}$  root,  $P_3$ - $M_2$ .  
 LAET 235, lt. female mand. frag.,  $P_{3-4}$ , broken  $\bar{C}$  and  $M_1$ .  
 LAET 242, lt.  $I_1$  (possibly same individual as 243/244).  
 LAET 243/244, female mand. lacking rami, broken through symphysis just right of midline, lt.  $P_3$ - $M_2$ , rt.  $\bar{C}$ - $M_3$  (almost erupted but base missing).  
 LAET 245, rt.  $I_2$  (found with LAET 242, 243, 244, but not associated).  
 LAET 5434, rt.  $M^{22}$ .  
 LAET 5439, rt.  $P^{24}$ .  
*Loc. 9* LAET 4568, rt. mand. frag.,  $M_3$ .  
*Loc. 9S* LAET 1489, weathered lt.  $M^{21}$  or  $dP^4$ , cranial and tooth frags.  
 LAET 3035, female mand. frag. rt.  $P_3$ - $M_3$ , alveoli  $I_1$ - $\bar{C}$ .  
*Loc. 10* LAET 483, rt. mand. frag.,  $M_{2-3}$ .  
 LAET 1209, subadult female lt. mand., lacking condyle,  $\bar{C}$ - $M_3$  ( $M_3$  roots open, not fully erupted).  
 LAET 2379, rt. max. frags., broken  $M^1$ ,  $M^2$  and  $M^3$ .  
 LAET 5269, male rt.  $\bar{C}$ , broken  $P^3$ ,  $M^2$ ,  $M^3$ .  
 LAET 5276, rt. or lt. heavily worn  $M^1$ .  
 LAET 5288, ? male mand. frag., rt.  $P_{3-4}$  erupting.  
 LAET 5307, rt. mand. frag.,  $dP_3$ , broken  $\bar{C}$ , root  $I_2$ .  
 LAET 5373, rt.  $P^4$ .  
 LAET 5374, rt.  $M^{22}$ .  
*Loc. 10E* LAET 2283, anterior portion rt. calcaneus.  
*Loc. 10W* LAET 419, rt.  $M^{23}$ .  
*Loc. 11* LAET 996, lt. mand. frag., damaged lt.  $M_{1-2}$ .  
 LAET 997, tooth frag. (may be associated with LAET 996).  
 LAET 998, rt. mand. frag.,  $dP_{3-4}$ , erupting  $\bar{C}$  and  $I_2$ .  
 LAET 2714, damaged lt.  $P^4$  and tooth frag.  
 LAET 3228, lt.  $dP_4$  (found with LAET 3229 but probably not associated).  
 LAET 3229, part rt.  $M^2$ .  
 LAET 4566, chipped lt.  $M_{21}$ .  
 LAET 4593, lt.  $M^{22}$ .  
 LAET 5465,  $M^{22}$ .  
*Loc. 21* LAET 3372c, rt.  $M^{22}$ .  
*Loc. 22* LAET 4911, complete proximal phalanx.
- (c) Mary Leakey collection, localities uncertain:  
 LAET 4592, rt.  $M^{23}$ .  
 LAET 4595, female rt. and lt. mand. and part symphysis, rt.  $P_3$ - $M_3$ , isolated lt.  $I_{1-22}$ ,  $P_3$ - $M_1$ , rt.  $I_{21-22}$ .
- Description.* *Parapapio ado* is a small to medium-sized papionin (Plate 4.1, Tables 4.4-7). The holotype is a relatively small female mandible with weathered teeth. The  $P_4$  is broken linguallally and occlusally, the  $M_2$  lacks its medial third and the buccal face of the  $M_3$  protoconid is chipped. The ramus is missing but the body is complete as far back as the middle of  $M_3$ . There is a large mental foramen under the  $P_4$ - $M_1$  contact area, but only a slight fossa on the lateral face of the body. Most of the teeth are worn, especially  $P_3$  and  $M_1$ .
- The best of Dietrich's specimens, MB 1938.1, is about the largest female and one of the largest mandibles in the whole sample. As Dietrich (1942) did not specifically fix a type of *P. serengetensis* we now designate MB 1938.1 as lectotype in accordance with his concept. The types of the two nominal species involved thus stand roughly at opposite ends of the variation range for females. Only three mandibular fragments which can certainly be said to be male are present. LAET 322, a complete symphysis; MB 1939.16.2, a partial symphysis and body; and MB 1938.2, a partial right body. Only two  $P_4$  and  $M_3$  and only one  $P_3$  and  $M_3$  are present among the associated teeth. These teeth are larger than those of large females. In view of this and given the large size variation in the female dentition it is to be expected that a similar size variation would occur among the males indicating that sexual dimorphism may have been evident in all teeth of this species and not only limited to the  $P_3$ s and canines. The complete male symphysis is significantly larger than any female symphysis in the collection.
- A few postcranial elements can be hesitantly referred to *P. ado*. LAET 3904 includes a number of hand bones and one foot bone associated with an isolated  $P_4$ . The  $P_4$  could perhaps be identified as colobine but it matches *P. ado* specimens in size. Among the associated hand bones, a left m/c I (9.0 mm wide, 23.5 mm long) is similar in proportion to *Papio cynocephalus* and confirms the cercopithecine

