

Molar Wear Stages in *Theropithecus gelada*
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Questions of paleoecology are among the most challenging and difficult to deal with of those confronting the student of the past. Once fossil remains have been recovered, once basic taxonomic assignments have been made and possible phylogenetic lines traced, it remains to attempt a synthesis of all the available geological and paleontological evidence, guided by principles derived from contemporary studies of ecology and environments. For such an analysis of the past it becomes important to have data on factors such as the number of individuals preserved per species, portion of the body preserved per individual, and population parameters such as the sex and age of preserved specimens. These are features which are of relatively little importance during the initial phase of taxonomic description, but which become vital for more complex analyses. Interest in taphonomy, the study of all the processes which intervene between the living and fossil assemblages, is currently increasing in paleoanthropology (Behrensmeyer 1975, 1976). As detailed cases are studied and principles established, taphonomic considerations will undoubtedly be more explicitly involved in interpretations of all kinds of fossil occurrences. It will probably never be possible to eliminate the effects of all the factors which have acted to distort our view of the past. The best we can hope for is to minimize these. To do this we must extract as much information as possible from the faunal and floral remnants which have been preserved and from their geological context.

In recent years there has been a noticeable increase in interest in and publication on fossil Cercopithecidae (Delson 1975; Jolly 1972; Freedman 1976; Leakey and Leakey 1973a, 1973b). In African Plio-Pleistocene fossil localities, monkeys are frequently recovered. Probably the largest collection of fossil cercopithecids is that from the Omo Group deposits of southwestern Ethiopia (Eck 1976). At this writing the Omo fossil catalog maintained in Dr. F.C. Howell's laboratory contains 6363 cercopithecoid entries. Of these, 2563 have been identified as *Theropithecus*. With such a large sample, it seemed reasonable to attempt a detailed study of the number of individuals present and the nature of their remains throughout a span of about two million years (Meikle, in progress).

As a preliminary to this projected study of Plio-Pleistocene fossil *Theropithecus* (*Simopithecus*) from the Omo Valley, an attempt has been made to construct a relative scale of molariform tooth wear for the living

gelada monkey, *Theropithecus gelada*. Criteria of age determination in fossil mammals are limited to symphyseal union and sutural closure and to dental eruption, replacement, and wear. Since fossil collections rarely include associated body parts and so frequently consist largely of jaws and teeth, attempts to assign relative or absolute ages to fossils will almost always be confined to the use of dental events.

Bramblett (1969) has established an age scale based on tooth wear for *Papio*, following the method used for *Homo sapiens* by Miles (1963; see also Zuhrt 1956; Mann (1975) has assigned ages to South African australopithecines in a similar way). This method consists essentially of the following: for all applicable members of a sample, observe the state of wear or dentine exposure of each molar of a toothrow which has a more posterior molar just erupting. If ages of eruption and occlusion are known, one can correlate the "functional age" of a tooth, the length of time it has been in use, with the amount of wear which has occurred on its occlusal surface. By reversing this procedure, individuals of unknown age can be assigned an age based on the amount of wear on their teeth. For example, assume that, in humans, the M1 comes into occlusion at age six years, the M2 at twelve years, and the M3 at eighteen years. At twelve, just as the M2 becomes functional, M1 will have been in use for six years. At eighteen, M3 will be erupting, M2 will have a functional age of six years, and M1's functional age is twelve. Therefore, if rates of wear are constant, the M2 should now have approximately the same wear pattern as M1 did when the person was twelve. Similarly, M3 should reach this "six-year" pattern when the individual is about twenty-four, at which time M2 (functional age of twelve) will be as worn as M1 at eighteen, and M1 will have a functional age of eighteen. By extrapolating it is possible to extend such a relative system well into adulthood, where such criteria as age of eruption or replacement of teeth are no longer useful. See Miles (1963) for more details and complications; he suggests that, in *Homo sapiens* at least, the rate of wear is not exactly the same for all three molars. However, Mann (1975:51) did not encounter this problem in australopithecine samples.

