



## A deciduous and permanent dental wear stage system for assessing the age of *Trachypithecus* sp. specimens (Colobinae, Primates)

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### ABSTRACT

Although Colobine monkeys are one of the most common prey hunted by Southeast Asian prehistoric humans, no data concerning tooth eruption and wear are available for these species. Dental wear eruption and attrition are used for attributing ages to individual fossils in order to construct mortality curves, and are also useful in reconstructing fossil life histories. Such wear sequences partly exist for Cercopithecines. Although Cercopithecines and Colobines are both bilophodont, they present significant differences in terms of diet, detailed tooth morphologies and occlusion. This paper aims to formulate a guide for the dental eruption and attrition of extant *Trachypithecus* specimens, the most folivorous of all the Colobines. We also propose to calibrate the eruption and wear stages that we define here with absolute ages available in the literature.

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### 1. Introduction

The abundance of non-human primate remains in recently excavated Asian archaeological sites raises questions concerning the human hunting strategies of these prey (Sémah et al., 2004; Setiagama Fadjar, 2006; Ingicco, 2010; Sémah and Sémah, in press). Hunting strategies are commonly explored by zooarchaeologists through age-at-death profiles, by identifying the peaks and lows of longitudinal age classes in both natural and archaeological populations. Age attribution methods based on patterns of the timing of anatomical modifications include post-cranial epiphyseal unions, craniofacial sutural closures, tooth growth, dental replacement sequences and tooth attrition (e.g. Tappen and Severson, 1971; Wintheiser et al., 1977; Cheverud, 1981). Tooth eruption and attrition are among the most common methods used in zooarchaeological studies, as dental modifications occur over the entire lifespan (Grant, 1982; Klein and Cruz-Uribe, 1984; Reitz and Wing, 2008). The predominance of this method may also be explained by the better preservation of teeth in palaeontological and archaeological assemblages (Swindler and McCoy, 1965). This is particularly true in Asian archaeological sites, where bones are intensively gnawed by porcupines and only tooth crowns are

preserved (Storm and de Vos, 2006; Wang, 2009). The dental wear age attribution system is certainly the best adapted system for establishing Colobine age-at-death profiles for fossils recovered from Asian archaeological sites. However, data from extant specimens are very scant for non-human primates, especially for Colobines.

The main work concerning dental wear sequences in non-human primates is the study by Welsch (1967) of the tooth attrition of 7126 specimens, representative of all the primate families. He established a tooth wear sequence for each genus studied. Although this work constitutes a detailed illustration of wear, very few stages are described ( $n = 4$ ). Delson (1973) summarized the general evolution of molar and premolar wear in Cercopithecines. He proposed a cusp wear gradient corresponding to a score. The scores of each cusp of a given tooth are then added together to obtain the relative age of the individual. Unlike the Welsch sequence (1967), the sequence proposed by Delson (1973) presents an adequate number of stages but appears too simple to eliminate the inter-observer error margin. Gantt (1979) described wear stages mainly for Cercopithecine molars (*Macaca nemestrina*, *Macaca mulatta* and *Papio cynocephalus*). The inadequacy of these systems for zooarchaeological purposes is underlined by the development of personal unpublished dental wear sequences by different scholars (Brain, 1981; Piper et al., 2008). It is thus necessary to elaborate a reference system that can be used by the whole community and that will produce

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comparable data. We provide here such a system for Colobines, that will be a complement to the already existing tables for Cercopithecines.

### 1.1. The Colobines diet

The Colobine diet consists principally of leaves. Seeds are also present in their nutrition in varying degrees, depending on the species considered and the season of the year. The unique Colobine diet is sustained by their multi-chambered stomach and forestomach (Kool, 1992). We decided to focus our study on the *Trachypithecus* clade, which is the most folivorous genus of the primates (Caton, 1999; Nijman et al., 2000), but the wear system that we propose here can be used for all the Colobines as teeth are very conservative in this group (Jablonski, 2002). Following Chivers (1994), leaves represent 54% of the *Trachypithecus* diet, fruit and flowers account for 14% each and seeds for 13%. Kool (1993) notes similar proportions with 46% of leaves (young leaves accounting for 45%), 15% of fruit and seeds and 7% of seeds only. The original Colobine diet partly reflects their habitat preference which tends to be more confined to forests and woodlands than Cercopithecines (Bennett and Davies, 1994). Such different ecologies between Colobines and Cercopithecines could give rise to different hunting strategies in prehistoric groups.

