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LATE MIOCENE PROCAVIID HYRACOIDS (HYRACOIDEA: *DENDROHYRAX*) FROM LEMUDONG'O, KENYA

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ABSTRACT

A small sample of hyracoid fossils from the late Miocene (~6.1 Ma) deposits at Lemudong'o, Narok, Kenya, belong to *Dendrohyrax*. This genus was unknown in the fossil record until recently, when almost simultaneously it was discovered at Lukeino (6 Ma) and Lemudong'o, both in Kenya. The fossils from Lemudong'o belong to a small species of the genus, not very different from *Dendrohyrax validus*. The Lukeino specimens are larger, and have been attributed to a new species *Dendrohyrax samueli*. The presence of tree hyraxes at these sites is indicative of forest at the time of deposition of the strata.

Introduction

Lemudong'o Locality 1 is a late Miocene (~6.1 Ma) mammalian-dominated fossil locality within the Narok District of Kenya (Ambrose et al., 2003; Ambrose, Bell, et al., 2007; Ambrose, Kyule, and Hlusko, 2007; Ambrose, Nyamai, et al., 2007; Deino and Ambrose, 2007). The primary fossil assemblage derives from the mudstone horizon and is dominated by specimens attributed to Bovidae and Cercopithecidae. However, the Hyracoidea are the third most commonly found taxon, comprising approximately 9% of the collection (112 specimens) (Ambrose, Bell, et al., 2007). This large proportion of the total mammalian assemblage is rare among Miocene and Plio-Pleistocene fossil localities in eastern and southern Kenya, and provides an uncommon insight into the paleoecology of this region.

All extant members of the Hyracoidea are classified within the family Procaviidae. The living Procaviidae are classified into two or three genera, depending on which authority one reads. All researchers are agreed that *Procavia* is distinct from the *Heterohyrax*/*Dendrohyrax* pair, but it is the relationship between the latter two that is subject to debate, with some researchers, such as Ellerman and Morrison-Scott (1951), Roche (1972) , and Hoeck (1978), classifying *Heterohyrax* as a subgenus of *Dendrohyrax*, and others (Hahn, 1934; Bothma, 1967, 1971; Skinner and Smithers, 1990, p. 553–563; Rasmussen et al., 1996) accepting that they represent distinct genera. Even though their dentitions are similar to each other in many ways, the cranial morphology, reproductive biology, life history variables, territoriality and vocalization reveal that they represent two separate genera, the view accepted here.

Fossil Procaviidae are known from many Plio-Pleistocene localities in East and South Africa (Churcher, 1956; Kitching, 1965; Jaeger and Wesselman, 1976; McMahon and Thackeray, 1994; Schwartz, 1997), but Miocene occurrences are rare, the only ones known prior to publication of this paper being from Namibia (Rasmussen et al., 1996) and Kenya (Fischer, 1986). In both the latter occurrences, the procaviids were identified as *Heterohyrax*. Procaviids have recently been collected at two late Miocene sites in Kenya, Lukeino in the Tugen Hills (Pickford, 2005), and Lemudong'o, near Narok.

At Lukeino, the Aragai palate is complete enough to reveal that it belongs to a new species of *Dendrohyrax*, *D. samueli* (Pickford, 2005). The Lemudong'o fossils in contrast are fragmentary and many of the features that are diagnostic for identifying *Heterohyrax* and *Dendrohyrax* are lacking. However, the base of a symphysis preserves morphology that is usually only found in *Dendrohyrax* (presence of roughened ridges separated from the body of the symphysis by grooves), and the ectoloph morphology of the upper molars suggests the same identification.

The dental remains from Lemudong'o plot within the ranges of metric variation of both *Dendrohyrax* and *Heterohyrax*. If they are *Heterohyrax* then they represent a large species of the genus, but if they are attributed to *Dendrohyrax*, then they would denote a small species of the genus. The assumption is that only one

Table 1. Measurements of the upper teeth (in mm) of *Dendrohyrax* sp., from Lemudong'o, Kenya.

Specimen	Tooth	Length	Breadth
KNM-NK 40909	left I1/ male	3.9	4.1
KNM-NK 42257	left I1/ female	3.5	4.2
KNM-NK 41460	left I1/ female	3.6	4.1
KNM-NK 44804	right P1/	3.8	2.9
	right P2/	5.0	4.5
	right M2/?	6.2	6.4
	left M1/?	5.7	6.3
	left M3/	6.2	7.0
KNM-NK 42300	left M3/	6.7	7.0

Table 2. Measurements of the lower teeth (in mm) of *Dendrohyrax* sp., from Lemudong'o, Kenya.

