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Expression Types for Two Cercopithecoid Dental Traits (Interconulus and Interconulid) and Their Variation in a Modern Baboon Population

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*Studies of cercopithecoid systematics include the analysis of quantitative and qualitative dental variation. Much of the qualitative variation involves the expression of cingular remnants on molars. Qualitative variation in the cingular remnant has been defined and described in several ways by researchers. The differences in terminology and definition confound cross-study comparisons. I introduce a formalized typology for two nonmetric molar traits, the interconulus and interconulid. Each trait includes 5 degrees of expression, with written and photographic descriptions for each character state. I scored a large sample (n = 329) of dental casts from a captive breeding colony of savannah baboons (*Papio hamadryas sspp.*) for the expression types and assessed the variation statistically. The baboon colony shows a large amount of variation in the two traits. Use of these formalized types will facilitate cross-study comparison and analysis, effectively increasing sample sizes and our understanding of the evolution of primate dentitions.*

KEY WORDS: nonmetric traits; dental variation; Carabelli's Cusp; *Papio hamadryas sspp*.

INTRODUCTION

Reasearchers study primate dentitions for many reasons ranging from phylogentic modelling to dental development to functional morphology. Teeth are the most frequently preserved parts of fossil primates and the only available structures for some extinct taxa. The dentition is adapted for many

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functions, including mastication, food preparation, and social interactions, and they contain a record of their growth. As such, studies of dental variation address a variety of paleontological and odontological hypotheses.

Most studies of primate dental variation focus on metric variation (Baume and Lapin, 1983; Eck, 1975; Freedman, 1957; Hayes *et al.*, 1990; Jolly *et al.*, 1997; Kieser and Groeneveld, 1988; Olivier *et al.*, 1979; Swindler, 1976). However, qualitative features are commonly used in systematic studies, especially for the purpose of alpha taxonomy (e.g. Benefit, 1993; Delson, 1975; Delson and Andrews, 1975; Hayes *et al.*, 1990; Hornbeck and Swindler, 1967; Jablonski and Yumin, 1991; Jolly *et al.*, 1997; Strasser and Delson, 1987; Swindler, 1976). Unlike metric characters though population-level variation in these traits is poorly quantified and understood.

The presence or absence of accessory cuspules on the sides of molar teeth is a qualitative character that is particularly common. They are thought to be remnants of the primitive primate cingulum (Dahlberg, 1950; Scott and Turner, 1997; Swindler, 1976) and are frequently present in anthropoid primates (Swindler, 1976). A large amount of attention has been given to the human maxillary cingular remnant, Carabelli's Cusp (von Carabelli, 1842), which is differentially expressed in human populations. A series of well-defined expression types for Carabelli's cusp was established by Dahlberg (1963) and is widely used (Hanihara, 1963; Scott, 1980; Turner *et al.*, 1991). Numerous researchers have incorporated this data collection protocol, using the well-described variation in Carabelli's cusp to differentiate populations and determine degrees of affinity among them (Scott and Turner, 1997).

Cingular remnant features in catarrhines have been identified by a variety of names: protostylid, protostyle, interconulus, interconulid, Carabelli's cusp, and groove cusp. Swindler's (1976) use of "interconulus" for styles between the protocone and hypocone of maxillary molars and "interconulid" for stylids between the protoconid and hypoconid of mandibular molars is preferable for cercopithecoids because they do not imply a special relationship with the protocone/id, which they do not display in cercopithecoids. Carabelli's cusp is inappropriate *in lieu* of interconulus given the human-specific implication of the term and the different molar morphology of humans versus cercopithecoids. The human expression of cingular remnants is morphologically distinct from that of nonhumans. In humans, Carabelli's cusp is generally a cuspule extending from the protocone. On cercopithecoid maxillary molars, the cuspules (or styles) are between the protocone and hypocone, rather than being associated exclusively with the protocone. The features in cercopithecoids are more appropriately called styles or stylids since they are not minor cusps. Due to the different morphology, the expression states established for human Carabelli's cusps are not appropriate for analysis of the variation of cingular remnants in cercopithecoids. The establishment of expression types for the interconulid and interconulus provides uniformity in the terminology used for these traits and the morphology associated with each term.