INSECTIVORA, GALAGINAE, AND CERCOPITHECIDAE

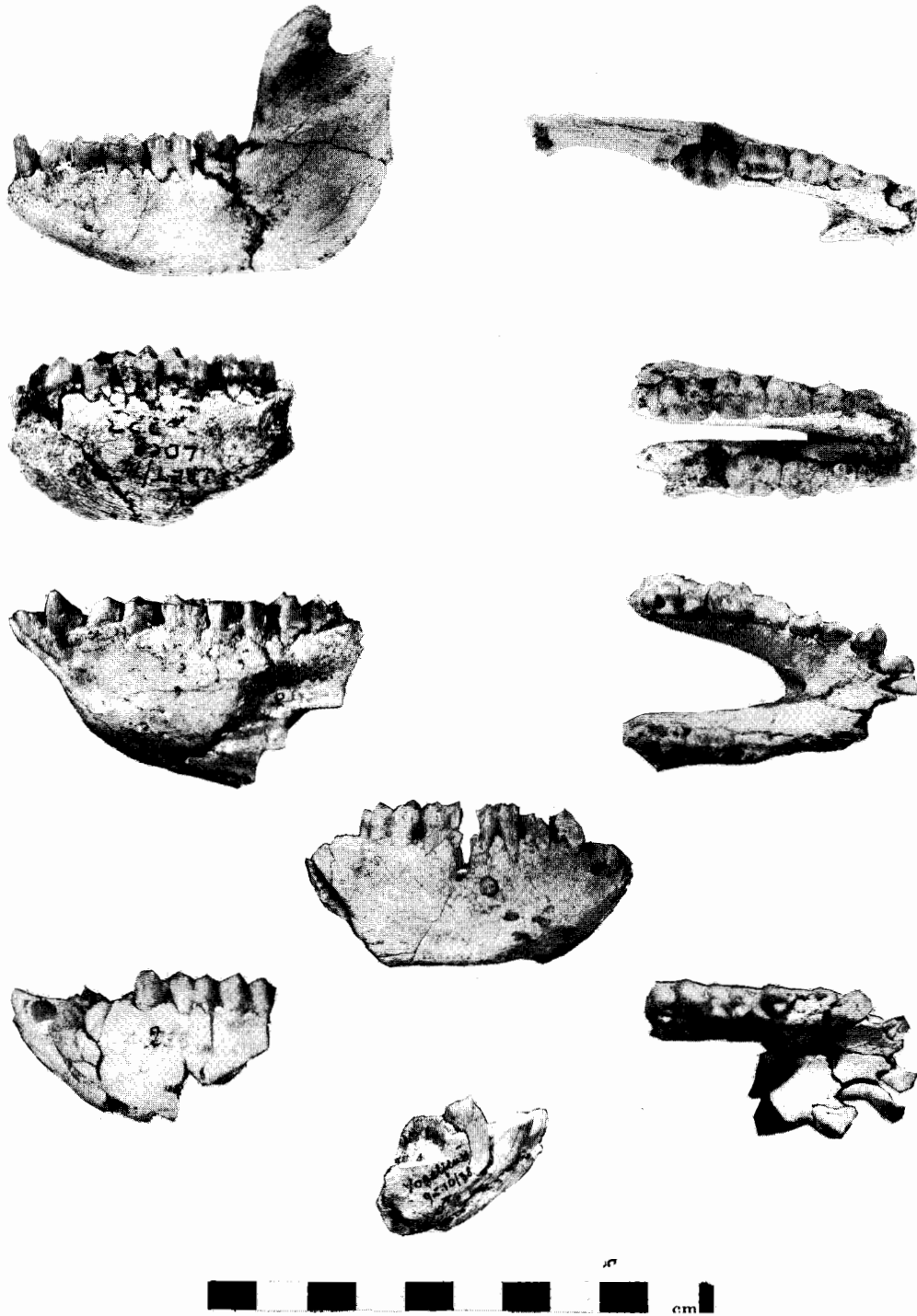


PLATE 4.1. Mandibles of *Parapapio ado*. Left and centre, lateral aspect; right, occlusal aspect. In descending order: LAET 209 ♀; LAET 223 ♀; MB. 1938.1 ♀; BM(NH). M14940 ♀ type specimen (centre); MB 1939.16.2 ♂ (left and right lateral aspect shown).

rather than colobine identification as this element is absent or reduced in colobines. A distal left m/c V, a complete proximal phalanx and a left capitate are all relatively close to female *Papio cynocephalus* in size and morphology, but the cuboid is distinctive in being narrow across its distal latero-medial width and in having the distal articular facets for m/t IV and V meet at less of an angle than in *Papio*. LAET 4911, a complete proximal phalanx (9.7 mm wide, 28.9 mm long) is longer and narrower than LAET 3904 but may be from the fourth or fifth digit of the foot, in which case it would be close in size to that of a male *Papio cynocephalus*. LAET 2283 is the anterior half of a small weathered calcaneus which closely matches *Papio* in what is left of its morphology. It has an elongated middle facet for the talus typical of the Papionini; in the Colobinae this facet is more circular.

The teeth of *P. ado* conform to the pattern typical of papionins; there are no apparent morphological peculiarities. Apart from one subadult ramus and some undiagnostic fragments, the mandibular body is the only cranial element represented in the sample and it is typical of a small *Parapapio* in lacking a marked fossa on the lateral face. Because of this, these specimens are allocated to the genus *Parapapio* despite the lack of diagnostic features of the muzzle and face.

Assignment of this collection to a species of *Parapapio* presents a number of problems. In South Africa, four *Parapapio* species are recognized: *P. jonesi*, *P. broomi*, *P. whitei*, and *P. antiquus*. *P. jonesi* and *P. broomi* are smaller than *P. whitei*, while *P. antiquus* is of similar size to *P. broomi* but is only known from Taung. Freedman (1957), Freedman and Stenhouse (1972), Maier (1971) and Eisenhart (1974) have discussed the question of separating the South African sample into species on the basis of dental size and have provided tables of metrical data. They are all basically agreed that size is a poor criterion for the separation of an essentially continuous pattern of variation but retain the four named species pending a detailed study of cranial morphology and variation.

We have compared measurements of  $P_4-M_3$  and  $M^{2-3}$  for *P. jonesi* (N=12-25) and *P. broomi* (N=48-67). The measurements included maximum lengths, width of  $P_4$ , and anterior and posterior widths of the molars. The anterior width/length indices were also calculated. The measurements were mainly those of Eisenhart with some additions and refinements by one of us (E.D.). In order to test the supposed distinctions between these two species, a series of *t*-tests was performed. In order to avoid stochastic errors due to the numerous tests (multivariate tests could not be performed due to small sample sizes and incomplete

data), we raised the confidence level for rejecting the null hypothesis of the equality means from 95% (0.05) to 0.005, or 0.001 for even greater significance (equivalent roughly to 99% (or 0.01) for a group of one or two tests). This is only an approximation, but is better than accepting differences at too low a level of confidence.

On the 28 tests performed, only the lower and upper  $M_3^3$  and the upper  $M^2$  showed significant difference in length (all  $< 0.0001$ ). But the lower teeth,  $P_4-M_3$ , were absolutely narrower in *P. jonesi* ( $< 0.0001$ ) and the upper  $M^{2-3}$  also tended to be narrower. The anterior width/length indices showed  $P_4-M_2$  to be relatively narrower as well but the latter difference was suppressed if teeth of comparable stages of wear were compared. The differences between these two species thus appear to be somewhat tenuous and relate more to a reduction in the size of the  $M_3$ s in *P. jonesi* and a tendency to narrower cheek teeth rather than to differences in the overall size of the molars and  $P_4$ .

We then computed *P. ado* (N=7-18) with both *P. broomi* and *P. jonesi* using the same measurements and indices. There was no significant difference in the length of the teeth of *P. broomi* and *P. ado* but the absolute widths of  $P_4-M_3$  were significantly smaller in the latter. When the anterior width/length indices were compared these teeth were significantly narrower in *P. ado*, but again the differences tended to be suppressed if teeth of similar wear stages were compared.  $M^2$  of *P. ado* was also relatively narrow. Finally we compared *P. ado* with *P. jonesi*. In this case  $M^2$  and  $M_3$  were significantly shorter in *P. jonesi* while the anterior breadth/length indices showed  $P_4$ ,  $M_1$ ,  $M^2$  and  $M^3$  to be relatively narrower in *P. ado*.

It thus appears that *P. ado* may be said to differ from both the South African species by a tendency for narrower molars and  $P_4$ . However these differences are insufficient to define an additional species of *Parapapio*. No good differential diagnoses have been published separating the South African *Parapapio* species; it may well be that *P. broomi* and *P. jonesi* are synonymous. Szalay and Delson (1979, p. 346) give criteria which roughly distinguish *P. broomi* from *P. whitei*, but *P. jonesi* is generally identified by its smaller size. As we have shown, this distinction is not very clear and the size range, when the two species *P. jonesi* and *P. broomi* are combined, is small compared with that of a modern species such as *Macaca mulatta*. It may be that fewer species of *Parapapio* should be recognized.

