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News and views

Possible change in dental morphology in *Gigantopithecus blacki* just prior to its extinction: Evidence from the upper premolar enamel-dentine junctionYingqi Zhang ^{a,*}, Reiko T. Kono ^b, Changzhu Jin ^a, Wei Wang ^c, Terry Harrison ^d^a Key Laboratory of Vertebrate Evolution and Human Origin of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China^b Division of Human Evolution, Department of Anthropology, National Museum of Nature and Science, Tsukuba 305-0005, Japan^c Guangxi Museum of Nationalities, Nanning 530021, China^d Center for the Study of Human Origins, Department of Anthropology, New York University, New York, NY 10003, USA

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Introduction

The extinct giant ape, *Gigantopithecus blacki*, inhabited southern China and northern Vietnam during the Early and Middle Pleistocene. Several researchers have inferred that its extinction occurred at 380–310 ka (thousands of years ago) (Rink et al., 2008) or 0.3 Ma (millions of years ago) (Wang, 2009), at the end of the Middle Pleistocene (Zhao and Zhang, 2013). The recently discovered *G. blacki* specimens from Hejiang Cave in Guangxi, South China (Zhang et al., in press), which are well dated to 400–320 ka, provide additional evidence for the Last Appearance Datum of the species. Twelve localities with *G. blacki* are currently known (Table 1), seven inferred to be Early Pleistocene in age and five Middle Pleistocene. However, no record of *G. blacki* older than the Early Pleistocene has been discovered in China or Vietnam.

The earliest well dated occurrence of *G. blacki* is from Longgupo, Wushan, Chongqing, with an age of 1.96 Ma based on paleomagnetic

correlations and electron spin resonance (ESR) dating (Huang and Fang, 1991; Huang et al., 1995). Jin et al. (2009) reported *G. blacki* from Sanhe Cave, with an estimated age of approximately 1.2 Ma. Ciochon et al. (1996) identified the co-occurrence of *G. blacki* and *Homo erectus* from Tham Khuyen Cave dating to 475 ka. Rink et al. (2008) published dates for *Gigantopithecus* Cave, Heidong, and Bulalishan using combined ESR and uranium–thorium (²³⁰Th/²³⁴U) isotopic analysis of tooth enamel, of 940–1206 ka, 308–380 ka, and 481–745 ka, respectively. These results are consistent with consensus age estimates based on biochronology, although the teeth sampled for dating were not necessarily contemporaneous with the *G. blacki* remains given the complex stratigraphic context of the cave deposits. The samples used to date the Hejiang Cave came from flowstones that stratigraphically bracket the *Gigantopithecus*-bearing depositional unit, so it reliably constrains the *G. blacki* remains to the 400–320 ka time interval (Zhang et al., in press). Therefore, the *G. blacki* specimens from Hejiang Cave should be considered the youngest securely dated representatives of the species. This implies that *G. blacki* survived for more than 1.5 million years from the Early Pleistocene to the end of the Middle Pleistocene.

Three mandibles and thousands of isolated teeth have been attributed to *G. blacki*, mostly from cave deposits in southern China. Current evidence points to the geographically and chronologically distant *Gigantopithecus giganteus* (or *Indopithecus giganteus*) from the Late Miocene Siwaliks of India as a potential precursor to *G. blacki* (Simons and Chopra, 1969; Szalay and Delson, 1979; Cameron, 2003; Patnaik, 2008). The phylogenetic status of *G. blacki* has been much debated in the past (Weidenreich, 1945; Pei and Woo, 1956; Simons and Ettl, 1970; Eckhardt, 1973, 1975; Szalay and Delson, 1979), but the current consensus view is that it represents a specialized pongin (Kelley, 2002; Cameron, 2003; Harrison, 2010; Begun, 2013; Fleagle, 2013). In addition, study of the paleobiology of *G. blacki* has included aspects of its diet (Ciochon et al., 1990; Daegling and Grine, 1994; Kupczik and Dean, 2008; Zhao et al., 2011; Zhao and Zhang, 2013; Kono et al., in press), dental caries (Han and Zhao, 2002), body mass estimation

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Table 1
Upper premolar samples included in the EDJ morphological analysis and the other *Gigantopithecus blacki* sites.

