

## Dental Variation among Asian Colobines (Nonhuman Primates): Phylogenetic Similarities or Functional Correspondence?

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**Ruliang Pan and Charles Oxnard (2003)** Dental variation among Asian colobines (nonhuman primates): phylogenetic similarities or functional correspondence? *Zoological Studies* 42(1): 93-105. In order to reveal variations among Asian colobines and to test whether the resemblance in dental structure among them is mainly associated with similarities in phylogeny or functional adaptation, teeth of 184 specimens from 15 Asian colobine species were measured and studied by performing bivariate (allometry) and multivariate (principal components) analyses. Results indicate that each tooth shows a significant close relationship with body size. Low negative and positive allometric scales for incisors and molars (M2s and M3s), respectively, are each considered to be related to special dental modifications for folivorous preference of colobines. Sexual dimorphism in canine eruption reported by Harvati (2000) is further considered to be associated with differences in growth trajectories (allometric pattern) between the 2 sexes. The relationships among the 6 genera of Asian colobines found greatly differ from those proposed in other studies. Four groups were detected: 1) *Rhinopithecus*, 2) *Semnopithecus*, 3) *Trachypithecus*, and 4) *Nasalis*, *Pygathrix*, and *Presbytis*. These separations were mainly determined by differences in molar structure. Molar sizes of the former 2 groups are larger than those of the latter 2 groups. This scenario is considered to be relevant to differences in their dietary selection and ecological niche adaptation, and to variations in latitude geographically. Snub-nosed monkeys (*Rhinopithecus*), especially those in China, are specialized colobines in many respects. The findings also imply that the geographical landscape and vegetation, being greatly shaped by tectonic modification and glaciation in Asia over the last 2 million years, have already forced Asian colobine monkeys to adapt to remarkably different diets and niches. The study of the colobines can thus provide an ideal model for interpreting the relationship between natural selection and adaptation. <http://www.sinica.edu.tw/zool/zoolstud/42.1/93.pdf>

**Key words:** Asian colobines, Dental variation, Functional adaptation, Geographic distribution, Dietary preference.

Colobines comprise 2 tribes distributed on the African and Asian continents, respectively. Asian species, in the tribe Presbytina, as is the case for macaques in the same area, are among the most successful nonhuman primates in terms of radiation, diversity, and distribution (Fleagle 1988, Davies and Oates 1994, Rowe 1996, Brandon-Jones 1998, Kirkpatrick et al. 2001, Pan and Groves in press). They are now found from tropical to subtropical forests (e.g., Java leaf monkey, *Presbytis comata*), swamp forests (e.g., proboscis monkey, *Nasalis larvatus*), along coastlines in regions which include plains and mid-sized

mountains (e.g., silvered leaf monkey, *Trachypithecus cristatus* and gray langur, *Semnopithecus entellus*), on high mountains at elevation of more than 3000 m (some populations of the gray langur and snub-nosed monkey), and finally in mountains as high as 4700 m of elevation on the Qinghai-Tibet Plateau, where no other nonhuman primates can survive except for 1 species of snub-nosed monkey (*Rhinopithecus bieti*). These distributions imply that Asian colobines occupy an enormous variety of niches which have resulted from gigantic tectonic changes and impacts of global glaciations during the Neogene (Pliocene and Pleistocene) in

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Asia. Some remarkable geographic alterations in this period included the disappearance of the Tethys Sea, the rapid uplift of the Qinghai-Tibet Plateau, and the junction/disjunction between continent and islands, and between archipelagos, following sea level changes (Pan and Jablonski 1987, Fa 1989, Jablonski and Peng 1993, Brandon-Jones 1998, Pan and Oxnard 2001a). In other words, the distribution of Asian colobines has been greatly modified, and might have resulted in their present significant differentiation in functional adaptations, behavior, locomotion, and dietary selection. Thus, some species, such as *Rhinopithecus* (snub-nosed monkey) and some populations of *Semnopithecus entellus* (gray langur), which are now confined to regions with increased seasonality and cold high-elevation climates, may have adapted quite different dental morphologies compared with others.

Even though having been generally regarded as folivorous primates (Table 1) in contrast to their partner (cercopithecines) in the Cercopithecidae, Asian colobines show great variation in dietary selection and diversity when the proportions of different dietary components are considered. According to Fleagle (1988), Rowe (1996) and Oates et al. (1999), some species in the genus *Presbytis*, such as, *P. vetulus* (purple-faced leaf monkey) and also *T. johnii* (Nilgiri langur), are more folivorous than *S. entellus* and can subsist almost exclusively on leaves. *Presbytis melalophos* (banded leaf monkey) feeds primarily on young leaves, seeds, and fruits and rarely on mature leaves. Some species in the genus *Trachypithecus* have different food habits, such as *T. obscurus* and *T. cristatus* (dusky and silvered leaf monkeys) which eat plant-based diets containing 55%-80% leaves. *Nasalis larvatus* (proboscis monkey) principally eats leaves. *Pygathrix nemaeus* (douc langur) prefers leaves and buds. Species of *Rhinopithecus* are more specialized compared with other colobines. They feed principally on leaves, grass, buds, bark, and lichens in temperate, coniferous-lichen forests (Mu and Yang 1982, Wu and He 1989, Kirkpatrick 1998, Li et al. 2000, Kirkpatrick et al. 2001).