### 1.2. Occlusion and eruption patterns

Both Colobines and Cercopithecines share the same dental formula with other Catarrhines (2-1-2-3 in each quadrant) and the same general tooth morphology, as they are bilophodont (meaning that molar cusps are linked two by two by transversal ridges called lophs). However, important differences exist between the two clades in terms of occlusion and detailed tooth morphology (Fig. 1) (Verheyen, 1962). The tendency to underbite is very common in leaf-monkeys (Swindler, 2002). Miles and Grigson (1990) note this occurrence in 35.9% of 985 leaf-monkey specimens, for only 1% in Cercopithecines. Colobines have higher cusps linked by sharper lophs and separated by deeper notches on molars compared to Cercopithecines. Following Kay (1977), this morphology allows for better occlusion than in Cercopithecines. For their part, Lucas and Teaford (1994) propose that the sharp lophs in Colobines are mainly dedicated to fracturing seeds. Food is sheared by the crests and the buccal cusps and crushed mainly by the lingual cusps (Kay and Hiiemae, 1974).

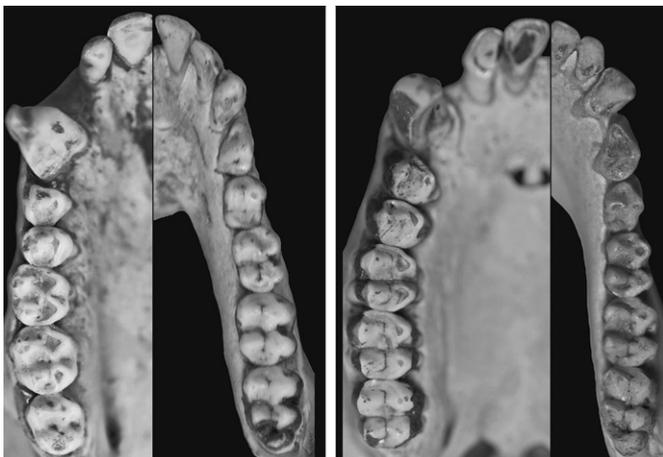


Fig. 1. Comparison between Cercopithecine (left) and Colobine (right) teeth.

Also, the sequence of eruption of permanent teeth is not the same in Colobines and Cercopithecines. The main difference is the inverted eruption of the second incisors and the second molars. In Colobines, the second molars erupt before the second incisors, and the fourth premolars before the third premolars (Harvati, 2000), while the opposite occurs in Cercopithecines (Schultz, 1935; Cheverud, 1981; Smith, 1994). On the other hand, no data is available for the emergence of the deciduous tooth sequence. Yet there is a close relationship between the gradient of tooth wear on an arch and the date of tooth eruption (Reitz and Wing, 2008). Both are informative for the construction of age-at-death profiles. Moreover, the relative length of tooth eruption is important for life histories (Harvati, 2000; King, 2004; Harvati and Frost, 2007; van der Geer and Dermitzakis, 2008; Borries et al., 2011). This point was already raised in the work of Schultz (1935), but has not been taken into account by all the later studies (King, 2004). Schultz (1935) referred to the length of eruption as the resting period.

### 1.3. Permanent dentition

The upper lateral incisors are canine-like and the lower lateral incisors have a salient lateral cusp (Olivier, 1955). As in all Cercopithecids, the mesial lingual face of the upper canines and the distal face of the lower canines are hollowed into a groove (Lucas and Teaford, 1994). Nevertheless, the groove is not as deep in Colobines as in Cercopithecines. The distal heel present on the lower canines is less developed than in Cercopithecines (Lucas and Teaford, 1994; Olivier, 1955). The protocone is reduced in Colobine third upper premolars compared to Cercopithecines (Delson, 1973; Swindler, 1976; Lucas and Teaford, 1994). Colobines differ mainly from Cercopithecines in that they have a less prominent distolingual crest extending from the fourth lower premolar protoconid. The fourth lower premolars are molariform in Cercopithecines and similar to the third lower premolars in Colobines (Hornbeck and Swindler, 1967). In Colobines, the fourth lower premolars have a wider protoconid than metaconid whereas the opposite is true of Cercopithecines (Delson, 1973). The trigonid fossa is much narrower than the talonid fossa in Colobines, unlike in Cercopithecines (Hornbeck and Swindler, 1967). The morphologies of upper and lower Colobine and Cercopithecine molars are completely different. The cusps are more prominent in Colobines with a wider inter-cusp width than in Cercopithecines (Fig. 1) (Olivier, 1955; Delson, 1973; Kay, 1977; Lucas and Teaford, 1994; Swindler, 2002). The lingual cusps on Colobine lower molars and the buccal cusps on the upper molars are the tallest. A fifth additional distal cusp (hypoconulid) is present on the third lower molar (Willis and Swindler, 2004).

