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The deciduous dentition of *Griphopithecus alpani* from Paşalar, Turkey

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Abstract

Seventy-four hominoid primary teeth have been recovered from the middle Miocene site of Paşalar, Turkey, constituting the largest sample of deciduous teeth for any species of fossil ape. Morphological features that characterize the permanent teeth of *Griphopithecus alpani* from the site have also been identified in some of these deciduous teeth, including a lingual pillar on the di^1s. These features plus the overwhelming preponderance of *G. alpani* permanent teeth at the site suggest that all of the deciduous teeth belong to this species. Contrary to the situation in the permanent teeth, nothing in the morphology of the primary dentition suggests the representation of a second species. The age profile of the nonadult hominoids was reconstructed based on the degree and type of wear recorded on the dp4s, the most abundant deciduous tooth in the sample, assuming a similar eruption chronology to that of *Pan troglodytes*. This analysis indicates underrepresentation of very young individuals in the sample and high mortality for individuals belonging to the 3–5-years age cohort, a situation that could be due to the effects of stress related to weaning. The coefficient of variation and range-index values obtained for the majority of tooth types are equal to or greater than the comparable values in a sample of *P. troglodytes*, in some cases at much smaller sample sizes. One possible explanation for this is that there was greater sexual dimorphism in the *G. alpani* deciduous dentition than in *Pan*, which would mirror the condition of the permanent dentition.

Keywords: Miocene; Hominoidea; Fossil apes; Teeth; Variation; Development

Introduction

Among the nearly 2000 fossil hominoid specimens recovered from Paşalar through 1999 are 74 deciduous teeth, all of them isolated. Two species are represented in the Paşalar collection as a whole (Martin and Andrews, 1993; Kelley et al., 2008), one common and the other much less so, with the former representing more than 96% of the total numbers of specimens. The common species is attributed to *Griphopithecus alpani*, while the less common species has been assigned to a new species of *Kenyapithecus*, *K. kizili* (Kelley et al., 2008). However, only the former appears to be represented among the deciduous teeth (see below).

Deciduous teeth are uncommon at fossil sites because they are not as robust as permanent teeth. They are, therefore, much more susceptible than are permanent teeth to destructive factors during accumulation and to diagenetic and other taphonomic processes after deposition. As a consequence, the potential utility of primary teeth to provide important ontogenetic, phylogenetic, and paleobiological information has not been fully realized.

The primary aim of this study is to provide complete morphological descriptions of all the tooth types represented by the Paşalar deciduous teeth (Alpagut et al., 1990) and to evaluate the degrees of metric variation in the sample (Mortzou, 1999). In addition, we attempt to reconstruct the age profile of the nonadult individuals in the sample and to interpret the demographic implications of this profile.

Materials and methods

The 74 deciduous teeth from Paşalar are listed in Table 1, which also shows the year of recovery, indicated by the letter prefix of each specimen number. The abbreviation BP stands for ‘‘Bursa, Paşalar’’ and refers to the initial discoveries

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Table 1
Paşalar deciduous teeth according to tooth type and excavation number (A, collection year 1983, B, collection year 1984, etc.)

Tooth type	Specimen number
di_1	D81
di^1	F544, G1639, K1308, K1326, L1549, M924
di_2	D826
di^2	D300, D805, D857, G1137
dc_1	B564, C183, D767, D926
dc^1	–
dp_3	D296, D702, D911, L1575, M958
dp^3	D763, D865, F483, K1312, K1319, K1320, L1567, L1563, M1874
dp_4	BP16, A5, C110(b), C243, C244, C246, E574, F154, H840, K1386, L1554, M956, M1860, N1508, R1633, S1113, S1123
dp^4	BP80, BP81, BP82, BP1312, B585, C110(a), C245, C247, C262, D765, D912, D924, F134, H486, H939, H1658, K1324, K1374, K1392, L1517, L1537, L1576, K1812, M955, M957, N1509, T580

made by the Turkish-German team in 1969 (Andrews and Tobien, 1977). When fieldwork was resumed in 1983, an alphabetical coding system was employed, with the letter A representing the first season and so on (Alpagut, 1990). The letters I, J, O, P, and Q were not used.