Such complex profiles in dietary preferences make it difficult or impossible to carry out integrated field work involving a large number of different Asian colobines. A functional laboratory study on the masticatory apparatus would certainly be useful to set up criteria to describe variations among them and to provide a scientific basis for field workers. Although there is a study on this issue

carried out by one of the authors of this paper and his colleagues (Jablonski et al. 1998), that work was made with references to the mandible, and other Old World monkeys were involved. According to recent studies on macaques, mandibles and dentition may or may not reflect the same profile when used to reveal morphological similarities and to estimate specific adaptive tendencies (Pan 1998, Pan and Oxnard 2000). For instance, these 2 anatomic elements display separate variation patterns when inter- and intraspecific differences are analyzed simultaneously. That is, the variation between species is revealed along the 1st axis of the principal components analysis (PCA), but that between sexes (within species) along the 2nd axis. This similarity, however, does not mean that they have the same functional adaptation since the 2 jaws have other nonmasticatory roles, e.g., in facial structure development. Teeth differ from jaws in terms of function and ontogenetic development. For instance, their development does not necessarily reflect phylogenetic relationships, but is more likely to mirror diet and life history (Smith 1994). In another study, teeth showed variation patterns different from those illustrated by the maxilla and mandible which, later generally reflect the resemblance in phylogeny when relationships with body size are considered (Pan and Oxnard 2002).

Dental eruption sequences of Asian colobines were analyzed by Schultz (1935) and Harvati (2000). They stated that the colobines (including African species) differ from other catarrhines in terms of eruption sequence. The permanent 2nd and 3rd molars tend to erupt early relative to the other teeth. However, it is still unknown whether a tooth appearing earlier will ultimately have a larger size than one erupting later, and vice versa. This actually can be tested through a study of the relationship between teeth and body size in adults. Another finding in Harvati's study was of sexual dimorphism in the eruption of the canines. It would be interesting to test whether this phenomenon has resulted in different allometric patterns in the 2 sexes of Asian colobines.

The main purposes of this study include: 1) to reveal allometric relationships between teeth and body size of Asian colobines; 2) to investigate how some teeth with a specific eruption sequence are related to body development; 3) to reveal how far each genus deviates from the baselines representing all Asian colobines; 4) to test whether some taxa, such as snub-nosed monkeys, exhibit a special dental structure; 5) to infer dietary scenarios

for some species whose records from the wild are rare or not available, and finally 6) to test whether differences among them are principally functionally or phylogenetically related.

## MATERIALS AND METHODS

The species and sample sizes used in this study are listed in table 1. All specimens were adult as judged by the full eruption of the M3s. There has been more controversy about the systematics and phylogeny of Asian colobines than for almost any other primates in the same region. They have been classified in from 3 to 9 genera (Groves 1970 2001, Hill 1972, Honacki et al. 1982, Pan and Groves in press). The taxonomy of the genera in this study is from Groves' recent report (Groves 2001). Thus, the species used are categorized as belonging in 6 genera. The maximum lengths and widths of each tooth were measured

at a number of different universities, museums, and academic institutions (see Table 1). Dental structure has been widely used in studies of classification, evolution, phylogeny, and functional adaptation because its special role in morphology is used for identification and its function is closely related to natural selection of the diet as well as being the most frequently available feature in fossil material.

There is a great variety of body sizes among colobine species, ranging from *T. pileatus* (capped leaf monkey) with a body weight of 5.1 kg for a female, to *R. bieti* (black snub-nosed monkeys) with a weight of 30 kg for a male (Ye et al. 1987, Rowe 1996). Variations in body size among taxa tend to outweigh variations due to shape, which is more useful for revealing both phylogenetic and functional differences. Thus, size variation has to be 'filtered out' or minimized, especially if functional aspects are to be considered. This is even more necessary where there are large differences

**Table 1.** Species and samples used in this study

Species	Common name	N (F+ M)	Storage	Diet preference	Reference	Distribution
<b>Odd-nosed group</b>						
<i>Rhinopithecus roxellana</i>	Golden snub-nosed monkey	8+10	NMNH, NUCH, KIZ	Leaf, bud, lichen, and fruit	Kirkpatrick (1998), Li et al., (2000)	Central China
<i>R. bieti</i>	Black snub-nosed monkey	9+8	KIZ,	Lichen, grass, leaf, and fruit	Wu and He (1989), Kirkpatrick et al. (2001)	Southwestern China
<i>R. brelichi</i>	Gray snub-nosed monkey	1+3	KIZ	Bud, leaf, and fruit	Bleisch et al. (1993), Bleisch and Xie (1998)	Southern China
<i>R. avunculus</i>	Tonkin snub-nosed monkey	2+2	ZD	Fruit, leave, and seed	Boonratana and Canh (1998)	Northern Vietnam
<i>Pygathrix nemaeus</i>	Red-shanked douc langur	8+9	ZD, NMNH, FMUS	Leaf, bud, fruit, seed, and flower	Bennet and Davies (1994), Caton (1998)	Vietnam, Laos, and Cambodia
<i>Nasalis larvatus</i>	Proboscis monkey	3+5	ZD	Leaf, seed, fruit, flower, and animal	Banks (1949), Bennet and Sebastian (1988)	Borneo (Indonesia)
<b>Normal-nosed group</b>						
<i>Prosbitytis rubicunda</i>	Maroon leaf monkey	7+5	ZRC	Leaf, seed, fruit, and flower	Davies et al. (1988), Davies (1991)	Borneo and Karimata (Indonesia)
<i>P. comata</i>	Javan leaf monkey	3+4	ZD	Leave, fruit, flower and fungus	Adiputra (1994)	Java (Indonesia)
<i>P. melalophos</i>	Banded leaf monkey	5+5	ZD	Leaf, seed, fruit, and flower	Curtin (1980)	Sumatra (Indonesia)
<i>Semnopithecus entellus</i>	Gray langur	5+5	ZD	Leaf, fruit, bud, flower, animal, bark, herb, and twig	Hladik (1977), Newton (1992), Bennet and Davies (1994)	India, Pakistan, Bangladesh, Tibet, Sri Lanka, and Burma
<i>Trachypithecus vetulus</i>	Purple-faced leaf monkey	5+3	ZD	Leaf, fruit, and flower	Hladick (1977)	Sri Lanka
<i>T. phayrei</i>	Phayre's leaf monkey	9+8	KIZ, ZRC	Fruit, leaf, and petiole	Stanford (1988), Li (1993)	Laos, Burma, Vietnam, Thailand, and China
<i>T. francoisi</i>	Francois' leaf monkey	7+8	KIZ, GXF, BIZ	Leaf, bud, and flower	Li (1993)	Vietnam, Laos, and China
<i>T. obscurus</i>	Dusky leaf monkey	10+10	ZRC	Fruit, seed, leaf, and flower	Curtin and Chivers (1978)	Thailand and Malay Peninsula
<i>T. cristatus</i>	Silvery leaf monkey	9+8	ZD	Leaf, bud, and fruit	Brotoisworo and Dirgayusa (1991)	Burma and Indochina to Borneo (Indonesia)

N: specimen number. F and M: Female and male.