### 1.4. Lacteal dentition

The Colobines deciduous dental formula is the same as that of other Catarrhines (2di,1dc,2dp in each quadrant). In contrast to the permanent incisors, the lateral deciduous incisors are larger than the central ones (Olivier, 1955). A talon, almost individualised as a cusp, is present on the distal face of the deciduous canines (Olivier, 1955). As for the permanent molars, the deciduous premolars have four cusps, but the teeth are more elongated. Although the second upper deciduous premolars are similar in size to the first upper permanent molars, the inter-cusp width is narrower. The same is true of the second lower deciduous premolars. This tooth also has a well-developed mesial shelf (Olivier, 1955).

Considering all the specificities of Colobines compared with Cercopithecines, the available dental replacement sequences and tooth attrition tables are inadequate. The purpose of this paper is to

propose a complete dental eruption and attrition sequence for juveniles and adults of the *Trachypithecus* clade. We also indicate the resting period between the eruption of two teeth. The aim is to provide a guide for zooarchaeologists to tooth wear in this taxon and new data for the *Trachypithecus* life history. A relative age system for Colobines may also be applied to efforts to track the demography of threatened populations.

**2. Materials and methods**

Our sample is composed of 141 adults and 47 juveniles wild shot individuals of the *Trachypithecus* genus from five species: *Trachypithecus auratus* (n = 137), *Trachypithecus cristatus* (n = 35), *Trachypithecus obscurus* (n = 6), *Trachypithecus vetulus* (n = 8) and *Trachypithecus johnii* (n = 2). The specimens are curated at the Natuurhistorische Museum (Leiden, the Netherlands) and at the Muséum national d'Histoire naturelle (Paris, France). No pathological individuals were included in our sample.

We decided to group males and females together as no differences have been correlated to gender, including the relative wear degree of the canines and the third lower premolars. All the individuals without all their permanent teeth in occlusion were considered as juvenile.

The eruption, replacement of deciduous by permanent teeth and attrition of deciduous and permanent dentition were visually assessed on maxilla and mandibles and each tooth was assigned to one stage. For juveniles, the eruption of a new tooth implies a new stage. Since the wear on a tooth is a continuous process, the definition of a new stage in adults is more subjective. We change stages in function of the gradient of wear on each cusp. This is the principle already used by Welsch (1967) and Delson (1973) for non-human primates and Grant (1982) for domestic pigs. Each stage is illustrated in Figs. 3 and 4.

We preferred not to use metrics in the definition of stages, as the simplest method is the description of the sequence and this is the easiest to use in the field by zooarchaeologists. When left and right sides presented different wear stages, the less worn side was taken into account. Thus, an intermediate wear stage described here would be classified in the lower stage.

The duration of tooth eruption is registered by recording the time when the tooth pierces the gingiva and the time it enters into occlusion. This enabled us to construct Table 1, which summarizes the chronological order and the relative duration of tooth emergence. Also, the term “erupted” used in the results and conclusions refers to a tooth in occlusion.

We employ here the zoological and morphological terminology for teeth used by Swindler (2002, p. 11).

**3. Results**

**3.1. Complete dental eruption sequence**

The complete dental eruption sequence is described in Table 1, and introduces the simultaneous presence of deciduous and permanent teeth.

In the genus *Trachypithecus*, the eruption of di1 and di2 is synchronous. This is very quickly followed by the eruption of dp1. Then dc erupts and finally dp2. This sequence was observed on both the maxilla and the mandible. The sample size for the different specimens is small but all the eruption stages of deciduous teeth are represented, including individuals without any erupted teeth.

M1 is the first permanent tooth to erupt and takes place behind dp4. The I1 erupts, replacing di1. The same sequence is observed for M2 and I2. M2 takes place behind M1 and I2 replaces di2. P4 pierces the arch bone, and before entering into occlusion, P3 does the same. When P4 is in occlusion, M3 pierces the arch bone. Then, P3 fully erupts. C pierces the arch bone and fully erupts before M3 enters into occlusion. This sequence is true for both the maxilla and the mandible.

**3.2. Dental wear sequence**

Fig. 3 presents the dental wear stages for juveniles and Fig. 4 shows the dental wear stages for adults. Stages beginning by the letter J refer to juveniles and stages beginning by the letter A refer to adults. Although this illustration is self-contained, we describe the different wear stages here.

*Stage J1:* Synchronous eruption of di1, dc and dp1.

*Stage J2:* Eruption of di2. di1, dc and dp1 are not yet worn.

