Tooth eruption in two agile gibbons (*Hylobates agilis*)

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Although the eruption stage of teeth is often used for a quick assessment of maturation in mammals, little is known about tooth-eruption in gibbons in general and specifically about the eruption of permanent teeth. In this study, we present longitudinal data on tooth-eruption in two captive agile gibbons (*Hylobates agilis*). The eruption of the deciduous dentition started around the age of one week, and was completed around the age of five months. This result was similar to findings of earlier studies on other gibbon species. The eruption of permanent teeth started at the age of 1.4 years and was completed at the age of around 6.6 years. There were individual differences between subjects both in the age at which certain teeth erupted and in the sequence of their eruption. A comparison with data on other primates suggests that ages of individual teeth eruptions in agile gibbons were similar to those of Japanese macaques, but occurred earlier than in chimpanzees and humans. As our gibbon sample is very small, observations on additional individuals are required in order to assess the generality of this result.

Introduction

The value of tooth eruption data is now well established for the comparisons of growth rate and life history of primate species (Smith *et al*., 1994; Swindler, 2002). Smith *et al*. (1994) compiled comprehensive data on the ages of eruption of all teeth for a wide array of primates and pointed out the glaring deficiency of data on gibbons (Hylobatidae). Our present knowledge of tooth eruption in gibbons can be summarized as follows.

Published information on deciduous tooth eruption encompasses 14 individuals, but several reports provide fragmentary data only (Badham, 1967; Ibscher, 1967, p. 56; Keith, 1931, p. 57; Robinson, 1925; Schultz, 1944, p. 41). The few cases that are described in more detail include a hybrid gibbon (*Hylobates lar* x *H. moloch*) and a siamang (*Symphalangus syndactylus*) at the San Diego Zoo (Rumbaugh, 1967a, 1967b), and seven white-handed gibbons (*H. lar*) and one crested gibbon (*Nomascus leucogenys*) at the Takarazuka Zoological and Botanical Gardens (Araki *et al*., 1989). These two studies suggested that the eruption of the deciduous dentition in gibbons starts soon after birth and is completed at the age of about six months. Intervals of dentition checks were unspecified in all previous studies, making it impossible to assess the accuracy of reported ages at which eruptions occurred. The number of the available samples is too small to determine whether there are differences among gibbon genera or species.

There does not appear to be any published information on the ages of permanent tooth eruption in gibbons. Based on their evaluation of earlier reports (Keith, 1931; Schultz, 1933, 1935, 1956), Smith *et al*. (1994) suggested that the first molar erupts around the age of 1.75 years and the dentition was complete at the age of about 7.5 years, but noted that this result was highly tentative, because the exact age of most gibbon specimens used in these studies was unknown.

As suggested by the above, there is a great need for data on dental eruption in gibbons of exactly known age. For this purpose, we monitored the ages of each tooth eruption as well as eruption sequence in two captive-born agile gibbons (*H. agilis*).

Animals and methods

Subjects were two male agile gibbons at the Primate Research Institute of Kyoto University (KUPRI), Japan. They were full brothers, named Tsuyoshi and Raja (Fig. 1).

Tsuyoshi was born on 9th June, 1998. His mother showed various improper behaviours toward her baby, the biggest problem being that she refused to suckle. As a result, nursery rearing began eight days after birth. Tsuyoshi was fed baby formula ten times per day in the early phase of rearing, and thereafter gradually weaned at the age of two years. Various foods were then fed at least three times per day, including fruits, vegetables, eggs, meal worms, nuts, and monkey chow. Tsuyoshi was thus raised by the authors and other KUPRI staff. At the same time, daily meetings with adult gibbons, including Tsuyoshi's biological mother were scheduled to facilitate his social development as a gibbon. When Tsuyoshi was one year of age, his younger brother Raja was born. Since then, the two have been reared together. At 2.5-years-old, Tsuyoshi was returned to his mother's cage. She showed receptive behaviours to him, such as grooming and playing. He lived with her until her death, at which time he was six years old. He has not suffered from any major illness, and has remained very healthy up to the present.

