

Peculiar Tooth Homologies of the Greater Bamboo Lemur (*Prolemur* = *Hapalemur simus*)

When is a Paracone Not a Paracone?

Jukka Jernvall, Christopher C. Gilbert and Patricia C. Wright

Introduction

Among living primates, bamboo lemurs provide a rare case of adaptation to feeding on fibrous vegetation. Bamboo makes up a significant portion of the diet of all three living species, *Hapalemur griseus*, *H. aureus*, and *H. simus* (now also known as *Prolemur simus*, Groves, 2001). The latter, the greater bamboo lemur, has perhaps the most monotonous plant diet of all primates. Long term studies on wild greater bamboo lemurs (Tan, 1999) have shown that 95% of its diet is composed of one species of bamboo (*Cathystachyum madagascariensis*). *H. simus* is also the only species that routinely breaks open and eats the culms (the bamboo's trunk) of mature bamboo. Even the remaining portion of the diet is made mostly of other bamboo species, with fruit and other foods (mostly soil and mushrooms) making 2% of the diet.

Bamboos, which are grasses belonging to the family Poaceae, are highly fibrous. Bamboo culms contain close to 50% cellulose with the remaining material made mostly of lignin and polyose (hemicellulose) (Fengel and Shao, 1984). Additionally, bamboo contains silica bodies (or phytoliths). Taken together, these factors make bamboo a challenging food to consume and digest. It is then perhaps to be expected that the challenge of bamboo feeding should be reflected in the dentition of bamboo lemurs. Indeed, H. O. Forbes in the Allen's Naturalist's Library (1894) described the *Hapalemur* dentition to be "peculiar and characteristic". While several "peculiarities" have been documented in the bamboo lemur dentition (Tattersall, 1982), in this paper we will focus on one, namely the molarization of premolars.

Jukka Jernvall

Developmental Biology Program, Institute of Biotechnology, University of Helsinki
PO Box 56, FIN-00014, Helsinki, Finland
jernvall@fastmail.fm

Molarization of Premolars but how?

Several mammalian groups have species with molariform premolars. Of the living species, elaborate molariform premolars are found in species with a fibrous, plant-based diet. For example, horses and hyraxes, which rely heavily on grass, have molars and premolars which form a single cheek-tooth battery. Based on their namesake diet, bamboo lemurs provide further evidence of the relationship between a dietary reliance on fibrous plant material and molarized premolars. Furthermore, as might be expected based on the extreme specialization to bamboo feeding, *H. simus* shows the greatest degree of premolar molarization among the bamboo lemurs (Tattersall, 1982).

In contrast to other Lemuriformes (Ankel-Simons, 2007), all species of bamboo lemur have molariform features on their posterior, upper fourth, premolars (P⁴) (see Fig. 1). Molariform features, in this context, refer to the addition of buccal and lingual cusps on the premolars as well as the position of these cusps. In general, lemur taxa have tribosphenic molars with three cusps: the paracone, protocone, and metacone (e.g., see Swindler, 2002). Some lemur taxa, such as *Hapalemur*, add a fourth cusp, the hypocone, as well. The more closely a premolar mimics the number and position of these cusps as typically observed on a molar, the higher the degree of molarization.

In most lemur taxa, the anterior upper premolars (P²–P³) are marked by only one prominent cusp, the buccally-positioned paracone (Swindler, 2002). The upper third premolar (P³) of *H. simus*, however, has a well-developed lingual cusp, the protocone, making it more molariform than the P³ of any other lemur taxon. Additionally, the prominent buccal cusp (i.e., the paracone) of the P³ is flanked by shorter mesial and distal cusps (Fig. 1).

While lemur species are variable in P⁴ morphology, this tooth typically displays two cusps, a prominent paracone and a smaller protocone (Swindler, 2002). In contrast, the P⁴ of *H. simus* has a squared-off occlusal shape and appears almost completely molariform. In addition to a paracone and protocone, the P⁴ of *H. simus* has also developed a second buccal cusp, the metacone. In many individuals one can even detect incipient development of a second lingual cusp, the hypocone, from the postprotocingulum (Fig. 1).