Specimen	Tooth	Length	Breadth
KNM-NK 41304b	left m/3	6.9	4.3
KNM-NK 40993	right m/3	7.0	4.0
KNM-NK 36575	right p/2	4.9	2.8
	right p/3	4.9	3.3
	right p/4	5.4	3.7
	right m/1	5.3	3.6
	right m/2	5.8	3.9
KNM-NK 42395	left m/1	5.8	3.5
KNM-NK 36534	left p/4	6.0	3.9
	left m/1	6.0	3.9
	left m/2	6.2	4.3
KNM-NK 41289	right p/2	4.8	2.9
	right p/3	5.0	3.5

genus is present at the site, and, if so, then it is a *Dendrohyrax* close in size to *D. validus*.

Sample and Methods

The entire collection of procaviids from Lemudong'o consists of 112 fossils. As recommended by White (2000), we agree that the best approach for describing fossils is to work with original material. However, due to circumstances at the National Museums of Kenya that were beyond the control of the authors, the first author was able to examine only a minor part of the collection, and this only in the form of casts and photographs. Therefore, this study focuses on the 18 most complete specimens of the Procaviidae assemblage, and size measurements of the other dental specimens (taken by the second author). Therefore, the results and conclusions presented herein are qualified with this unavoidable hindrance. Measurements of the cheek teeth were taken twice by L. H. and averaged. These are presented in Tables 1 and 2. Measurements of the upper incisors and the humeri were taken on casts by M. P.

Abbreviations

KNM stands for the National Museums of Kenya, and NK for the Narok District, in which the site of Lemudong'o occurs. Maxillary teeth are indicated with capital letters and the numerical tooth position followed by a back-slash (e.g., M2/ for maxillary second molar). Mandibular teeth are indicated with lower case letters and the numerical tooth position preceded by a back-slash (e.g., m/2 for mandibular second molar). Dental terminology is based on Rasmussen and Simons (1988).

Systematic Paleontology

Order Hyracoidea Huxley, 1869
Family Procaviidae Thomas, 1892
Genus *Dendrohyrax* Gray, 1868
Dendrohyrax cf. *D. validus* True, 1890
Figure 1

Referred material

KNM-NK 36534, left mandible with p/4–m/2; KNM-NK 36575, right mandible with p/2–m/2; KNM-NK 36934, fragment of mandible with molar; KNM-NK 40909, left I1/ male; KNM-NK 40993, right mandible with m/3; KNM-NK 41006, base of mandibular symphysis; KNM-NK 41289, right mandible with p/2–p/3; KNM-NK 41304a, edentulous mandible fragment; KNM-NK 41304b, left mandible with m/3; KNM-NK 41304c, fragment of right mandible; KNM-NK 41304d, edentulous mandible fragment; KNM-NK 41460, left I1/ fragment female; KNM-NK 42257, right I1/ female; KNM-NK 42272, distal end right humerus; KNM-NK 42300, left M3/; KNM-NK 42395, left mandible with m/1 and roots m/2; KNM-NK 44776, distal end of left humerus; KNM-NK 44804, various pieces of maxilla and mandible, one with right P1/–P2/, one with two worn molars, and three isolated unworn upper teeth.

Description

Mandible

The base of a mandible, KNM-NK 41006 (Figure 1E) lacks teeth, but has the floors of the alveoli of the left and right i/2 preserved. The external surface of the symphysis is marked by two distinct swollen ridges which extend parallel to the sagittal plane from a point 8 mm from the rear of the symphysis upwards for a distance of 8.5 mm.

Upper dentition

Three upper incisors in the examined sample are tusklike, permanently growing teeth (Table 1). One specimen has a sharp anterior ridge with concave sides, indicating that it is from a male individual, while the other two have a blunter ridge with less concave or even convex sides, indicating female status.

The P1/ in maxilla fragment KNM-NK 44804 has a prominent steep ectoloph with two buccal ridges descending from apex towards cervix either side of a central groove (Table 1). Lingually, in line with the two buccal ridges, there are two transverse crests which extend to the lingual side of the crown, but which are separated throughout their length by a deep valley. These internal ridges correspond to the protocone and hypocone, but the cusps are not as clearly differentiated as those in the posterior premolars and the molars. The postprotocrista curves distally as it extends towards the lingual side of the tooth. There is a low parastyle at the anterior limit of the ectoloph, from the base of which a low cingulum extends lingually and distally, but there is no metastyle. The tooth has three roots, one lingual, the other two buccal.