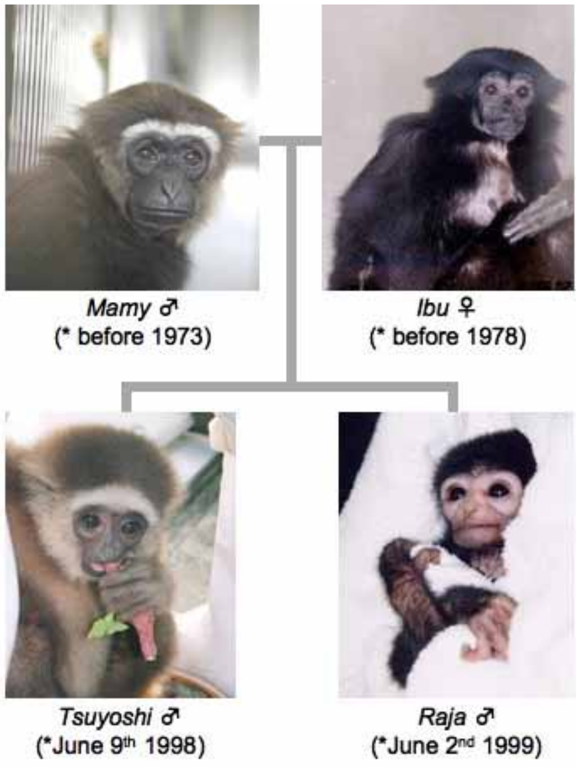

Fig. 1. Agile gibbons (and their date of birth) at the Primate Research Institute of Kyoto University (KUPRI). The subjects of this study, Tsuyoshi and Raja, were sons of the same pair. – *Die Schwarzhandgibbons und ihre Geburtsdaten am Primatenforschungs-institut der Universität Kyoto (KUPRI). Die beiden Studientiere Tsuyoshi and Raja waren Söhne desselben Paares*.

Raja was born on 2nd June, 1999 (Fig. 2). His history was very similar to Tsuyoshi's. He was moved to nursery rearing at the age of 12 days. He was raised with Tsuyoshi from the start, and lived with his biological mother from the age of 1.5 to 5 years. One important difference was that Raja was severely bitten by his father at the age of 96 days. The injury on his left forearm was sutured and treated by veterinary staff (Fig. 3), and eventually healed. He also suffered from external piles soon after the injury described above. After getting over these disorders, he grew up in good health.

Study period for this article was from June 17th 1998 to August 27th 2005. Subjects were observed about five hours per day during the study period by the first author. This was a version of the Participant observation (Spradley, 1980; Matsuzawa, 2006), as the authors participated in the everyday activities of the subjects. Daily records on the gibbons were kept in a notebook, in cooperation with other caretakers and researchers. Dentitions were checked virtually every day when the subjects opened their mouths. Opportunities for this were common during the gibbons' daily activity, for instance when they were laughing, yawning, eating, or biting (Fig. 4). However, the upper molars were often relatively difficult to see.

Tooth eruption was defined as projection of any portion of tooth through gums, referred to as "standard gingival emergence" (Smith *et al.*, 1994). As the minimum unit, age in days after birth was used here. Ages recorded were converted to the larger units according to need (1 month = 30.4375 days, 1 year = 365.25 days). The tooth arrangements were depicted in pattern diagrams, filling in the age and order of eruption of each tooth in turn.

Tooth names were abbreviated as follows. Deciduous teeth were written in lowercase letters, and permanent teeth in capitals. Tooth type was expressed by the initial letter: i or I = incisor, m or M = molar, c or C = canine, P = premolar. The number following the letter identified the position of the tooth; for example, i1=central incisor.

Fig. 2. Raja clinging to his mother Ibu soon after birth. Photo: N. Maeda. – *Raja klammert sich an seine Mutter kurz nach seiner Geburt*.

Fig. 3. Raja three days after being bitten by his father. The left forearm is swollen; the injury had to be sutured. – *Raja drei Tage nachdem er von seinem Vater gebissen wurde. Der linke Unterarm ist geschwollen und die Bisswunde musste genäht werden*.