It would seem logical to include the Laetoli sample in one of the South African species, either *P. broomi* or *P. jonesi*, pending revision of the South African papionins but 'ado' has priority; Hopwood named

*Cercocebus ado* in 1936, while Jones named *P. broomi* in 1937 and Broom named *P. jonesi* in 1940. It is clear that a revision of the South African species to include good differential diagnoses of *Parapapio* is called for. When this happens it may well be that both *P. jonesi* and *P. broomi* will be found to be synonymous with *P. ado*. Certainly, having studied the Laetoli material, we can offer no criteria to separate these East and South African species unequivocally.

Three other East African sites of comparable age to Laetoli have yielded a small papionin. Patterson (1968) reported a partial male mandible which he referred to *P. jonesi* from Kanapoi, Kenya, a site which may be of similar age to or younger than Laetoli. Patterson *et al.* (1970) and Behrensmeyer (1976) report three dates of 2.9, 2.5, and 2.7 Ma for the basalt at Kanapoi, but it is uncertain how much older the fauna may be. M. G. and R. E. F. Leakey (1976) redescribed the Kanapoi specimen (KNM-KP 286), noting its similarity to *Cercocebus ado* but calling it Papionini genus et species indet. B. They further reported a damaged isolated right M<sub>3</sub> (KNM-KP 287) from Ekora, a locality close to Kanapoi in age (Harris and White, 1979), which they referred to the same indeterminate taxon. Szalay and Delson (1979) referred both these specimens to ?*Parapapio ado*. The Ekora M<sub>3</sub> is smaller than the M<sub>3</sub> of the Kanapoi mandible, but only its mesial width may be accurately determined. The Kanapoi specimen, although of a male, is significantly smaller than any of the three male mandibles in the Laetoli collection. From the Hadar Formation in the Afar, Ethiopia, numerous cercopithecoid fossils, including cranial and postcranial specimens of a small species of *Parapapio*, have been recovered from locality AL 363, high in the Kadar Hadar Member. This member lies below the BKT<sub>2</sub> tuff which has a K-Ar age of 2.9 Ma (Walter and Aronson 1982) and above the Denen Dora Member which has yielded suid material indicating an age close to 3.0 Ma (Cooke 1978). The Hadar remains will be described in detail by Eck, Delson, and Johanson.

#### Genus *Papio* Erxleben, 1777

*Diagnosis.* The genus is characterized, particularly in the males, by an elongated snout. In profile, dorsal surface of muzzle shows sharp, distinct drop in interorbital region and then a much more gradual slope down to the alveolar point. Particularly in the males, muzzle dorsum is greatly flattened and maxillary ridges are well developed. A maxillary fossa and a fossa on the lateral face of the mandibular corpus are usually present. Supraorbital tori are large. Incisors

are large relative to posterior dentition. Molar cusps are more or less subequal although anterior pair is almost invariably slightly larger than posterior. Molars flare markedly towards cervix; this is most pronounced on buccal aspect of lower molars and on lingual aspect of uppers. Sexual dimorphism is marked in all the species of this genus. The postcranium is strongly adapted to terrestrial life (after Freedman 1957).

#### cf. *Papio* sp.

##### *Material.*

*Loc. 5* LAET 4925, distal humerus.

*Loc. 11* LAET 4765, rt. dP<sup>4</sup>.

*Discussion.* These two specimens confirm the presence of a very large papionin at Laetoli. The distal humerus (Plate 4.2) is well preserved except for slight damage to the trochlear edges on the posterior and inferior surfaces and to the posterior edge of the medial epicondyle. The deciduous premolar is worn and the roots broken, but the crown is complete. As there is no other monkey of similar size among the Laetoli fossils, it was considered that these specimens might be intrusive, perhaps from the overlying Ndolanya Beds. Matrix adhering to the fossil humerus could be matched with the sedimentary sequence at Locality 5 (Drs Mary Leakey and Richard Hay, pers. comm.). The dP<sup>4</sup> had no adhering matrix but almost certainly derives from the Laetoli Beds. It is not possible to assign these specimens with certainty to genus, much less to species.

The distal humerus is comparable in size to the large *Theropithecus oswaldi* from Bed II at Olduvai Gorge and from the stratigraphic level of the Koobi Fora Tuff east of Lake Turkana (about 1.5 Ma), but it shows some morphological differences. In particular, the medial epicondyle is relatively small and more posteriorly directed as in *Papio* rather than *Theropithecus*. Unfortunately no postcranial elements of *Papio* (*Dinopithecus*) *ingens* or any other baboon of equivalent size to the large *Theropithecus oswaldi* have yet been recovered or described.

The dP<sup>4</sup> is clearly papionin, having similarities with a large *Papio* such as *Papio* (*Dinopithecus*) *ingens*. It is moderately worn and there is slight chemical weathering of parts of the enamel. In addition, on the posterior half of the tooth the enamel is broken and missing at the cervix on the lingual side. The identification of this tooth as deciduous was originally doubted by one of us (E.D.) in view of the very small posterior breadth measurement; the measurements closely match those of a *P. ado* M<sup>3</sup>. However this posterior breadth



PLATE 4.2. Above, distal humerus of cf. *Papio* sp. compared with *Papio hamadryas cynocephalus*. Left, anterior aspect; right, posterior aspect. Below, proximal femur of cf. *Paracolobus* sp. compared with *Paracolobus chemeroni* (KNM-BC 3). Left, posterior aspect; right, anterior aspect.

measurement is misleading. Because of the steep slope of the lingual face, the damage to the enamel at the cervix, although only affecting a small area, causes a significantly reduced breadth. This tooth has to be deciduous for the following reasons: firstly, for an equivalent stage of wear on a permanent molar the crown height is much greater; secondly, the roots were apparently directed outwards as in a deciduous molar; and thirdly, the crown flares outwards from the cervix on both the anterior and posterior sides as in a deciduous upper molar.

On the basis of the ratio of humeral bi-epicondylar width to  $M^1$  length in sixteen specimens of *Papio hamadryas anubis* (average 3.5, range 3.1–4.1), the width of the Laetoli humerus (46.5 mm) suggests an

$M^1$  length for this individual of about 13.3 mm (between 11.3 and 15 mm at least). This is far above the observed range for  $M^1$  length in *Parapapio ado* (Table 4.5) but comparable with dentitions of *Papio (Dinopithecus) ingens* from Swartkrans (Freedman 1957) and those of *P. (D.) cf. ingens* from the lower members of the Shungura Formation (Delson 1982). The Swartkrans specimens are about 2 Ma younger than those from Laetoli but the lower part of the Shungura Formation is only slightly younger than the Laetoli Beds. SK 554, a specimen from Swartkrans assigned to *P. (D.) ingens*, includes a  $dP^4$  of equal length (11.0 mm) while the length of  $M^1$  of this specimen is 13.3 mm, equal to that estimated for the individual with the large humerus LAET 4952. These

specimens clearly represent a large baboon but its taxonomic status may not be resolved without further and more complete material.