Notes: BIZ = Beijing Institute of Zoology, Beijing, China; FMUS = Field Museum of Natural History, Chicago, IL, USA; KIZ = Kunming Institute of Zoology, Kunming, Yunnan, China; GXF = Guangxi Forest Department, Nanning, Guangxi, China; NMNH = National Museum of Natural History, Washington, DC, USA; NUCH = Nanchong Teachers' College, Nanchong, Sichuan, China; ZD = Department of Mammalogy, British Museum (Natural History), London, UK; ZRC = Zoological Reference Collection, National University of Singapore.

in overall sizes between species (deWinter 1997).

Tooth size has been commonly regarded as closely related to body size, so it is frequently used to predict body size. Thus, variations in body size will naturally lead to similar magnitudes in variations in teeth. Tooth size can be estimated using different dimensions, such as length, width, and height. Crown area (maximum length multiplied by maximum width) is a feature combining 2 dimensions and is a better estimate of tooth size (Gingerich et al. 1982, Kieser and Groeneveld 1990). Crown area is used to represent dental size in this study.

Residuals or deviations from an allometric baseline are a useful way to provide a measure of how much an individual deviates from a baseline after allometric elements are removed (Smith 1983, Bouvier 1986). The allometric formula,  $Y = aX^b$  or  $\log Y = \log a + b \log X$ , where  $Y$  (the dependent variable) is the square root of the tooth crown area, and  $X$  (the independent variable) is cranial length which frequently has been used as a substitute for body size (e.g., Pilbeam and Gould 1974, Gould 1975, Kay 1975, Pan and Oxnard 2001b). In order to maintain the same geometric scale between dependent and independent variables (mm), the square root (SR) of each tooth crown area is calculated before the logarithmic transformation, that is, log-transformed SRs are examined against another log-transformed independent variable, linear cranial length.

The deviation of a tooth size from a specified allometric baseline is estimated by the difference between the original and the predicted sizes. According to Smith (1981), this deviation (D) is:

$$D = \text{antilog}(\text{original value} - \text{predicted value}).$$

The original value is the SR recorded for each tooth area, while the predicted value is the SR predicted with reference to a specific allometric baseline. If D is equal to 1, then the predicted value, as expected theoretically, is equal to the original. Whether a tooth shows a larger/smaller size than expected is determined by D being larger/smaller than 1. Size here is a different concept from that originally measured. It is now a size scaled in reference to a baseline determined from all Asian colobines. Thus, how far a taxon varies from a "common base" can be estimated using this new scale.

Principal components analysis (PCA) is used in this study. Its purpose is to test whether or not there is notable variation among colobines with reference to the differences detected through dental allometric analysis when all deviations are consid-

ered simultaneously. In this technique, the information inherent in all deviations is reduced to that within the 1st few axes (normally the first 3). It may, therefore, be unnecessary to look at the algebraically far more confusing multidimensional model of original deviations. In addition to this data reduction effect, such an analysis may achieve 2 other effects. It can demonstrate, first, where a noticeable separation exists among groups (species in this study) when they are treated as a single universe of data. Then, in achieving these placements of the original specimens, variables may be arranged in groups. A correlation matrix, instead of covariance, transformation is used for the analysis. This is because the former is considered to be more suitable for anatomical data that include different dimensions (lengths, widths, etc.). In this way a well-defined group of variables can be provided for interpretation (Jolliffe 1986, pp. 46-49). Another advantage of a correlation matrix in defining a PCA is that results of analyses of different sets of random variables are more directly comparable than they are for analyses based on covariance matrices.

## RESULTS

The allometric relationships between cranial length and each tooth size of the Asian colobines are listed in table 2. Each tooth shows a significant close correlation with cranial length. In regard to the upper teeth, three others, the canine, M<sup>2</sup>, and M<sup>3</sup>, differ from the other teeth which are negatively scaled, in being positively scaled. The lower

**Table 2.** Allometric relationships between dental size and the independent variable (cranial length). The correlation coefficient between dental size and cranial length, and the exponent in allometric analysis are represented by  $r$  and  $b$ , respectively

Variable	Upper teeth		Lower teeth	
	$r$	$b$	$r$	$b$
I1	0.665	0.686	0.619	0.665
I2	0.614	0.560	0.657	0.678
C	0.778	1.218	0.751	1.156
P3	0.735	0.756	0.771	1.114
P4	0.789	0.838	0.806	0.831
M1	0.819	0.888	0.788	0.839
M2	0.848	1.086	0.840	1.158
M3	0.838	1.216	0.836	1.289

teeth which are positively scaled include the canine, P<sub>3</sub>, and the last 2 molars (M<sub>2</sub> and M<sub>3</sub>); the rest of lower teeth are negatively allometric.

Comparisons of dental deviations among the 6 genera are illustrated in figures 1-6. For upper teeth, in contrast to *Pygathrix*, *Rhinopithecus* and *Semnopithecus*, *Nasalis*, and *Trachypithecus* show smaller incisors; I<sup>1</sup> in *Presbytis* is similar to that in *Nasalis* and *Trachypithecus* (Fig. 1). Two genera, *Semnopithecus* and *Trachypithecus*, display bigger canines than expected, even being larger than those in other genera. *Semnopithecus* is characterized by its 2 larger premolars which show larger variation compared to the rest of the teeth (Fig. 2). Six genera are arranged as 3 clear groups based on deviations of the 3 molars (Fig. 3). That is: 1)

*Nasalis*, *Presbytis*, and *Pygathrix* show the smallest sizes because they have the lowest negative deviation (<1); 2) *Rhinopithecus* and *Semnopithecus* display the largest size (positive deviation greater than 1), and 3) *Trachypithecus* with values close to those expected (Fig. 3).