*Stage J3:* Eruption of dp2. di1, di2, dc and dp1 begin to wear, at the top of the occlusal face for the buccal teeth and on the lingual side of the dp<sup>1</sup> and the buccal side of the dp<sub>1</sub>.

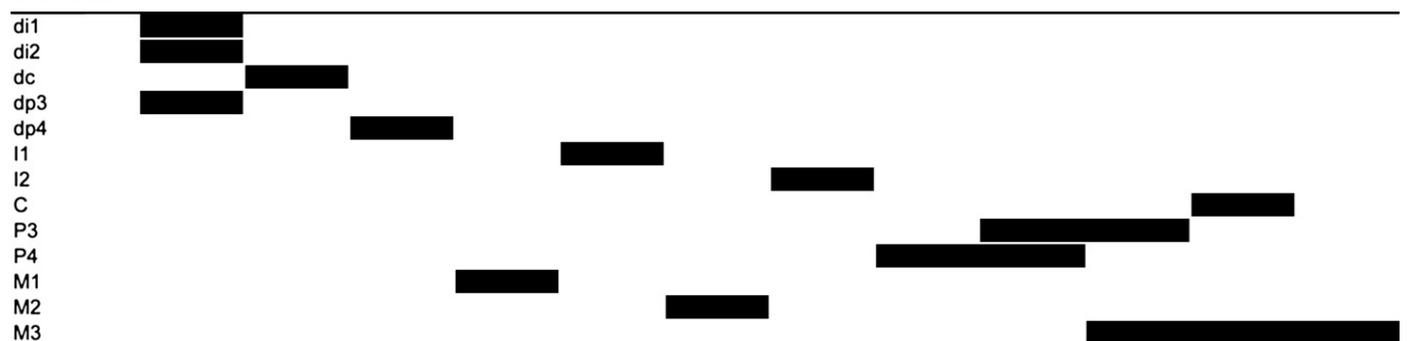
*Stage J4:* Eruption of M1, then I1. The wear of deciduous labial teeth develops on more than half of the occlusal face and the wear of the buccal deciduous teeth extends on the buccal cusps for dp<sup>1</sup> and dp<sup>2</sup> and lingual cusps for dp<sub>1</sub> and dp<sub>2</sub>.

*Stage J5:* Eruption of M2, then I2. The wear of dc occurs on all of the occlusal face and the wear of dp1 and dp2 develops between cusps. A loss of enamel appears on the apical face of I1 as a polish on the apical face of I2. The top of the lingual cusps of M<sup>1</sup> and of the buccal cusps of M<sub>1</sub> begins to wear.

*Stage J6:* Eruption of P4, loss of dc and dp1. C and P3 pierce the bone. The wear of lingual cusps on M<sup>1</sup> and buccal cusps on M<sub>1</sub>

**Table 1**

Eruption sequence and resting periods of deciduous and permanent dentition. The black bars represent the relative length of tooth eruption. For example, M3 pierces the arch before C but fully erupts after this one. Then, the black bar for M3 begins before C and ends after C. This diagram enables us to visualize with precision the synchronous eruption of two teeth.



enlarges. A polish develops on the  $M^2$  paracone and the  $M_2$  protoconid.

*Stage J7:* Eruption of P3 followed by C. The loss of enamel continues on the  $M^1$  lingual cusps and  $M_1$  buccal cusps. A polish develops on the  $M^2$  metacone and the  $M_2$  hypoconid, as on the P4 metaconid.

The eruption of the last tooth, the M3, is the sign of maturity. The wear of the permanent teeth continues. The following stages characterize adult individuals.

*Stage A1:* The wear of I and C extends bucco-lingually on the apical face. Wear appears on the P4 paraconid. The wear facet on the lingual side of the occlusal face of  $M^1$  and the buccal side of  $M_1$  is goose foot-shaped. The wear on the lingual face of  $M^2$  and buccal face of  $M_2$  expands. There is no visible dentine.

*Stage A2:* Wear on I and C covers the whole apical face. A dot of dentine appears on the P3, on the  $M^3$  metacone and the  $M_3$  hypoconid. The wear facet on P4 enlarges. Wear extends on the buccal side of the occlusal face of  $M^1$  and the lingual side of  $M_1$ . The wear facet on the lingual side of the occlusal face of  $M^2$  and the buccal side of  $M_2$  spreads.

*Stage A3:* The wear facet of I and C extends towards the crown base. The wear facet of the premolars extends, as does the wear facet of the M1 entoconid. A dot of dentine appears on the  $M^2$  and  $M^3$  paracone and metacone and on the  $M_2$  and  $M_3$  metaconid and entoconid, as on the hypoconulid. The wear facet is goose foot-shaped on the lingual side of the occlusal face of  $M^2$  and  $M^3$  and on the buccal side of  $M_2$  and  $M_3$ .