Subfamily COLOBINAE Jerdon, 1867

Genus *Paracolobus* R. Leakey, 1969

*Diagnosis.* An extinct colobine with moderately long, wide muzzle, wide face, and wide frontal process of zygoma. Interorbital region wide, nasals short, zygomatic region moderately wide, nasal aperture long with relatively thick lateral margins and straight lateral profile. Postorbital constriction marked, temporal lines prominent and meeting at bregma. Supraorbital tori moderately thick, postglabellar sulcus present. Gonial region sometimes inflated, ramus moderately high with axis vertical to occlusal plane. Superior border of coronoid slightly higher than condyle. Premolars relatively large, P<sup>3</sup> with small protocone, upper molars wide relative to length and flaring at cervix. Postcranial elements mainly display features typical of arboreal colobines but some traits are intermediate between colobines and terrestrial cercopithecines. Distinguished from other colobines by its postcranial elements and larger size. Also differs from *Cercopithecoides* in deep slender mandible, wide muzzle, and P<sup>3</sup> with protocone. Differs from *Rhinocolobus* in short wide muzzle and relatively larger cheek-teeth compared with cranium size (Leakey 1982).

*Type species.* *Paracolobus chemeroni* R. Leakey, 1969.

**cf. *Paracolobus* sp.**

*Material.*

- (a) Early collections, locality uncertain;  
 BM (NH) M18774, mand. frag. heavily worn rt. and lt. I<sub>1</sub>.  
 MB 1939.16.4, lt. ?female mand. frag. M<sub>2-3</sub>. Base preserved below M<sub>2</sub> and forward to below broken C̄-P<sub>3</sub> area.  
 MB 1939.16.5, lt. mand. frag., M<sub>2-3</sub>.  
 MB 1939.16.6, rt. mand. frag., M<sub>3</sub>.  
 MB 1939.16.9, lt. max. frag., P<sup>4</sup>-M<sup>1</sup>, rt. M<sup>1</sup>.  
 MB 1939.16.10, lt. max. frag., P<sup>3</sup>-M<sup>1</sup> (?male).  
 MB 1939.16.12, rt. female max. frag., C̄-P<sup>3</sup>.  
 MB 1939.16.17, rt. female max. frag., C̄-P<sup>4</sup>.  
 MB 1939.16.21, broken lt. M<sup>22</sup>.  
 MB 1939.16.23, lt. P<sup>22</sup>.  
 MB 1939.16.25, rt. max. frag., M<sup>22</sup>.  
 MB 1939.16.26, lt. max. frag., broken M<sup>1</sup> or <sup>2</sup>.  
 MB 1939.16.28, lt. M<sup>1</sup> or <sup>2</sup>.  
 MB 1939.16.29, rt. mand. frag., M<sub>3</sub>.  
 MB 1939.16.30, rt. M<sup>23</sup>.  
 MB 1939.16.31, rt. M<sup>22</sup>.  
 MB 1939.16.32, rt. M<sup>21</sup>.  
 MB 1939.16.35, mand. frag., rt. and lt. I<sub>1</sub> erupting.

(b) Mary Leakey collection, localities known;

- Loc. 1* LAET 1974, lt. M<sup>22</sup>.  
*Loc. 2* LAET 1915, broken lt. M<sub>3</sub>.  
 LAET 2523, female lt. P<sub>3</sub>-broken M<sub>1</sub> and M<sub>2</sub>.  
 LAET 2847, molar frag.  
 LAET 3740, lt. M<sub>2</sub>.  
*Loc. 3* LAET 247, female max. frags., rt. C̄, M<sup>1-2</sup>, lt. P<sup>3</sup>, M<sup>2</sup>, temporal frag. with articular facet, proximal rt. femur.  
*Loc. 6* LAET 295, female max./premax. frag., rt. I<sup>1</sup>, roots I<sup>2</sup>-C̄, P<sup>3</sup>-M<sup>3</sup>.  
*Loc. 7* LAET 321, rt. max. frag., dP<sup>3</sup>-M<sup>1</sup>, I<sup>1</sup> in crypt, unerupted lt. I<sup>1</sup> and skull frags.  
 LAET 327, distal femur.  
*Loc. 9* LAET 1469/1560, damaged rt. C̄-M<sub>2</sub>, lt. C̄, broken P<sub>4</sub>, two skull frags.  
*Loc. 10* LAET 2011, rt. M<sub>2</sub>.  
*Loc. 10W* LAET 4126, rt. max. frag., broken P<sup>3</sup>-M<sup>3</sup>.  
*Loc. 17* LAET 4596, male rt. mand. frag., roots P<sub>3-4</sub>, and M<sub>1-3</sub>, lt. mand. frag. M<sub>2-3</sub>, isolated I<sub>1</sub>, P<sub>4</sub>, and broken M<sub>1</sub>.  
*Loc. 21* LAET 3372b, rt. M<sub>3</sub>.  
 LAET 4156, rt. M<sub>2</sub>.  
 LAET 5340, rt. M<sub>1</sub> (these three specimens may be associated).  
 LAET 5352, male lt. C̄.

(c) Mary Leakey collection, locality uncertain;

LAET 4565, very weathered rt. M<sub>3</sub>.

*Description.* These specimens represent a medium-sized colobine (Plate 4.3, Tables 4.8 and 4.9). M. G. Leakey (1982) has recently discussed the larger Plio-Pleistocene fossil colobines of Africa, recognizing three genera, *Paracolobus*, *Rhinocolobus*, and *Cercopithecoides*, which are readily distinguished by their cranial morphology. She recognized a new species *Paracolobus mutiwa*, from the Turkana basin, distinct from *P. chemeroni* from the Baringo basin although of similar size. Unfortunately separation of these taxa on the basis of isolated teeth and partial jaws such as comprise the Laetoli sample is not easy.

Metrically, the preserved teeth from Laetoli are indistinguishable from those of *Rhinocolobus turkanaensis* from Omo and Koobi Fora, while they are smaller than specimens assigned to the two species of *Paracolobus*. However, the morphology of the mandibular fragments and in particular that of an associated proximal femur (LAET 247) indicates affinities with *Paracolobus* in spite of the smaller size.

As well as differing cranial morphology, *Paracolobus* is distinguished from *Rhinocolobus* on the basis of its comparatively larger teeth compared to skull size. Unfortunately there is insufficient cranial material from Laetoli to use this criterion here although the larger pieces show this tendency. The Laetoli speci-