Although cercopithecoid cingular remnants differ from human homologues, their morphology is similar across cercopithecoid taxa (Swindler, 1976). Several authors have taken both metric and nonmetric approaches to evaluate the variation (Eck, 1975; Jablonski and Yumin, 1991; Teaford, 1983). However, a consistent methodology to assess them had not been established. For example, Eck (1975) measured the length, number and bilaterality of accessory styles on maxillary and mandibular molars. In contrast, Teaford (1983) restricted his assessment of the trait to a count of the accessory cuspules, or styles. Given the similarity of expression among cercopithecoid taxa, the establishment of formal expression types will facilitate comparisons among data sets and will unify the terminology used in discussions. Terminological uniformity is necessary in light of the prominent role the interconulus and interconulid have played in studies of taxonomy, phylogeny, functional morphology, and more recently, developmental genetics.

Delson and Andrews (1975) inferred accessory cuspules for the last common ancestor of the Catarrhini, and they have been used to diagnose various living and extinct primates (*Prohylobates tandyi*: Delson, 1979; *Colobus satanas*: Harrison and Harris, 1996; *Microcolobus tugenensis*: Benefit and Pickford, 1986; *Komba minor*: McCrossin, 1992).

Several researchers have hypothesized a functional role for cingular remnants (Benefit, 1993; Delson, 1975; Haeussler *et al.*, 1989; James 1960; Macho and Spears, 1999; Mizoguchi, 1993; Spears and Macho, 1998), though no definitive evidence is available to support or to reject any of them. The hypotheses remain speculative until we understand more about the genetic and developmental processes that result in the presence of either a complete cingulum, or its remnants, or its absence.

The expression of accessory cusps is also potentially important for quantitative genetic studies of dental development. However, it is first crucial to establish a consistent nomenclature and to define basic morphological variation in the traits.

I used variation in 329 baboons (*Papio hamadryas sspp.*: Jolly, 1993) to establish expression types for two cingular remnant traits: the interconulus and interconulid (Swindler, 1976). The interconulus is an accessory style on the lingual surface of maxillary molars between the protocone and hypocone. The interconulid is an accessory stylid on the buccal surface of mandibular molars between the protoconid and hypconid. The interconulus and interconulid vary greatly within the sample, with their expression ranging from no style to multiple styles. Using the range of variation of the two traits, I describe, 5 expression types (character states) for each of them.

MATERIALS

I examined teeth of 329 pedigreed baboons, *Papio hamadryas sspp.* (Jolly, 1993), which are part of a much larger breeding colony at the Southwest Foundation for Biomedical Research (SFBR) in San Antonio, Texas. Jolly's (1993) taxonomy comprises one species with 5 subspecies of savanna baboon: *Papio hamadryas anubis*, *P. h. cynocephalus*, *P. h. hamadryas*, *P. h. papio*, and *P. h. ursinus*. The SFBR sample includes individuals from 2 subspecies: olive baboons (*Papio hamadryas anubis*), yellow baboons (*Papio hamadryas cynocephalus*), and their hybrids (Williams-Blangero *et al.*, 1990). Savanna baboons have a high amount of dental variation, possibly related to the diverse subspecies within *Papio hamadryas*. Hybridization and large amount of variation is typical of wild baboon populations as the hybridize in natural contact zones in Kenya (Jolly, 1993; Kingdon, 1971; Maples and McKern, 1967; Samuels and Altmann, 1986).

The use of hybrid baboons to establish the expression types is of minimal concern. The trait varies within other cercopithecoids and the range of variation within them is as extreme as that in the SFBR baboon colony, ranging from some individuals having no expression of either trait to multistyle/id expression (Swindler, 1976). Accordingly, the level of phylogenetic distance among savanna baboons is irrelevant to the establishment of expression types for the interconulus and interconulid.