The P2/ in the same maxilla is more molariform. It is a bigger tooth, trapezoidal in outline, with four roots. The ectoloph is steep with two prominent buccal ridges fading out towards the cervix. The protocone and hypocone are oriented obliquely with their anterior crests positioned centrally, and their distal crests ending near the lingual side. There is a deep central fovea and there is no sign of transverse spurs.

KNM-NK 42300, a left M3/, has an ectoloph with a prominent parastyle and mesostyle but a weaker metastyle (Table 1). These

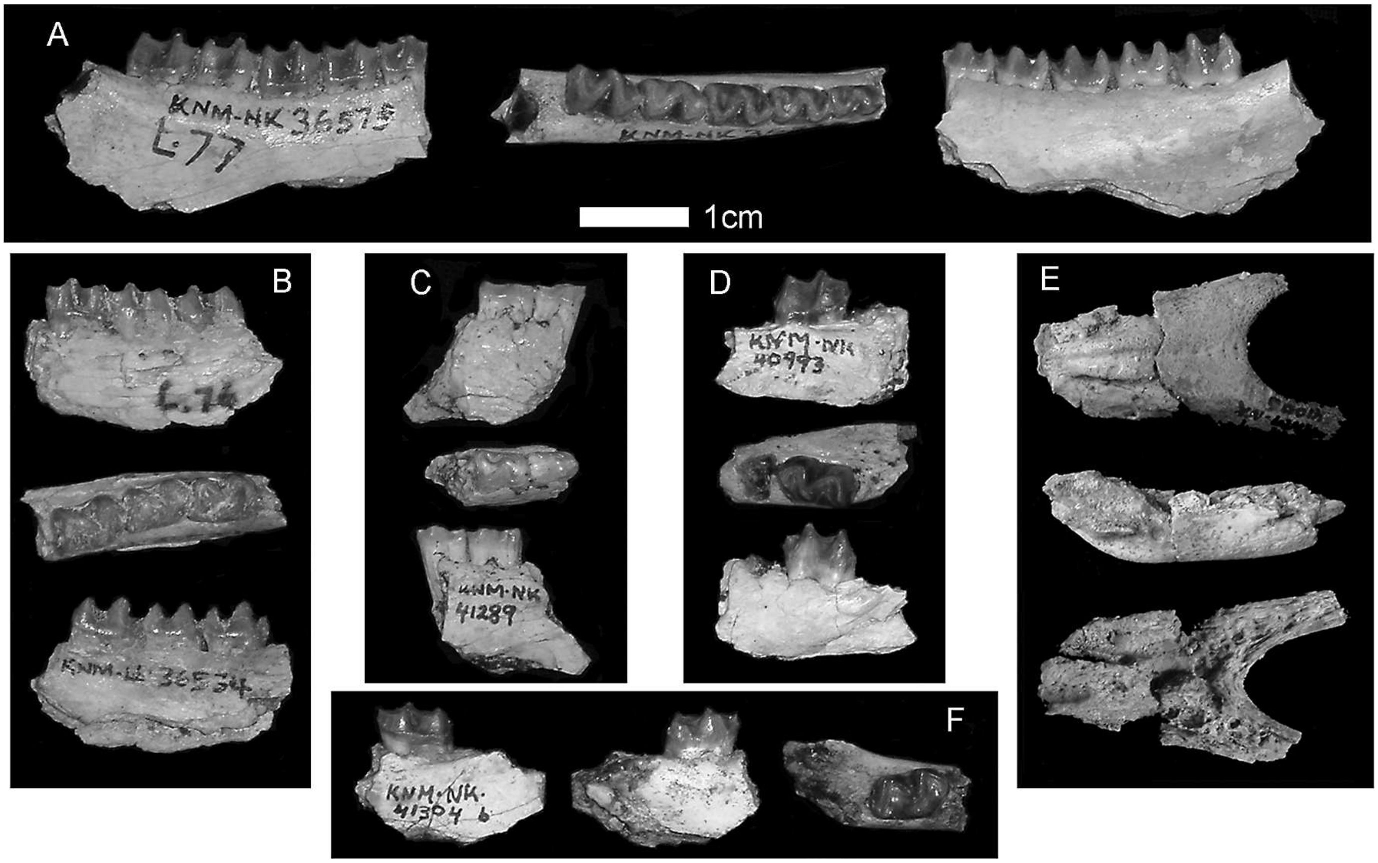

Figure 1. *Dendrohyrax* sp., Lemudong'o, late Miocene (~6.1 Ma), Kenya. A. KNM-NK 36575, right mandible with p/2–m/2 (m/3 in crypt). From left to right: buccal (mesial is to the right), occlusal (mesial is to the right), and lingual (mesial is to the left) views. B. KNM-NK 36534, left mandible with p/4–m/2. Top to bottom: buccal (mesial is to the left), occlusal (mesial is to the right), and lingual views (mesial is to the right). C. KNM-NK 41289, right mandible with p/2–p/3. Top to bottom: buccal (mesial is to the right), occlusal (mesial is to the right), and lingual (mesial is to the left). D. KNM-NK 40993, right mandible fragment with m/3. Top to bottom: buccal (mesial is to the right), occlusal (mesial is to the left), and lingual (mesial is to the left). E. KNM-NK 41006, mandibular symphysis. From top to bottom: inferior, left lateral, and superior views (anterior is to the left). F. KNM-NK 41304b, left mandible fragment with m/3. Left to right: buccal (mesial is to the left), lingual (mesial is to the right), and occlusal (mesial is to the right). Scale = 1 cm

styles are almost vertical with respect to the cervical plane. The paracone and metacone, in contrast, are inclined lingually, which imparts a strongly zigzag cutting edge to the ectoloph. The protocone and hypocone are oriented obliquely. There is no sign of spurs. The tooth has a fifth root which leans distally and is located distinctly behind the two main distal roots, rather than between, or immediately behind, them. The disposition of the roots indicate that this tooth is an M3/.