For the lower teeth, the 2 incisors of *Trachypithecus* are characterized by the smallest negative deviations (Fig. 4). *Presbytis* and *Semnopithecus* show the largest deviations in I<sub>2</sub> compared to the other genera. There is very little difference in the canine among genera except for *Presbytis* which shows a small deviation (Fig. 5). *Semnopithecus* is distinguished from others by its 2 large premolars. *Nasalis* and *Rhinopithecus* display large and small P<sub>3</sub>, respectively. As for the

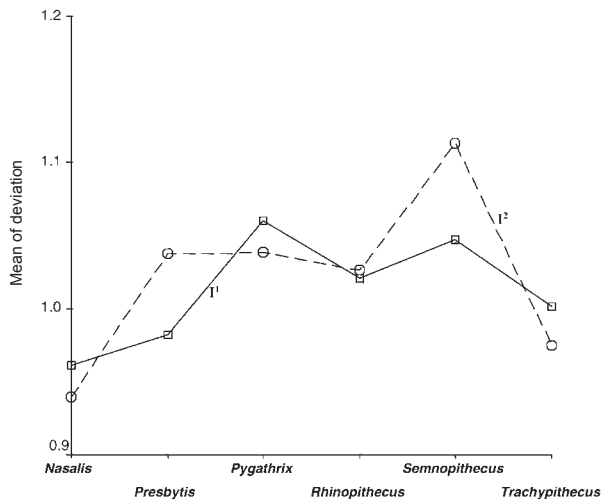


Fig. 1. Upper incisor deviation in reference to the baseline for Asian colobines.

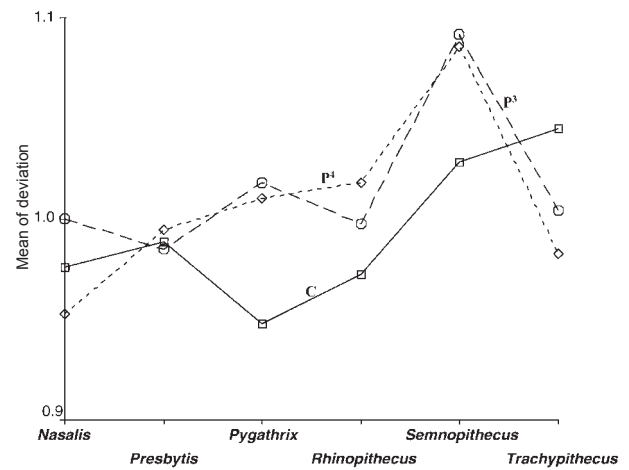


Fig. 2. Upper canine and premolar deviation in reference to the baseline for Asian colobines.

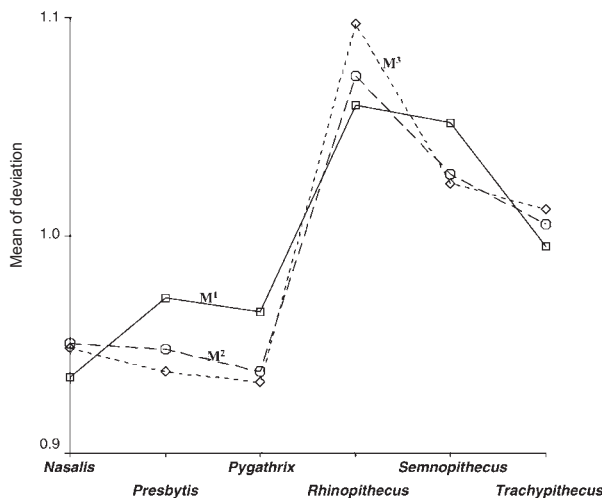


Fig. 3. Upper molar and deviation in reference to the baseline for Asian colobines.

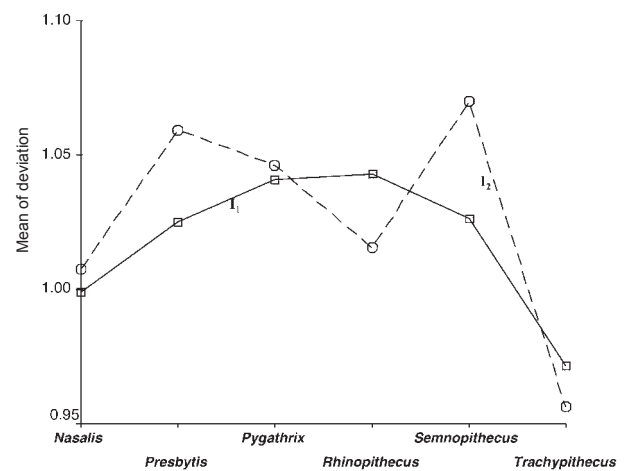


Fig. 4. Lower incisor deviation in reference to the baseline for Asian colobines.