Whereas the ecological context of premolar molarization appears to be diet, the way premolars acquire molar shapes is not necessarily clear. One of the best studied cases is the molarization of premolars in a lineage of Eocene perissodactyls. Beginning in *Hyracotherium*, the Eocene “dawn horse”, the premolars began to expand lingually and attain molariform features in this lineage (Granger, 1908; Butler, 1952; Van Valen, 1982). On the P⁴, the protocone has been reconstructed to have evolved first, followed by the hypocone distal to the protocone. This mode of cusp evolution is to be expected because it follows the ancestral mode of lingual expansion of molars themselves. Furthermore, the identity of cusps and their names are based on their relative location to other cusps and crown features. Regardless of the shape, the single or mesial lingual

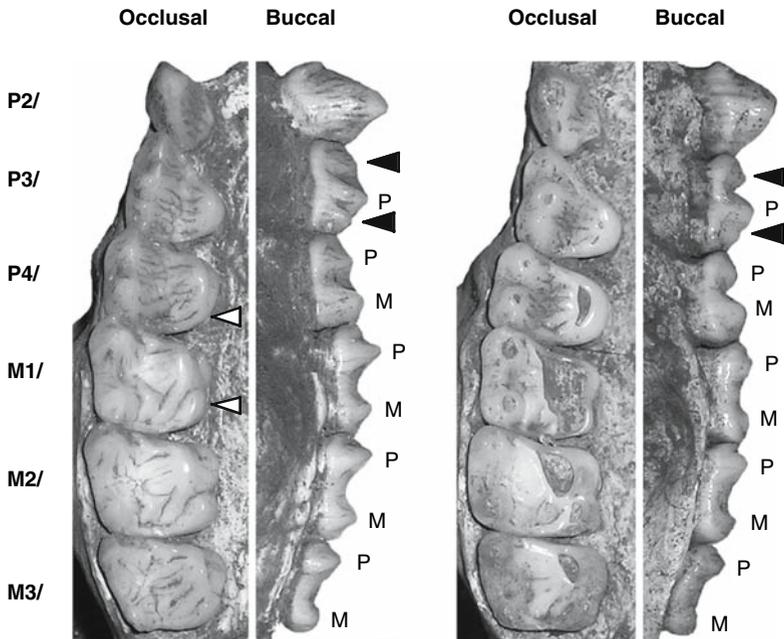


Fig. 1 Two examples of the greater bamboo lemur postcanine tooth rows. The buccal views have the paracone (P) and the metacone (M) cusps marked. The open arrow heads mark the postprotocingulum on P4/ and the hypocone on M1/. The closed arrow heads mark the two accessory cusps mesial and distal to the paracone on P3/ (see text for details). Note the presence of the lingual cusp (the protocone) on the premolars of both specimens. Also note the presence of the homologous trough between the paracone and the mesial accessory cusp on P3/ and the metacone and paracone on P4/ in the specimen on the right (buccal view). DPC 7939 on the left, DPC 7854 on the right

cusp is called the protocone, but this is also where the *Hyracotherium* P³ has turned out to be interesting. When the P³ of *Hyracotherium* evolved a new lingual cusp, this cusp appeared not distal, but mesial to the protocone. Nevertheless, both P⁴ and P³ eventually evolved similar molariform morphologies in perissodactyls. In this instance, the molarization of P³ happened by the protocone shifting distally and changing its “identity” to the hypocone whereas the new, mesial lingual cusp, by definition, became the protocone.

This shift in cusp position during molarization between P³ and P⁴ was first noted by Granger (1908) and discussed in connection to cusp homology by Van Valen (1982; 1994). The problem is that whereas we could label the single lingual cusp of the *Hyracotherium* P³ as the “hypocone”, and thus solve the shift in cusp identity, this is only possible by the benefit of hindsight. That is, if the P³ molarization had stopped at the single lingual cusp, we would be content in calling this cusp the protocone.

Why knowing about shifts in cusp homology may matter is in the connection to phylogenetic studies in which one relies on comparison of homologous

characters across species. As the molarization of *Hyracotherium* premolars suggests, in certain situations the historical continuity of cusp homologies may break, a view that gains further support from developmental biology studies. Evidence of mammalian tooth development indicates that molar cusps may appear during ontogeny as an iterative replay of the same set of developmental regulatory genes (Salazar-Ciudad and Jernvall, 2002). Experimental work on mice has shown that decreasing or increasing the production of a single signaling molecule required for cusp formation causes many of the existing cusps to fuse or new cusps to appear, respectively (Kangas et al., 2004). Thus there might not be a unique genetic code for the protocone, for example, but cusps evolve as a result of changes in the overall interplay between molecular signaling and tissue growth (Salazar-Ciudad and Jernvall, 2002; Kangas et al., 2004).