In the lot of specimens labelled KNM-NK 44804, there is an unworn isolated right upper molar with a fifth root vertically oriented and lying between the two main distal roots. This tooth is probably an M2/. Its crown morphology is similar to that of the M3/ described above. There is another specimen with the fifth root leaning distally, and this is likely an M3/ (Table 1). A further specimen is a rootless crown, which is smaller than the other molars. It is possibly an M1/. With the same catalog number there is a maxilla fragment with deeply worn and damaged molars or posterior premolars. This specimen indicates that there is more than one individual represented by this catalog number.

Lower dentition

KNM-NK 36575 is the most complete of the mandibular specimens, and its teeth are barely worn (Figure 1A). It has five cheek teeth in occlusion, and a sixth one in its crypt distally. KNM-NK 41304b (Figure 1F) and KNM-NK 40993 (Figure 1D) are small mandible fragments each bearing m/3. By a process of elimination it is possible to determine that the teeth in occlusion in KNM-NK 36575 are the p/2 to m/2, and the tooth in the crypt is the m/3. This inference is supported by the evidence of the root of the ascending ramus, which terminates anteriorly opposite the rear of m/2, and the eruption pattern (in lateral view the cervix of m/1 is located distinctly higher than that of p/4).

In occlusal view the cheek teeth of KNM-NK 36575 are formed of two V-shaped crescents arranged one behind the other to form an overall W-shaped occlusal surface. The rear limb of each V is almost at right angles to the long axis of the tooth row, whereas the anterior part of the V is obliquely oriented. The paraconid is lower than the rest of the cusps and it is centrally positioned. The protoconid, metaconid, hypoconid, and entoconid are high. The