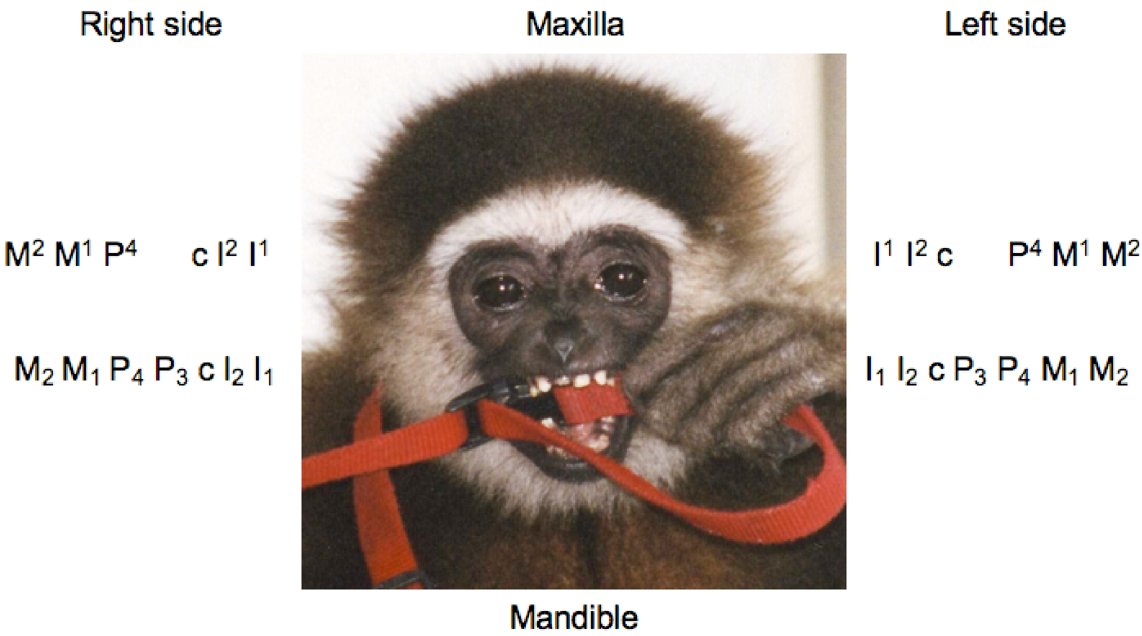

Fig. 4. The gibbons' dentitions were monitored by inspecting their mouths during daily activity. This photo was taken when Tsuyoshi was 1,512 days old. The shorthand description of his dentition on that day is also shown in the figure (see text for abbreviations). He fractured his right upper I1. Tips of his lower P3 are just projecting through the gums. – *Die Bezahnung der Gibbons wurde während ihrer täglichen Aktivitäten kontrolliert. Auf diesem Bild ist Tsuyoshi 1'512 Tage alt. Die Kurzbezeichnung seiner rechten, linken, oberen und unteren Zähne sind neben dem Bild angegeben. Die Spitzen seiner unteren Prämolaren P3 befinden sich im Durchbruch*.

Table 1. Sequence of tooth eruption in gibbons.[1] – *Reihenfolge des Zahndurchbruchs bei Gibbons*.

Reference		**Sequence of eruption**	
		Deciduous teeth	Permanent teeth
Schultz (1944)		i1 - i2 - m1 - c - m2	M1 - I1 - I2 - M2 - P3 & P4 - C - M3
Uchikoshi & Matsuzawa (this study)	Tsuyoshi	i1 - i2 - m1 - c - m2	M1 - I1 - I2 & M2 - P4 - P3 - C & M3
	Raja	i1 - i2 - m1 - c & m2	M1 - I1 & I2 & M2 - P3 & P4 - M3 & C

[1] Tooth types were listed from left to right in the sequence of their eruption. Abbreviations for tooth types, deciduous teeth: i1 = central incisor, i2 = lateral incisor, c = canine, m1=first molar, m2 = second molar; permanent teeth: M1 = first molar, I1 = central incisor, I2 = lateral incisor, M2 = second molar, P3 = first premolar, P4 = second premolar, C = canine, M3 = third molar.

