



Fossil *Pongo* from the Early Pleistocene *Gigantopithecus* fauna of Chongzuo, Guangxi, southern China



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ARTICLE INFO

Article history:

Available online 2 February 2014

ABSTRACT

More than seventy isolated teeth of fossil *Pongo* are reported from Baikong, Juyuan and Queque Caves in Chongzuo, Guangxi, southern China. This Early Pleistocene material dates from 2.0 to 1.0 Ma based on faunal correlations and paleomagnetic analyses. The teeth from Chongzuo are generally morphologically very similar to those of extant species of *Pongo*, but are much larger in size. All of the fossil specimens can be attributed to *Pongo weidenreichi*, which is a typical member of the Early and Middle Pleistocene fauna of southern China and Vietnam. The identification of more detailed species-specific characteristics of *P. weidenreichi* will require larger samples. In addition, many of the systematic problems associated with fossil *Pongo* remain unresolved, but a provisional taxonomic scheme is presented that better reflects our current understanding of species-level diversity. Five extinct species of *Pongo* are recognized: *P. weidenreichi* from the Early and Middle Pleistocene of China and the Middle Pleistocene of Vietnam, *Pongo palaeosumatensis* from the Late Pleistocene of Sumatra, *Pongo javensis* from the Late Pleistocene of Java, *Pongo duboisi* from the Late Pleistocene of Sumatra, and *Pongo devosi* from the Late Pleistocene of China and Vietnam. *P. weidenreichi*, which is the earliest-known species of orang-utan, is replaced during the Late Pleistocene by a smaller species, *P. devosi*. *Pongo* becomes extinct in China during the Late Pleistocene, but may have survived in Vietnam and Cambodia into the Holocene. In island Southeast Asia, orang-utans were present on Java by at least the Middle Pleistocene and they continued into the Late Pleistocene as *P. javensis*. The Javan lineage of *Pongo* is more diminutive, at least dentally, than broadly contemporary species on mainland Asia, Sumatra and Borneo. Two species of *Pongo* are recognized from Late Pleistocene localities in the Padang Highlands of Sumatra. A relatively large species, *P. duboisi*, is known from Lida Ayer and Djambu, while a somewhat smaller species, *P. palaeosumatensis*, is known from slightly younger deposits from Sibrambang. The latter two taxa possibly represent time-successive members of the *Pongo abelii* lineage or are members of an older lineage of *Pongo*, broadly distributed across Sundaland, that was the sister taxon of *Pongo pygmaeus* and *P. abelii*. As noted by previous researchers, the fossil record provides evidence of a trend in *Pongo* to reduce the size of its dentition during the Pleistocene, but this overall trend was apparently influenced by various extrinsic factors that resulted in spatio-temporal heterogeneity in dental size.

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1. Introduction

Orang-utans (*Pongo pygmaeus* and *Pongo abelii*) are restricted today to Borneo and northern Sumatra, but during the Pleistocene they were widely distributed throughout island and mainland southeast Asia as far north as southern China. Fossil and subfossil *Pongo* specimens have been recovered from Pleistocene sites in Borneo, Sumatra, Java, Thailand, Vietnam, Laos, Cambodia,

Peninsular Malaysia and China (Pei, 1935; Hooijer, 1948, 1960; Kahlke, 1972; Delson, 1977; Aigner, 1978; Han and Xu, 1985; Gu et al., 1987, 1996; Olsen and Ciochon, 1990; Cuong, 1992; Nisbett and Ciochon, 1993; Schwartz et al., 1994, 1995; Drawhorn, 1995; Harrison, 1996, 1998, 2000; Tougaard and Ducrocq, 1999; Bacon and Long, 2001; Zhou, 2002; Harrison et al., 2006; Bacon et al., 2008a,b; 2011; Zhao et al., 2009, 2014; Ibrahim et al., 2013). By the close of the Pleistocene, *Pongo* became increasingly rare or extinct across much of its former range in mainland Southeast Asia, though it may have survived into the Holocene in Vietnam and Cambodia (Tan, 1985; Drawhorn, 1995).

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Fossil orang-utans have been known from Pleistocene cave sites in southern China since the 1930s. The first described specimens were purchased from apothecaries in mainland China, Hong Kong and Manila (but presumed to have originated from localities in southern China) (Teilhard de Chardin et al., 1935; Von Koenigswald, 1935; Weidenreich, 1937), as well as excavated from cave sites in Guangxi and Yunnan (Young, 1932; Pei, 1935; Bein and Chia, 1938). Since then, more than 30 occurrences have been recorded from Pleistocene sites in Yunnan, Guangxi, Guangdong, Guizhou, Hainan, Hubei and Chongqing (Kahlke, 1972; Gu et al., 1987; Ho et al., 1995; Drawhorn, 1995; Zhou, 2002; Wang et al., 2009; Zhao et al., 2009, 2014).

The aim of the current contribution is to place on record new finds of fossil orang-utans from Early Pleistocene karst cave sites in the area of Chongzuo, Guangxi, southern China, and to assess their taxonomic affinities. The new finds of *Pongo*, comprising more than seventy isolated teeth, have been recovered from three cave sites in the region – Baikong, Juyuan, and Queque. *Pongo* specimens from the Early Pleistocene of Sanhe Cave are the subject of a separate report (Zhao et al., 2014). The material can all be referred to a single species, *Pongo weidenreichi*, which is distinguished from extant taxa primarily by having considerably larger teeth. It is the largest of the extinct species of *Pongo*. The *Pongo* specimens from these cave sites are associated with a diverse primate fauna, which includes *Gigantopithecus blacki*, as well as two other much rarer hominoids – a species of hylobatid (probably referable to *Nomascus* sp.) and an unnamed hominoid. The latter taxon is smaller in dental dimensions than *P. weidenreichi*, and is probably the same taxon as the “mystery ape” (*sensu* Ciochon, 2009, 2010) known from contemporary sites in southern China, such as Chuifeng, Liucheng, Jianshi, Longgupo, and Mohui (Wang et al., 2007; Wang, 2009; Jin et al., 2009a; Ciochon, 2009, 2010). In addition to hominoids, there are at least seven species of cercopithecids, belonging to *Macaca* (three species), *Procynocephalus*, *Rhinopithecus*, *Trachypithecus*, and *Pygathrix* (Takai et al., 2014).