*Stage A4:* The wear facet on I and C extends from the apex to the crown base. The wear facet links the cusps of the premolars and the M1. Wear develops on the  $M^2$  and  $M^3$  paracones and metacones and on the metaconid and entoconid of  $M_2$  and  $M_3$ , as on the hypoconulid.

*Stage A5:* I and C reduce in size. The wear facet reaches the trigonid fossa on the premolars. A thin filament of enamel remains on the M1 contour. The wear facet links the cusps of the M2 and M3.

*Stage A6:* A thin filament of enamel remains on the incisors and C, and the pulp is visible under the dentine of the latter. The wear facet of the M1 reaches the crown base. The relief of the P3, P4, M2 and M3 cusps is no longer visible.

*Stage A7:* The incisors and C are worn out and the pulp is visible below the remaining dentine. A thin filament of enamel remains on the contour of the premolars. There is no more enamel on the M1. The wear facet of the second and third molars reaches the base of the crown.

### 3.3. Absolute age designation

The detailed presentation of tooth wear in the toothrow (Figs. 3 and 4) helps to estimate age and link isolated teeth with partial fossil dentition, such as upper and lower teeth from a palaeontological population.

As it stands, this method can only be used to give an indication of the relative ages of animals which is sufficient to calculate the minimal number of individuals in an archaeological site. Histograms can easily be constructed from these tables in order to establish the age structure of an archaeological or palaeontological population. Nevertheless, dental wear stages may be useful once ages are assigned to each specimen. From the data available in the literature, many of the stages presented in Figs. 3 and 4 may be correlated with an absolute age. Bolter (2011) mentions that under 4 months, all the deciduous teeth have not yet erupted, meaning that they are not yet in occlusion. This corresponds to stages J1 and J2. These two stages also correspond to the neonate category of Schillaci (2007). From 4

months to 1 year, all the deciduous teeth have erupted and no permanent tooth is present on the dental arch (Bolter, 2011; Godfrey, 2001). This is stage J3. This latter stage corresponds to the infant category of Schillaci (2007). For Schultz (1940), the infant category corresponds to stage J3 grouped with stages J1 and J2. The M1 erupts between 1 and 2 years old, corresponding to stage J4, and the M2 erupts between 2 and 3 years, corresponding to stage J5 (Bolter, 2011; Godfrey, 2001). Those two stages correspond to the juvenile or juvenile I category (Schultz, 1940; Schillaci, 2007). Stages J6 and J7 correspond to the juvenile II or subadult category (Schultz, 1940; Schillaci, 2007). Sexual maturity, corresponding to the full eruption of the M3, takes place between 3 and 5 years old (Bolter, 2011), or a mean of 3 years and 9 months for Harvati (2000). This is stage A1. On the other hand, no data is available for adult stages. Nowak (1999, p. 603) mentions an age at death of 31 years and 1 month for a *T. cristatus* individual maintained in captivity. Shelmedine et al. (2009) mention the existence of a 25 year old female in the Bronx zoo. Incidentally, it is difficult to correlate these maximal ages from captive individuals with stage A7 defined here on wild individuals, who supposedly have a shorter lifespan. It is also noteworthy that the growth of non-human primates in captivity is reported to be accelerated (Phillips-Conroy and Jolly, 1988).

## 4. Discussion and conclusion

We provide here new information for Colobine life histories by presenting the eruption sequence of deciduous teeth. Synchronous eruptions seem to occur for the di1 and di2, but this may be due to our limited sample for these early stages. The dp3 erupts early, synchronous with the deciduous incisors, and the dp4 erupts after the dc (Table 1 and Fig. 3). This deciduous dental eruption sequence is similar to that of hominids (Permar, 1974), as the dp3 erupts before the canine. Deciduous dental eruption in Cercopithecines is different as the emergence is gradual along the dental arch from the labial to buccal teeth (di1, di2, dc, dp3 and dp4) (Lawrence et al., 1982). The opposite occurs with permanent dental eruption as Cercopithecines share the same sequence with hominids (M1 I1 I2 M2 P3 P4 C M3) while Colobines have a different sequence (M1 I1 I2 M2 I2 P3 P4 C M3) (Figs. 2 and 3). Synchronous tooth eruption is often mentioned for non-human primates. Harvati (2000) notes the simultaneous eruption of the P4 and P3. There is in fact, as shown in our results, a little difference in timing, and the P4 always erupts before P3. P3 pierces the arch before P4 is fully erupted. The