Sample sizes range from one in the case of the lower incisors up to 17 and 27, respectively, for the lower and upper dp4s. No upper deciduous canines have been found, but this tooth is the only type entirely absent. The minimum number of individuals (MNI) is 15 based on the frequency of the left dp^4, using all teeth that were sufficiently well-preserved to allow reliable identification and to provide useful metric data.

Because sample sizes for some teeth are small, we have calculated range-based statistics in addition to the coefficient of variation (CV). Range-based statistics underestimate variation at small sample sizes, while the CV tends to overestimate it (Martin and Andrews, 1993; Plavcan and Cope, 2001; Humphrey and Andrews, 2008). The maximum/minimum index (MI) is defined as the maximum value divided by the minimum value; the mean-adjusted value of the range (R%) is defined as (maximum − minimum)/mean × 100 (Martin and Andrews, 1993).

All measurements were taken with a sliding digital caliper and were recorded to within 0.1 mm. Sample parameters were calculated for each tooth type where sample size exceeded four. The intraobserver measurement error was within the range of 0.5 and 2.7%, while the interobserver error (measured independently by PA and GM) was within the range of 0.7 and 3.3% (calculated according to the method described in White, 1991: 292).

The same measurements and indices were obtained from a comparative sample of 30 infant, juvenile, and/or subadult *Pan troglodytes* specimens from the Natural History Museum, London. Both maxillary and mandibular dentitions were present on 25 of these individuals, although in more than half of the specimens, various teeth were either damaged or missing. The remaining five individuals were represented by three mandibles and two maxillae, again with varying degrees of dental preservation.

Chimpanzees were chosen for the comparative sample for two reasons. First, chimpanzee deciduous teeth are closer in overall morphology to those of *Griphopithecus alpani* than are those of any other extant ape. This criterion was important for the analysis of morphology and for estimating developmental stages based on deciduous teeth. Orangutans have complex secondary wrinkling of the teeth that makes morphological comparisons difficult. Their dental development is also poorly known (Dean, 2000). Second, eruption data for deciduous and permanent teeth are better for chimpanzees than for other extant apes (eruption being equated with gingival emergence) (Smith et al., 1994: Tables A32, A62, A63). Following the system introduced by Smith et al. (1994), age estimates for the Paşalar specimens are given in decimal years (i.e., days were divided by 365, months by 12, etc.), and data are not separated by sex. Smith et al. provided separate tables for chimpanzee males and females, which we combined to produce a species mean for the purposes of this study.

Descriptions

Upper central incisors (right di^1s: K1308, K1326; left di^1s: F544, G1639, L1549, M924)

The presence of two species at Paşalar is based in part on the presence of two distinct morphologies among the permanent I^1s (Alpagut et al., 1990; Martin and Andrews, 1993; Kelley et al., 2008). The morphology of the six Paşalar di^1s is identical to that of the more common morph at Paşalar, assigned to *Griphopithecus alpani* (see Alpagut et al., 1990; Kelley et al., 2008) The crown is low though robust, and the mesiodistal length is greater than either the labiolingual breadth or crown height (Fig. 1). The appearance is that of a broad but labiolingually compressed tooth, an impression that is further enhanced by the relatively flat and smooth buccal surface, which lacks the convexity typical of di^1s. In addition, the crown is strongly asymmetric due to the gently sloping and rounded distal-end corner of the tooth incisally, which contrasts strongly with the sharply angled mesial corner.

The distinctive character of this incisor morphology lies in the lingual surface of the crown. The cingulum is of moderate size, and extends over the entire length of the lingual surface. At the mesial and distal margins of the tooth, it rises towards the incisal edge, thus forming the mesial and distal marginal ridges, respectively. These are well defined (the mesial one more so) and follow the general outline of the crown; accordingly, the former is longer and straighter, while the latter is shorter and weaker, meeting the sloping distal incisal margin at a lower level. At the approximate midline of the lingual surface, a robust and broad pillar rises from the cingulum towards the incisal edge. The pillar is triangular in outline, broad at its base and progressively narrowing to a pointed apex shortly before it reaches the incisal edge of the crown. Fossae are present between the lingual pillar and the two marginal ridges.

Metrically, the Paşalar di^1s are both smaller and less variable than those of the chimpanzee sample (Tables 2 and 3), although the lower variability is expected given the much smaller size of the Paşalar sample.