INSECTIVORA, GALAGINAE, AND CERCOPITHECIDAE

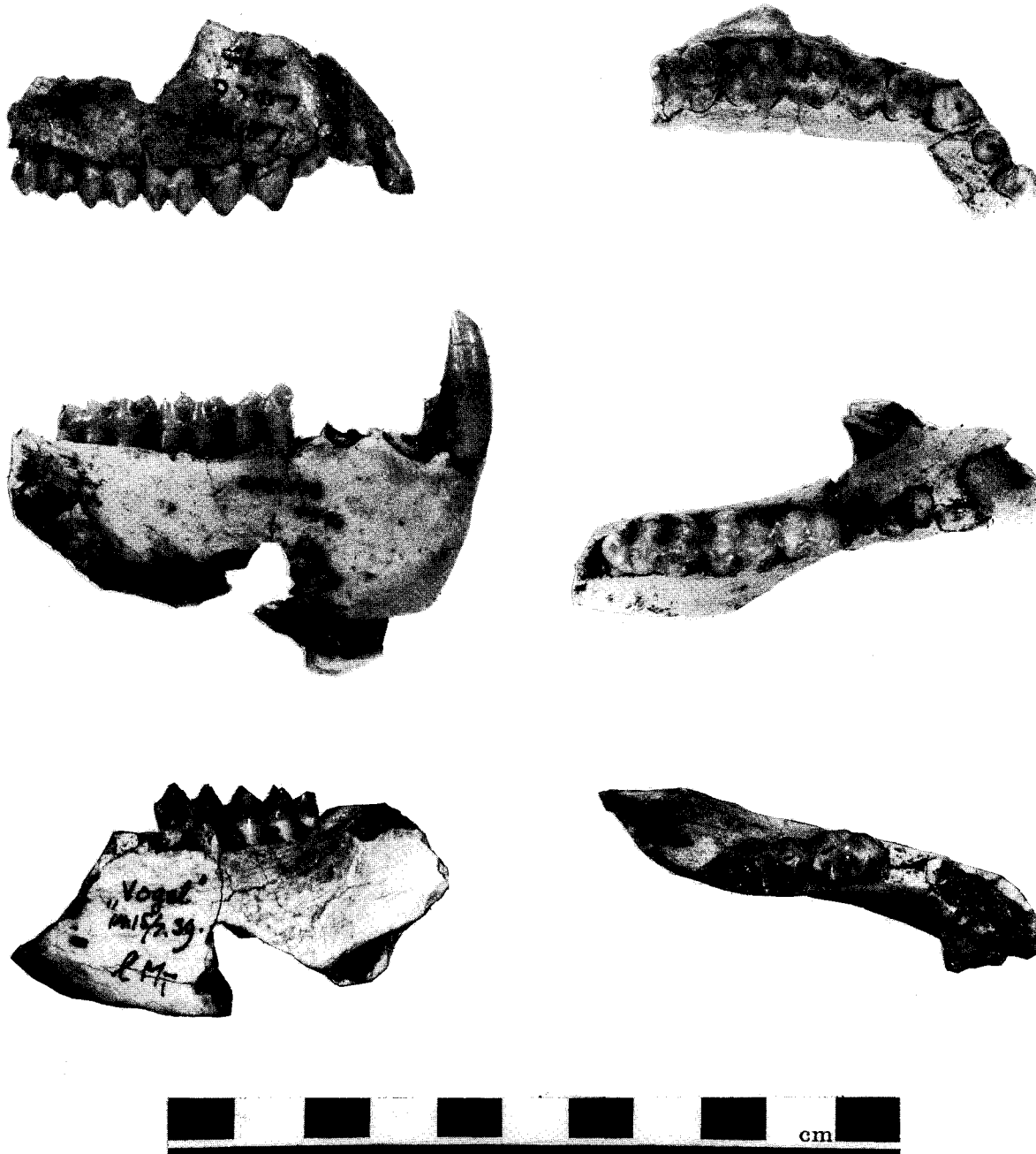


PLATE 4.3. cf. *Paracolobus* sp. Left, lateral aspect; right, occlusal aspect. Above, LAET 295 (maxilla); centre, LAET 4596 (rt mandible); below, 1939.16.4 (lt mandible).

mens are distinguished from the third genus, *Cercopithecoides*, by a more rounded muzzle and by the morphology of the femur. In addition, a number of metrical distinctions were found separating the Laetoli teeth from those of *Cercopithecoides*.

Only two Laetoli mandibles, MB 1939.14.4, a female, and LAET 4596, a male, provide more than

fragments of the mandibular body, but even these are broken. The former is complete below  $M_2$  but lacks  $M_1$ , while the latter although complete at the symphysis, lacks the base posterior to this. Thus it is not possible to take comparable measurements.

A few postcranial elements may be referred to this taxon, although we look forward to publication of the

detailed studies of Mark Birchette (Johns Hopkins University) on East African Plio-Pleistocene colobine postcrania for a more extensive basis for comparison. LAET 247 (Plate 4.2), a proximal femur associated with maxillary fragments and teeth compares well with that of *P. chemeroni* in head shape and hafting but its lesser trochanter is relatively smaller and the trochanteric fossa more proximal. Of significance is the small proximal extension of the greater trochanter which is characteristic of the Colobinae and particularly marked in *Paracolobus*. LAET 327, a distal femur, is of comparable size to LAET 247.

While we tentatively allocate the medium-sized Laetoli colobine to cf. *Paracolobus* sp., more material is required to make a specific identification. The dental remains are smaller than those of *P. chemeroni* and *P. mutiwa*. If the generic allocation is correct, a new species may eventually have to be erected.

#### Colobinae gen. et. sp. indet.

##### Material.

(a) Early collection, localities unknown;  
MB 1939.16.20, rt. P<sup>4</sup>.  
MB 1939.16.27, rt. P<sup>24</sup>.

(b) Mary Leakey collection, localities known;

Loc. 1 LAET 672, lt. cuboid.

Loc. 7 LAET 4578, rt. P<sup>24</sup>.

Loc. 10W LAET 1817, prox. lt. femur lacking greater and part of lesser trochanter.

Loc. 21 LAET 3372a, rt. P<sup>4</sup>.

*Description.* These four isolated teeth are smaller than homologous teeth of cf. *Paracolobus* sp. (Table 4.10), and appear to represent a second colobine taxon. Although one specimen, LAET 3372a was found associated with two other teeth, one of which (LAET 3372b) is an M<sub>3</sub> referred to *Parapapio ado*, it seems unlikely that the association is biological. LAET 3372b, the colobine M<sub>3</sub> is among the smaller *Paracolobus* M<sub>3</sub>s but it does appear to fit well into the observed range of the taxon and may be associated with other teeth of cf. *Paracolobus* sp. from Locality 21 (see above). A small partial femur, LAET 1817, is included here as its short neck and head hafting appear colobine and it is much smaller than the cf. *Paracolobus* sp. femur, LAET 247. However it may conceivably be a *P. ado* specimen instead. LAET 672, a left cuboid, is close in size to LAET 3904 (referred to *Parapapio ado*) but it contrasts with this specimen in being wider distally and having a rather concave dorsal surface.

In their reports on the cercopithecoid fossils from East Turkana and the Omo respectively, M. G. Leakey (1976) and Eck (1976) discussed fragmentary

colobine remains intermediate in size between modern *Colobus* and the several larger fossil genera. The Laetoli small colobine may have affinities with these specimens and with material of comparable size (including a fine partial skeleton) recovered from Hadar and other sites in the Afar region of Ethiopia.

#### Indeterminate specimens

##### Material.

(a) Early collection, localities unknown;  
MB 1939.16.19, juvenile symphysis with erupting I<sub>2</sub> P<sub>3</sub>.  
LAET '59 462, lt. male C crown.

LAET '59 598, lt. male C crown, lacks tip.  
LAET '59 599, rt. male C.

(b) Mary Leakey collection, localities known:

Loc. 1 LAET 744, lt. calcaneus lacking posterior surface.

Loc. 6 LAET 1177, lt. broken talus.

LAET 4693, weathered rt. M<sub>1</sub> and dP<sub>3</sub>.

LAET 4721, edentulous symphysis.

Loc. 8 LAET 240, frag. premaxilla.