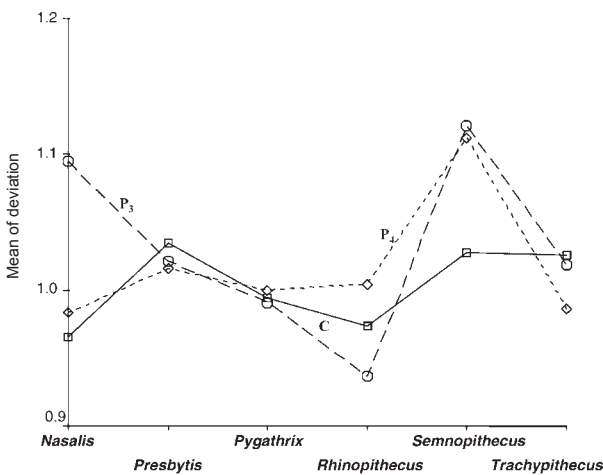


upper teeth, three groups are labeled by regarding the deviations of the 3 molars (Fig. 6): 1) *Nasalis*, *Presbytis*, and *Pygathrix* show the smallest sizes; 2) *Rhinopithecus* and *Semnopithecus* display the largest sizes apart from  $M_3$  in *Semnopithecus*, but which is still larger than that in the 1st group, 3)

**Table 3.** Total variation explained by the first 3 axes of PCA and the related eigenvectors based on dental deviations from allometric baselines

Eigenvector	Component		
	1	2	3
Total variation (%)	41.30	15.11	14.11
Cum. variation (%)	41.30	56.41	70.52
<b>Upper teeth</b>			
I1	0.374	0.205	0.825
I2	0.412	0.264	0.560
C	-0.072	0.690	-0.351
P3	0.558	0.350	-0.372
P4	0.745	0.252	-0.139
M1	0.912	-0.039	-0.070
M2	0.899	-0.178	-0.137
M3	0.824	-0.197	-0.180
<b>Lower teeth</b>			
I1	0.460	0.363	0.876
I2	0.296	0.428	0.669
C	-0.236	0.770	-0.218
P3	-0.031	0.715	-0.437
P4	0.637	0.251	-0.172
M1	0.873	-0.097	-0.096
M2	0.929	-0.109	-0.082
M3	0.849	-0.263	-0.164

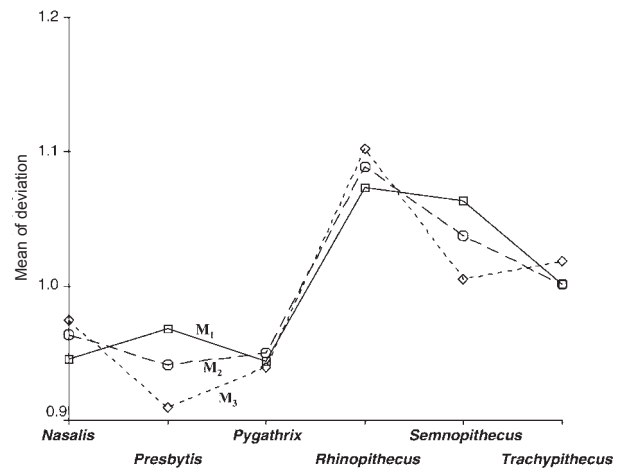
Variables making the highest contributions to the axes are shadowed.



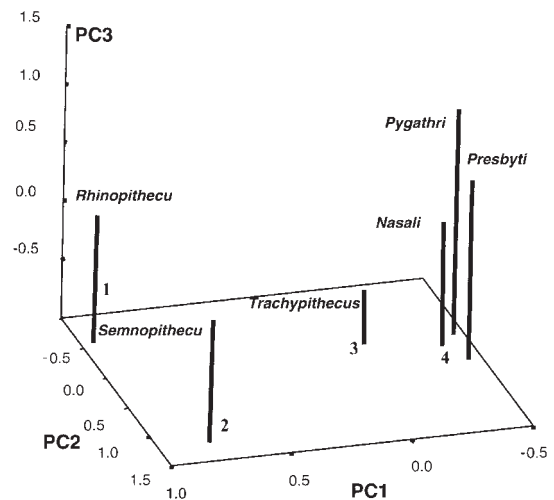
**Fig. 5.** Lower canine and premolar deviation in reference to the baseline for Asian colobines.

*Trachypithecus* shows sizes that are almost equal to those expected.

In principal components analysis based on deviations, the first 3 axes account for 70.52% of the total variation of which 41.30%, 15.11%, and 14.11% are explained by the 1st, 2nd, and 3rd axes, respectively (Table 3). Referring to eigenvectors, three molars in both jaws make the highest contributions to the 1st axis, which can then be regarded as the 'molar axis'. This means that the dispersion of taxa is mainly determined by the variation in molars. In the 2nd axis, the 2 canines and  $P_3$  that express negative eigenvectors on PC1 make the highest positive contributions, but molars show low negative eigenvectors. In contrast to the



**Fig. 6.** Lower molar deviation in reference to the baseline for Asian colobines.



**Fig. 7.** Generic dispersion of the colobines on the first 3 axes of the principal components analysis based on deviations from the baselines for Asian colobines.

remaining teeth which show negative eigenvectors, the 4 incisors make the highest positive contributions to the 3rd axis. Thus, the 2nd and 3rd axes can be regarded as 'canine and P<sub>3</sub>' and 'incisor' axes, respectively.

The dispersion of the 6 genera of Asian colobines in the first 3 axes of PCA is illustrated in figure 7. *Rhinopithecus* and *Semnopithecus* are closely gathered and clearly separated from the remaining genera along the 1st axis. They are, however, allocated at the 2 poles of the 2nd axis. The 3 genera, *Pygathrix*, *Nasalis*, and *Presbytis*, are clustered together with reference to both the 1st and 2nd axes. *Trachypithecus* is notably isolated from the remaining colobines along the 1st axis.

## DISCUSSION

The results found from this study provide sound evidence of relationships between tooth and body size and variation among Asian colobines. The results can also be used to test differences in dietary preferences in the wild, and to clarify whether dental variation is mainly associated with the dissimilarities in phylogeny or functional adaptation.