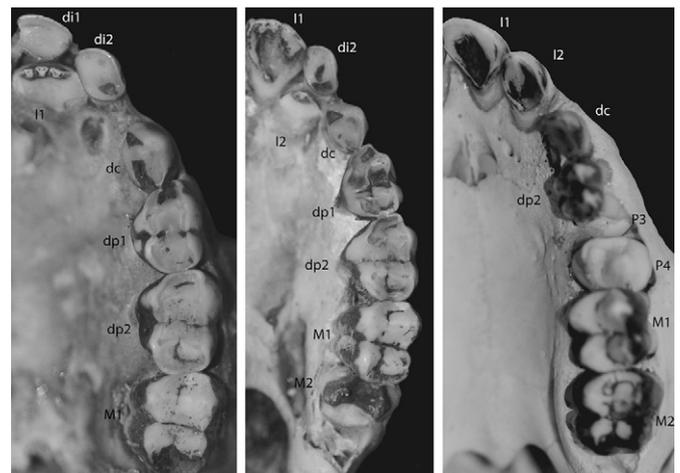
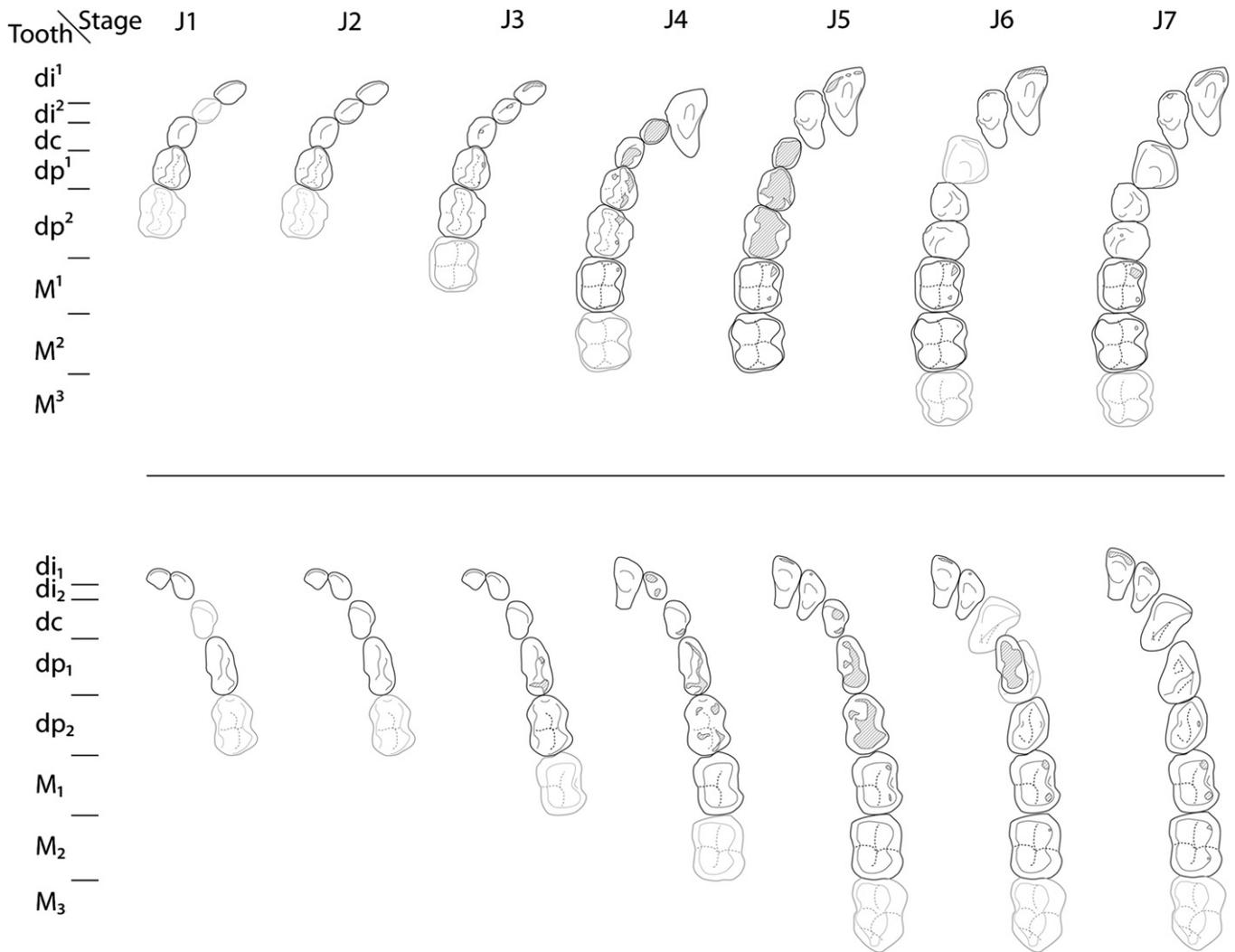


Fig. 2. Presence and absence of teeth during the eruption of the first incisor (left), second incisor (central) and fourth premolar (right). We can see that the fourth premolar has not fully erupted when the third premolar pierces the arch.