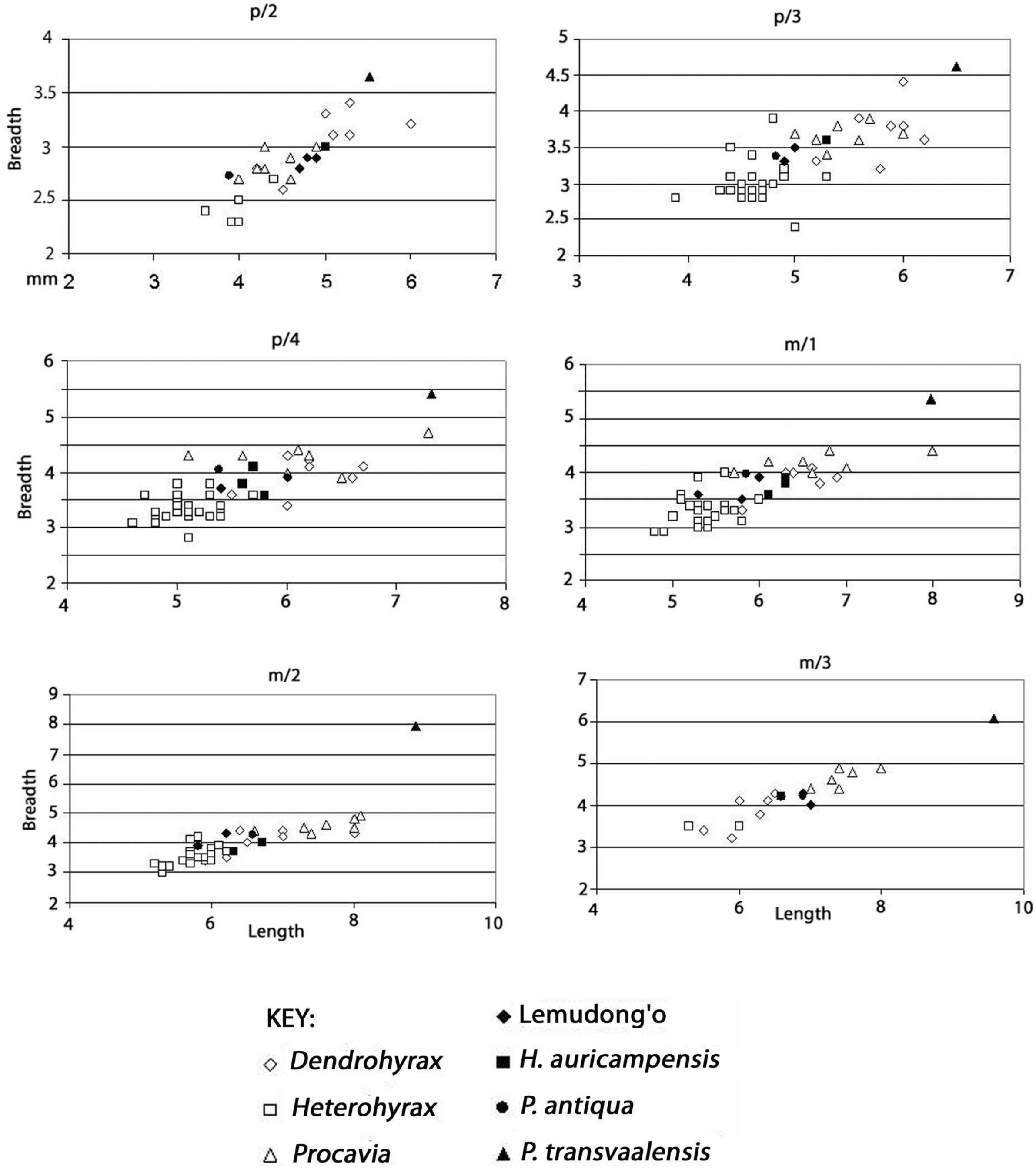

Figure 2. Scatter diagrams of length vs. breadth (in mm) of p/2–m/3 of extant and fossil Procaviidae (open symbols = extant species, solid symbols = fossils).

cristid obliqua descends gently from the hypoconulid and terminates beneath the summit of the flattened metaconid. There is a well formed buccal cingulum which extends onto the distal surface of the tooth. The trigonid and talonid basins are deep and open lingually slightly above cervix level.

KNM-NK 36534 (Figure 1B) contains left p/4 to m/2, similar in all details to those in KNM-NK 36575, and the teeth are in a similar stage of wear.

The m/3s in KNM-NK 40993 and KNM-NK 41304b are W-shaped in occlusal view, and they do not have a third lobe. Nevertheless, in both specimens the distal cingulum rises in the center to form a low, vertical, distal ridge that fades out at about half the height of the crown. This ridge is probably the remnant of a third lobe.

The premolars in KNM-NK 41289 (Figure 1C) are deeply worn, but the W-shaped occlusal outline is preserved. The buccal cingula are low but rounded.

Humerus

Two distal ends of humeri from Lemudong'o, KNM-NK 42272 and KNM-NK 44776 (not shown), are typically procaviid in articular morphology. The specimens are compatible in size with the available dental elements. The epiphyses are 13.5 and 13.3 mm in mediolateral dimensions respectively.

Discussion

The most diagnostic specimen for the purposes of determining the generic status of the Lemudong'o hyracoid is the base of a mandible, KNM-NK 41006. Among extant procaviids, the mandibular symphyses of *Procavia* and *Heterohyrax* do not possess such ridges, being evenly curved from side to side. Mandibles of *Dendrohyrax* can be devoid of ridges, but many specimens possess them. In *Dendrohyrax* the ridges increase in size ontogenetically, and are often more strongly developed in males than in females. KNM-NK 41006 provides strong evidence that the genus *Dendrohyrax* is represented in the collection. The Lemudong'o hyrax fossils are close in size to the extant species *D. validus* True, 1890, but are smaller than *D. dorsalis* Frazer, 1852.