<i>Gigantopithecus blacki</i> sites	Reference	Age	P ³	P ⁴
Included sites and specimens				
<i>Gigantopithecus</i> Cave, Liucheng, Guangxi	Woo, 1962	Early Pleistocene	31	8
	Rink et al., 2008	940–1206 ka		
Sanhe Cave, Chongzuo, Guangxi	Jin et al., 2009	Early Pleistocene (1.2 Ma)	4	4
Hubei	Hsu et al., 1974	Unknown (Drugstore)	8	5
Guangzhou	Pei and Woo, 1956	Unknown (Drugstore)	0	1
Nanning	Pei and Woo, 1956	Unknown (Drugstore)	0	1
Hejiang Cave, Chongzuo, Guangxi	Zhang et al., in press	400–320 ka	2	1
The other sites				
Longgupo, Wushan, Chongqing	Huang and Fang, 1991	2.0 Ma		
	Huang et al., 1995	1.96 Ma		
Longgudong, Jianshi, Hubei	Zheng, 2004	Early Pleistocene		
Baeryan, Bijie, Guizhou	Zhao et al., 2006	Early Pleistocene		
Chuifeng Cave, Tiandong, Guangxi	Wang, 2009	Early Pleistocene		
Mohui Cave, Tiandong, Guangxi	Wang et al., 2005, 2007	Early Pleistocene		
Nomoshan, Bama, Guangxi	Chang et al., 1975	Middle Pleistocene		
Bulalishan, Wuming, Guangxi	Chang et al., 1973	Middle Pleistocene		
	Rink et al., 2008	481–745 ka		
Heidong, Daxin, Guangxi	Pei and Woo, 1956;	Middle Pleistocene		
	Rink et al., 2008	308–380 ka		
Tham Khuyen Cave, Lang Son, Vietnam	Ciochon et al., 1996	475 ka		

For more detailed information on the included specimens, see SOM Table S1.

(Johnson, 1979) and paleoecology (White, 1975; Cheng et al., 2006; Zhao et al., 2011). However, the possibility that *G. blacki* has undergone morphological change through time during the early part of the Pleistocene has been largely overlooked. Given that a number of other mammalian lineages associated with the *G. blacki* faunas, such as *Ailuropoda* (Jin et al., 2007) and *Tapirus* (Tong, 2005), exhibit discernable morphological changes and speciation events during this same time period, the possibility that *G. blacki* might exhibit a similar temporal trend should be entertained. Indeed, there is already some evidence to support such a conclusion. Zhang (1982, 1983) analyzed more than 600 isolated teeth of *G. blacki* and concluded that the species tended to increase in dental dimensions from the Early Pleistocene to the Middle Pleistocene.

The present study aims to investigate in more detail the possibility that there were morphological changes in the dentition of *G. blacki* through time. In order to address this question, the morphology of the enamel-dentine junction (EDJ) of the upper premolars of *G. blacki* was studied using data derived from micro-computed tomographic (micro-CT) scanning. Study of the sub-occlusal morphology has been shown to be phylogenetically and taxonomically informative (Suwa et al., 2007, 2009; Skinner et al., 2008; Smith and Tafforeau, 2008), and allows for comparisons between teeth at different wear stages. The samples analyzed include upper premolars from Hejiang Cave, which are representative of a late surviving population of *G. blacki* close in time to the probable extinction of the species. The Hejiang specimens are compared with a large sample of upper premolars from the Early Pleistocene Liucheng and Sanhe cave sites, and with drugstore specimens of uncertain age and provenance.

Materials

To investigate possible intraspecific change in dental morphology over time in *G. blacki*, three upper premolars from Hejiang Cave (Zhang et al., in press) were selected with the presumption that they represent the latest occurrence of the species just prior to its extinction. For comparison, 39 upper premolars from the Early Pleistocene Liucheng *Gigantopithecus* Cave, the largest *in situ* sample of *Gigantopithecus* (Woo, 1962) dating within the range of 940–1206 ka (Rink et al., 2008), are included in the study. A further eight upper premolars from the Early Pleistocene Sanhe

Cave (~1.2 Ma) and 15 upper premolars from drugstore collections of uncertain age and provenance from Guangdong, Guangxi and Hubei (Pei and Woo, 1956; Hsu et al., 1974) are also included. Details of the *G. blacki* upper premolar samples are presented in Table 1.