I made impressions of dentitions while the subjects were anesthetized intramuscularly with ketamine followed by intravenous RAAK (Rompun, Atropine, Acepromazine, and Ketamine) to affect relaxation. I used a mouth splint to hold the subject's mouth open. I wiped the teeth with gauze and brushed them with a toothbrush when necessary. I molded the postcanine dentition and incisors with a rapidly setting impression dental material (Coltene President© gel). The procedure is approved by the Institutional Animal Care and Use Committee, in accordance with established guidelines. I poured positive casts with plaster $\leq$ 1 week after making the molds.

DESCRIPTION OF TYPES

I used third maxillary molars casts to exemplify the interconulus and second mandibular molar cast to exemplify the interconulid.

Interconulus

The interconulus is an accessory style on the lingual surface of maxillary molars between the protocone and hypocone. A score of zero indicates that

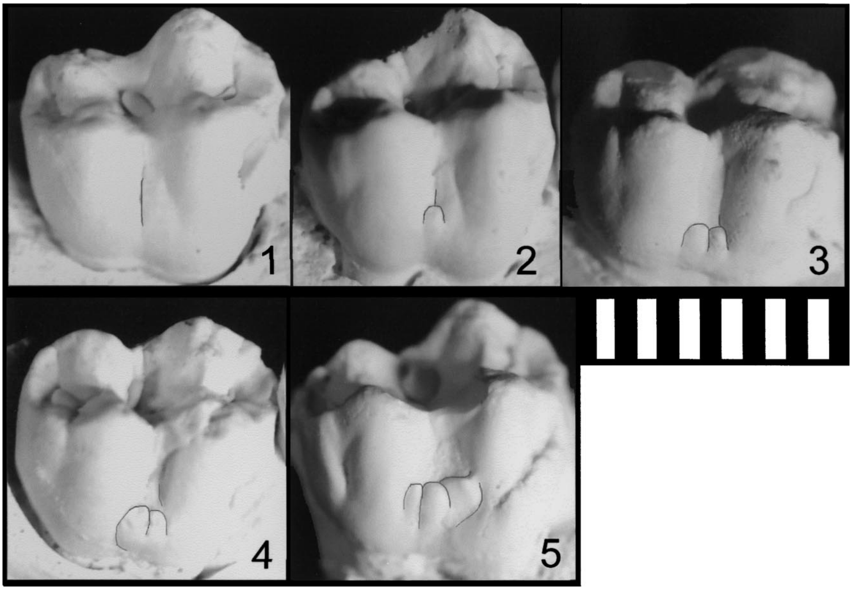

Fig. 1. Interconulus expression types. All photographs are the lingual view of right maxillary third molars. The interconulus is highlighted with line drawings to accentuate the morphology described in the text. Scale = mm.

the trait is obscured, too worn, or otherwise not ascertainable. One is its lowest expression and, 5 is its strongest expression (Fig. 1):

1 – There is no expression of a style. The lingual surface between the paracone and metacone is either completely smooth or just slightly swollen though the swells from the two cusps do not meet to form a style.
2 – A small style close to but separate from both lingual cusps.
3 – There is a double style close to but separate from the two lingual cusps.
4 – The styles are large and extend lingually to, or beyond, the most lingual point of either the protocone or hypocone when viewed occlusally.
5 – There are multiple styles that extend mesiodistally onto the protocone and hypocone and often extend lingually beyond the most lingual point of the lingual cusps.

