第56卷　第3期
2018年7月

古 脊 椎 动 物 学 报
VERTEBRATA PALASIATICA

pp. 248–263
figs. 1–3

DOI: 10.19615/j.cnki.1000-3118.180403

Fossil gibbons (Mammalia, Hylobatidae) from the Pleistocene of Chongzuo, Guangxi, China

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Abstract Recent fieldwork at Pleistocene cave sites in the Chongzuo area in Guangxi Zhuang Autonomous Region has yielded 33 isolated teeth of fossil hylobatids. Comparisons indicate that the teeth can all be referred to a single species of *Nomascus*, but the material is insufficient to assign it to a particular species. The molars are slightly larger on average than those of extant species of *Nomascus*, but unlike contemporary great apes from the Pleistocene of southern China, the hylobatids do not seem to have undergone a change in dental size through time. *Nomascus* is not present in the Chongzuo area today, but historical records indicate that the genus may have been widely distributed across southern China in the recent past.

Key words Chongzuo, Guangxi; Pleistocene; *Nomascus*; taxonomy; isolated teeth; evolution; dental size

Citation Zhang Y Q, Jin C Z, Wang Y et al., 2018. Fossil gibbons (Mammalia, Hylobatidae) from the Pleistocene of Chongzuo, Guangxi, China. Vertebrata PalAsiatica, 56(3): 248–263

1 Introduction

Extant hylobatids (gibbons and siamangs) are currently included in four genera: *Hylobates*, *Hoolock*, *Nomascus*, and *Symphalangus* (Mittermeier et al., 2013; Roos, 2016; Rowe and Myers, 2016). The phylogenetic relationships between these taxa have not been fully resolved (Meyer et al., 2012; Wall et al., 2013; Carbone et al., 2014; Harrison, 2016), but the molecular clock estimates indicate a date of ~20–17 Ma for the divergence of hylobatids from the other hominoids, and ~9–5 Ma for the divergence of the crown hylobatid lineages (Fabre et al., 2009; Matsudaira and Ishida 2010; Thinh et al., 2010; Chan et al., 2010, 2012; Perelman

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中国科学院战略性先导科技专项(编号：XDPB05)、国家自然科学基金(批准号：41625005)、现代古生物学和地层学国家重点实验室(中国科学院南京地质古生物研究所) (编号：173132)和纽约大学资助。

收稿日期：2017-10-23

et al., 2011; Israfil et al., 2011; Springer et al., 2012; Finstermeier et al., 2013; Carbone et al., 2014; Pozzi et al., 2014).

However, the fossil record of hylobatids is meager (Harrison, 2016). The family appears to have originated some time during the Early Miocene, but the only known stem hylobatid is *Yuanmoupithecus xiaoyuan* from the Late Miocene (~7–9 Ma) of Yunnan (Pan, 2006; Harrison, 2010, 2016). Otherwise, fossil hylobatids are known from Pleistocene localities in China, Vietnam, Thailand, Laos, Borneo, Sumatra, and Java (Harrison, 2016). These are mostly isolated teeth, making their taxonomic positions and phylogenetic affinities difficult to determine, but they can generally be assigned to extant genera. Today, gibbons in China (*Hylobates*, *Hoolock*, and *Nomascus*) are restricted to the southwest of the country including Tibet, Yunnan, Guangxi, and on the island of Hainan (Ji and Jiang, 2004; Geissmann, 2007; Fan and Huo, 2009; Mittermeier et al., 2013; Fan et al., 2017), but during the Pleistocene, and even in historic times, they were widely distributed across southern and central China (van Gulik, 1967; Groves, 1972; Gao et al., 1981; Gu, 1989; Geissmann, 1995; Gu et al., 1996; Jablonski et al., 2000; Jablonski and Chaplin, 2009; Harrison, 2016), gibbons have been largely extirpated in China within the last several hundred years because of the high level of anthropogenic pressure (Turvey et al., 2015).

The best-known hylobatid from the Pleistocene of China is a partial mandible with m2 and m3 from Yanjinggou in Chongqing Municipality (formerly part of Sichuan Province), described by Matthew and Granger (1923) as *Bunopithecus sericus*. A recent reanalysis of the specimen (Ortiz et al., 2015) has shown that *Bunopithecus* represents a distinct genus and is possibly the extinct sister taxon of *Hoolock*. Other Pleistocene hylobatids from China have been recovered from Yunnan, Guangxi, Hainan, Sichuan, Guizhou, Guangdong, and Hunan (Gu et al., 1996; Jablonski and Chaplin, 2009).