Upper premolars were chosen to investigate the EDJ morphology because these are the only teeth from Hejiang Cave that are not too worn or eroded, and for which there is adequate comparative material. A total of 45 P³s and 20 P⁴s were selected for comparison and analysis (Table 1). Among them, only two P³s and one P⁴ are from Hejiang Cave, but the relatively large samples from the Early Pleistocene cave sites and drugstores allow for statistically meaningful comparisons. It is important to note that there is a possibility that the left P³ (HD-90), right P³ (HD-76), and right P⁴ (HD-75) from Hejiang Cave belong to a single individual, given that they are all unerupted and have similar preservation and coloration. All of the teeth in the comparative sample are unworn or only slightly worn with no dentine exposure.

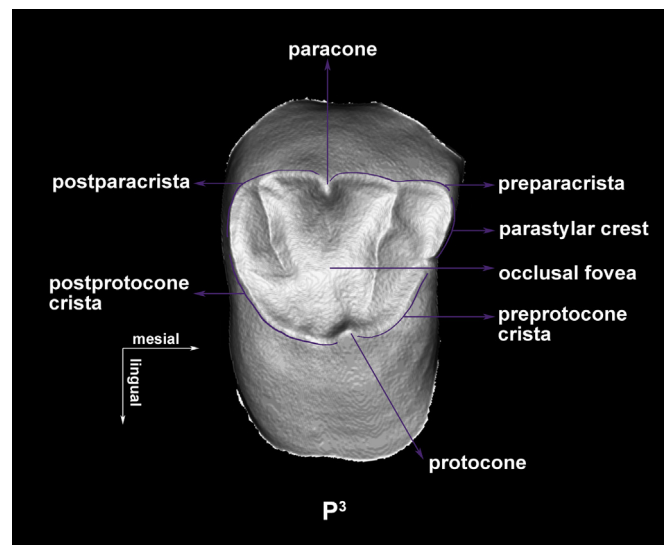


Figure 1. Terminology of EDJ morphological features used in this study (adapted from Szalay and Delson, 1979). The occlusal fovea is defined as the occlusal basin bordered by the main crests. The terminology for P⁴ differs from that for P³ only in a lack of the parastylar crest.

Methods

The EDJ takes shape early in dental development. It develops well before the functional emergence of the tooth, when enamel and dentine are deposited on the occlusal and basal surfaces of the basement membrane (membrane praeformativa) of the inner enamel epithelium of the enamel organ (Schour and Massler, 1940; Massler and Schour, 1946). The shape of the basement membrane is preserved on the EDJ because it does not remodel once its formation is complete. As a result, the morphology of the EDJ has been considered to be phylogenetically informative (e.g., Suwa et al., 2007, 2009; Skinner et al., 2008; Smith and Tafforeau, 2008). Examination of the EDJ morphology is especially advantageous for the study of *G. blacki* because the species is represented mainly by isolated teeth, many of which have suffered dental wear of varying degrees. In these circumstances, the EDJ has a greater chance than the outer enamel surface (OES) of preserving useful information pertaining to dental morphology. To examine the EDJ of the upper premolars of *G. blacki* the following methods were employed.

Micro-computed tomography of the *G. blacki* upper premolars was carried out using the TX225-Actis system (Tesco, Tokyo) at the University Museum, the University of Tokyo. Serial scans of entire tooth crowns were taken at isotropic voxel resolution of 40–60 μm , depending on the size of the tooth. Approximately 300–500 slices were obtained per tooth crown, usually parallel to the occlusal plane. Fossil teeth were scanned at 130 kv, 0.2–0.24 mA, with a copper pre-filter of 0.2 or 0.5 mm to minimize beam-hardening artifacts. Each scan was reconstructed in a 512×512 matrix from 720 or 900 views. Data output of this micro-CT system is in arbitrary units of ct value (and not in Hounsfield units).