Interconulid

The interconulid is an accessory stylid on the buccal surface of mandibular molars between the protoconid and hypconid. A score of zero indicates

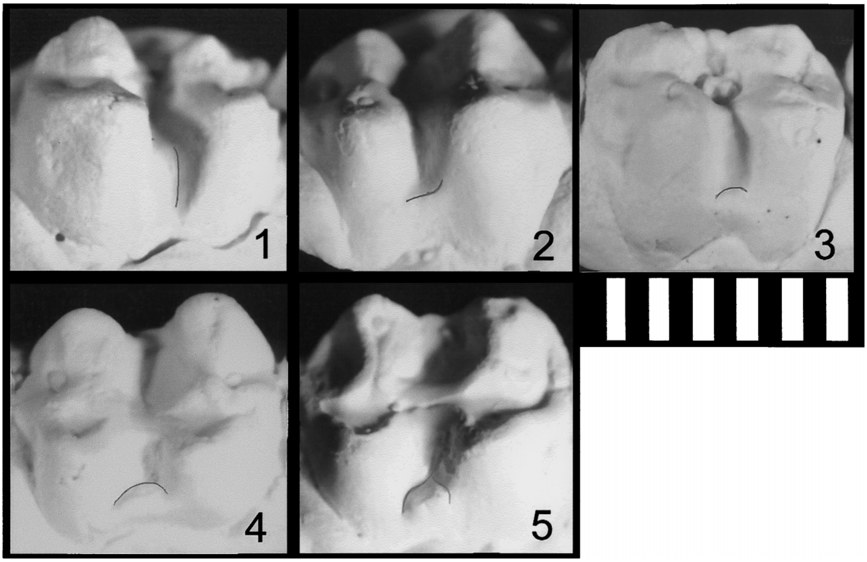

Fig. 2. Interconulid expression types. All photographs are the buccal view of second mandibular molars. All are right side molars except for 1 and 3. The interconulid trait is highlighted with line drawings to accentuate the morphology described in the text. Scale = mm.

Table I. Descriptive statistics for the interconulus and interconulid

	Interconulus		
	Mean	StDv	N
XLM1	1.59	0.71	318
XLM2	1.64	0.90	320
XLM3	2.09	1.24	305
XRM1	1.50	0.61	304
XRM2	1.58	0.82	310
XRM3	1.98	1.18	293
DLM1	2.80	0.78	292
DLM2	2.29	0.90	306
DLM3	2.12	1.18	255
DRM1	2.64	0.82	299
DRM2	2.06	0.91	303
DRM3	1.88	1.15	264

Note. X = maxillary; D = mandibular; L = left; R = right; 1, 2, or 3 designates molar number.

Table II. Frequency data for the interconulus and interconulid

Score	XRM1	XRM2	XRM3	XLM1	XLM2	XLM3	DRM1	DRM2	DRM3	DLM1	DLM2	DLM3
No data	25	19	36	11	9	24	30	26	65	37	23	74
1	170	183	138	164	181	138	15	81	138	11	51	102
2	119	88	74	129	94	67	123	152	62	86	152	71
3	13	26	45	20	25	55	120	45	33	145	73	42
4	2	13	20	3	18	26	36	20	20	47	24	29
5	0	0	16	2	2	19	5	5	11	3	6	11
Total	329	329	329	329	329	329	329	329	329	329	329	329

Note. X = maxillary; D = mandibular; L = left; R = right; 1, 2, or 3 designates molar number.

it is obscured, too worn, or otherwise not ascertainable. One is its lowest expression and 5 is its strongest expression (Fig. 2):

1 – The buccal crown is completely smooth.
2 – There is slight evidence of an interconulid, but it appears only as a smoothed shelf.
3 – The interconulid is a distinctive shelf that wraps slightly onto the adjacent cusps. In occlusal view the shelf does not extend beyond the buccal dimension of the protoconid and hypoconid.
4 – The interconulid is a distinctive shelf that not only wraps onto the adjacent cusps but also protrudes buccally beyond them when viewed occlusally.
5 – The interconulid is like state 4, but there is also a stylid rising above the level of the interconulid shelf.

VARIATION OF TRAITS

I assessed the interconulus and interconulid in the SFBR baboon sample ($n = 329$). I scored each molar twice, with one week between assessments. I conducted a third assessment for teeth whose first and second scores did not match. The two scores that matched were used as the final data point for a molar. A third scoring was necessary for <35% of the sample.