2. Geology and chronology

The cave sites are located in the vicinity of the Chongzuo Ecological Park, Guangxi Zhuang Autonomous Region, southern China, about 100 km southwest of Nanning (Fig. 1). Caves are formed in the karst peaks on both sides of the Zuojiang River valley. Due to different phases of uplift and valley floor incision during the Plio-Pleistocene, cave openings occur at six different elevations, with those located at the highest levels being the oldest (Jin et al., 2009a). The *Pongo* specimens included in this study are derived from the fifth level, located at about 200 m above sea level, and dating to the Early Pleistocene (Jin et al., 2009a,b).

Baikong Cave (22°17.755'N, 107°29.997'E, elevation 212 m) on Liyu Mountain has two fossiliferous horizons comprising sandy and silty breccias. The mammalian assemblage is typical of Early Pleistocene faunas, such as those from Liucheng, Longgupo, Mohui and Chuifeng (Pei, 1987; Huang and Fang, 1991; Wang et al., 2005, 2007; Wang, 2009). The biochronological and paleomagnetic evidence indicates an estimated age of ~2.0 Ma (Sun et al., 2014). The fossiliferous sediments of Juyuan Cave (22°17.375'N, 107°30.667'E, elevation 206 m) on Boyue Mountain consist of at least two horizons of silty and sandy breccias. The mammalian fauna (Jin et al., 2014) and paleomagnetic evidence (Sun et al., 2014), indicate an age slightly younger than that from Baikong Cave, with an estimated age of ~1.8 Ma. The fossils from Queque Cave (22°16.367'N, 107°30.367'E, elevation 198 m) on Wuming Mountain are derived from sandy silts. The mammal fauna and paleomagnetic results indicate a late Early Pleistocene age, with an estimated age of ~1.0 Ma (Sun et al., 2014).

3. Evolutionary history and taxonomy of *Pongo*

The two extant species of orang-utans can be distinguished from each other based on hair color and length, distribution of facial hair, the size and shape of the throat pouches and cheek flanges in males, and a number of cranial features (MacKinnon, 1973; Groves,

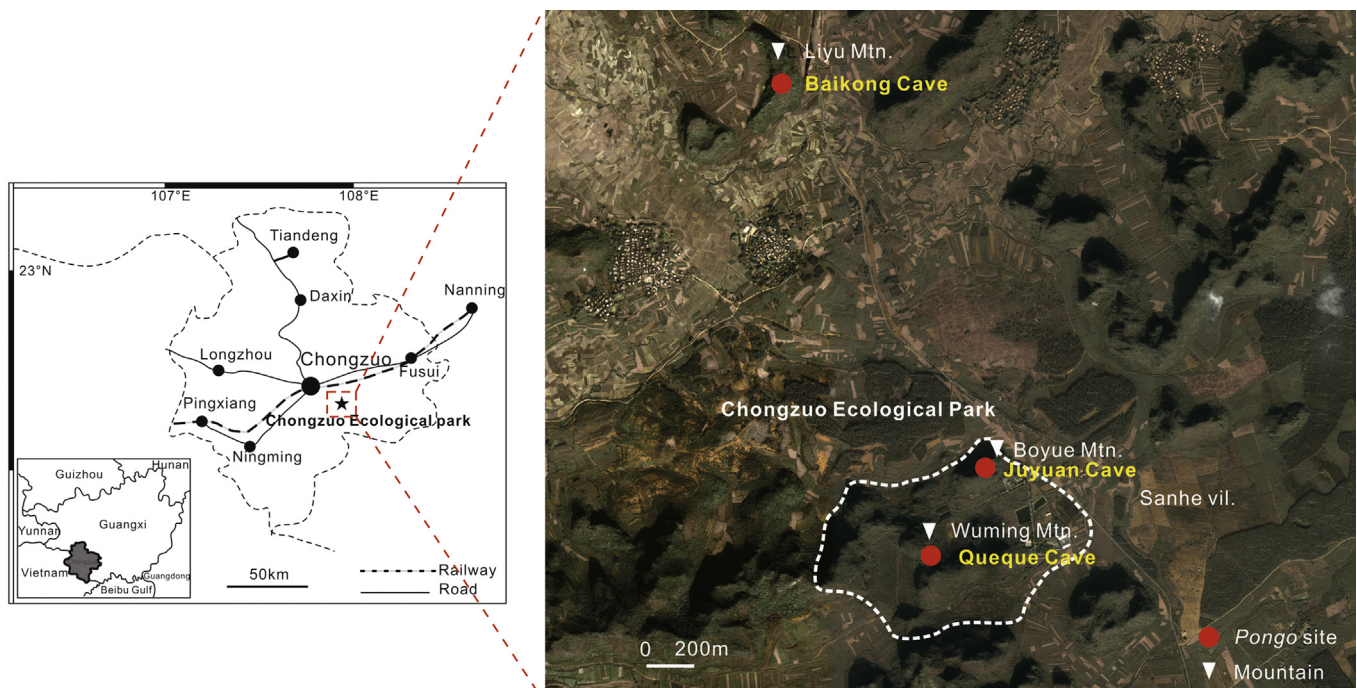


Fig. 1. Map and satellite image showing the location of the early Pleistocene cave sites in the Chongzuo area of Guangxi Zhuang Autonomous Region in southern China.

1986, 2001; Courtenay et al., 1988; Weitzel et al., 1988). Although Sumatran orang-utans have slightly larger teeth on average than Bornean orang-utans (Cameron, 2001), and there are some minor morphological differences in the postcanine dentition (Uchida, 1998), mixed samples of isolated teeth would be impossible to separate. However, molecular data provide strong support for the separation of extant *Pongo* into two species. Based on this evidence, a range of estimated divergence dates (0.4 Ma–6.0 Ma) for the two species have been inferred (Ryder and Chemnick, 1993; Xu and Arnason, 1996; Zhi et al., 1996; Karesh et al., 1997; Steiper, 2006; Arora et al., 2010; Israfil et al., 2011; Locke et al., 2011; Matsui and Hasegawa, 2012; Finstermeier et al., 2013), but it seems likely that the extant species diverged during the mid-Pliocene to Early Pleistocene (see Harrison et al. (2006)).