Visualization and segmentation of the outer enamel surface and the EDJ were done by means of the half-maximum-height method, using the Rugle series software Vol-Rugle (Medic Engineering Inc., Kyoto). After segmentation, the occlusal views of the OES and EDJ surfaces were rendered for further analysis (see Supplementary Online Material [SOM] Fig. S1 for details).

Complexity analysis of the morphology of the occlusal fovea (see Fig. 1) on the upper premolar EDJ was carried out (see SOM Fig. S1

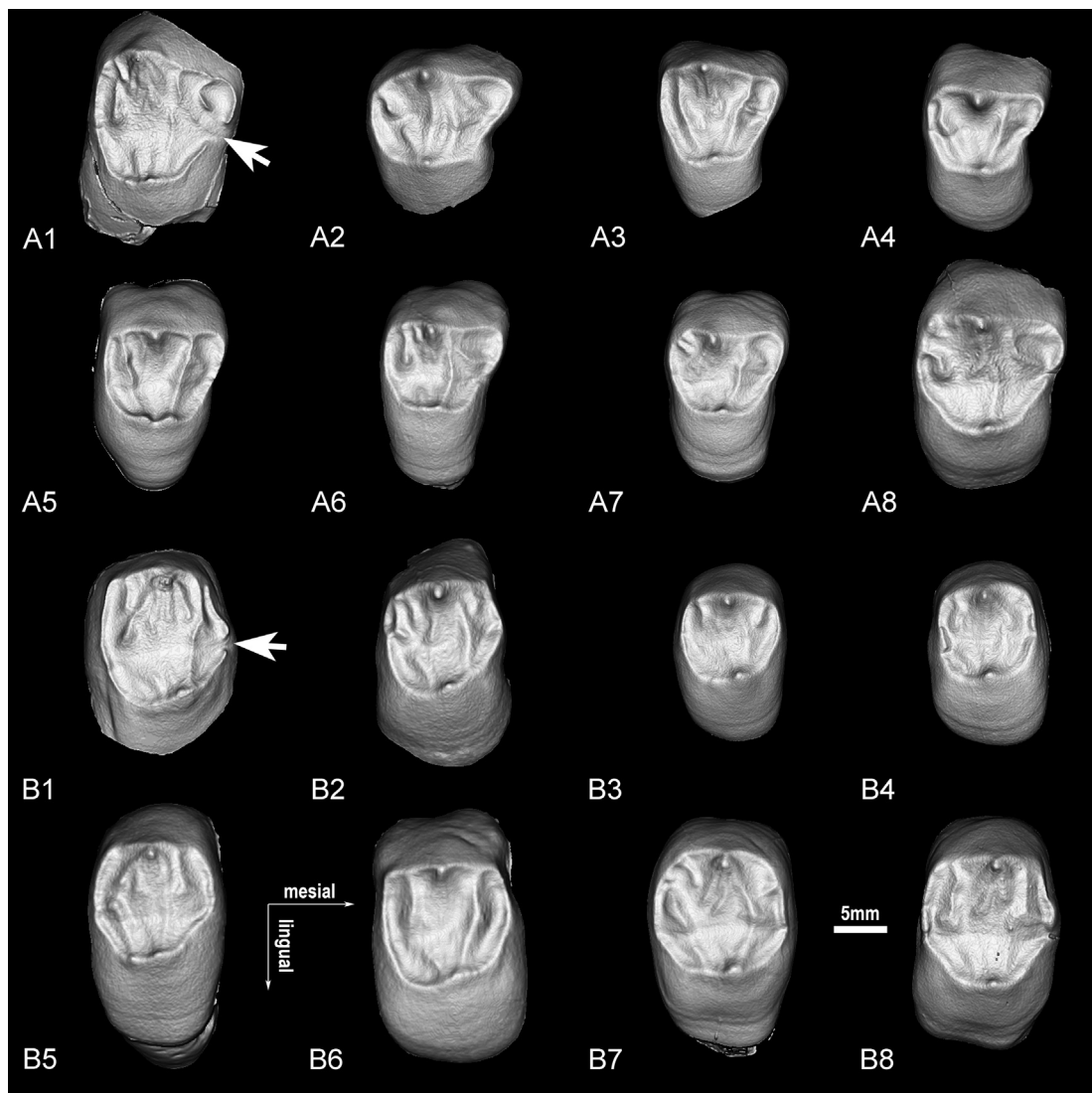


Figure 2. Upper premolar EDJ morphology of *G. blacki* from Hejiang Cave and other sites. P³: Hejiang Cave, A1. HD-76 (R); Liucheng, A2. A2-1-3-5 (L), A3. A2-1-4-6 (L), A4. A2-1-6-4 (L); Hubei, A5. A7-1-3-4 (L), A6. A7-1-3-5 (L), A7. A7-1-4-4 (R); Sanhe Cave, A8. SD-239 (R), P⁴: Hejiang Cave, B1. HD-75 (R); Liucheng, B2. A2-1-1-4 (R), B3. A2-1-2-5 (R), B4. A2-1-2-8 (R); Guangzhou, B5. A5-1-8-4 (R); Nanning, B6. A5-1-8-7 (R); Hubei, B7. A7-1-5-6 (R); Sanhe Cave, B8. SD-242 (L). All left premolars are mirrored as right ones to facilitate comparison. Arrows indicate the sulcus between the parastylar crest and the preprotocone crista on the P³ and between the preparacrista and the preprotocone crista on the P⁴ from Hejiang Cave.

for details of the procedure). The EDJ surface rendered in the former step is used to perform the complexity analysis employing 3D-Rugle (Medic Engineering Inc., Kyoto). Three parameters were calculated and plotted: (1) curvedness sum, (2) ridge area, and (3) total area of the occlusal fovea. The curvedness sum is calculated by adding the curvedness of each pixel of the ridges that occur in the occlusal fovea. Ridge area is the area where mean curvature <0 on the occlusal fovea (see Fig. 3: A1 and B1 for example). Total area is the total area of the occlusal fovea. Because the left P^3 (HD-90) from Hejiang Cave is broken, only the right P^3 (HD-76) and the right P^4 (HD-75) are included in the complexity analysis.