The scale devised and illustrated by Bramblett (1969) for *Papio cynocephalus* works on exactly the same principle. However, since the teeth, especially the molariform teeth, of *Theropithecus* are quite distinct from those of *Papio* (Jolly 1972), it is not possible to use the same scale for this genus. The unique morphology

of *Theropithecus* molars has been described by Jolly (1972) and Delson (1975), and does not need to be repeated here. Because of such features as greater relative crown height and columnar cusps, molars of *Theropithecus* display a wear pattern which differs considerably from that of *Papio*, although certain elements are shared by the patterns of both genera.

As pointed out by Jolly (1970), there is a relatively steep wear gradient in the molars of *Theropithecus* compared, for instance, to *Papio*. This means that at any given age, more anterior molars show heavier wear relative to that of more posterior teeth than in other cercopithecines. In addition, there are clear differences in detail of molar wear pattern between *Papio* and *Theropithecus*. In *Papio*, wear at first heavily affects the buccal half of lower molars (lingual of uppers), while only gradually affecting the opposite half. Only after considerable wear is there dentine exposure across an entire loph(id); very shortly after this stage, surface detail of the tooth is obliterated, leaving a dentine "lake" surrounded by an enamel rim (see drawing in Bramblett 1969:163). In *Theropithecus*, on the other hand, attrition soon produces more even dentine exposure across the width of the loph(id)s. This might be caused by a greater horizontal component in the *Theropithecus* chewing cycle, compared to *Papio*. Because of the height of *Theropithecus* cusps and the depth of the clefts and basins, the *Theropithecus* molar retains occlusal surface features longer than *Papio* molars. This is reflected in the amount of time during which dentine "lakes" exist separately on the loph(id)s and in the persistence of the "hourglass"-

figure once it develops (see below). Jolly (1972:20) points out that *T. (Simopithecus)* is also distinguished by the length of this stage. Wear scales based on *Papio* cannot help but give inconsistent ages for *Theropithecus* under these conditions. Therefore, a new scale for *Theropithecus* has been constructed.

Since upper and lower molars of *Theropithecus* are in some ways close to being mirror images of each other (Jolly 1972) and since both members of an occluding pair have been consistently found to display similar amounts of wear, quite similar wear stages can be defined to describe upper and lower dentitions. These will be outlined separately below. The stages described here were developed by study of the dentition of nine *Theropithecus gelada* now in Dr. F.C. Howell's laboratory at the University of California, Berkeley. Six of these animals had been wild-shot in Ethiopia; the other three died in zoos. They range from juvenile (M2 just erupting; dC, dP3-4 still present) to adult; five are male and four are female. Although this sample is small, the pattern of molar wear observed is so consistent in all these animals that I have considerable confidence in its generality for *T. gelada*. In addition, the observed wear patterns have been found to be similar to those in the much larger sample of fossil *Theropithecus* from the Omo. Terminology follows Delson (1975).

Molar Wear Stages (see Figure 1)

Lower dentition: Stage 1. Tooth unworn. Used for molars which are unerupted or otherwise not yet in occlusion. Once full occlusion is reached, the tooth does not remain at this stage very long.