Unfortunately, the nomenclature of fossil *Pongo* is convoluted, and the proliferation of species-group names will undoubtedly prove unsustainable with further detailed study. Given that the fossil taxa are almost exclusively based on samples of isolated teeth, and that the dentitions of modern orang-utans are notoriously highly variable and difficult to discriminate at the species level, it will not be an easy task to satisfactorily resolve all of the taxonomic and nomenclatural issues. Nevertheless, this contribution offers a provisional taxonomy of *Pongo* that, while still imperfect, will hopefully help to facilitate communication and provide a basis for further comparative research and discussion (see Table 1).

Table 1
Species of *Pongo* recognized in this study.

Species	Geographical distribution	Temporal range
<i>Pongo pygmaeus</i> (Linnaeus, 1760)	Borneo	Late Pleistocene to Recent
<i>Pongo abelii</i> Lesson, 1827	North Sumatra	Recent
<i>Pongo palaeosumatrensis</i> Hooijer, 1948	Sibrambang, Padang, central Sumatra	Late Pleistocene
<i>Pongo weidenreichi</i> Hooijer, 1948	South China and Vietnam	Early and Middle Pleistocene
<i>Pongo javensis</i> Drawhorn, 1995	Punung, south central Java	Late Pleistocene
<i>Pongo duboisi</i> Drawhorn, 1995	Lida Ayer and Djambu, Padang, central Sumatra	Late Pleistocene
<i>Pongo devosi</i> Schwartz et al., 1995	South China and Vietnam	Late Pleistocene

The earliest fossil record of *Pongo* is from the Early and Middle Pleistocene of southern China. This material was described as a distinct subspecies, *P. pygmaeus weidenreichi*, by Hooijer (1948) based principally on the overall larger size of the teeth. It is elevated here to a separate species, *P. weidenreichi*. Also included in this species are the associated lower molars of “australopithecines” from Longgudong Cave, Jianshi, Hubei (Gao, 1975) and the *Hemantropus peii* teeth purchased from traditional medicine stores in Hong Kong (Von Koenigswald, 1957). The occlusal areas of the cheek teeth of *P. weidenreichi* from Guangdong and Guangxi are on average ~20% larger than those of extant *Pongo* (Gu et al., 1987). During the Late Pleistocene *P. weidenreichi* is replaced in southern China by a smaller species of *Pongo*. This species is referred to here as *Pongo devosi* (see below), which is slightly larger in size than the extant species. *Pongo* survived in China until at least the Late Pleistocene. At Early and Middle Pleistocene sites in southern China, *P. weidenreichi* is typically associated with *G. blacki*, but the latter species continues after the last appearance of *P. weidenreichi* and overlaps temporally with *P. devosi*.

Similar material from Middle to Late Pleistocene sites in Vietnam can also be referred to *P. weidenreichi*. The largest samples are from the late Middle Pleistocene cave sites of Tham Khuyen, Tham Om and Lang Trang, which are found in association with

Gigantopithecus at Tham Khuyen (Ciochon et al., 1990; Cuong, 1992; Schwartz et al., 1994, 1995). *Pongo* teeth from these sites are ~25–30% larger on average than those of their modern counterparts, and comparable in size or slightly larger than the teeth of *P. weidenreichi* from southern China. Those from the Late Pleistocene site of Hang Hum are smaller, being only ~6% larger on average than extant *Pongo*, which provides additional support for the replacement of *P. weidenreichi* by a smaller species during the Late Pleistocene.

Schwartz et al. (1995) recognized a number of new hominoid taxa from the Pleistocene cave sites in Vietnam, including *Langsonia liquidens* (from Tham Khuyen), *Pongo hooijeri* (from Tham Khuyen and Tham Hai), *Pongo pygmaeus ciochoni* (from Lang Trang), *P. pygmaeus devosi* (from Hang Hum), *Pongo pygmaeus kahlkei* (from Tham Khuyen), and *Pongo pygmaeus fromageti* (from Tham Om). Our assessment of the published evidence provides insufficient grounds to maintain the distinctiveness of most of these taxa (see Harrison, 2000). The *Pongo* specimens from Tham Khuyen, Lang Trang and Tham Om can all be accommodated in *P. weidenreichi* (with *P. hooijeri*, *P. pygmaeus ciochoni*, *P. pygmaeus kahlkei* and *P. pygmaeus fromageti* identified as junior synonyms). Previously, Harrison (2000) questioned the validity of *L. liquidens* from the Middle Pleistocene of Vietnam, but it does seem likely that there is a hominoid species from Tham Khuyen with distinctive molar morphology that is smaller in size than *P. weidenreichi*.

The more diminutive *Pongo* from the Late Pleistocene of Hang Hum is here recognized as a separate species, *P. devosi*. The similar-sized specimens from the Late Pleistocene of southern China are also provisional referred to this taxon. In this scheme, the earlier *P. weidenreichi* is replaced by *P. devosi* in China and Vietnam during the Late Pleistocene. The finding that the fossil orang-utans from the Late Pleistocene of Zhiren Cave, Mulanshan, Chongzuo, dating to 110 ka (Zhao et al., 2009; Jin et al., 2009b), are intermediate in size (with teeth ~16% larger on average than modern *Pongo*), implies that diminution of the dentition in *Pongo* in southern China may have been the result of a gradual evolutionary transformation within a single *P. weidenreichi*–*P. devosi* lineage rather than due to a relatively abrupt cladogenetic event.

A number of Middle and Late Pleistocene sites with fossil orang-utans are known from Java, Sumatra and Borneo. Von Koenigswald (1940), Widianto (1991) and Aziz and Saefudin (1996) have reported isolated teeth of fossil orang-utans from Middle Pleistocene deposits at Sangiran in Java. In addition, two upper molars from the Middle Pleistocene of Trinil in Java, were originally assigned to *Pithecantropus erectus* (Dubois, 1896), but subsequently referred to *Pongo* (Weidenreich, 1937; Hooijer, 1948; Harrison et al., 2006). However, de Vos and Sondaar (1982) and Von Koenigswald (1982) and de Vos (1983, 1984) expressed doubts about this latter identification. Most recently, Smith et al. (2011) have shown that the dental development and structure of the Trinil molars are more similar to those of *Homo erectus* than to *Pongo*.