**Fig. 3.** Wear stages for juvenile *Trachypithecus*. Hatches correspond to wear with exposed dentine. In grey are the teeth that have begun to pierce the arch but have not yet fully erupted.

permanent dental eruption in Colobines is thought to be accelerated by the early eruption of the M2 (Harvati, 2000; Harvati and Forst, 2007; Borries et al., 2011). The early eruption of dp3 may then also be interpreted as an accelerated deciduous dental eruption. This particularity has already been observed by Borries et al. (2011). The accelerated growth rate appears to be strongly correlated with diet, as this condition is found in many folivorous primates. As already mentioned, the *Trachypithecus* clade is one of the most folivorous primates (Caton, 1999; Nijman et al., 2000).

Gantt (1979) observed that in Welsch's (1967) illustrations, wear patterns are similar among Cercopithecoidea. Nevertheless, a major difference occurs between Colobines and Cercopithecines in the timing of the wear of the lophs. Lophs are worn after buccal cusps and before lingual cusps in Colobines, while in Cercopithecines, buccal cusps are worn first, then lingual cusps, and finally lophs (Welsch, 1967). Thus the sharp occlusal relief of Colobine molars is preserved over a longer time period than in Cercopithecines. This condition was previously reported by Lucas and Teaford (1994) and interpreted by them as the consequence of seed chewing.

The important role of leaves in the *Trachypithecus* diet may explain another peculiarity observed on the wear of permanent molars. On upper molars, the mesial buccal cusp is the first

buccal cusp to wear, whilst on the lower molars, the distal lingual cusp is the first lingual cusp to wear (Fig. 4). Therefore the mirror condition is not respected between upper and lower molars. This particularity was already observed by Delson (1973) for all Cercopithecines, but in Welsch's drawings (1967), this condition only applies to the *Trachypithecus* clade. For all of the other species, the mesial lingual cusp is the first to wear on the lingual side of the lower molars. This character thus appears to be a reliable criterion for *Trachypithecus* genus fossil identification among Colobine molar teeth. Gantt (1979), who reports that wear patterns are remarkably regular throughout Old World monkeys, notes that wear patterns are strongly correlated with enamel thickness. In consequence, investigations should be conducted on the enamel thickness of *Trachypithecus* molars. Furthermore, the validity of the *Trachypithecus* genus as a different clade from *Semnopithecus* or even *Presbytis* has long been discussed (Brandon-Jones et al., 2004; Ingicco et al., 2011). Differences in enamel thickness could be an important characteristic for differentiating the *Trachypithecus* clade.

Although the dental wear chronology in *Trachypithecus* is original among primates, the fact that Colobine teeth are invariable validates the utilisation of this table for all the clade. The system that we propose here is composed of the same number of stages for