Each tooth showed a significant close relationship with cranial length. This again confirms that dental size is tightly related to body size as proposed by other researchers (e.g., Gingerich 1977, Gingerich et al. 1982). The interesting finding in this study is that none of the teeth was isometric relative to body size. They were scaled either positively or negatively. In other words, a change in dental size varied differently from that of body size in Asian colobines. It seems that different dental areas, e.g., incisor, canine, premolar, and molar for both mandibular and maxillary teeth, displayed different relationships with body size. Those with a positive allometric scale ( $b > 1.0$ ) include canines, M2s, and M3s in both jaws and P<sub>3</sub>. The remaining teeth were negatively scaled. This could be associated with differences in ontogeny. That is, different dental areas have genetic developmental trajectories (see below) correlated with specific functional adaptations (Schultz 1935, Kay and Hylander 1978, Christopher 2000, Harvati 2000). It has been shown that a developmental emphasis in a specific dental region is closely associated with a special functional adaptation; for example incisors usually characterize frugivorous primates. This selection

result from an adaptation to more-frequent usage of front teeth in fruit grasping, cutting, and biting. On the other hand, such an emphasis occurs for molars in folivorous primates. Functionally this means having a large crown surface for chewing, shearing, and grinding the hard fibers of leaves (Hylander 1975a b). Colobines, quite different from cercopithecines, are categorized as folivorous primates or are generally regarded as "leaf-eating monkeys" (Smith 1983, Smith et al. 1983, Struhsaker and Leland 1987, Rowe 1996, also see Table 1). Some dental features found in this study could be considered to be associated with folivorous preferences in colobines. In a study involving a number of anthropoids (Kay and Hylander 1978), colobines were significantly separated from cercopithecines by their small incisors which showed lower negative allometry to body size compared with others in the cercopithecines. These teeth in some species, such as *Papio*, *Macaca*, *Mandrillus*, and *Theropithecus*, are much developed and it has been suggested that they are used for frugivorous food processing. The lowest negative allometric relationships between incisors and body size revealed in this study (Table 2) seem to confirm this differentiation in incisors between colobines and cercopithecines. Positive allometric relationships between M2s and M3s with body size, however, imply that a molar region is more emphasized in colobines than in cercopithecines.

Dental growth and eruption sequences have been considered to be related to patterns of life history and to special functional adaptations (Shultz 1935 1960, Leigh 1994). An allometric analysis of adult specimens can test whether a specific tooth experienced a long period of growth or an increased growth rate relative to body size. It was reported in Asian colobines that the eruption of the incisors is quite variable (Harvati 2000). With regard to the permanent teeth, I<sub>1</sub>s erupt before M2s in *Nasalis*, and in *Trachypithecus* I<sub>1</sub> erupts after M<sub>2</sub>, while I<sub>2</sub> appears before M<sub>2</sub> in some species. M2s erupt after I<sub>1</sub>s in other species. M2s always appear before I<sub>2</sub>s in *Presbytis* and *Pygathrix*. The results found in this study imply that the less-developed incisors (being very lowly negatively scaled) in Asian colobines may result from either a shorter developmental period or a slower growth rate than M2s which are scaled positively.

The allometric patterns exhibited by molars in this study and the specific growth rate of M1s indicate that molars in colobines undergo different individual ontogenetic trajectories even though

they finally form a region that is more developed than in cercopithecines (Schultz 1953, Oates et al. 1994, Harvati 2000). That is, the first molars (M1s), as in most of the other nonhuman primates, always erupt first, and their appearances are also regarded as a significant indication of the occurrence of some behavioral and physical developments, such as weaning time and a brain size that has reached about 90% of its expected volume (Ashton and Spence 1958, Smith 1989 1991). According to table 2, this tooth in both jaws greatly differ from M2s and M3s, by exhibiting a negative allometric relationship to body size. This implies that even though this tooth begins growing earlier, it may experience either a shorter growth period or a slower developmental rate than the other 2 molars that are positively scaled even though they erupt later, especially M3s.

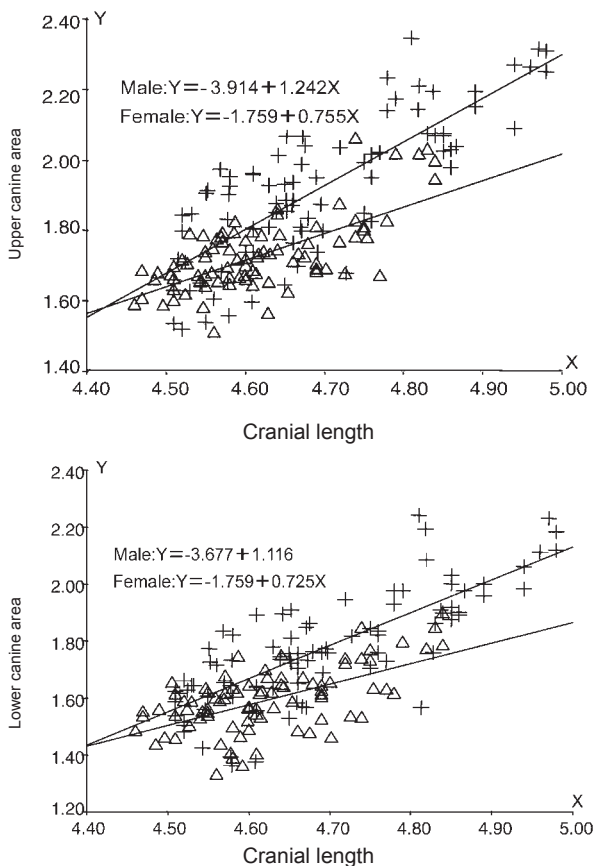
Compared with other primates, a tendency for early eruption of the molars in colobines has been considered to be relevant to their special functional adaptation to dietary components. That is, more folivorous components require extensive

chewing, shearing, and compressing between the upper and lower molar crowns (Schultz 1935, Kay and Hylander 1978, Leigh 1994). So it is not surprising that M2s and M3s in this study showed a positive allometric relationship with body size.

