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Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*

Erin R. Vogel [a,b,*], Janneke T. van Woerden [c], Peter W. Lucas [d], Sri S. Utami Atmoko [e], Carel P. van Schaik [b], Nathaniel J. Dominy [a]

[a] Department of Anthropology, 1156 High Street, University of California Santa Cruz, CA 95064, United States
[b] Anthropological Institute and Museum, University of Zürich, Winterthurerstrasse 190, 8057-Zürich, Switzerland
[c] Department of Behavioral Biology, University of Utrecht, P.O. Box 80.086, 3508 TB, Utrecht, The Netherlands
[d] Anthropology Department, The George Washington University, Hortense Amsterdam House, 2110 G Street, NW, Washington, DC 20052, United States
[e] Biology Faculty, Universitas Nasional – Jakarta, Jl. Sawo Manila, Pejaten, Pasar Minggu, Jakarta 12520, Indonesia

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Abstract

The divergent molar characteristics of *Pan troglodytes* and *Pongo pygmaeus* provide an instructive paradigm for examining the adaptive form-function relationship between molar enamel thickness and food hardness. Although both species exhibit a categorical preference for ripe fruit over other food objects, the thick enamel and crenulated occlusal surface of *Pongo* molar teeth predict a diet that is more resistant to deformation (hard) and fracture (tough) than the diet of *Pan*. We confirm these predictions with behavioral observations of *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii* in the wild and describe the mechanical properties of foods utilized during periods when preferred foods are scarce. Such fallback foods may have exerted a selective pressure on tooth evolution, particularly molar enamel thinness, which is interpreted as a functional adaptation to seasonal folivory and a derived character trait within the hominoid clade. The thick enamel and crenulated occlusal surface of *Pongo* molars is interpreted as a functional adaptation to the routine consumption of relatively tough and hard foods. We discuss the implications of these interpretations for inferring the diet of hominin species, which possessed varying degrees of thick molar enamel. These data, which are among the first reported for hominoid primates, fill an important empirical void for evaluating the mechanical plausibility of putative hominin food objects.

Keywords: Diet; Frugivory; Young's modulus; Fracture toughness; Functional morphology

Introduction

The physical characteristics of foods are predicted to exert a selective pressure on many aspects of primate biology, with a particular emphasis on dental functional morphology (Lucas, 2004). For instance, Kay (1981) observed an association between molar enamel thickness and dietary proclivity. Primate species with relatively thin molar enamel rely on leaves and/or soft fruit, whereas those with thicker enamel tend to consume hard foods. Kay (1985) suggested that the thick enamel of hard-object feeders was an adaptation to strengthen the tooth crown (cf. Macho and Spears, 1999); additionally, it is also plausible that natural selection favored thicker molar enamel because it delays tooth senescence in the face of abrasion (Jolly, 1970; Molnar and Gantt, 1977). In support of this second hypothesis, the longevity and reproductive fitness of individual primates has been linked directly to tooth durability and efficacy (DeGusta et al., 2003; King et al., 2005). As a result of these two mutually compatible views, an adaptive relationship between molar enamel thickness and obdurate food has become widely accepted.

* Corresponding author. University of California Santa Cruz, Department of Anthropology, CA 95064, United States.
E-mail addresses: evogel@ucsc.edu (E.R. Vogel), J.T.vanWoerden@students.uu.nl (J.T. van Woerden), pwlucas@gwu.edu (P.W. Lucas), suci-azwar@yahoo.co.id (S.S. Utami Atmoko), vschaik@aim.unizh.ch (C.P. van Schaik), njdominy@ucsc.edu (N.J. Dominy).

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Kay's (1981) concept of food hardness was based on the subjective impressions of human observers. In the 25 years since, relatively few quantitative data have emerged on the hardness of primate foods (Kinzey, 1978; Peters, 1987; Kinzey and Norconk, 1990, 1993; Dumont, 1995; Ungar, 1995; Yamashita, 1996; Lambert et al., 2004). In general, the results of these studies support Kay's observation; thickly enameled species are more durophagous. Such findings indicate resource partitioning on the basis of food hardness, but they are difficult to interpret in a broader comparative context. Each study differed methodologically and in the usage of mechanical terms. Thus, an adaptive relationship between molar enamel thickness and the mechanical properties of foods, particularly among hominoid primates, continues to be based largely on inductive reasoning, notwithstanding the fact that enamel thickness itself can vary greatly depending on the measurement protocol used (Martin, 1985; Nagatoshi, 1990; Schwartz, 2000; Kono, 2004; Smith et al., 2005; Olejniczak and Grine, 2006).