A large collection of subfossil orang-utans, comprising more than four thousand specimens, mostly isolated teeth, was recovered by Eugene Dubois in the late 19th Century from four cave sites (i.e., Sibrambang, Djambu, Lida Ayer and an unnamed locality) in the Padang Highlands of west central Sumatra (Dubois, 1891). Based on the associated mammalian fauna, the localities are all Late Pleistocene in age, with Sibrambang possibly being slightly younger than Lida Ayer (Drawhorn, 1995). Hooijer (1948) included all of the material from the Padang Highlands in a new subspecies, *Pongo pygmaeus palaeosumatrensis*. The taxon was distinguished from extant orang-utans by its overall larger size, greater degree of canine sexual dimorphism and differences in the relative proportions of the permanent dentition (Hooijer, 1948). Badoux (1959) and Kahlke (1972) argued that the differences are insufficient to merit a taxonomic distinction. However, Harrison (2000) provided

additional support for a separation by showing that the teeth from the Padang Highlands are on average ~15% larger by area than those of extant orang-utans, with every tooth locus being larger on average than its homologue. However, [Drawhorn \(1995\)](#) correctly noted that the samples from the individual localities should not necessarily be pooled or presumed to belong to a single taxon. He contends that the sample from Sibrambang (the type locality of *P. pygmaeus palaeosumatrensis*) and those from Lider Ayer and Djambu are distinct enough to recognize as separate species. Consequently, [Drawhorn \(1995\)](#) named a new species and two new subspecies to accommodate the variation within the Padang samples – *Pongo duboisi lidaayerensis* from Lida Ayer and Djambu and *Pongo duboisi djamboensis* from Djambu. The Sibrambang sample does exhibit teeth that are larger than modern *Pongo*, especially in the size of the premolars and molars (occlusal areas of the cheek teeth are 8.6% larger on average), and merits being recognized as a distinct species, *P. palaeosumatrensis* (see [Table 4](#)). *P. duboisi* from Lida Ayer and Djambu can be distinguished from *P. palaeosumatrensis* and extant *Pongo* by having larger teeth (the occlusal areas of the cheek teeth in *P. duboisi* are 10.6% and 19.4% larger on average, respectively).

Table 2

Dimensions of teeth of *Pongo weidenreichi* from the Early Pleistocene of Chongzuo, Guangxi.

Locality – Field#	Element	Measurements		
		MD	BL	BHT
Baikong Cave				
40	L p4.	13.6	14.2	
45	R M3.	14.1	15.3	
865	R dP4.	9.6	10.8	
874	L m1.	17.2	13.9	
875	L m2.	18.2	15.7	
876	R m1. Crown incomplete.	16.2	—	
877	L m3.	14.6	12.7	
878	R m2.	16.3	14.9	
879	L I2. Germ. Antimere of 880.	11.4	11.0	13.4(—)
880	R I2. Germ. Antimere of 879.	11.5	—	13.9(—)
881	R p3. Germ. Male.	—	11.3	
933	R dC. Germ.	8.5	8.9	9.0
935	R dc.	9.7	7.0	9.5
1085	R m2.	16.8	15.8	
1086	L m3.	18.2	16.8	
1087	R m3.	18.3	16.8	
1089	R P3.	14.8	17.9	
1091	R M2.	16.6	18.6	
1115	L p3. Male.	18.1	11.4	12.2
1118	L M3.	17.2	17.0	
1119	R M1.	14.2	15.2	
1120	L p4. Weathered.	15.5	16.1	
1121	L p3. Male.	17.8	11.5	
1129	R i1. Germ.	9.5	10.5	18.3(—)
1139	R m2.	17.2	15.5	
1154	R m3.	16.6	15.2	
1168	L p4. Germ. Fragmentary.	—	—	
1181	L m1.	15.7	14.2	
1188	R p4. Germ.	14.1	14.2	
1189	L m3.	16.3	16.0	
2508	R I2. Germ.	11.4	11.7	12.3(—)
	R m3.	14.8	13.3	
	L M1.	13.5	14.5	
	L I2.	9.5	—	
Juyuan Cave				
P037	L c. Male.	19.6	16.1	28.6
P041	R m2.	17.8	16.4	
P042	R m2.	18.9	18.2	
P043	L m2.	18.0	15.8	
P044	R m1.	15.0	13.6	
P045	L i2.	8.5	11.8	13.5(—)
P046	L p4.	13.1	13.6	
P047	R p4.	13.6	13.9	

Table 2 (continued)

Locality – Field#	Element	Measurements		
		MD	BL	BHT
P048	R M1.	14.0	15.0	
P049	R dC.	11.0	9.3	11.2
P050	L dc.	10.5	7.7	14.8(–)
P051	L i1.	–	10.7	
P057	R p3. Female.	17.6	10.9	10.7
Queque Cave				
0704-25	R M3.	13.6	13.9	
0704-274	R M3.	13.8	15.0	
0704-275	L m1.	14.3	12.2	
0704-276	R M3.	12.3	13.7	
0704-277	R m3.	16.0	15.2	
0704-278	R m2.	17.8	16.3	
0704-279	L M2.	13.0	15.5	
0704-281	L P3.	11.4	16.1	
0704-282	R m3.	19.7	15.6	
0704-294	R M3.	14.3	15.8	
0811-1	R m2.	16.0	13.9	
0811-2	L M3.	14.6	16.2	
0811-3	L M2.	13.3	15.6	
0811-4	R m2.	16.3	14.6	
0811-76	R m1.	13.9	13.0	
0904-2	R m1.	14.4	12.2	
82.1	R m3.	18.1	15.4	
SN 27	L m3.	17.6	15.4	
SN 28	R m1.	14.0	12.7	
SN 32	L p4.	13.1	13.2	
SN 33	L M1.	12.7	14.8	
SN 34	R M2.	14.9	16.1	
SN 35	R M1.	14.0	14.1	
SN 36	R m2.	17.0	14.8	
SN 37	L M3.	12.4	13.3	
SN 40	L P4.	11.3	15.7	
SN 47	L p3. Male.	19.0	13.2	–
SN 48	L p3. Male.	19.6	12.0	–
SN 49	R P4.	11.2	13.8	
SN 50	R m1. Partial crown.	–	–	

Abbreviations: R, right; L, Left; MD, mesiodistal length; BL, buccolingual breadth; BHT, buccal height; (–) minimum dimension.