Results

Deciduous Teeth

Results are described separately for Tsuyoshi and Raja.

When Tsuyoshi was separated from his mother at the age of 8 days, 4 central incisors and 2 lower lateral incisors had already erupted. Other teeth erupted in the sequence shown in Fig. 5, and the deciduous dentition was completed by the age of 134 days (or 4 months).

In the case of Raja, the first teeth erupted at the age of 13 days, slightly later than in the case of his brother (Fig. 5). The projection of the last tooth occurred at the age of 206 days (or 6 months), which was 2 months later than in Tsuyoshi.

The age at eruption of each tooth in each gibbon is specified in Fig. 5, and the sequence of tooth eruption is summarized in Table 1.

Comparison with previous gibbon studies

Combining data from earlier work with those from the present study, ages at which each tooth erupted and those of completion are listed in Table 2. There were individual differences in ages of each eruption; minimum range was 8 days in the case of central incisor eruption, and maximum range was over 101 days in canine eruption. Completion and eruption of the 2nd molar in Tsuyoshi occurred earlier than in other gibbon individuals (Raja, Gabrielle, Sarah, Con-chan). Tsuyoshi completed his deciduous dentition at the age of 134 days, representing the earliest recorded case. Conversely, completion and eruption of four tooth types occurred later in Raja than in other individuals. Raja completed his dentition at the age of 206 days, and this was representing the slowest recorded case. Tsuyoshi and Raja were not particularly similar to each other in their tooth eruption patterns, in spite of their close relatedness.

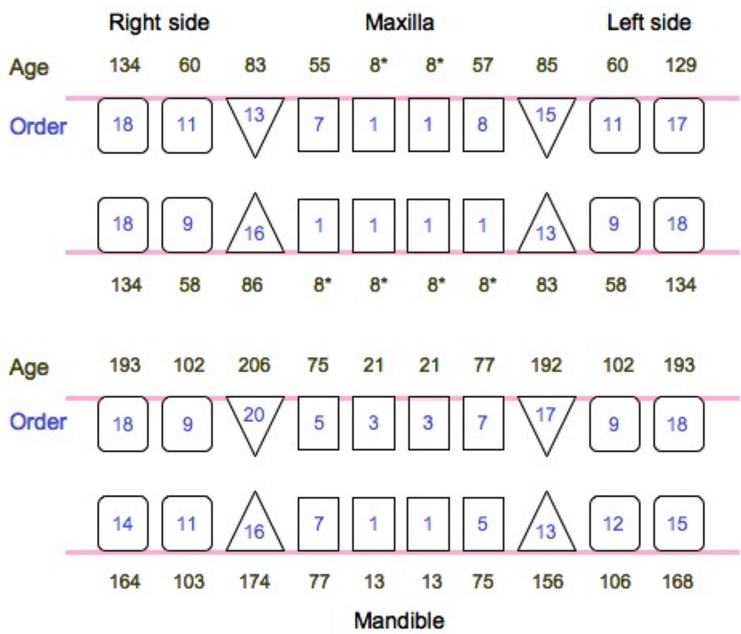

Fig. 5. Deciduous tooth eruption in Tsuyoshi (above) and Raja (below). This diagram shows the dentition from an anterior view. The pink horizontal line represents the gum line. Teeth symbols include rectangles for incisors, triangles for canines, and rounded rectangles for molars. Ages in days of each tooth eruption were indicated in the gum area of each teeth row. Tooth eruptions in several teeth may have occurred slightly earlier than we first detected them (judging by the amount of tooth projection). These teeth are identified by an asterisk. Sequences of eruption are written inside the teeth symbols in blue. – *Durchbruch der Milchzähne bei Tsuyoshi (oben) und Raja (unten). Das Diagram zeigt das Gebiss in Frontalansicht. Die waagrechten rosa Linien stellen das Zahnfleisch dar. Quadrate stehen für Schneidezähne, Dreiecke für Eckzähne und gerundete Quadrate für Molaren. Die Zahlen im Bereich des Zahnfleisches sind das Alter bei Durchbruch des betreffenden Zahnes. Aufgrund des Durchbruchsstadiums könnte der Durchbruch mancher Zähne begonnen haben, bevor wir ihn entdeckten. Solche Zähne sind mit Stern gekennzeichnet. Die Reihenfolge des Durchbruchs wird durch die blauen Zahlen innerhalb der Zahnsymbole Sequences angegeben.*