Canines and  $P_3$  are another three teeth that showed positively allometry. Canines in colobines, as in a macaque species (*Macaca nemestrina*), are characterized by significant sexual dimorphism in eruption times (Harvati 2000). This variation was considered to be relevant to differences in growth period and rate (Smith 1994, Harvati 2000). This tooth tends to erupt after the premolars in males, but before premolars in females (Oates et al. 1994). Thus, it seems that the 2 sexes show great variation in growth trajectories. That is, even though this tooth appears earlier in females, it has a slower growth rate or a shorter developmental period than it does in males. So it is positively scaled in males and negatively scaled in females with respect to body size when they were analyzed independently (Fig. 8). An analysis of covariance for the 2 regression models indicates that the 2 sexes show 2 significantly different regression slopes. This implies that they have quite different patterns in terms of the relationship between the canines and body size.

A strongly developed canine in male Asian colobines can be considered to be functionally associated with the phenomena of social structure and behavior. For example, a polygamous mating system is very common in these species. For some species, such as gray, dusky, and douc langurs, and snub-nosed monkey, populations are composed of multi-male/multi-female individuals (Napier and Napier 1967, Jablonski and Pan 1995, Rowe 1996). In such a social structure, frequency and intensity of competition are very great for mates, hierarchical status, territorial arrangement, and food accessibility. Snub-nosed monkeys are remarkable not just among colobines but also among Old World monkeys because of their extremely high sexual dimorphism in canine and body size which was considered to be higher than that reported for other colobine monkeys (Jablonski and Pan 1995).

Significant sexual dimorphism in the canine tooth was reported to be accompanied by the same scenario in  $P_3$  at about the same level in colobus and snub-nosed monkeys (Leutenegger 1977, Pickford 1986, Jablonski and Pan 1995). This correspondence of development is an adaptation to extensive and heavy cutting and shearing between upper and lower canines. A two-way



**Fig. 8.** Comparison of allometric relationships between canine area and cranial length in the 2 sexes of Asian colobines. +:males;Δ:female.



ANOVA analysis for an interaction test between species and sex shows that a significant interaction between these 2 factors was detected for the sizes of the canines and  $P_3$ , but not for the rest remaining teeth. This implies that, in addition to a significant differentiation between sexes, there must be another important variation among species in terms of patterns of sexual dimorphism when these 2 teeth are considered. Further analysis of this issue is necessary.

When all dental deviations were considered simultaneously, the results from PCA showed that the 6 genera of Asian colobines were clustered into 4 groups (Fig. 7), that is, into *Rhinopithecus*, *Semnopithecus*, *Trachypithecus*, and the combination of *Presbytis*, *Nasalis*, and *Pygathrix*. This profile greatly differs from those based on other morphological parts of the skull, which illustrates their similarities in systematics, evolution, and phylogeny. That is, all Asian colobines can be regarded as 2 big groups: odd-nosed and normal-nosed (Peng and Pan 1994, Jablonski 1998, Groves 2001, Pan and Groves in press, also see Table 1), but this also reflects similarities in ecology, habitat, and dietary preferences.

Even though all Asian colobines are generally categorized as folivorous primates, as mentioned above, a great diversity exists between genera, species, and even in populations within a species (Bennett and Davies 1994, Oates et al. 1994, Rowe 1996). Unfortunately, a comparative study of dietary components in the field has not been made, except for some isolated studies, such as between *T. vetulus* and *S. entellus*. The former was regarded as more folivorous than the latter (Hladik 1978). Furthermore, between *T. obscurus* and *P. melalophos* in Malaya (Curtin 1976), the former was thought to be more folivorous than the latter. Other non-comparative field studies related to the species studied in the present investigation and some dietary data for single species are available, such as those for *T. francoisi* and *T. phayrei* (Li 1993, Das 1998). Studies on other Asian colobines are also available. They are frequently described as consumers of leaves, fruit, seeds, flowers, and other tender plant parts (Table 1), but it is difficult to quantitatively compare differences between species. On the other hand, as occurs in most groups of animals, dietary selection in colobines greatly varies between populations in different geographic regions and even within the same species. This is because of variations in ecological backgrounds (Bennett and Davies 1994). The importance of the availability of a cer-

tain food is dependent on a specific season. Thus, there is no doubt that different observation results may have been reported on the same species. For example, leaves taken by the proboscis monkey were evaluated as being from 44% to 52% of their total diet (Yeager 1989, Dierenfeld and Koontz 1992, Yeager et al. 1997).

Other reports, however, have provided some support for the results of this study. Species of snub-nosed monkeys are significantly isolated from the other colobines. This, as mentioned above, may be linked to their special niches, especially those on the Qinghai-Tibet Plateau. The habitat of this genus is mainly comprised of coniferous or mixed temperate coniferous-deciduous broad leafed forest. Some diets taken by monkeys greatly differ from those chosen by other Asian colobines, for example, vines, nuts, bark, and lichens in coniferous forests (Shi et al. 1982, Hu et al. 1989, Li and Shi 1989, Liu 1989), mosses found in fir-larch forests and on the ground where snow is found all year around, and the bark of China fir for Chinese species (Li and Shi 1989, Bleisch et al. 1993, Bleisch and Xei 1998, Kirkpatrick et al. 2001).

Snub-nosed monkeys illustrate larger molars than expected (Figs. 3, 6), and this makes the highest contribution to PC1 (Table 3). The more strongly developed molars than other Asian colobines implies that they are very specialized in terms of dietary selection and adaptation. The special habitats to which they are adapted have already made them distinguishable from other colobines in Asia in terms of food selection. For instance, in cold climates, tree bark, lichens, moss, and nuts are composed of fibers that are harder than those of the leaves, buds, and seeds found in tropical-subtropical rain forests to which groups 3 and 4 are adapted. On the other hand, in colder climates, especially in winter, the choice of palatable food items is greatly reduced, and animals are forced to rely on a few species with lower nutritional contents that have to be consumed in greater quantities (Li et al. 2000, Kirkpatrick et al. 2001). Such food is more resistant to mastication. The remarkable dietary separation of snub-nosed monkeys from other colobines was previously suggested by results based on mandibular structure (Jablonski et al. 1998), a feature in which they differ significantly from other Old World monkeys. They displayed an unusually strongly robust mandibular corpus and symphysis that were considered to be capable of resisting the high peak strains during mastication adapted for a long period of heavy chewing in the molar area (Hylander

1979, Bouvier 1986). The strong development of the molars found in this study obviously needs a strong mandibular structure.