Notes: Lower case and upper case letters for teeth indicate lower and upper teeth respectively; d prefix refers to deciduous teeth. MD and BL measurements of p3, c and C are maximum length and perpendicular breadth respectively.

Table 3

Dimensions of *Pongo weidenreichi* cheek teeth from southern China.

		<i>Pongo weidenreichi</i> from Guangdong and Guangxi (Gu et al., 1987)			<i>Pongo weidenreichi</i> from Chongzuo, Guangxi (this study)		
		N	Mean	Range	N	Mean	Range
p3	MaxL	8	16.8	14.4–18.1	5	18.4	17.6–19.6
	PerpB	8	10.6	9.4–11.0	6	11.7	10.9–13.2
p4	MD	12	12.1	10.3–14.8	6	13.8	13.1–15.5
	BL	12	12.1	10.9–13.5	6	14.1	13.2–16.1
m1-2	MD	7	15.6	13.5–17.2	19	16.4	14.0–18.9
	BL	6	13.8	11.6–15.3	18	14.7	12.2–18.2
m3	MD	10	14.3	13.5–16.2	10	17.1	14.6–19.7
	BL	10	12.4	11.2–13.8	10	15.2	12.7–16.8
P3	MD	5	11.4	10.0–12.4	2	13.1	11.4–14.8
	BL	5	13.7	12.3–14.5	2	17.0	16.1–17.9
P4	MD	7	11.1	10.2–11.9	2	11.3	11.2–11.3
	BL	7	14.7	13.0–16.1	2	14.8	13.8–15.7
M1	MD	12	13.5	11.6–14.5	5	13.7	12.7–14.2
	BL	12	14.4	13.1–15.6	5	14.7	14.1–15.2
M2	MD	4	14.3	13.5–15.5	4	14.5	13.0–16.6
	BL	4	14.5	13.2–15.0	4	16.5	15.5–18.6
M3	MD	6	12.3	11.2–13.5	8	14.2	12.3–17.2
	BL	6	13.9	12.5–15.5	8	14.7	13.3–17.0

Abbreviations: BL, buccolingual breadth; MD, mesiodistal length; MaxL, maximum length; PerpB, perpendicular breadth; N, number of specimens.

Notes: Lower case and upper case letters for teeth indicate lower and upper teeth respectively.

Table 4

Occlusal areas (length $\times$ breadth) of the permanent teeth of fossil *Pongo* from southern China compared with those of Late Pleistocene *Pongo* from SouthEast Asia and extant orang-utans (see text for explanation).

	N	Standard deviation intervals from the mean values of extant orang-utans								
		–3SD	–2D	–1SD	+1SD	+2SD	+3SD	+4SD	+5SD	+6SD
Extant <i>Pongo</i> spp. (Borneo, Sumatra) ^{a,b}	822	4	136	304	235	113	29	1		
	100%	0.5%	16.5%	37.0%	28.6%	13.7%	3.5%	0.1%		
<i>Pongo pygmaeus</i> (Niah Cave, Sarawak, Borneo) ^b	65		3	24	30	7	1			
	100%		4.6%	36.9%	46.2%	10.8%	1.5%			
<i>Pongo palaeosumatrensis</i> (Sibrambang, Sumatra) ^a	1251		48	345	446	288	94	20	4	6
	100%		3.8%	27.6%	35.7%	23.0%	7.5%	1.6%	0.3%	0.5%
<i>Pongo duboisi</i> (Lida Ayer & Djambu, Sumatra) ^a	1419		24	247	471	367	229	67	14	
	100%		1.6%	17.4%	33.2%	25.9%	16.1%	4.7%	1.0%	
<i>Pongo javensis</i> (Punung, Java) ^c	171	5	37	69	49	11				
	100%	2.9%	21.6%	40.4%	28.7%	6.4%				
<i>Pongo cf. devosi</i> (Zhiren, Chongzuo, Guangxi) ^d	13			2	4	5	2			
	100%			15.4%	30.8%	38.5%	15.4%			
<i>Pongo weidenreichi</i> (Baikong, Chongzuo, Guangxi)	25				3	3	9	3	5	2
	100%				12.0%	12.0%	36.0%	12.0%	20.0%	8.0%
<i>Pongo weidenreichi</i> (Juyuan, Chongzuo, Guangxi)	10				1	2	3	3	0	1
	100%				10%	20.0%	30.0%	30.0%	0%	10.0%
<i>Pongo weidenreichi</i> (Queque, Chongzuo, Guangxi)	29				5	10	9	4	1	
	100%				17.2%	34.5%	31.0%	13.8%	3.4%	
<i>Pongo weidenreichi</i> (Combined, Chongzuo, Guangxi)	64				9	15	21	10	6	3
	100%				14.1%	23.4%	32.8%	15.6%	9.4%	4.7%

^a Data from Hooijer (1948).

^b Data from Harrison (1996, 2000).

^c Data from Badoux (1959), Drawhorn (1995).

^d Data from Zhao et al. (2009).

From an evolutionary perspective, the orang-utan samples from Padang might plausibly represent extinct time-successive members of the *P. abelii* lineage, which have undergone dental diminution during the course of the Pleistocene. It has been well documented that reduction in dental size is a common phenomenon in many lineages of Southeast Asian mammals, including primates, during the Pleistocene (Medway, 1959, 1964, 1966a,b; Hooijer, 1961, 1962; Cranbrook, 1986; Harrison, 1996, 2000). Alternatively, *P. palaeosumatrensis* and *P. duboisi* might possibly represent taxa belonging to a more ancient lineage of *Pongo* that was broadly distributed across Sundaland (and possibly related to the contemporary *P. devosi* in mainland Asia) and constitutes the sister taxon to *P. pygmaeus* + *P. abelii*.