Results

Based on qualitative morphological comparisons of the EDJ (Fig. 2, SOM Figs. S2–3), the major crests on the Hejiang Cave premolars appear markedly sharper and better defined than those on all of the comparative specimens (see Fig. 1 for terminology). The minor crests on the Hejiang Cave premolars, especially those

that radiate from the paracone, are also much better defined and more numerous. Usually the postparacrista and the postprotocone crista extend medially and join together to form the distal boundary of the occlusal fovea on all specimens. However, the morphology on the mesial half is different. The preprotocone crista does not join the parastylar crest on the P^3 and the preparacrista on the P^4 from the Hejiang Cave (Fig. 2). As a result, a wide sulcus interrupts the mesial margin of the occlusal fovea. In the comparative sample these two crests meet on most of the P^3 s and P^4 s, or are separated by a narrower gap (e.g., Fig. 2: A8 and B8).

The quantitative complexity analysis of the EDJ of the occlusal fovea produced the following results (Fig. 3, SOM Table S2). The bivariate plots of the ridge area against the total area of the occlusal fovea for both P^3 and P^4 show a clear positive linear relationship between the two parameters. The Hejiang Cave P^3 and P^4 do not show much distinctiveness, but the P^3 has high values for the two parameters, being similar in size to the premolars from Sanhe Cave. The bivariate plot of the curvedness sum of the ridge area against the ridge area highlights the