Table 2. Comparison of the ages in days at which each deciduous tooth erupted in various gibbons.[1] – *Alter in Tagen beim Durchbruch der einzelnen Zähne für verschiedene Gibbons.*

Reference	**Taxon**	**Individual**	**Tooth**					**Comple-tion**
			i1	i2	c	m1	m2	
Rumbaugh (1967a, b)	*S. syndactylus*	Sarah	10	by 48	–	–	–	by 180
Rumbaugh (1967a, b)	*H. lar* x *H. moloch*	Gabrielle	–	by 34	by 55	by 48	by 151	by 158
Araki *et al*. (1989)	*H. lar*	mean±SD[2]	6±1.4	26±17.5	96±25.0	60±16.9	141±20.0	169±13.6
Araki *et al*. (1989)	*N. leucogenys*	Con-chan	5	5	87	68	169	190
Uchikoshi & Matsuzawa (this study)	*H. agilis*	Tsuyoshi	by 8	by 8	83	58	129	134
	H. agilis	Raja	13	75	156	102	164	206
Range			5-13	5-75	by 55-156	by 48-102	129-169	134-206

[1] The age of the earliest eruption is shown.

[2] The number of individuals varies (maximum number: 7).

As suggested by the data compiled in Table 2, the eruption of the deciduous teeth in gibbons appears to begin at the age of around one week and to end at the age of about five months.

Sequences of tooth eruption in subjects were compared with the “typical sequence in gibbons” proposed by Schultz (1944), which was based on his examination of 22 infantile gibbon skulls. In Tsuyoshi, the sequence of tooth type eruption was [i1 i2 m1 c m2], identical to that reported by Schultz. In Raja, however, the last tooth to erupt was an upper canine, not an m2.