Molarization of Premolars and the Discontinuity of Homology

In contrast to the molarization of premolars in the extinct evolutionary lineage of Eocene perissodactyls, the premolars of the greater bamboo lemur provide a living example of what may happen to cusp homologies during molarization. Theoretically, studying an extant taxon allows for a better appraisal of morphological variation as well as the opportunity to study developmental genetic correlates in a laboratory setting. Unfortunately, extant *H. simus* is too rare and endangered to study in the laboratory and only one social group is habituated enough to obtain dental measurements for the study of subtle morphological variation. However, the field work of Elwyn Simons has provided us with an extensive sample of recently extinct *H. simus* populations. His work demonstrates that *H. simus* was widespread and probably present throughout Madagascar, except in the south (Godfrey et al., 2004). One specimen has been dated to 4560 ± 70 BP (Simons et al., 1995) and, at least from a paleontological perspective, it is likely that all the studied specimens are drawn from a relatively short time interval. We therefore focused on a sample of *H. simus* specimens from Ankarana Massif, where a large number of individuals have been recovered. By examining correlated morphological variation within a large sample, we can record the pattern of cusp change during the premolar molarization process.

Because *H. simus* shows a slightly lesser degree of molarization than the Eocene perissodactyls, we focused on the variation in buccal cusps. From a sample of 15 relatively unworn specimens, we measured the distance between buccal cusps of P^3 , P^4 , and M^1 . As a proxy for molarization of the P^4 , we measured the distance between the mesial and distal cusps, the paracone and the metacone. The distances between these cusps in our sample of P^4 s was then compared to the distances between these cusps in our sample of corresponding M^1 s. The closer a distance measured on P^4 approximates the same distance measured on a corresponding M^1 , the higher the degree of premolar

molarization. The values seen within P⁴ range from 65 to 80% of the corresponding distance in M¹, showing that in some individuals the P⁴ is indeed very close to the M¹ in cusp spacing.

Next we tested whether the increased molarization of P⁴ is associated with a corresponding increase in the molarization of P³. The third premolar has one buccal cusp, the paracone, often with one mesial and one distal accessory cusp. We measured whether the relative P⁴ distance between paracone and metacone correlates with the relative distance between the P³ paracone and its distal cusp or its mesial cusp (Fig. 2). The former correlation would indicate that increased molarization of P⁴ results in increased molarization of P³ by distal extension, and the formation of the metacone in the normal distal position. The latter option would show that the increasing P³ molarization is obtained by further development of the mesial part of the tooth and by formation of a new mesial cusp. Hence, in this latter case a new paracone is formed and the “original” paracone becomes the metacone (Fig. 2). These hypotheses assume that the molarization affects all the premolars but at a decreasing strength in the anterior teeth. Developmentally, this kind of shift in cusp homology may stem from development affecting the overall high-level complexity of teeth rather than individual cusp positions (Evans et al., 2007).

The results demonstrate that the P³ paracone to distal cusp distance shows no correlation with the P⁴ molarization ($r_s = -0.31, p = 0.252$). In contrast, the P³ paracone to mesial cusp distance increases with increasing P⁴ molarization ($r_s = 0.70, p = 0.009$, Fig. 3). This indicates that, developmentally, the paracone-metacone pair of the P⁴ are homologous to the mesial cusp-paracone pair of the P³. Thus, in *H. simus*, the P³ paracone is in the process of becoming the metacone by shifting distally. This shift represents a break in homology.