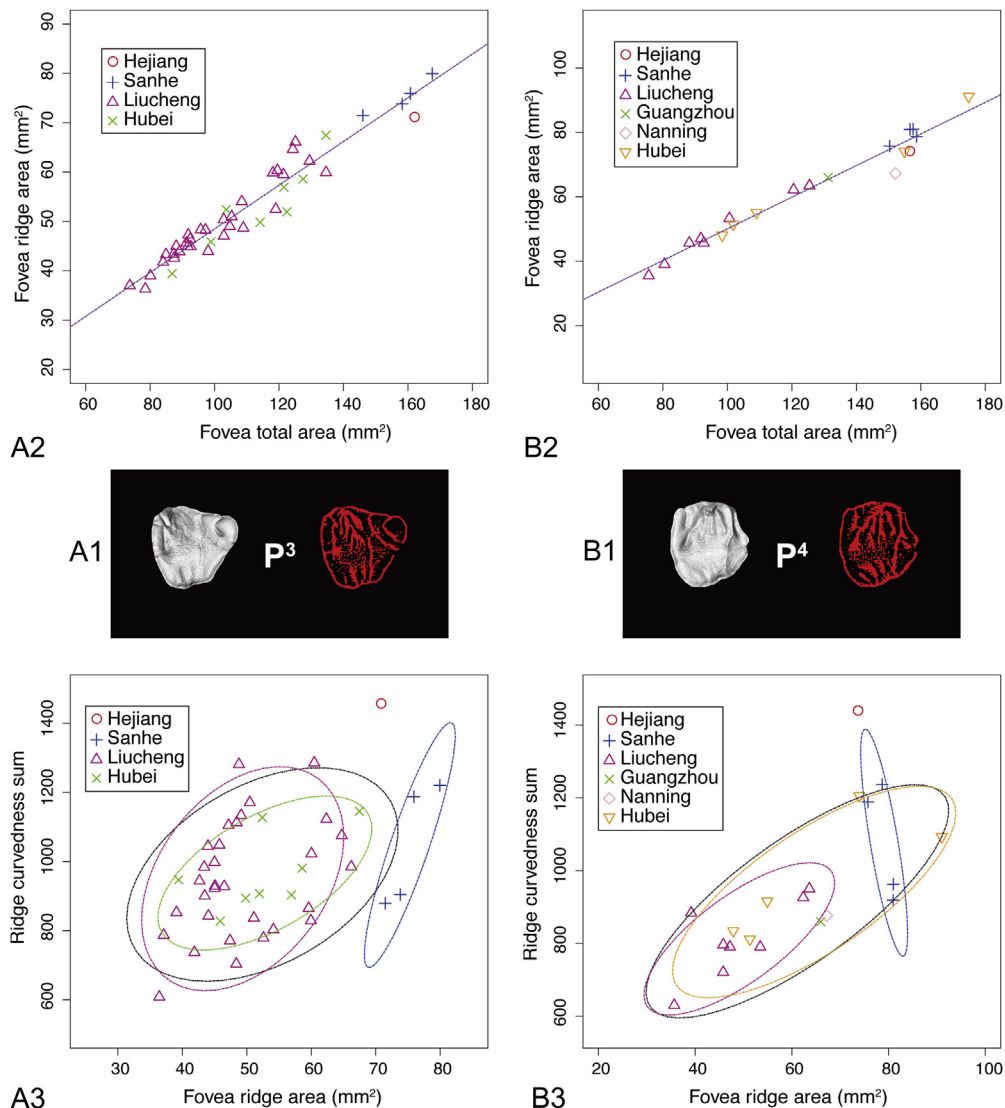


Figure 3. Upper premolar EDJ complexity analysis of *G. blacki* from Hejiang Cave and other sites. A. for P^3 and B. for P^4 (A1 and B1 show the Hejiang Cave P^3 (HD-76) and P^4 (HD-75), respectively). 1 The occlusal fovea manually extracted from the EDJ surface and the ridge mask; 2 Bivariate plot of the ridge area against the total area of the occlusal fovea, where the dashed straight lines indicate a positive linear relationship between the two variables; 3 Bivariate plot of the ridge curvedness sum against the fovea ridge area, where the 95% confidence ellipses are drawn for each comparative group (distinguished by colors) and all of the comparative specimens as a whole (black). The Hejiang Cave P^3 and P^4 show higher complexity and fall outside the confidence intervals. I've ordered the color printing of this figure for the paper version.

distinctiveness of the Hejiang Cave specimens. They fall outside the 95% confidence ellipses of all of the comparative specimens. These results show that the crests of the occlusal foveae of the Hejiang Cave P^3 s and P^4 have higher curvatures and the major and minor ridges are more sharply defined than in the comparative sample. Overall, the occlusal fovea of the Hejiang Cave upper premolars exhibit much higher degrees of morphological complexity relative to the other *G. blacki* samples.