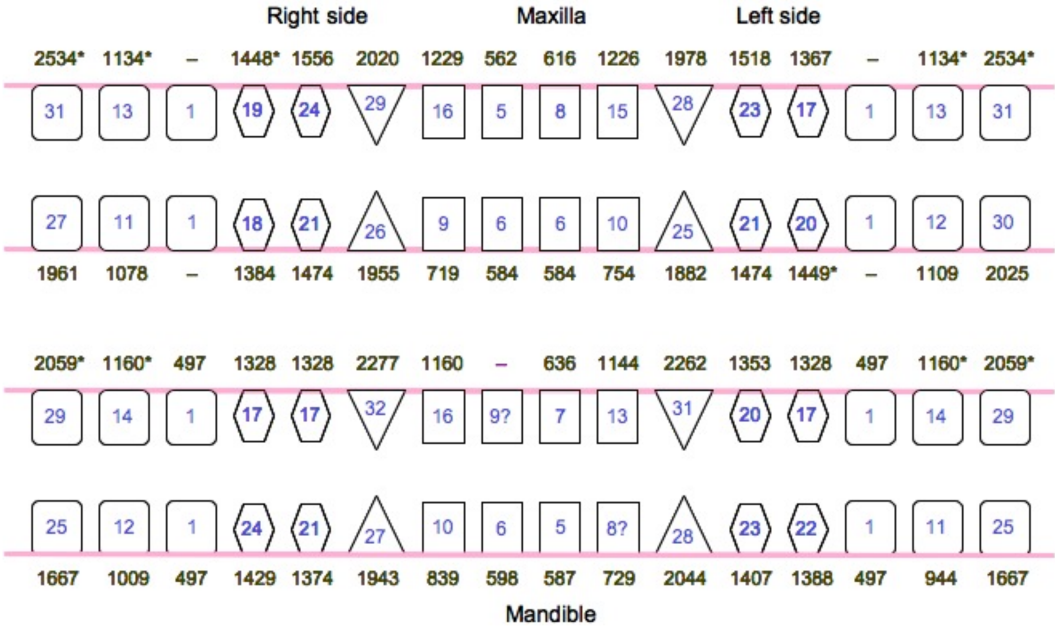

Fig. 6. Permanent tooth eruption in Tsuyoshi (above) and Raja (below). Symbols as for the deciduous teeth (Fig. 5), but hexagons are added to identify premolars. The ages at which the 1st molars in Tsuyoshi, and the upper right central incisor in Raja erupted, were not recorded. Tooth eruptions in several teeth may have occurred slightly earlier than we first detected them (judging by the amount of tooth projection). These teeth are identified by an asterisk. – *Durchbruch der Dauerzähne bei Tsuyoshi (oben) und Raja (unten). Die Zahnsymbole sind dieselben wie in Fig. 5; zusätzlich stehen Sechsecke für Prämolaren. Das Alter, bei dem die ersten Molaren von Tsuyoshi und der erste Schneidezahl oben rechts von Raja durchgebrochen sind, wurden nicht erfasst.*

Permanent teeth

In Tsuyoshi, we missed the eruption of the first permanent tooth. The reason for this loss of data was that it occurred early beyond the authors' expectation. At the age of 562 days (or 1.5-years-old), a central incisor erupted. At that point, all 1st molars had already projected (Fig. 6). By the age of 2,534 days (or 6.9-years-old), all permanent teeth had erupted.

In Raja, the first permanent teeth appeared at the age of 497 days (or 1.4-years-old); all 1st molars projected simultaneously (Fig. 6). Raja completed his dentition at the age of 2,277 days (or 6.2-years-old); earlier than in Tsuyoshi, unlike in the case of deciduous teeth completion.

Sequences of eruption for each tooth in the two subjects are shown in Fig. 6, summed up by tooth type in Table 1. There were differences between subjects in the order of eruption. For example, the last erupted tooth in Tsuyoshi was the upper 3rd molar, whereas it was a canine in Raja.

Comparison with earlier gibbon studies

Smith *et al*. (1994) suggested that the first molar erupts at the age of about 1.75 years, and the dentition is complete at the age of about 7.5 years. These stages occurred slightly earlier in our study gibbons. Schultz (1944) described the typical sequence based on observation of 118 immature, mostly wild-shot *H. lar* (Table 1). Whilst our subjects followed Schultz's order roughly, they differed from it in several points. After the permanent 1st molars, orders in the two subjects were somewhat irregular.

Discussion

Basic data on tooth eruption were collected by observing two agile gibbons for 7 years. Ages of deciduous tooth eruption in the subjects were comparable to two earlier studies (Rumbaugh, 1967a, b; Araki *et al*., 1989), though there were individual differences (Table. 2). Combining our data with this earlier work suggested that gibbons seem to erupt deciduous teeth from around 1 week of age to around 5month of age (Table 2). However, later completions were reported in two other articles. Ibscher (1967) observed a female hybrid gibbon (*H. pileatus* x *H. lar*), whose deciduous dentition was completed at the age of 8 months. Badham (1967) mentioned that a male pileated gibbon (*H. pileatus*) of 7 months had 16 teeth other than four molars. Later ages of completion in these two individuals could have been caused by several reasons. Firstly, differences in methods of observation: the gibbon studied by Ibscher was reared by her mother, which may have made checking her dental development more difficult than in the nursery-reared gibbons of this and other studies (Araki *et al*., 1989; Rumbaugh, 1967a, b). The pileated gibbon studied by Badham had experienced improper care from his mother, and had been removed from her at the age of 5.5 months. As the infant's body weight at the age of 7 months was 0.9 kg, it was much lighter than other gibbons of the genus *Hylobates* that weighed more than 1.4 kg at about the same age (Tsuyoshi, Raja, and Gabrielle). This suggests that the pileated gibbon of the study may have developed later or more slowly than usual. In order to determine standard body weights of immature gibbons for each age, however, larger samples are still required.