A small collection of isolated teeth ($n = 13$) of orang-utans from Jambunan and Paku Flats in the Bau area of Sarawak in Borneo are similar in size to those of *P. palaeosumatrensis* (with teeth that are on average 14.3% larger in occlusal area than those of the corresponding teeth in extant *Pongo*) (Harrison, 2000). The age of the material is unknown, but, based on the degree of mineralization and the accompanying fauna, it cannot be older than Late Pleistocene. These specimens could be interpreted either as support for a broad distribution of *P. palaeosumatrensis* across Sundaland during the Late Pleistocene or for the occurrence of a large-toothed population of the *P. pygmaeus* lineage that underwent dental reduction during the course of the Pleistocene.

Recently described fossil orangutan teeth from the Middle Pleistocene Badak Cave C and the Late Pleistocene Batu Cave in Peninsular Malaysia (Ibrahim et al., 2013) may also be referred to *P. palaeosumatrensis*. Although the samples are small (only 9 teeth), two of the cheek teeth from Batu Cave do exceed the upper size limit of extant *Pongo* and fall with the range of *P. palaeosumatrensis*.

A large sample of isolated teeth ($n = 214$) of fossil orang-utans is known from three Late Pleistocene fissure-fillings at Punung in Java (Badoux, 1959; Drawhorn, 1995; Storm et al., 2005; Westaway et al., 2007). Although Badoux (1959) considered the material to be morphologically and metrically indistinguishable from extant *Pongo*, Drawhorn (1995) recognized distinctive features of the

dentition (i.e., m2 significantly smaller,¹ P3 relatively broader, cusps less peripherally placed, stronger cingulum development on molars, and possibly thinner enamel) that provided the basis for naming a new subspecies, *Pongo pygmaeus javensis*. Our reanalysis of the metrical data indicates that all of the cheek teeth loci are consistently smaller on average than their homologues in extant *Pongo* (with the exception of m3, which is poorly sampled) (see Table 4). The cheek teeth are on average 10.3% smaller than those of extant *Pongo*. The range of the occlusal areas of the teeth from Punung fall within the overall range of extant orang-utans, but the sample is markedly skewed towards the smaller end of the distribution, with ~65% of teeth falling below the mean value of their respective homologues (see Table 4).

The evidence indicates that a relatively small species of *Pongo*, referred to here as *P. javensis*, occupied Java during the Late Pleistocene. This species was considerably smaller than its contemporary, *P. palaeosumatrensis*, on Sumatra. As noted previously (Harrison, 2000; Cameron, 2001), the fossil record provides evidence of a general trend in *Pongo* to reduce the size of its dentition during the Pleistocene, but vicariance and ecogeographic factors acting differentially on populations at the regional and local levels resulted in spatio-temporal diversity in dental size. In this regard, it should be noted that the teeth of *Pongo* from the Middle and Late Pleistocene of Java are similar in size or smaller than those of extant *Pongo*, implying that, compared to their contemporaries elsewhere in Asia, an accelerated rate of dental diminution may have been characteristic of Javan populations. A comparable trend is seen in other mammalian taxa from the Pleistocene of Java (Hooijer, 1952).

Late Pleistocene–Holocene cave sites in Borneo, including Niah and Gua Sireh in Sarawak and Madai in Sabah, have yielded the remains of *Pongo* (Hooijer, 1961; Harrison, 1996, 1998, 2000; Harrison et al., 2006). These are identical in size and morphology

¹ Throughout the text, a lower case letter indicates lower teeth and an upper case letter indicates upper teeth.

to the modern-day Bornean orang-utan (see Table 4), and can be referred to *P. pygmaeus*.

4. Fossil *Pongo* from Chongzuo

The new specimens of *Pongo* from the Chongzuo area consist of 77 isolated teeth, mostly permanent upper and lower cheek teeth (Table 2, Figs. 2 and 3). The samples are derived from three Early Pleistocene cave sites, Baikong, Juyuan and Queque, which date from ~2.0 to 1.0 Ma. The material can all be referred to a single species, *P. weidenreichi*, which is primarily distinguished from the extant species by having considerably larger teeth on average.

The fossil teeth are morphologically indistinguishable from those of the extant species of *Pongo*, but they are considerably larger in their overall dimensions (the occlusal areas of the cheek teeth are on average 42.9% larger than extant *Pongo*). Descriptions of the individual teeth are unnecessary until larger samples are available to allow identification of more detailed species-specific characteristics. The specimens from all three localities can be attributed to *P. weidenreichi*, which is typical of Early and Middle Pleistocene sites in southern China. As noted above, *P. weidenreichi* was initially described as a subspecies of *Pongo pygmaeus* by Hooijer (1948). However, in conjunction with the recognition of two extant species, there are adequate grounds to recognize it as a distinct species. As noted by Hooijer (1948), *P. weidenreichi* is distinguished from other species of *Pongo* by its larger size and by its lower crowned canines. The holotype, figured by Weidenreich (1937: Plate VII, Fig. 61; Plate XXVII, Fig. 258), is a right lower canine