As discussed above, the advantage of investigating the EDJ morphology in fossils is that it is likely to be better preserved than the OES. Another advantage is that the EDJ has a simpler morphology compared with the OES in the case of *Gigantopithecus*, which makes it easier to analyze. Nearly all of the secondary structures on the OES have different degrees of expression on the EDJ. Conversely, all of the visible secondary structures on the EDJ are always more strongly expressed on the OES (Fig. 4). The Hejiang Cave upper premolars demonstrate a more complicated and crenulated OES than those in the comparative sample due to the presence of secondary crests that radiate from the paracone and protocone and originate from the preparacrista and postparacrista.

Discussion and conclusions

Although there is a possibility that all three Hejiang Cave upper premolars belong to one individual, the complex EDJ morphology of the Hejiang Cave upper premolars is sufficiently distinct from all other *G. blacki* samples to rule out the possibility that the teeth merely represent the extreme end of the range of intraspecific variation. Given the extent of the differences and the age of the Hejiang specimens, it seems likely that the differences reflect an evolutionary change towards greater complexity in dental morphology in terminal members of the *G. blacki* lineage. The morphological complexity of the upper premolar EDJ in the 15 drugstore specimens shows greater similarity with that of the Early Pleistocene specimens (Fig. 3: A3 and B3), and possibly indicates that they were obtained from sites that are earlier in age than the Hejiang Cave. However, given their unknown provenance it is not possible to ascertain their age, so any consideration of their morphology in relation to time has to be disregarded in order to avoid circular reasoning. Nevertheless, their inclusion in the analysis does serve to highlight the morphological distinctiveness of the Hejiang Cave