LAET 3549, molar frag.

Loc. 10E LAET 1207, male rt. C.

Loc. 11 LAET 990, skull and tooth frags.

LAET 5509, tooth frag.

Loc. 16 LAET 2966, partial frontal.

LAET 3870, rt. talus.

Loc. 22 LAET 3611, prox. rt. metatarsals IV and V.

LAET 4907, prox. rt. radius.

*Description.* This material includes a number of complete or partial but identifiable remains too fragmentary or undiagnostic to allocate to one of the taxa recognized at Laetoli. The juvenile symphysis (MB 1938.16.19) may belong to the same individual as MB 1939.16.35, a fragment of mandible with erupting lower incisors referred above to cf. *Paracolobus* sp. The four male upper canines vary greatly in size and may belong to one or other of the common taxa, but not enough associated canines are known to identify them unequivocally. LAET 1207 is the largest and is larger than the male canine LAET 322 referred to *P. ado*.

Of the postcrania, LAET 3870, a large talus, matches that of *Paracolobus chemeroni* in size but has a relatively shorter neck and pronounced lateral extension of the lateral process. It differs from *Papio cynocephalus* by its wider trochlear surface. It is possible that this specimen and a second talus fragment, LAET 1177 of similar size, belong to the large cf. *Papio* sp. LAET 744, a large calcaneus lacking the posterior surface, is not unlike that of *P. chemeroni* but has a longer middle articular facet for the talus. In colobines this facet tends to be more circular. The remaining specimens are too fragmentary to merit comment.

## SPECIMENS FROM YOUNGER DEPOSITS

In addition to the specimens from the Laetolil Beds, cercopithecids have also been recovered from younger deposits in the region. Teeth quite similar to those from the Laetolil Beds have been recovered from the overlying Upper Ndolanya Beds in Locality 7E. LAET 5472 is a damaged and worn right  $M_3$ , not unlike that of *Parapapio ado*. Its mesial breadth is too damaged to measure, but its distal breadth (9.4 mm) is greater than that of *P. ado*, while its length (15.0 mm) is comparable, suggesting a relatively wider tooth. LAET 5123 is a nearly complete isolated right  $I_1$  (width 5.8 mm, length 6.4 mm, height 8.6 mm) which is probably colobine and matches that of the maxilla LAET 295 referred to cf. *Paracolobus* sp.

Kohl-Larsen collected two large jaw fragments referable to the modern *Papio hamadryas* cf. *anubis*, as indicated briefly by Dietrich (1942). The provenance of these two specimens is unknown but their modern aspect would appear to suggest that they are from younger horizons than the Ndolanya Beds.

## DISCUSSION

Dated at about 3.5 Ma, the Laetoli collection of cercopithecids represents one of the largest and most complete collections of African Pliocene monkeys. Langebaanweg, the only site of comparable age in South Africa has yielded only two partial premolars referable to the Cercopithecidae (Grine and Hendey 1981), while the oldest of the Transvaal sites, Makapansgat, although yielding a rich cercopithecoid fauna, is unlikely to be older than 3 Ma. Cercopithecids are rare at East African sites of equivalent age. Only from the Sidi Hakoma and Denen Dora Members of the Hadar Formation, Ethiopia has a collection of Cercopithecidae been recovered which approaches that of Laetoli in age and in the number of specimens.

A total of 130 identifiable cercopithecoid remains are known from the Laetolil Beds, of which 83 derive from known localities. Table 4.11 summarizes the distribution of the four recognized taxa by locality. *Parapapio* is clearly the most common cercopithecoid and is represented by 71 specimens, of which only 9 were juveniles. Of the remaining 62 adults and subadults, 9 can be identified as female and 3 as male. *Paracolobus* sp. represents a further one-third of the total specimens. Localities 7, 8, 10, and 11 have yielded the most cercopithecoids, being especially rich in *Parapapio*. At localities 1, 2 and 21 *Paracolobus* specimens outnumber those of *Parapapio*. The small

colobine is present at three localities (7, 10 and 21), that have also yielded both other taxa. The large papionin is known from Locality 5, where it is the sole recognized cercopithecoid, and from Locality 11 where *Parapapio* is common.

Geological and faunal interpretations provided in this volume suggest that the Laetoli deposits were probably laid down in an environment of savanna and wooded savanna with seasonal rains but no large bodies of water. The sediments are largely subaerial deposits of ash and contrast both with the lacustrine and fluvial Plio-Pleistocene deposits elsewhere in eastern Africa and with the cave sediments of South Africa. The fossilized remains from Laetoli, as is typical of subaerial deposits, are fragmentary and broken which makes taxonomic identification difficult. Footprints are often preserved in such deposits and those at Laetoli are spectacular. Cercopithecoid trails are preserved at three sites, C, D, and F. These tracks have not been studied by us, but as reported by M. D. Leakey and Hay (1979), foot lengths measure between 10 and 20 cm, with stride lengths between about 20 and 50 cm. Given the overlap in size between taxa and the large size-range between juveniles and adult males it is not possible to determine to which taxon the prints belong.

The high frequency of *Parapapio* and the absence of *Theropithecus*, of which a small form is known at other African localities of comparable age, may be a consequence of the Laetoli palaeoenvironment. Unfortunately, few African sites of comparable age to Laetoli are known. In the Sidi Hakoma Member of the Hadar Formation at Afar in Ethiopia, between 3 and 3.5 Ma (Cooke 1978), a small *Theropithecus* predominates, with a small *Parapapio*, and a small and a large colobine being much rarer. At the Omo, the cercopithecoid remains from the lower Shungura and Usno Formations (about 3 Ma), are rather fragmentary consisting mainly of isolated teeth. *Theropithecus* is the common genus but other taxa are represented (Eck 1976). At Koobi Fora the lower levels (about 3 Ma) have yielded few cercopithecoid fossils. Kanapoi and Lothagam on the west side of Lake Turkana have yielded *Parapapio* and a small colobine but only one *Theropithecus* molar. These sites are all from sedimentary regimes which are largely fluvial but include lacustrine episodes.

On the other hand, papionins are the dominant cercopithecoids in southern Africa where the faunas lack aquatic elements. Unfortunately these sites are not accurately dated, but Makapansgat and Sterkfontein are thought on palaeomagnetic and faunal evidence to date from 3 to 2.3 Ma (McFadden *et al.*

1979; Harris and White 1979). *Parapapio* species are the most common cercopithecids at these sites, with the terrestrial colobine *Cercopithecoides williamsi* less abundant. In addition, two species of *Papio* occur at Sterkfontein, and at Makapansgat *Theropithecus darti*, cf. *Cercocebus* sp. and a large colobine have been recorded. Vrba's (1980) analysis of the fossil Bovidae of the Sterkfontein valley suggest an open habitat with low bush cover for this site. The relatively open palaeoenvironment at Laetoli has yielded a similar fauna dominated by *Parapapio*. That neither of the Laetoli colobines is referable to *Cercopithecoides* may be due to the antiquity of the site since the environment appears to have been suitable.