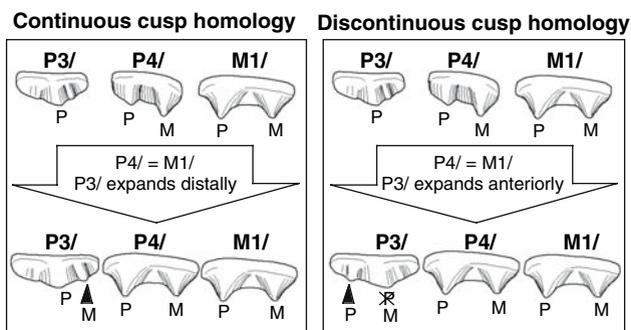


Fig. 2 Two possibilities for the molarization of P³/ in *H. simus*. Illustrations show buccal views with the paracone (P) and the metacone (M) cusps marked. On the left the P⁴/ becomes fully molarized and the posterior part of P³/ expands giving rise to the metacone. On the right the P⁴/ becomes fully molarized but the mesial portion of P³/ expands giving rise to a new paracone whereas the old paracone becomes the metacone, braking the continuity of historical homology

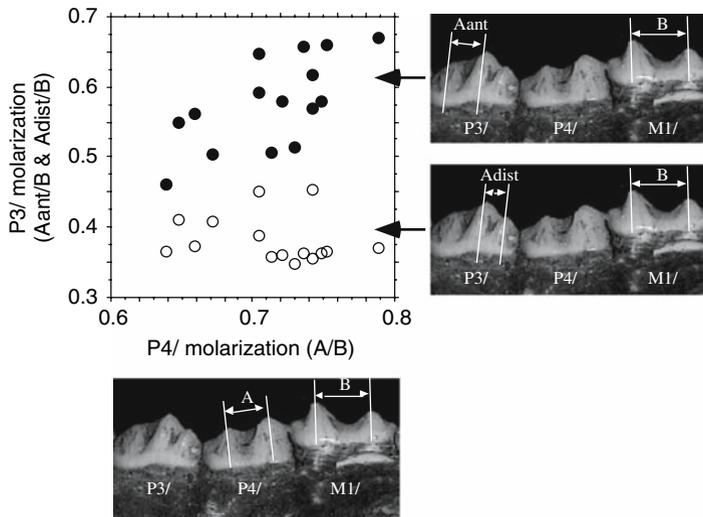


Fig. 3 The relative molarization of P4/ and P3/. As the paracone-metacone distance (A) of P4/ approaches that of M1/ (B), the relative P3/ paracone-anterior accessory cusps distance (Aant) increases (see dark circles, $r_s = 0.70$, $p = 0.009$). In contrast, the relative P3/ paracone-distal accessory cusps distance (Adist) shows no molarization effect (see open circles, $r_s = -0.31$, $p = 0.252$). These correlation analyses indicate that the anterior accessory cusp on P3/ is homologous to the paracone on P4/. Measurements were taken from digital buccal views (DPC 6755, 6811, 7854, 7938, 7939, 10942, 10956a, 10956b, 10978a, 10978b, 10978c, 10980, 10983, 11714, 20705)

The interpretation presented here is further supported by one *H. simus* specimen in which a well developed trough between the P⁴ paracone and the metacone is paired with a corresponding trough between the P³ mesial cusp and the paracone (Fig. 1, specimen on the right). It is also quite possible that the shift in homology of cusps is not limited to P³ because in every studied case on P⁴, the P⁴ paracone was shorter than the P⁴ metacone. This is noteworthy because in mammals relative cusp height correlates with the initiation of cusp development (Berkovitz, 1967, Kangas et al., 2004) and thus the P⁴ metacone may well have been the paracone in the ancestor of *H. simus*. This prediction could be testable with a Tertiary fossil record, which is, unfortunately, currently unavailable in Madagascar (see Tattersall, 2008).

Conclusions

Our study indicates that the molarization of upper premolars in *H. simus* takes place through a process in which the paracone is shifted distally to become the metacone and a new mesial buccal cusp (paracone) is developed. This process represents a discontinuity in cusp homology. Although we often assume the

development of cusps follows a standard sequence, it is clear from Eocene perissodactyls and *H. simus* that cusp homologies are not always as they appear. The paracone of one tooth may become the metacone of another tooth. Similarly, the protocone of one tooth may become the hypocone of another tooth. These changes can occur within species, such as *H. simus*, and between species as documented by the Eocene perissodactyl lineage. Researchers must be cautious in assuming cusp homologies without studies of cusp development, whether through experimental lab work or through morphological observations such as those presented here.