Ages of permanent tooth eruption were revealed by the present study. Based on data from two subjects, it seems that permanent teeth in agile gibbons start to erupt at the age of 1.4 years, and complete at the age of about 6.6 years. More cases are doubtless needed to confirm the generality of this result. Accumulation of data will make it possible to investigate existence or non-existence of differences among gibbon genera or species.

The sequences of tooth eruption differ among the taxa in various ways. The first permanent tooth to erupt in all primates is the first molar; however, the last tooth to erupt is extremely variable; it may the 3rd molar, a canine, or even a premolar (Swindler, 2002). Schultz (1944) described the typical eruption sequence for gibbons based on a cross-sectional examination of 22 infantile skulls and 118 juvenile specimens of several species but mostly *H. lar*. Although the eruption sequence of our agile gibbons resembles the one published by Schultz, there are some differences (Table 2). And although the two agile gibbons were full brothers, their dental eruption patterns also differed in several respects, suggesting the occurrence of "emergence sequence polymorphisms" such as those reported for chimpanzees (Conroy and Mahoney, 1991).

A preliminary comparison of the age at the earliest eruption of each tooth type for four primate species is shown in Fig. 7. Samples were humans (mean ages, 239 individuals for deciduous teeth and 3075 males for permanent teeth), chimpanzees (mean ages, 58 individuals for deciduous teeth and 8 males for permanent teeth), Japanese macaques (median ages, 76 individuals for deciduous dentition and 59 males for permanent dentition) and agile gibbons (mean ages of two males). The figure suggests that ages of tooth eruption in agile gibbons are similar to those of Japanese macaques, whereas the same teeth erupt later in chimpanzees and later again in humans. This finding appears to be consistent with the results of morphological formation of gibbon teeth (Dirks, 1998). Probably, teeth erupt earlier in gibbons than in chimpanzees because gibbons exhibit a much lower body weight of only about one 8th of chimpanzees (Geissmann, 1993; Leigh and Shea, 1995; Rowe, 1996). In previous studies, the mean age of tooth eruption is strongly related to size, measured as mean adult body weight (Smith *et al.*, 1994). There must be many other factors which contribute to differences in life history traits; such as metabolic rate, brain weight, diet, age-specific mortality, infant care strategy, social system, phylogeny, etc. (Allman *et al.*, 1998; Dirks, 2003; Kappeler and Pereira, 2003).

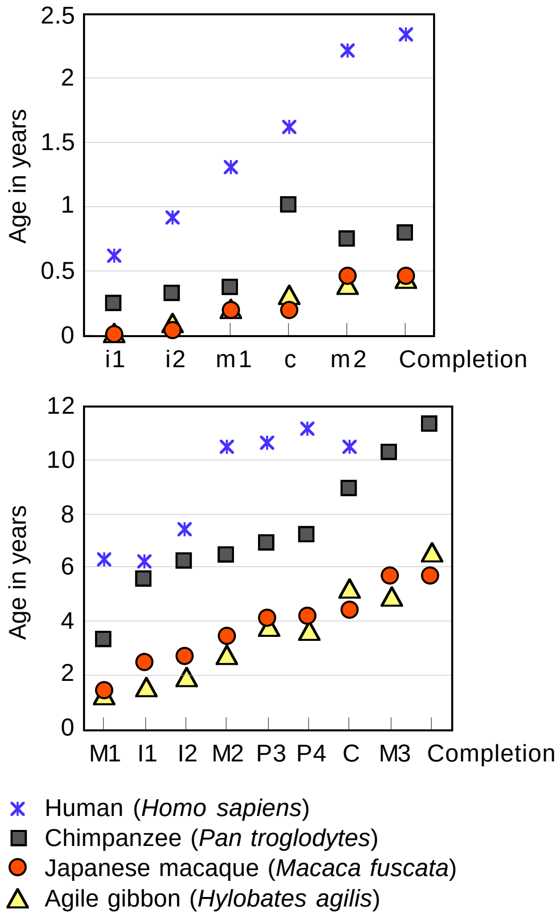

Fig. 7. Age at the earliest eruption of each tooth type for four primate species. Graph of deciduous teeth above, and that of permanent teeth below. Data for species other than gibbons are from Smith *et al.* (1994). – *Alter des frühesten Durchbruchs für jeden Zahntyp bei vier Primatenarten. Obere Graphik: Milchbezahnung; untere Graphik: Dauerbezahnung. Die Daten für die Nicht-Gibbons stammen von Smith et al. (1994)*.