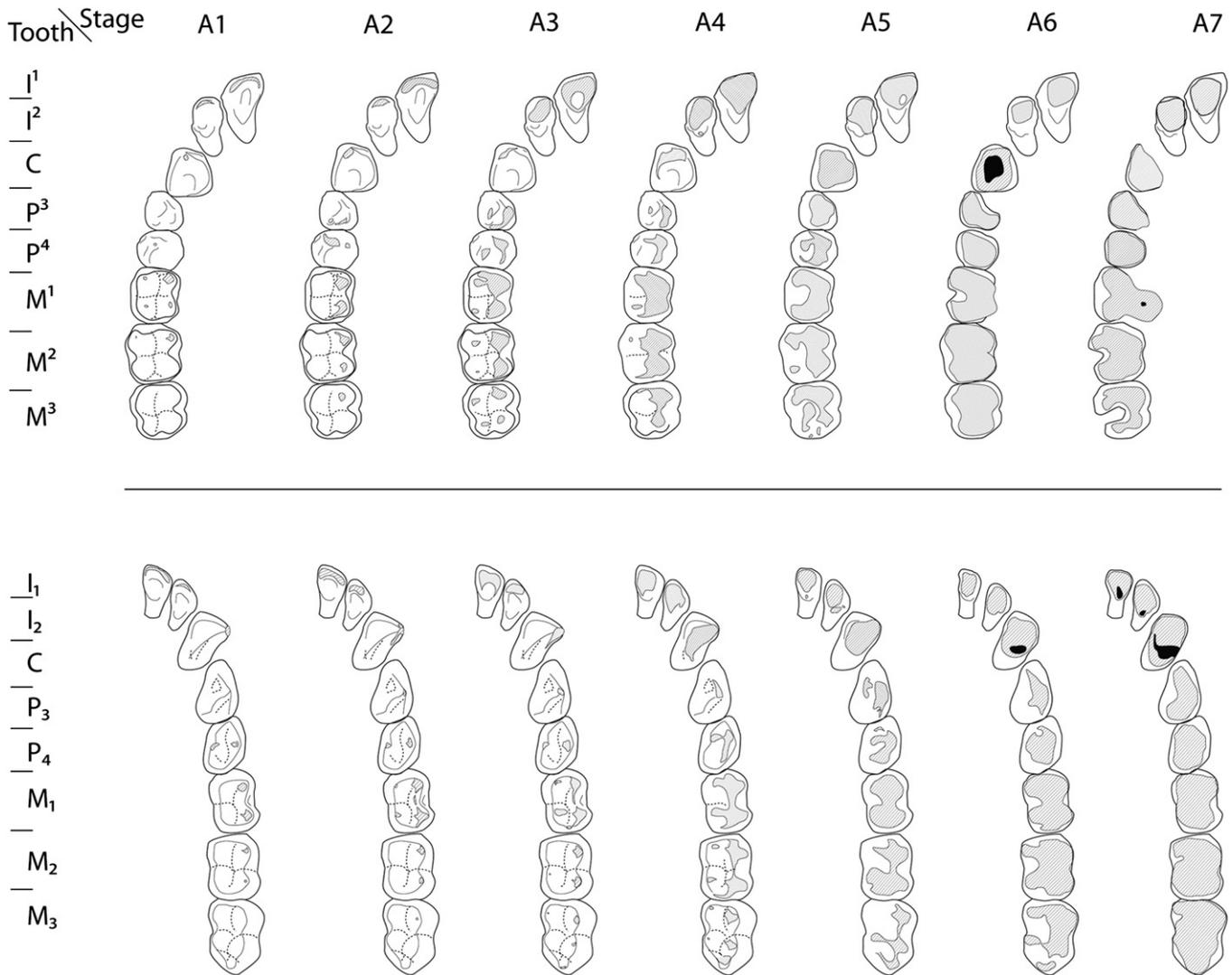


Fig. 4. Wear stages of adult *Trachypithecus*. Hatches correspond to wear with exposed dentine. In black the pulp cavity is visible through the dentine.

juvenile and adult periods, although the duration of these two periods is different. The juvenile period is more detailed. Neither of those sequences, juvenile or adult, reflects equally time-spaced stages. But, in our sample, no individual was deemed difficult to classify. The limited number of stages and the accurate drawings of tooth attrition (Figs. 3 and 4) limit the inter-observer error margin. We also believe that these figures and their definitions are easy and fast to use.

The tables can be used for both complete and incomplete dental arches. They can also be used to predict the wear stages of missing teeth in a very straightforward manner and thus facilitate refitting of two fragments and maxilla-mandible associations. For example, an isolated I1 with an A2 wear stage would be assimilated to any dental row fragment missing an I1 or even to isolated teeth with the same wear stage. The minimum number of individuals (MNI) by age class is consequently easy to estimate for any archaeological population with this system. Histograms illustrating the MNI per age class would then provide age-at-death profiles. Such profiles could in turn be interpreted by comparison with extant primate species mortality profiles (Lyman, 1987). Comparisons between natural and archaeological profiles would lead to the interpretation of the different hunting strategies used by prehistoric human groups. Two main kinds of mortality profiles characterize fossil

populations: a catastrophic profile, with a decrease in the MNI from young to old classes, and an attritional profile, with an over-representation of young and old individuals (Lyman, 1987). Hence, comparisons between Colobine mortality profiles obtained with our system and Cercopithecine profiles in a given archaeological site would enable differences in hunting strategies for those two clades to be identified.

As it stands, these tables are useful not only for zooarchaeologists, but also for primatologists focussing on animal tracking. Future research should investigate correlations between this relative age system and absolute ages from captive or wild specimens of known ages. Although such data are not relevant for zooarchaeologists, they are of interest to primatologists tracking the demography of threatened populations.

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