The 2nd group consists of the gray langur which is close to the snub-nosed monkey. This species is characterized by its strongly developed molars, which are very similar to those of *Rhinopithecus*. This species differs from other Asian colobines in terms of its distribution and dietary components. It was reported to take more fruits, about 45% of its total intake (Amerasinghe et al. 1971, Muckenhirn, 1972) or to be extremely frugivorous compared with other colobines (Kay and Hylander 1978). According to Bennet and Davies (1994) this species is characterized by its feeding on a great range of plants (53 species) due to its extensive distribution, from the coastline to the Himalayan hills up to 4000 m in elevation; it also takes more insects than any other colobines. The very similar molar size and a close association between *Semnopithecus* and *Rhinopithecus* in PC1 may be explained by some similarities between their diets, such as bark and twigs in the snowy winter (Rowe 1996), and in their niches; some populations of *S. entellus* are distributed in the coniferous forests in the high mountains adjacent to the Qinghai-Tibet Plateau where the snub-nosed monkey (*R. bieti*) is also found. They can even be found in mountains at elevation more than 4000 m (Rowe 1996), which is even higher than that of the other 3 species of snub-nosed monkeys (*R. avunculus*, *R. brelichi*, and *R. roxellana*). So it is reasonable to propose that the sub-nosed monkeys and the gray langur have been shaped by the same adaptations in terms of ecology, diet, and geographic modification.

*Trachypithecus* and *Presbytis* are noticeably separated (Fig. 7). Species of *Trachypithecus* are generally found in evergreen moist deciduous forest. Dietary information about them is very scant and isolated. According to Bennett and Davies (1994), *T. vetulus* is sympatric with *S. entellus* in Sri Lanka, and fruit consumption was most common for both species in the fruiting season. *Trachypithecus phayrei* and *T. obscurus* are largely folivorous. The latter was regarded as being much more folivorous than *P. melalophos* (Curtin 1976). Another study showed that *Trachypithecus* has a higher foliage intake than *Presbytis*, in which foliage usually comprises of about 60% of the annual diet, with 20%-40% of it being mature foliage (Bennett and Davies 1994). The profile shown in figure 7 also implies that the species in this genus differs from those in *Presbytis* and are

closer to snub-nosed monkeys and the gray langur.

Three genera, *Nasalis*, *Pygathrix*, and *Presbytis*, form the 4th group (Fig. 7). According to figures 3 and 6, they are characterized by smaller molars. This relationship may reflect some similarities in their niches (coastline tropical rain forest) and dietary adaptations. They may be more folivorous compared with the previous 3 groups.

The proboscis monkey is distributed in coastal swamps and riverside forests and was described as a species taking a very high proportion of leaves. It feeds on young leaves, buds, and shoots of mangrove and pedata trees. These can form 95% of its diet (Banks 1949, Davies 1962, Kern 1964). This species was also reported to eat a lot of seeds (Yeager 1989).

The douc langur feeds primarily on leaves in tropical deciduous moist forest and semi-deciduous forest (Bennett and Davies 1994, Lippold 1995). It had been regarded as relatively folivorous within the colobines and its dietary leaf proportion can reach 82.0% (Chivers 1994, Lippold 1998). Morphology of the stomach in the douc langur also differs considerably from that of the snub-nosed monkey even though they are phylogenetically closely related (Groves 2001, Pan and Oxnard 2001a), but it is very similar to that of the proboscis monkey (Caton 1998). Thus, it is not surprising that they were categorized into 1 group and there is significant separation from the snub-nosed monkey based on dental structure in this study.

*Presbytis* monkeys are found in evergreen tropical rain forests and have been regarded as typical representatives of folivorous primates among nonhuman primates (Napier and Napier 1967, Rowe 1996), so the name 'leaf-eating monkey', was suggested to name them only (Oates et al. 1994).

Thus, quite different from the scenarios revealed by genetic and molecular analyses, and other morphometric studies, the relationships among Asian colobines revealed in this study mainly reflect their similarities in ecology, dietary adaptations, and latitudinal geographic distributions, rather than similar evolutionary processes or phylogenetic development. This also confirms that some factors, such as the extensive tectonic movements in Asia since the Pliocene, especially of the Himalayas and the Qinghai-Tibet Plateau, and the last global glaciation which profoundly shaped the vegetation (Brandon-Jones 1998), have already forced Asian colobines to adapt to

different niches. Their dental structures was accordingly modified. This is a good example of natural selection and adaptation.

## CONCLUSIONS

The results of this study reveal some biological features of Asian colobines. 1) Each tooth showed a significant relationship with body size and was allometrically scaled relative to body size. A positive allometry for the canines and P<sub>3</sub> could be considered to be related to their multi-male/multi-female mating system and behavioral differences in social activities between the sexes. The same scaling for M2s and M3s is regarded as a functional adaptation to a folivorous preference in food. 2) Sexual dimorphism in the eruption sequence of the canines has resulted in a clear difference in allometric patterns between the 2 sexes. These teeth in both upper and lower jaws were scaled positively and negatively in males and females, respectively. 3) Relationships between groups did not reflect variations in evolution and phylogeny as revealed in other studies, but in functional adaptations. 4) Different from other species, the snub-nosed monkey and gray langur are characterized by their larger molar size. This was suggested as being related to their special dietary selection in temperate and coniferous forests, and 5) finally, tectonic modifications and climate changes in Asia since the Neogene have already significantly forced various species to adapt to different ecological niches.

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