It has been suggested (Szalay and Delson 1979) that, on the basis of the apparent ancestral retentions of facial form (shared with *Macaca*) and its relative conservatism, *Parapapio* may be considered as the ancestral 'archetypal' African papionin. It is unfortunate that the ages of the South African *Parapapio* species are not known but the contemporaneous occurrence of *P. ado* and cf. *Papio* sp. at Laetoli confirms that the common ancestor of these two genera will only be encountered at earlier localities. Similarly the contemporary occurrence of cf. *Paracolobus* sp. with the small Colobinae sp. indet. suggests that the radiation of the colobines which resulted in the great variety of colobine species later in the Plio-Pleistocene between 2.5 and 1.5 Ma (M. G. Leakey 1982) began prior to the accumulation of the Laetoli Beds.

While cercopithecids are known in Africa in the late Lower Miocene at Gebel Zelten, Libya (Delson 1979) and Wadi Moghara, Egypt (Simons 1969), and in the Middle Miocene at Maboko, Kenya (Koenigswald 1969; Delson 1975), the first unquestionable colobine is a mandible recovered from the 9 Ma deposits at Ngeringerowa, Kenya, by Martin Pickford. Thus the divergence of the two subfamilies must have occurred before this. The divergence of the genera within each subfamily most probably took place in the period between 9 and 4 million years ago, a time sparsely represented in the fossil record in Africa.

## SUMMARY

The Laetoli Beds have yielded 130 cercopithecid specimens, the largest and most complete collection of cercopithecids yet described from the middle Pliocene of Africa. Over half of these belong to a medium-sized papionin previously called *Cercocebus ado* or *Papio serengetensis*, but here recognized as *Parapapio ado* (Hopwood 1936). This species is nearly identical in dental size to *Parapapio jonesi* of South Africa with

which it may be synonymous. If this is found to be the case, *P. ado* has priority. A medium-sized colobine is represented by about one-third of the specimens. On the basis of mandibular morphology and an associated femur, it seems to be referable to the genus *Paracolobus* rather than to the similar-sized *Rhinocolobus turkanaensis*. Four upper premolars and a partial femur are considered to represent a smaller colobine, similar in size to specimens recognized from the Omo, Koobi Fora, and Hadar. A single distal humerus and an isolated dP<sup>4</sup> document the presence of a very large papionin; while the humerus is comparable in size to the much later *Theropithecus oswaldi*, morphologically it is closer to *Papio*. The dominance of *Parapapio* and the absence of the small *Theropithecus* common at Hadar and Makapansgat may be a reflection of the distinctive Laetoli palaeoenvironment. The variety of species represented at Laetoli is consistent with the hypothesis that the diversification within the two subfamilies of Cercopithecidae took place in Africa between 9 and 4 million years ago.

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*Note added in proof:* Current geochronological data on the Ethiopian and Kenyan sites mentioned may be found in Brown *et al.* (1985) and references therein. Delson (1984) provided an interim list of cercopithecoid taxa at over 60 African Plio-Pleistocene site units including those discussed here and suggests biochronological correlations.

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TABLE 4.4. Measurements of the upper cheek-teeth of *Parapapio ado*, *P. broomi*, and *P. jonesi*

	P <sup>4</sup>			M <sup>1</sup>			M <sup>2</sup>			M <sup>3</sup>		
	L	B	B/L	L	B	B/L	L	B	B/L	L	B	B/L
<i>P. ado</i>												
mean	6.81	8.10	1.17	8.97	8.10	0.91	11.24	10.42	0.93	10.83	10.16	0.94
n	7	6	6	4	4	4	12	12	11	7	7	7
range	6.1-7.5	7.8-8.3	1.1-1.3	8.0-9.9	7.5-8.4	0.9-1.0	9.9-12.3	8.5-12.0	0.9-1.1	9.4-11.8	8.2-11.3	0.9-1.0
S.D.	0.4	0.2	5.3	0.8	0.4	8.0	0.88	1.1	5.5	0.9	1.1	5.6
C.V.	6.4	2.0	4.5	9.4	5.0	8.8	7.81	10.8	5.9	8.6	11.1	6.0
<i>P. broomi</i>												
mean							11.0	11.09	1.01	10.89	10.91	1.00
n							60	54	53	52	50	49
range							9.7-12.3	9.4-12.3	0.9-1.1	9.6-12.2	9.4-12.2	0.9-1.1
S.D.							0.56	0.6	5.8	0.7	6.0	6.4
<i>P. jonesi</i>												
mean							10.23	11.09	1.00	10.17	10.36	1.01
n							13	54	12	16	15	15
range							9.3-10.7	9.1-12.2	0.9-1.2	9.0-11.1	9.4-11.5	0.9-1.1
S.D.							0.3	0.7	7.8	0.6	0.7	5.7

TABLE 4.5. Measurements of lower cheek-teeth of *Parapapio ado*, *P. broomi*, and *P. jonesi*

	P <sub>4</sub>			M <sub>1</sub>			M <sub>2</sub>			M <sub>3</sub>		
	L	B	B/L	L	B	B/L	L	B	B/L	L	B	B/L
<i>P. ado</i>												
mean	7.08	5.92	0.83	9.07	6.98	0.75	10.82	8.97	0.79	13.85	8.92	0.65
n	18	11	11	18	12	12	14	13	13	14	13	13
range	5.8-8.5	5.1-6.5	0.7-0.9	7.7-10.3	6.3-7.9	0.7-0.8	9.6-12.5	7.3-9.8	0.8-0.9	12.5-15.3	7.8-10.8	0.6-0.7
S.D.	0.7	0.6	5.5	0.7	0.5	3.2	0.7	0.7	3.4	1.0	0.8	3.8
C.V.	9.2	7.6	6.6	7.7	7.1	4.2	6.2	8.3	4.3	6.9	8.6	5.9
<i>P. broomi</i>												
mean	7.09	7.10	1.00	9.12	7.99	0.88	10.91	9.73	0.89	14.24	9.97	0.70
n	52	50	49	55	48	47	66	60	58	67	61	60
range	5.7-8.8	5.6-9.2	0.7-1.3	7.6-10.5	7.2-9.0	0.8-1.1	9.5-12.4	8.3-10.9	0.8-1.0	12.1-16.7	8.2-11.0	0.6-0.8
S.D.	0.6	0.7	1.0	0.6	0.5	7.0	0.6	0.5	6.1	1.0	0.6	4.6
<i>P. jonesi</i>												
mean	6.83	6.28	0.93	8.97	7.28	0.81	10.61	8.79	0.83	13.15	9.02	0.69
n	24	25	24	24	21	21	23	22	21	21	20	20
range	6.0-7.6	5.5-7.0	0.79-1.07	7.7-10.1	6.6-7.8	0.73-0.95	8.8-11.6	7.4-9.5	0.76-0.91	11.2-14.2	8.4-9.7	0.6-0.8
S.D.	0.4	0.3	7.5	0.6	0.3	5.5	0.7	0.5	4.9	0.8	0.4	4.7

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TABLE 4.6. Measurements of the anterior dentition and P<sub>3</sub> of *Parapapio ado*