The available material from *H. simus* also shows that there is subtle but detectable variation in the molarization of its premolars. Without further study of the temporal range of the specimens, it is not possible to test whether this variation may indicate differences in selective regimes through time and microhabitat. However, the effect of habitat might be testable in *H. griseus*, the smallest and widest ranging of the extant bamboo lemur species. Our observation regarding the discontinuity in homology of buccal cusps is a further indication of the dynamic nature of tooth development and evolution. This, together with the high degree of premolar molarization in *H. simus*, underscores the evolutionary uniqueness of this taxon and adds yet another reason to protect the species from extinction (Fig. 4). Finally, this study was largely made possible by the work of Elwyn Simons in Madagascar and his continued emphasis on studying both fossil and living primates.



Fig. 4 The extant greater bamboo lemur, *Hapalemur simus*. Photo by J. Jernvall

Acknowledgment We thank Prithijit Chatrath and Elwyn Simons for access to the subfossil *H. simus* material at the Division of Fossil Primates. We thank Elwyn Simons for his tireless fieldwork and inspiration. We also thank John Fleagle for his patience and helpful comments on an earlier version of this manuscript. This is DLC publication #1091.

References

- Ankel-Simons, F. (2007). *Primate Anatomy*. Elsevier, Academic Press, Burlington, MA.
- Berkovitz, B. K. B. (1967). The dentition of a 25-day pouch-young specimen of *Didelphis virginiana* (Didelphidae: Marsupialia). *Arch. Oral Biol.* 12: 1211–1212.
- Butler, P. M. (1952). Molarization of the premolars in the Perissodactyla. *Proc. Zool. Soc. London* 121: 819–843.
- Evans, A. R., Wilson, G. P., Fortelius, M., and Jernvall, J. (2007). High-level similarity of dentitions in carnivorans and rodents. *Nature* 445: 78–81.
- Fengel, D., and Shao, X. (1984). A chemical and ultrastructural study of the Bamboo species *Phyllostachys makinoi*. *Wood Sci. Technol.* 18: 103–112.
- Forbes, H. O. (1894). *A Handbook to the Primates: Allen's Naturalist's Library*. W. H. Allen & Co, London.
- Godfrey, L. R., Simons, E. L., Jungers, W. L., De Bliex, D. D., and Chatrath, P. S. (2004). New discovery of subfossil *Hapalemur simus*, the greater bamboo lemur in western Madagascar. *Lemur News* 9: 9–11.
- Granger, W. (1908). A revision of the American Eocene horses. *B. Am. Mus. Nat. Hist.* 24: 221–264.
- Groves, C. P. (2001). *Primate Taxonomy*. Smithsonian Institution Press, Washington, DC.
- Kangas, A. T., Evans, A. R., Thesleff, I., and Jernvall, J. (2004). Nonindependence of mammalian dental characters. *Nature* 432: 211–214.
- Salazar-Ciudad, I., and Jernvall, J. (2002). A gene network model accounting for development and evolution of mammalian teeth. *P. Natl Acad. Sci. USA* 99: 8116–8120.
- Simons, E. L., Burney, D. A., Chatrath, P. S., Godfrey, L. R., Jungers, W. L., and Rakotosamimanana, B. (1995). AMS C-14 dates for extinct lemurs from caves in the Ankarana Massif, northern Madagascar. *Quaternary Res.* 43: 249–254.
- Swindler, D. R. (2002). *Primate Dentition: An Introduction to the Teeth of Non-Human Primates*. Cambridge University Press, Cambridge.
- Tan, C. L. (1999). Group composition, home range size, and diet of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. *Int. J. Primatol.* 20: 547–566.
- Tattersall, I. (1982). *The Primates of Madagascar*. Columbia University Press, New York.
- Tattersall, I. (2008). Vicariance vs. dispersal in the origin of the Malagasy mammal fauna. In: Fleagle, J. G. and Gilbert, C. C. (eds.), *Elwyn Simons: A Search for Origins*. Springer, New York, pp. 397–408.
- Van Valen, L. (1982). Homology and causes. *J. Morphol.* 173: 305–312.
- Van Valen, L. (1994). Serial homology: The crests and cusps of mammalian teeth. *Acta Palaeontol. Pol.* 38: 145–158.