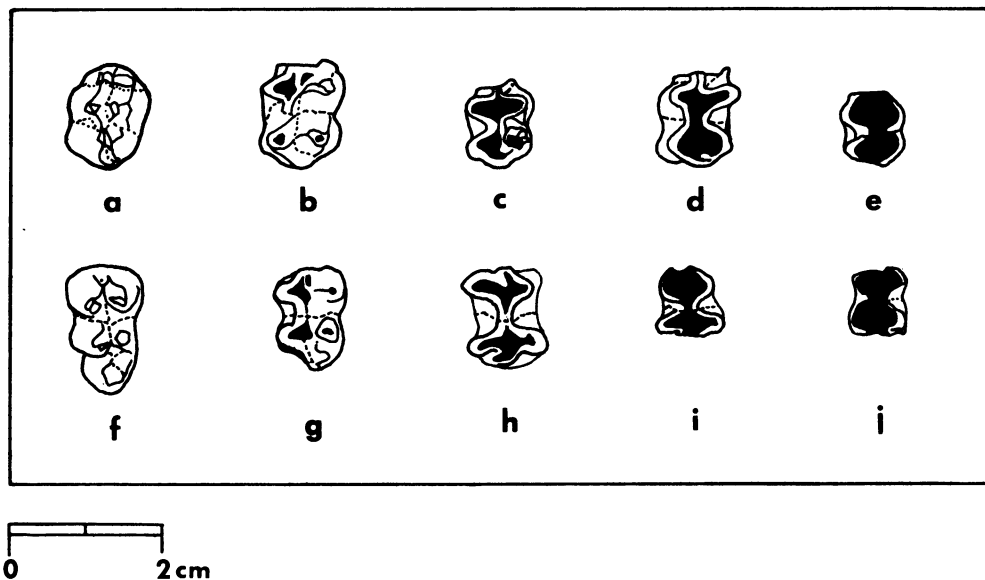


Figure 1. Occlusal views of *T. gelada* molars as examples of wear stages. (a)-(e) are upper molars, (f)-(j) are lowers. Stage 2:(a), (f); Stage 3:(b), (g); Stage 4:(c), (h); Stage 5:(d), (i); Stage 6:(e),(j). Enamel shown in white and and dentine in black. In Stage 2, enamel facets are indicated by encircled white areas. (Stages 1, 7, and 8 not illustrated)

Stage 2. "Facets" start to appear on the enamel; however, no part of the crown is worn enough to expose the underlying dentine. The enamel facets are best seen by holding the specimen under a good light and slowly turning it in various directions. The facets are shiny, reflecting surfaces, most of which appear at or towards the top of the columnar molar cusps. Further use and wear on these highest points on the tooth crown result in the next stage.

Stage 3. Circles of dentine appear on the tooth crown at the cusp apices. The buccal cusps are affected before the lingual ones. The protoconid is the first cusp with dentine exposure, and throughout this stage it continues to have the largest area of dentine. Usually the hypoconid is the second cusp affected and has the second largest dentine area. The metaconid is the last cusp affected. During this stage the size of all the dentine exposures increases, but there are no connections between them.

Stage 4. Total dentine area exposed is increased. The buccal and lingual areas of dentine start to merge along the metalophid and hypolophid, although dentine exposure is still noticeably greater on the buccal half of each lophid. Because of the relative height of the cusps and depth of the enamel-covered talonid basin and median buccal notch, there is no dentine contact between these mesial and distal dentine areas.

Stage 5. The dentine areas exposed form larger and more symmetrical "lakes", with more even contributions from buccal and lingual halves of each lophid. There is the beginning of mesio-distal dentine contact between the metalophid and hypolophid "lakes". Wear now starts to remove the enamel surface of the deepest parts of the talonid basin and of the median buccal cleft. Also during this stage, interstitial wear has progressed enough to result in the loss of the enamel margin at the mesial and distal borders of the tooth (mesially only in M_3). At first this dentine exposure along the margin occurs over only a small area, but it soon spreads buccally and lingually as interstitial wear continues. When viewed from above, teeth in this stage of wear display a very narrow-waisted "figure-eight" or "hourglass" of dentine. The removal of enamel rims by interstitial wear results in direct contact between dentine and the mesial and/or distal margins of neighboring teeth.

Stage 6. The hourglass-shaped dentine surface of the tooth remains well-defined by the enamel floors of the talonid basin and median buccal cleft. However, the waist becomes steadily wider as these floors are worn away. Interstitial wear also continues, widening the area of dentine contact with neighboring teeth initiated in the previous stage. Often teeth in this stage will have broad dentine-dentine contact with their neighbors because of this wear.

Stage 7. At this stage all or almost all crown detail of the molar has been removed by wear. The tooth is worn down almost to its neck. There is a simple, planar

dentine area filling the occlusal surface. This is bounded by a narrow enamel rim lingually and buccally; mesially and distally, interstitial wear has resulted in very broad dentine exposure, and little enamel remains along these rims. (This stage was approached, but not reached, in the *T. gelada* sample studied. It has been observed in fossil *Theropithecus* specimens.)

Stage 8. The entire crown is worn away. No enamel remains. Wear is progressing onto the roots. (This extreme stage has been found in only one fossil specimen so far. It was not found in the *T. gelada* sample.)