	I <sub>1</sub>		I <sub>2</sub>		C		C			P <sub>3</sub>		
	L	B	L	B	L	B	L	C	B	B	P <sub>3</sub>	L
<i>Upper</i>												
<i>Dentition</i>												
mean	—	—	—	—	11.25	8.90	5.30	6.35	6.07	7.10		
n	—	—	—	—	2	2	2	2	4	4		
range	—	—	—	—	10.5-12.0	8.6-9.2	4.7-5.9	6.3-6.4	5.4-6.5	6.5-7.9		
S.D.	—	—	—	—	1.1	0.4	0.9	0.1	0.5	0.7		
C.V.	—	—	—	—	9.4	4.8	16.0	1.1	7.9	10.3		
<i>Lower</i>												
<i>Dentition</i>												
mean	4.87	4.78	4.30	4.62	6.30	10.23	3.78	6.34	11.5	5.40	7.26	4.40
n	3	5	1	4	3	3	5	5	1	2	8	9
range	4.5-5.1	3.8-5.3	—	3.4-5.9	5.8-6.8	10.0-10.6	3.0-4.3	5.1-7.1	—	5.0-5.8	6.1-10.9	3.6-5.0
S.D.	0.3	0.6	—	1.8	0.5	0.3	0.5	0.8	—	0.6	1.5	0.4
C.V.	6.6	13.2	—	22.1	—	7.9	3.1	12.7	—	10.5	21.2	9.0

TABLE 4.7. Measurements of the deciduous dentition of *Parapapio ado*

	dI <sub>2</sub>		dC		dP <sub>3</sub>			dP <sub>4</sub>		
	L	B	L	B	L	B	B/L	L	B	B/L
<i>Upper dentition</i>										
mean	—	—	—	—	7.65	5.55	0.73	—	—	—
n	—	—	—	—	2	2	2	—	—	—
range	—	—	—	—	7.5-7.8	5.4-5.7	0.7-0.7	—	—	—
S.D.	—	—	—	—	0.2	0.2	0.8	—	—	—
C.V.	—	—	—	—	2.8	3.8	1.1	—	—	—
<i>Lower dentition</i>										
mean	3.00	2.00	2.70	4.65	7.58	4.28	0.56	8.04	5.64	0.70
n	1	1	2	2	5	5	5	5	5	5
range	—	—	2.7-2.7	4.3-5.0	6.8-8.5	4.0-4.7	0.5-0.6	7.6-8.4	5.4-6.0	0.7-0.8
S.D.	—	—	—	—	0.8	0.3	3.1	0.3	0.3	3.6
C.V.	—	—	—	—	10.2	7.3	5.4	4.1	4.6	5.6

TABLE 4.8. Measurements of the cheek-teeth and deciduous dentition of cf. *Paracolobus* sp.

	L	P <sub>3</sub>	B/L	L	P <sub>4</sub>	B/L	L	M <sub>1</sub>	B/L	L	M <sub>2</sub>	B/L	L	M <sub>3</sub>	B/L
	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
<i>Upper dentition</i>															
mean	7.1	7.78	1.10	7.18	8.66	1.21	9.38	8.76	0.93	9.85	9.95	1.01	10.95	9.95	0.91
n	5	5	5	5	5	5	6	5	5	4	4	4	2	2	2
range	6.9-7.4	7.4-8.3	1.0-1.2	6.8-7.6	8.6-8.8	1.2-1.3	8.7-10.0	8.4-9.2	0.9-1.0	9.4-10.3	9.7-10.3	0.9-1.1	10.5-11.4	9.8-10.1	0.9-1.0
S.D.	0.2	0.4	6.7	0.4	0.1	6.5	0.5	0.3	4.9	0.5	0.3	5.0	0.6	0.2	7.2
C.V.	2.8	5.3	6.1	5.0	1.0	5.3	5.5	3.7	5.3	4.7	2.5	5.0	5.8	2.1	7.9
<i>Lower dentition</i>															
mean				8.30	6.05	0.73	9.36	6.33	0.70	10.92	8.11	0.75	13.68	8.32	0.61
n				3	2	5	3	3	3	6	7	6	6	5	5
range				7.6-9.1	6.0-6.1	0.7-0.8	8.8-10.0	6.0-6.7	0.7-0.8	10.3-11.6	7.5-9.0	0.7-0.8	13.0-14.6	7.5-9.2	0.6-0.6
S.D.				0.8	0.1	8.4	0.4	0.4	6.0	0.5	0.5	2.4	0.7	0.6	2.4
				9.1	1.2	11.5	4.7	5.6	8.7	4.6	6.0	3.3	5.4	7.7	3.9
<i>Deciduous dentition (upper)</i>															
mean	6.3	4.4	0.70	7.6	5.9	0.78									
n	1	1	1	1	1	1									

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TABLE 4.9. Measurement of the anterior dentition and P<sub>3</sub> of cf. *Paracolobus* sp.

	I <sub>1</sub>		I <sub>2</sub>		C <sub>3</sub> ♂		C <sub>3</sub> ♀		P <sub>3</sub> ♂		P <sub>3</sub> ♀	
	L	B	L	B	L	B	L	B	L	B	L	B
<i>Upper dentition</i>												
mean	6.25	5.05	—	5.50	—	6.50	8.95	6.50	—	—	—	—
n	2	2	—	1	—	4	4	4	—	—	—	—
range	6.2-6.3	5.0-5.1	—	—	—	5.8-7.0	8.3-9.7	5.8-7.0	—	—	—	—
S.D.	—	—	—	—	—	—	0.6	0.5	—	—	—	—
C.V.	—	—	—	—	—	—	6.5	8.1	—	—	—	—
<i>Lower dentition</i>												
mean	4.90	5.53	—	—	7.20	11.60	—	—	11.50	5.80	8.90	4.50
N	3	3	—	—	2	2	—	—	1	1	1	1
range	4.2-5.4	5.3-5.8	—	—	6.1-8.3	10.9-12.3	—	—	—	—	—	—
S.D.	0.6	0.3	—	—	1.6	1.0	—	—	—	—	—	—
C.V.	13.0	4.6	—	—	21.6	8.5	—	—	—	—	—	—

TABLE 4.10. Measurements of teeth assigned to Colobinae gen. and sp. indet.

Specimen no.	Tooth	B	L	B/L
MB 1939.16.27	P <sup>4</sup>	6.6	5.7	1.16
MB 1939.16.20	P <sup>4</sup>	6.3	5.4	1.17
LAET 3372a	P <sup>4</sup>	7.5	5.7	1.32
LAET 4578	P <sup>4</sup>	5.9	5.1	1.16

TABLE 4.11. Distribution of cercopithecoid taxa from the Laetolil Beds by locality

Locality	1	2	3	5	6	7	8	9/gs	10	10E	10W	11	16	17	21	22	Total	
																	locality known	locality unknown
<i>Parapapio ado</i>	1	3	3	—	4	7	7	3	9	1	1	10	—	—	1	1	51	23
cf. <i>Papio</i> sp.	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—	2	—
cf. <i>Paracolobus</i> sp.	1	4	1	—	1	2	—	1	1	—	1	—	—	1	4	—	17	19
Colobinae indet.	1	—	—	—	—	1	—	—	—	—	1	—	—	—	1	—	4	2
Genus indet.	1	—	—	—	3	—	2	—	—	1	—	2	2	—	—	2	13	4
Total	4	7	4	1	8	10	9	4	10	2	3	13	2	1	6	3	87	48