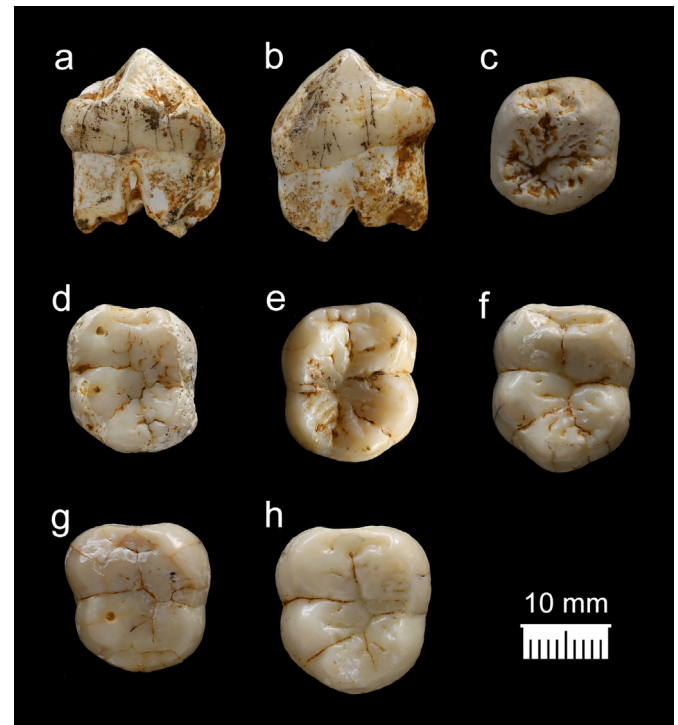


Fig. 3. Representative lower cheek teeth of *Pongo weidenreichi* from Chongzuo, Guangxi: (a) Baikong 1115, left p3, lingual view; (b) Baikong 1115, left p3, buccal view; (c) Baikong 1188, right p4, occlusal view; (d) Baikong 1181, left m1, occlusal view; (e) Queque SN 36, right m2, occlusal view; (f) Baikong 875, left m2, occlusal view; (g) Baikong 1189, left m3, occlusal view; (h) Baikong 1086, left m3, occlusal view. All to same scale.

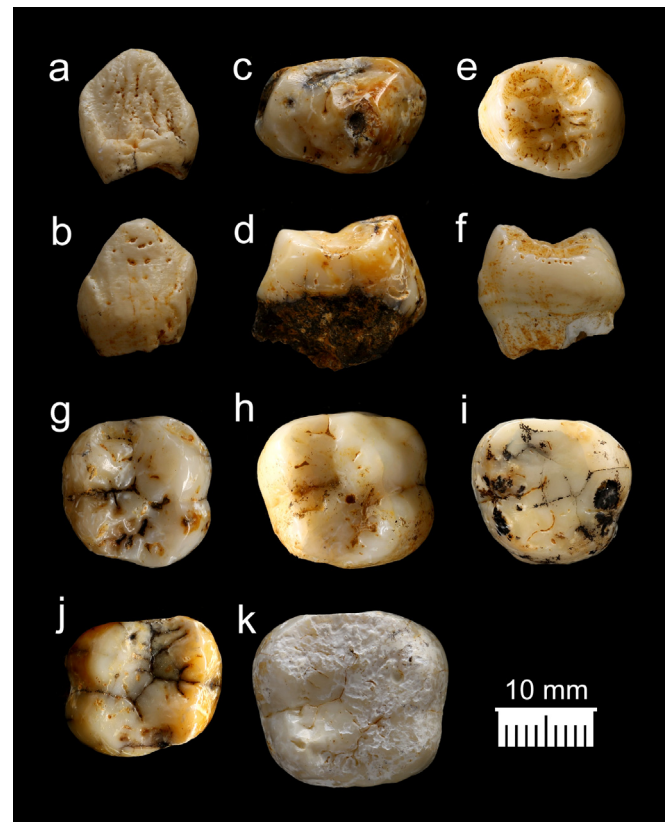


Fig. 2. Representative upper teeth of *Pongo weidenreichi* from Chongzuo, Guangxi: (a) Baikong 879, left I2, lingual view; (b) Baikong 879, left I2, buccal view; (c) Queque 0704-281, left P3, occlusal view; (d) Queque 0704-281, left P3, distal view; (e) Queque SN 49, right P4, occlusal view; (f) Queque SN 49, right P4, distal view; (g) Queque SN 35, right M1, occlusal view; (h) Queque SN 34, right M2, occlusal view; (i) Baikong 45, right M3, occlusal view; (j) Queque SN 33, left M1, occlusal view; (k) Baikong 1091, right M2, occlusal view. All to same scale.

of a female individual from the Middle Pleistocene cave site of Heshang in Yunnan (Bein and Chia, 1938). Broom (1946) suggested that this tooth might instead belong to *Gigantopithecus*, but we concur with Hooijer's assessment (Hooijer, 1948) that the lower canine is a better fit morphologically and metrically with *Pongo*. Additional isolated teeth attributed to *P. weidenreichi* have been recovered from Early and Middle Pleistocene cave sites in Yunnan, Guangxi, and Guangdong (Gu et al., 1987; Wang et al., 2009).

Analysis of the metrical data compiled by Gu et al. (1987) demonstrates that the occlusal areas of the cheek teeth of *P. weidenreichi* from Guangdong and Guangxi are on average 20.1% larger than extant *Pongo*. Comparisons show that the cheek teeth from Chongzuo are 26.5% larger than those included in the study by Gu et al. (1987), and that the mean values are higher for all cheek tooth loci (Table 3). How does one account for these differences? Measurement methods employed by different researchers may produce different results, but the differences are profound enough to rule out inter-observer error as fully accounting for the observed difference. Another important factor to be considered is sexual dimorphism. Gu et al. (1987) do not provide information on the inferred sex of their material, but from Chongzuo seven teeth can be reliably sexed, and six are from males (see Table 2). It is conceivable, therefore, that the Chongzuo sample has a skewed sex ratio, with the larger-toothed males predominating over females. Another potential confounding variable is that Gu et al. (1987) included samples from Middle and Late Pleistocene localities, which might have introduced the possibility that some smaller *Pongo cf. devosi* specimens were included in the composite sample. However, sample mixing would result in depressed mean values, but the upper ends of the ranges would be expected to be unaffected. Analysis of the data shows that the upper limits of the ranges of every class of cheek tooth from Chongzuo exceeds those

in Gu et al.'s study, implying that mixing of teeth from different taxa is unlikely to entirely explain the observed differences.

The most plausible explanation is that the difference in dental size is due to a temporal trend in *P. weidenreichi* from southern China. All of the Chongzuo *P. weidenreichi* samples in this study come from Early Pleistocene sites, whereas those sampled by Gu et al. (1987) are from the Middle Pleistocene (i.e., Maba, Daxin, Xiashan and Shanbei) and Late Pleistocene (i.e., Baipeng) (Gu et al., 1987, 1996; Drawhorn, 1995). *P. weidenreichi* may have undergone dental reduction during the Early to Middle Pleistocene, a general trend that was continued in the lineage leading to *P. devosi*. Counter to this general trend is the observation that *P. weidenreichi* from the Middle Pleistocene of Vietnam has larger teeth on average than its Early Pleistocene conspecific from southern China. Large samples from sites with reliable chronology will be needed to test for temporal trends and regional variation in dental size in *Pongo* during the Early and Middle Pleistocene of China and Vietnam.