Probably, features of gibbon development will become clear not only from tooth data, but also from considering the relationship between teeth and other domains, such as endocrine, morphological, cognitive and behavioural development. Comprehensive analysis of gibbon development is the next challenge, comparing data from multiple domains in the same subjects (Myowa-Yamakoshi and Tomonaga, 2001; Suzuki *et al.*, 2003). In contrast to tooth eruption, most behaviours appeared later in our subjects than in Japanese macaques, and earlier than in chimpanzees (Uchikoshi and Matsuzawa, 2002, and unpublished data; a similar view on gibbon behavioural development was suggested by Berkson, 1966). Speed differences between the growth of teeth and behavioural changes during early development might be a key feature of gibbons, assuming heterochrony (defined as a developmental change in the timing of events; see Gould, 1977).

Above, we discussed features of tooth eruption in agile gibbons, based on data from only two subjects. Further information will clarify the standard values; we therefore hope to see reports by researchers who have similar data in the future. Maybe, such data already exists, in unpublished form, in zoos, rehabilitation centres and sanctuaries. It is also possible that relevant work has been published in non-English language journals, and thus we are unaware of it. Since the observation of tooth eruption through daily interaction is completely non-invasive, it dose not have welfare implications. Not only from a scientific perspective but also from a bioethical view-point, we can broadly recommend tooth observation. Accumulation of knowledge on hylobatid tooth eruption will help age estimation for individuals who were brought into captivity before adulthood, thereby contributing to the progress of gibbon conservation and welfare.

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Zusammenfassung

Der Zahndurchbruch bei Schwarzhandgibbons (*Hylobates agilis*)

Obwohl Stadien des Zahndurchbruchs normalerweise zur raschen Beurteilung des Entwicklungszustandes und zur Altersschätzung von Säugetieren verwendet wird, ist nur wenig über den zeitlichen Verlauf des Zahndruchbruchs und insbesondere des Zahnwechsels bei Gibbons bekannt. In dieser Studie präsentieren wir Langzeitdaten zum Zahndurchbruch und –wechsel von zwei in Gefangenschaft geborenen Schwarzandgibbons (*Hylobates agilis*). Der Durchbruch der Milchzähne begann etwa im Alter von einer Woche und war im Alter von etwa fünf Monaten abgeschlossen. Dieses Resultat ähnelt den Befunden von früheren Studein an anderen Gibbonarten. Der Durchbruch der Dauerzähne begann im Alter von 1.4 Jahren und war mit 6.6 Jahren abgeschlossen. Obwohl die beiden untersuchten Gibbons Brüder waren, unterschieden sie sich sowohl im Alter, mit welchem einzelne Zähne durchbrachen, als auch in der genauen Reihenfolge des Durchbruchs einzelner Zähne. Dabei dürfte es sich um die ersten veröffentlichten Beobachtungen zum Durchbruch der Dauerzähne bei Gibbons von genau bekanntem Alter handeln. Ein Vergleich mit Daten von anderen Primaten zeigt, dass die einzelnen Zähne bei den untersuchten Gibbons ungefähr im selben Alter durchbrechen wie bei Rotgesichtsmakaken (*Macaca fuscata*), aber deutlich früher als bei Schimpansen (*Pan troglodytes*) und Menschen. Unsere Gibbon-Stichprobe ist jedoch noch sehr klein, und Beobachtungen an weiteren Individuen sind nötig, um die Allgemeingültigkeit unserer Schlussfolgerungen zu beurteilen.