One of the relatively uncontested viewpoints in studies of molar enamel thickness is that *Gorilla* and *Pan* possess comparatively thin enamel, while *Pongo* and modern humans possess varying degrees of thick enamel (Schwartz, 2000; Smith et al., 2005; cf. Shellis et al., 1998; Kono, 2004). This distinction is illustrated in Fig. 1. When compared to *Pan troglodytes*, the molar enamel of *Pongo pygmaeus* is thicker, particularly along the occlusal basin, an area associated with crushing during Phase II of the chewing power stroke (Kay, 1985; Schwartz, 2000). Such thickness predicts a relatively obdurate diet, as do a variety of additional craniodental characteristics (Walker, 1981; Teaford and Walker, 1984; Kay, 1985; Demes and Creel, 1988; Ungar, 1994, 1998; King et al., 1999; Galbany et al., 2005; Merceron et al., 2005, 2006; Taylor, 2006; Taylor et al., submitted).

The crenulated occlusal surface of *Pongo* molars is another distinctive trait. When compared to the molars of chimpanzees, *Pongo* molars exhibit higher average surface slopes and steeper molar-cusp slopes throughout the wear sequence (Ungar, 2006a). This distinction is illustrated in Fig. 1. Such relief increases the angularity of the enamel surface, and likely improves the extent to which foods are fractured (M'Kirera and Ungar, 2003; Ungar and M'Kirera, 2003). This pattern, together with relatively high shearing crest development, has led some authors to suggest that *Pongo* evolved to subsist on fracture-resistant leaves to a greater extent than *Pan* (Ungar and Kay, 1995; Ungar et al., 2004). Yet a resemblance of categorical foraging behavior—chimpanzees and Bornean orangutans tend to consume food objects in similar proportions (Rodman, 1984)—raises the possibility that *Pongo* evolved to cope with a tougher overall diet rather than a greater fraction of leaves per se.

In sum, the divergent molar characteristics of *Pan* and *Pongo* provide an instructive paradigm for testing hypotheses on the evolution of molar enamel thickness. Here we describe the mechanical properties of food objects in the diet of *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. The diet of *Pongo* is predicted to be more resistant to deformation and crack initiation (hard) and crack propagation (tough) than the diet of *Pan* (for detailed mechanical definitions, see Lucas et al., 2000; Lucas, 2004). We confirm these predictions and assess the importance of mechanically challenging food

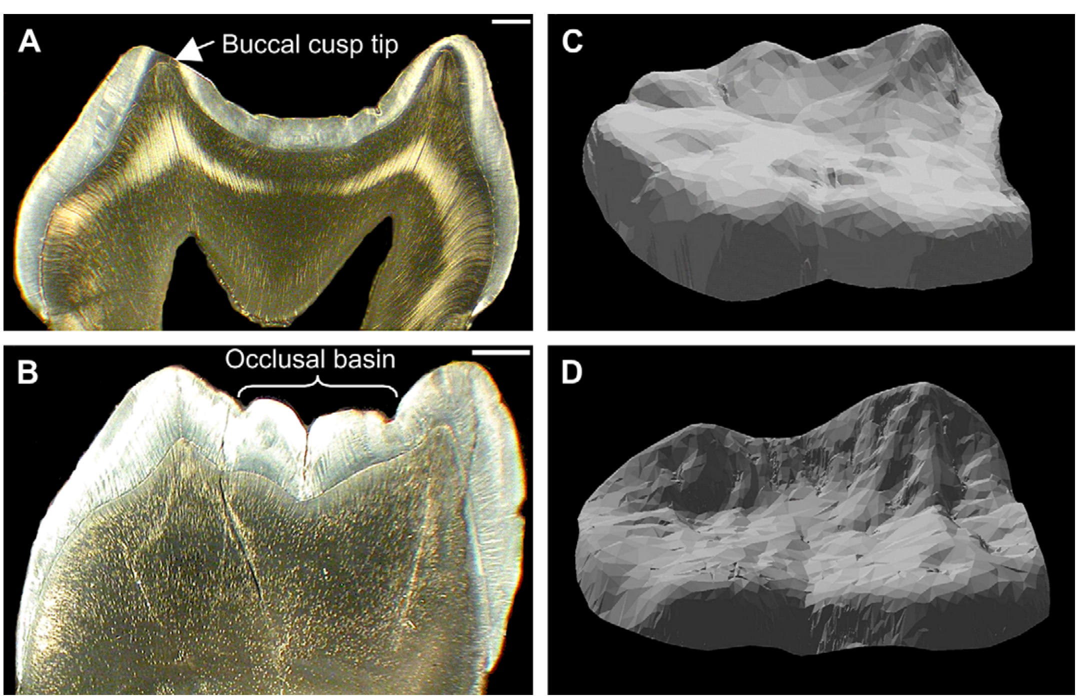

Fig. 1. M_2 cross-sectional images of (A) *Pan troglodytes* and (B) *Pongo pygmaeus*. The enamel of *Pan* is thinnest along the cusps, which may facilitate dentine exposure, as evident on the protoconid. The enamel of *Pongo* is thickest in the occlusal basin, an area associated with crushing. The triangulated irregular surface of M_2 at wear stage II is also depicted for (C) *Pan troglodytes* and (D) *Pongo pygmaeus*. When compared to *Pan*, the enamel of *Pongo* is more crenulated, exhibiting a greater degree of surface angularity. M_2 images are courtesy of T.M. Smith (A and B) and P.S. Ungar (C and D). The white scale bar = 1 mm.