Upper dentition (Since upper and lower wear stages are similar, these will be discussed in less detail):

Stage 1. Tooth unworn.

Stage 2. Enamel facets appear at or near cusp apices.

Stage 3. Dentine circles appear, first on the lingual cusps and then on the buccal ones. The protocone is affected first and at any time has the largest dentine exposure. Paracone and hypocone exposures are often about the same size. The metacone has the smallest dentine area. No connections exist during this stage between any of these dentine areas.

Stage 4. There is a dentine connection between protocone and paracone along the paraloph. Dentine exposure on the hypocone is noticeably greater than that on the metacone, and during this stage these areas start to merge along the metaloph. Mesio-distal connection between the dentine of these lophids is prevented by the enamel of the trigon basin and median lingual notch. Interstitial wear has reduced enamel thickness mesially and distally, but there is still a complete enamel rim around the tooth margins.

Stage 5. Both paraloph and metaloph are worn through to dentine. There is the beginning of dentine contact between the lophids, and a narrow-waisted hourglass of dentine is established. Interstitial wear breaks through the enamel of at least the mesial border of the tooth, if not both mesial and distal borders.

Stage 6. The hourglass waist widens as wear removes the enamel of the median lingual and buccal clefts. Interstitial wear continues.

Stage 7. Wear nears the tooth neck, leaving little surface detail. An enamel rim remains only along the lingual and buccal tooth margins.

Stage 8. The crown is worn away entirely. (As in the lower teeth, Stages 7 and 8 were not observed in the *T. gelada* sample.)

Application of these stages to assign ages to individual specimens depends on a kind of seriation by amount of wear. Functional ages are deduced by correlation with stage attained as more posterior molars come into occlusion. Assignment of "absolute ages" thus depends crucially on accurate knowledge of the interval between tooth eruptions. Obviously this information will never be available for fossil species. In

fact, I know of no published data on age of tooth eruption or interval between molar eruptions in *T. gelada*. The most useful substitute is probably data for *Papio*. It seems likely that age of eruption is correlated with body size and with length of developmental periods. Comparisons of *Papio* and *Macaca* show that the teeth, deciduous and permanent, of the former consistently come into occlusion later than those of the latter (Siegel and Sciulli 1973; compare also Reed 1967 and Freedman 1962 with Hurme 1960). Living geladas are within the considerable range of variation in size found in *Papio*. Many fossil *Theropithecus* specimens are quite large, but as a group they overlap the top of the *Papio* size range. Because of this lack of data, ages assigned to *Theropithecus* by this method are not truly "absolute." However, I am confident that they can be of the right order of magnitude. In any case, relative age attained at death can be accurately calculated.

There have been relatively few attempts to apply demographic methods of analysis to fossil mammal populations (Clark and Guensburg 1970; Kurtén 1953, 1958; Van Valen 1964a). Even if detailed studies are prevented by the incompleteness or scatter (through time and space) of specimens from the Omo, the attempt may still prove worthwhile. The nature of the fossil assemblages may provide clues as to how they accumulated, and thus to paleoenvironments. Taken in conjunction with detailed geological studies and with the evidence of other fossil remains, interpretations of associations or communities of the past may be possible. This, in turn, contributes to our understanding of the processes and contexts of human evolution. Previous attempts to reconstruct paleocommunities based on abundance and preservation of fossils (Shotwell 1955, 1958, 1963) have been seriously criticized because of their implicit assumptions (Voorhies 1969, 1970; Clark, Beerbower, and Kietzke 1967). There do not seem to have been very many efforts to derive information related to populations from the mammalian fossil record, or to establish limits on what can be derived (Guthrie 1967, 1968; Van Valen 1964b; Wolff 1973).

Of course, data from the fossil monkeys alone will clearly be insufficient to answer many questions. They form, after all, only a portion of the total preserved fauna from any site. However, it seems possible that a detailed study of this portion, which can be conveniently compared with ecological studies of living monkey species (Altmann and Altmann 1970), may provide significant information when combined with other available paleontological and geological evidence. This is only one step towards a better understanding of the past, but it may clarify what is possible and what kinds of inferences it is still impossible to draw in reconstructing the puzzles of evolution.

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