Both traits are bilaterally symmetrical such that expression of each trait on antimeres of the same individual is not significantly different. Approximately 40% of the baboon sample demonstrates some degree of expression (states 2–5) of the interconulus (Table I). The degree of expression of the interconulus increases distally along the tooth row, such that expression on the third molar is typically greater than is expression on the second molar, and expression on the second molar is greater than that on the first molar (Table II).

Virtually the entire sample (95%) showed some expression (character states 2–5) of the interconulid (Table I). Within the tooth row, the degree of expression of the interconulid shows the opposite pattern from that of the interconulus. First molar expression is generally greater than those of the second or the third molars (Table II).

CONCLUSIONS

Variation in degree of expression of the interconulus and interconulid in a modern savanna baboon population was used to establish formal expression states for use in cercopithecoid odontology. These traits have fallen under a wide-range of terminologies and are usually described in terms of qualitative presence or absence. The scoring system described here will enable this discontinuous variable to be more specifically incorporated into descriptions of fossils, species, and population-level variation. Such facility of languge will be beneficial to the wide fields of study that employ these traits, such as phylogenetics, dental functional morphology, and developmental and quantitative genetic analysis.

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REFERENCES

Baume, R. M., and Lapin, B. A. (1983). Inbreeding effects on dental morphometrics in *Papio hamadryas. Am. J. Phys. Anthropol.* 62: 129–135.

Benefit, B. R. (1993). The permanent dentition and phylogenetic position of *Victoriapithecus* from Maboko Island, Kenya. *J. Hum. Evol.* 25: 83–172.

Benefit, B. R., and Pickford, M. (1986). Miocene fossil cercopithecoids from Kenya. *Am. J. Phys. Anthropol.* 69: 441–464.

Corruccini, R. S. (1977). Crown component variation in hominoid lower third molars. *Z. Morph. Anthrop*. 68(1): 14–25.

Dahlberg, A. A. (1950). The evolutionary significance of the protostylid. *Am. J. Phys. Anthropol.* 8: 15–25.

Dahlberg, A. A. (1963). Analysis of the American Indian dentition. In Brothwell, D. R. (ed.), *Dental Anthropology*, Pergamon Press, London, pp. 149–178.

Delson, E. (1975). Evolutionary history of the Cercopithecidae. In Szalay, F. (ed.), *Approaches to Primate Paleobiology, Contributions to Primatology*, Vol. 5, Basel, New York, pp. 167–217.

Delson, E. (1979). *Prohylobates* (Primates) from the Early Miocene of Libya: A new species and its implications for cercopithecid origins. *Geobios* 12: 725–733.

Delson, E., and Andrews, P. (1975). Evolution and interrelationships of the catarrhine primates. In Luckett, W. P., and Szalay, F. S., (eds.), *Phylogeny of the Primates: A Multidisciplinary Approach*, Plenum Press, New York, pp. 405–446.

Eck, G. (1975). *Morphometric Variability in the Dentitions and Teeth of Theropithecus and Papio*, Phd Thesis, University of California, Berkeley.

Freedman, L. (1957). The fossil cercopithecoidea of South Africa. *Ann. Trans. Mus.* 23: 121–262.

Haeussler, A. M., Irish, J. D., Morris, D. H., and Turner, C. G. III. (1989). Morphological and metrical comparisons of San and central Sotho dentitions from southern Africa. *Am. J. Phys. Anthropol.* 78, 115–122.

Hanihara, K. (1963). Crown characters of the deciduous dentition of the Japanese-American hybrids. In Brothwell, D. R. (ed.), *Dental Anthropology*, Pergamon Press, New York, pp. 105–124.

Harrison, T., and Harris, E. E. (1996). Plio-Pleistocene cercopithecids from Kanam East, western Kenya. *J. Hum. Evol.* 30: 539–561.

Hayes, V. J., Freedman, L., and Oxnard, C. E. (1990). The taxonomy of savannah baboons: An odontomorphometric analysis. *Am. J. Primatol.* 22: 171–190.

Hornbeck, P. V., and Swindler, D. R. (1967). Morphology of the lower fourth premolar of certain Cercopithecidae. *J. Dent. Res.* 46(Suppl 5): 979–983.