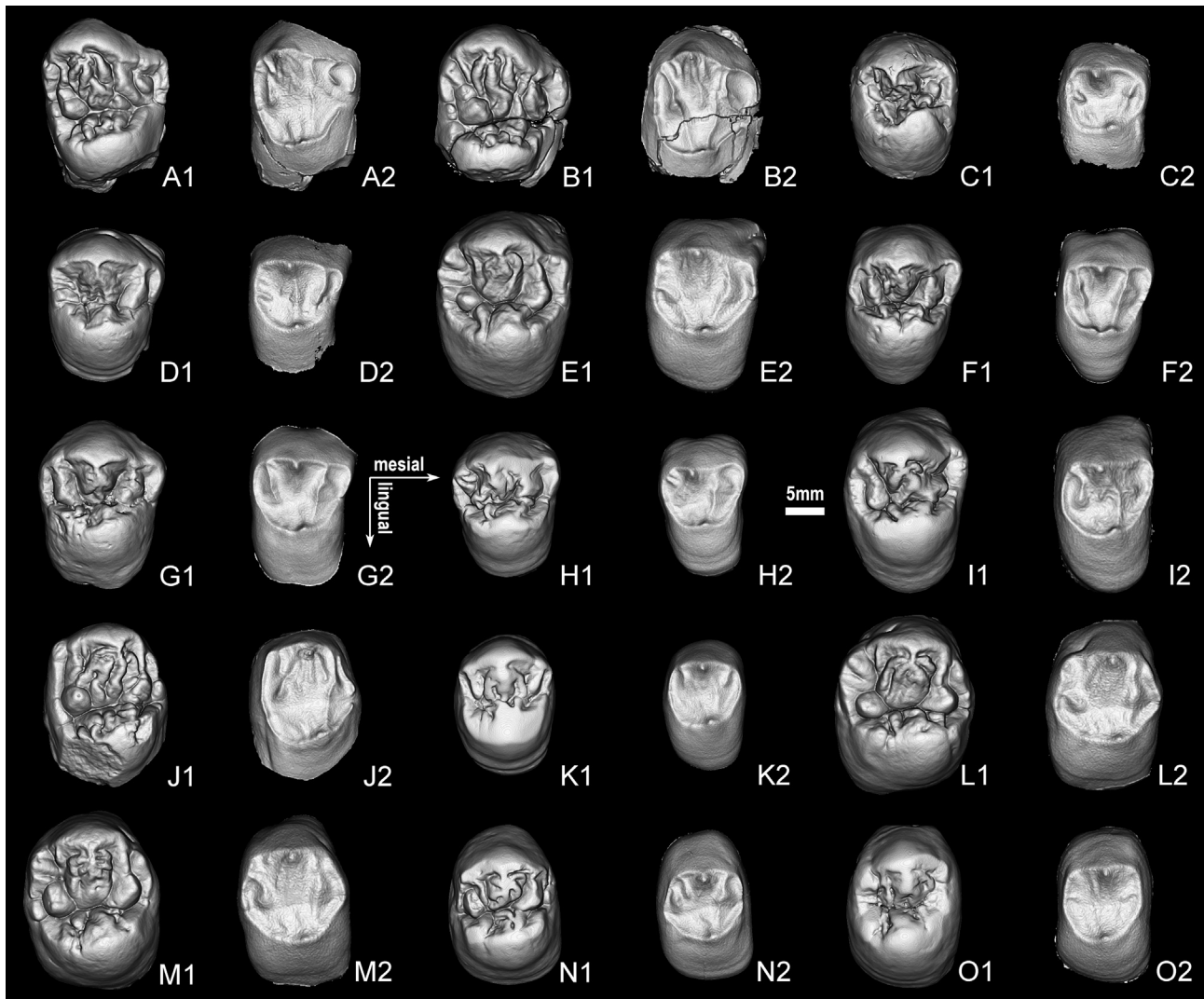


Figure 4. Morphological correspondence between OES and EDJ of *G. blacki* upper premolars. P^3 : Hejiang Cave, A. HD-76 (R), B. HD-90 (L); Liucheng, C. A2-1-2-1 (R), D. A2-1-3-6 (L); Sanhe Cave, E. SD-244 (R); Hubei, F. A7-1-3-4 (L), G. A7-1-3-8 (L), H. A7-1-4-4 (R), I. A7-1-4-6 (R). P^4 : Hejiang Cave, J. HD-75 (R); Liucheng, K. A2-1-2-5 (R); Sanhe Cave, L. SD-241 (L), M. SD-248 (R); Hubei, N. A7-1-5-4 (R), O. A7-1-5-5 (R). 1. for outer enamel surface (OES) and 2. for enamel-dentine junction (EDJ). All left premolars are mirrored as right ones to facilitate comparison.

premolars in relation to all other *G. blacki* specimens, including those from the drugstores.

There is a close morphological correspondence between the OES and EDJ. The OES morphology of *G. blacki* upper premolars from Baeryan (Zhao et al., 2006: Fig. 1,1), Mohui (Wang et al., 2007: Plate II, a, b, c), Chuifeng (Wang, 2009: Figure 5, 8–20), Longgupo (Huang and Fang, 1991: Plate IV, 2), Longgudong (Zheng, 2004: Figure 5.1, f), and the Bulalishan (Chang et al., 1973: Figure 1, 1–4) teeth do not exhibit the level of morphological complexity seen in those from Hejiang Cave. Preliminary data on the EDJ morphology of molars from the Hejiang Cave (e.g., HD-93: left M¹, HD-163.3: right M₃; Zhang et al., in press) also demonstrate greater complexity, such as higher and more pointed dental cusps on the only upper molar, and extra cusps mesial to the entoconid on the lower molars. These findings support the inference that *G. blacki* from Hejiang Cave represents a specialized terminal form of the species that is different in its dental morphology from all other Early Pleistocene and Middle Pleistocene specimens. If the temporal change in dental morphology in *G. blacki* is substantiated by additional comparative studies, these findings may have important implications for understanding the selection pressures and micro-evolutionary changes in the species in response to climatic and environmental changes that took place during the Middle Pleistocene. In addition, the nature and timing of these morphological changes could offer critical clues about the environmental factors that may have contributed to the eventual extinction of the species.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2014.06.010>.

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