The new material from Chongzuo also adds an additional feature that distinguishes *P. weidenreichi* from extant *Pongo*. Even though the sample is comprised entirely of isolated teeth, rather than associated tooth rows, there does appear to be a consistent difference in the proportions of the upper and lower molar series. Compared to extant *Pongo*, the second and third molars of *P. weidenreichi* tend to be considerably larger relative to the first molars. The proportions of occlusal areas of m1:m2:m3 in the Chongzuo sample is 100:156:144 and that of M1:M2:M3 is 100:118:104 (compared with 100:118:108 and 100:106:94 in extant *Pongo* respectively).

Following the method introduced by Harrison (1996, 2000), the size of the fossil teeth are compared against an extant *Pongo* reference standard (Table 4). Since there are only minor, non-significant differences in dental size between the two extant *Pongo* species (Hooijer, 1948; Drawhorn, 1995; Cameron, 2001), data for the Sumatran and Bornean species are combined in this analysis. The mean and standard deviation for the occlusal areas of each of the permanent teeth are used as a standard for comparison, and the distribution of the areas of individual teeth in relation to their deviation from the respective means is calculated. The use of occlusal areas, rather than linear dimensions, facilitates comparisons based on overall size, and the use of ranges of variation based on standard deviation from the mean allows comparisons to be made using data that pools teeth from the entire dental series. This analysis permits generalizations about the overall size of the teeth based on relatively small samples sizes, such as the fossil collections reported here. As shown in Table 4, the fossil *Pongo* teeth from Chongzuo are considerably larger in occlusal area than those of extant *Pongo*. All of the individual teeth of *P. weidenreichi* from the Early Pleistocene of Chongzuo are larger than the mean values of the modern species, with 29.7% of the teeth being more than 3 standard deviations larger.

Finally, Schwartz et al. (1995: 24) comment on the “extreme rarity” of *P. weidenreichi* specimens from southern China, and conclude that this is related to the species being at the northern limits of the geographical range of *Pongo*. While the fossil evidence confirms that the range of the genus does only extended as far north as the Yangtze River (at 27°N), coinciding with the limit of the subtropical Oriental faunal realm, we do not agree that *Pongo* was a particularly rare component of the fauna. *P. weidenreichi* specimens from the three localities included in this study constitute over 10% of all non-human primates; proportionally higher than one finds today for *P. pygmaeus* in Borneo (Rodman, 1978; Waser, 1987).

5. Summary and conclusions

More than seventy isolated teeth of fossil *Pongo* are reported from Baikong, Juyuan and Queque Caves in Chongzuo, Guangxi, southern

China. The specimens are Early Pleistocene in age and date from 2.0 to 1.0 Ma. The *Pongo* specimens are found in association with a diverse primate fauna, which includes *G. blacki*. The *Pongo* teeth from Chongzuo are generally morphologically indistinguishable from those of the extant species of orang-utans, but are much larger in size. All of the specimens can be attributed with confidence to *P. weidenreichi*. This species and its smaller relative, *P. devosi*, are now known from over thirty localities, and represent a typical constituent of the Pleistocene faunas of southern China and Vietnam.

P. weidenreichi is distinguished from the extant species by having considerably larger teeth on average, lower crowned canines, and relatively large second and third molars. The identification of more detailed species-specific characteristics of *P. weidenreichi* will require larger samples from sites in southern China (see Zhao et al., 2014). In addition, many of the systematic problems associated with fossil *Pongo* remain unresolved, but a provisional taxonomic scheme is presented here that better reflects our current understanding of species-level diversity. In addition to the two extant species, *P. pygmaeus* and *P. abelii*, five extinct species are recognized, including *P. weidenreichi* from the Early and Middle Pleistocene of China and Middle Pleistocene of Vietnam, *P. palaeosumatrensis* from the Late Pleistocene of Sumatra, *P. javensis* from the Late Pleistocene of Java, *P. duboisi* from the Late Pleistocene of Sumatra, and *P. devosi* from the Late Pleistocene of China and Vietnam. *P. weidenreichi* is replaced during the Middle to Late Pleistocene by a smaller species, *P. devosi*. *Pongo* apparently became extinct in China during the Late Pleistocene, but may have survived in Vietnam and Cambodia into the Holocene. Orang-utans were present on Java by at least the Middle Pleistocene and they continued into the Late Pleistocene as *P. javensis*. The Javan lineage appears to have been more diminutive, at least dentally, than broadly contemporary species on mainland Asia, Sumatra, and Borneo.

Two species of *Pongo* are recognized from Late Pleistocene localities in the Padang Highlands of Sumatra. A relatively large species, *P. duboisi*, is known from Lida Ayer and Djambu, while a somewhat smaller species, *P. palaeosumatrensis*, is known from the apparently younger locality of Sibrambang. These two taxa possibly represent time-successive members of the *P. abelii* lineage or are representatives of an older lineage of *Pongo*, broadly distributed across Sundaland, that was the sister taxon of *P. pygmaeus* and *P. abelii*. As noted by previous researchers, the fossil record provides evidence of a general trend towards dental reduction in *Pongo* during the course of the Pleistocene, but this is complicated by vicariance and ecogeographic factors operating differentially on populations at the regional and local levels to produce spatio-temporal heterogeneity in dental size.

Acknowledgments

We are grateful for assistance in the field from Wenshi Pan, Dagong Qin, Zuhong Liang and Yihong Liu. Peter Andrews, Christopher Bae, Russell Ciochon, Eric Delson, Wei Wang and Lingxia Zhao provided valuable advice and feedback. This study was supported by funding from Program of Chinese Academy of Sciences (KZZD-EW-03), National Natural Science Foundation of China (41072013) and the Program of China Geological Survey (1212011220519) (to CJ), and National Natural Science Foundation of China (41202017) and J0930007 (to YW). Additional funding was provided by an NYU travel grant (to TH).

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