Jablonski, N. G., and Yumin, G. (1991). A reassessment of *Megamacaca lantianensis*, a large monkey from the Pleistocene of north-central China. *J. Hum. Evol.* 20: 51–66.

James, W. W. (1960). *The Jaws and Teeth of Primates*, Pitman Medical Publishing Co., Ltd., London.

Jolly, C. J. (1993). Species, subspecies, and baboon systematics. In Kimbel, W. H., and Martin L. B., (eds.), *Species, Species Concepts, and Primate Evolution*, Plenum Press, New York, pp 67–107.

Jolly, C. J., Woolley-Barker, T., Beyene, S., Disotell, T. R., and Phillips-Conroy, J. E. (1997). Intergeneric hybrid baboons. *Int. J. Primatol.* 18(4): 597–627.

Kieser, J. A., and Groeneveld, H. T. (1988). Patterns of metric variability in the dentition of *Papio ursinus*. *Am. J. Primatol.* 14(2): 141–151.

Kingdon, J. (1971). *East African Mammals: An Atlas of Evolution in Africa*, Academic Press, New York.

Macho, G. A., and Spears, I. R. (1999). Effects of leading on the biomechanical behavior of molars of *Homo*, *Pan*, and *Pongo*. *Am. J. Phys. Anthropol.* 109, 211–227.

Maples, W. R., and McKern, T. W. (1967). A preliminary report on classification of the Kenya baboon. In Vagtborg, H. (ed.), *The Baboon in Medical Research*, Vol 2, University of Texas Press, San Antonio, TX, pp. 13–22.

McCrossin, M. L. (1992). New species of bushbaby from the Middle Miocene of Maboko Island, Kenya. *Am. J. Phys. Anthropol.* 89: 215–233.

Mizoguchi, Y. (1993). Adaptive significance of the Carabelli trait. *Bull. Nat. Sci. Mus., Ser. D* (*Anthropol*) 19: 21–58.

Olivier, T. J., Freedman, L., and Coppenhaver, D. (1979). Odontometric variation among local populations of Kenyan olive baboons. *J. Hum. Evol.* 8(6): 603–614.

Samuels, A., and Altmann, J. (1986). Immigration of a male Papio anubis into a group of *Papio cynocephalus* baboons and evidence for an anubis-cynocephalus hybrid zone in Amboseli, Kenya. *Int. J. Primatol.* 7: 131–133.

Scott, G. R. (1980). Population variation of Carabelli's trait. *Hum. Biol.* 52: 63–78.

Scott, G. R., and Turner, C. G., II (1997). *The Anthropology of Modern Human Teeth*, Cambridge University Press, New York.

Spears, I. R., and Macho, G. A. (1998). Biomechanical behaviour of modern human molars: Implications for interpreting the fossil record. *Am. J. Phys. Anthropol.* 106, 467–482.

Strasser, E., and Delson, E. (1987). Cladistic analysis of cercopithecid relationships. *J. Hum. Evol.* 16: 81–99.

Swindler, D. R. (1976). *Dentition of Living Primates*, Academic Press, New York.

Teaford, M. F. (1983). The morphology and wear of the lingual notch in macaques and langurs. *Am. J. Phys. Anthropol.* 60: 7–14.

Turner, C. G., II, Nichols, C. R., and Scott, G. R. (1991). Scoring procedures for key morphological traits of the permanent dentition: the Arizona State University Dental Anthropology system. In Kelley, M. A., and Larsen, C. S. (eds.), *Advances in Dental Anthropology*, Wiley Liss, Inc., New York, pp. 13–31.

von Carabelli, G. (1842). *Anatomie des Mundes*, Braumüller und Seidel, Wien.

Williams-Blangero, S., Vandeberg, J. L., Blangero, J., Konigsberg, L. W., and Dyke, B. (1990). Genetic differentiation between baboon supspecies: Relevance for biomedical research. *Am. J. Primatol.* 20: 67–81.