Both *Heterohyrax* and *Dendrohyrax* possess sexually dimorphic upper central incisors similar to the two specimens from Lemudong'o.

In the Lemudong'o hyrax upper molars the surfaces of the ectoloph on either side of the mesostyle are in line with each other as in *Dendrohyrax*, not offset from each other as in *Heterohyrax* (Allaerts et al., 1982, p. 221).

It is clear from the upper and lower molar morphology that the Narok hyrax does not represent *Procavia*. The available dental fossils resemble both *Dendrohyrax* and *Heterohyrax*. In favor of attribution to *Dendrohyrax* is the morphology of the ectoloph of the upper molars. As Allaerts et al. (1982, p. 221) pointed out, the parts of the ectoloph on either side of the mesostyle lie in the same plane in *Dendrohyrax* but are offset from one another in *Heterohyrax*. Whilst ectoloph morphology is somewhat variable in procaviids, and visual assessment of its morphology is affected by wear, the Lemudong'o specimens accord closely with *Dendrohyrax*.

None of the Lemudong'o mandibular material is complete enough to employ any of the usual criteria (ratio of lengths of premolar row to molar row, length of diastemata relative to premolar and molar rows, depth of mandible beneath the rear of m/1 relative to molar row) used to separate *Dendrohyrax* from *Heterohyrax*. The lower dentitions of these two genera are extremely similar to each other, and it is virtually impossible to determine to which genus isolated teeth or even partial tooth rows belong.

The m/3s appear to be relatively large when compared to the molars of other procaviids, falling above the scatter for extant *Dendrohyrax* species. All the other cheek teeth (Figure 2) plot at the small end of the range of variation of extant *Dendrohyrax*. Given the small sample available, and the uncertainties involved in measuring procaviid teeth that are incorporated in tooth rows, it is not possible to decide whether the Lemudong'o tree hyrax possessed relatively large third molars, or not. Considering the fragmentary condition of the examined sample of Lemudong'o procaviids, it is not realistic to attribute them to a species, although it is noted that they are close in size to extant *Dendrohyrax validus*.

Paleoecological Considerations

Extant *Dendrohyrax* is an arboreal, forest-dwelling mammal, although it sometimes lives in rocky areas especially in high altitude situations. It is generally nocturnal, highly territorial and is a browser. There are several species recognized, and many subspecies have been named, although there is almost no agreement in the literature about the quantity and geographic distribution of these subspecies. Three species are generally accepted (Skinner and Smithers, 1990, p. 553–563): *D. dorsalis* in the West African rainforest, *D. arboreus* in seasonal forests of East and South Africa, and *D. validus* in drier forests of East Africa. Some authorities recognise that the limits between the three species are gradational, and on this basis have argued that there is only one species of tree hyrax (*D. arboreus*) with 15 subspecies (Haltenorth and Diller, 1980). In general, *Dendrohyrax* from humid forests are larger than those from drier environments. The Lemudong'o fossils belong to quite a small species (Figure 2), from which it is surmised that even though the Lemudong'o area was forested in the late Miocene, it would probably have been a relatively dry forest rather than a humid tropical forest.

Conclusions

The Lemudong'o material is too incomplete for employment of many of the usual criteria used to determine to which of the genera (*Dendrohyrax* and *Heterohyrax*) it belongs. It is clearly not a *Procavia*. However, the morphology of the ectoloph of the upper molars suggests that it belongs to *Dendrohyrax*. The most convincing evidence that the fossils represent *Dendrohyrax*, rather than *Heterohyrax*, is the morphology of the base of the mandibular symphysis. The presence of two ridges on the ventral surface of the symphysis only occurs in *Dendrohyrax*. Young individuals of this genus sometimes show no sign of this structure, in which case they are difficult to distinguish from *Heterohyrax*, but when the ridges are present there is little doubt that the specimen belongs to *Dendrohyrax*.

Dendrohyrax, as its name implies, is indicative of forest, as this genus is arboreal, and usually lives in holes in trees. It is mostly nocturnal, but does have some diurnal activity when conditions are suitable. It is a browser, the cheek teeth being brachyodont. The presence of this genus in the late Miocene deposits at Lemudong'o, Kenya, can be taken to mean that the region was forested during the late Miocene, and on the basis of the small size of the species, probably dry forest rather than rain forest.

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