Gu (1986, 1989) published an account of hylobatid finds from Guangxi obtained under the direction of Pei Wen-Zhong (Pei Wen-Chung) in 1956–1957. The 37 isolated teeth, consisting primarily of upper molars, came from at least eight different cave sites, as well as medicinal supply companies. Gu concluded that the majority of the upper molars resembled *Nomascus concolor* (*sensu lato*) in retaining a lingual cingulum, while three upper molars lacking a lingual cingulum were more similar to *Hoolock*. Extant *Hoolock* species are distributed west of the Salween River from Bangladesh to western Yunnan, while *N. concolor* is distributed in Yunnan as well as in Laos and Vietnam. Neither species is currently found in Guangxi, although *N. nasutus* occurs in western Guangxi.

Recent fieldwork in the Chongzuo area in Guangxi Zhuang Autonomous Region (ZAR) has yielded a sample of isolated teeth of fossil hylobatids from eight cave sites that date from Early to Late Pleistocene (Fig. 1). Gibbons appear to be a rare component of the Pleistocene primate community in Chongzuo, constituting less than 1% of specimens (Takai et al., 2014). The aim of this contribution is to describe the newly discovered hylobatids from Chongzuo and to determine their taxonomic positions.

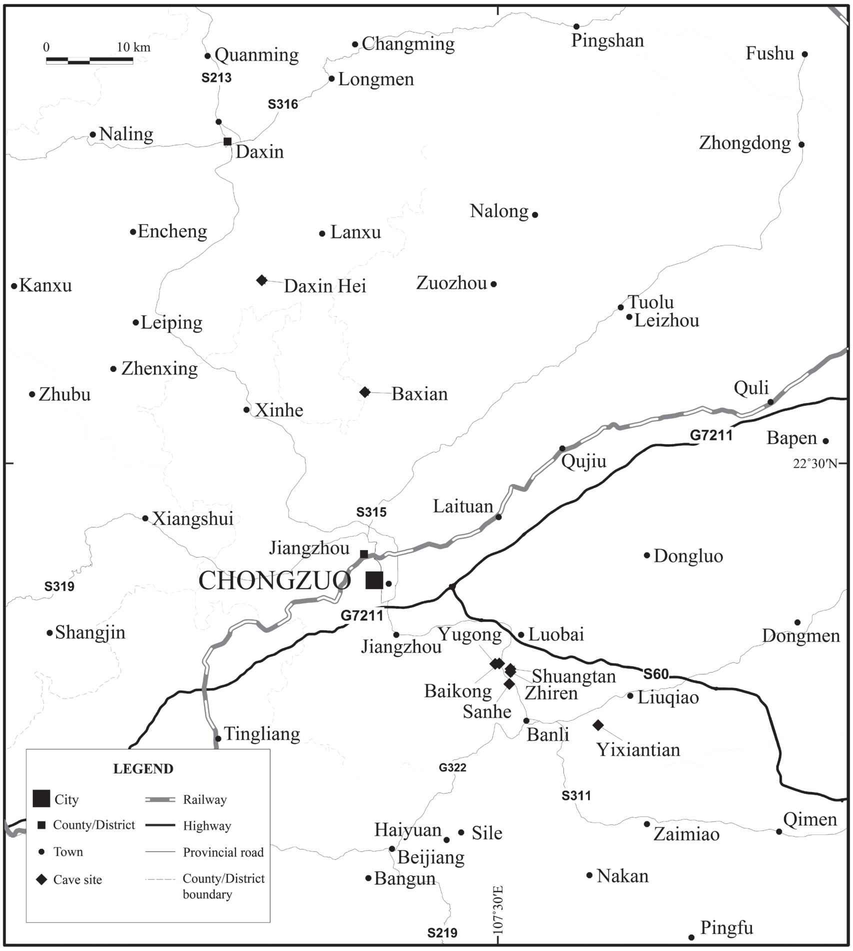

Fig. 1 Map of the Chongzuo area showing the location of the cave sites with hylobatid fossils

2 Materials and methods

The new fossil hylobatid specimens were recovered from cave sites in the area of Chongzuo in Guangxi ZAR. They consist of 33 isolated teeth, mostly upper and lower molars (Fig. 2; Table 1). All of the specimens are housed in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP). The ages of the specimens range from late Early Pleistocene to Late Pleistocene. The oldest specimens are from Baikong Cave, with an estimated age of ~2.0 Ma (Jin et al., 2014; Takai et al., 2014). The fossils were compared with extant hylobatids from the American Museum of Natural History in New York, the Smithsonian Institution in Washington D.C., the Natural History Museum in London, the Kunming Institute of Zoology in Kunming, the Institute of Zoology in Beijing, and the Biology Museum, School of Life Sciences at Sun Yat-Sen University in Guangzhou. Metrical and morphological comparisons indicate that the fossils can all be referred to a single species within the genus *Nomascus*.

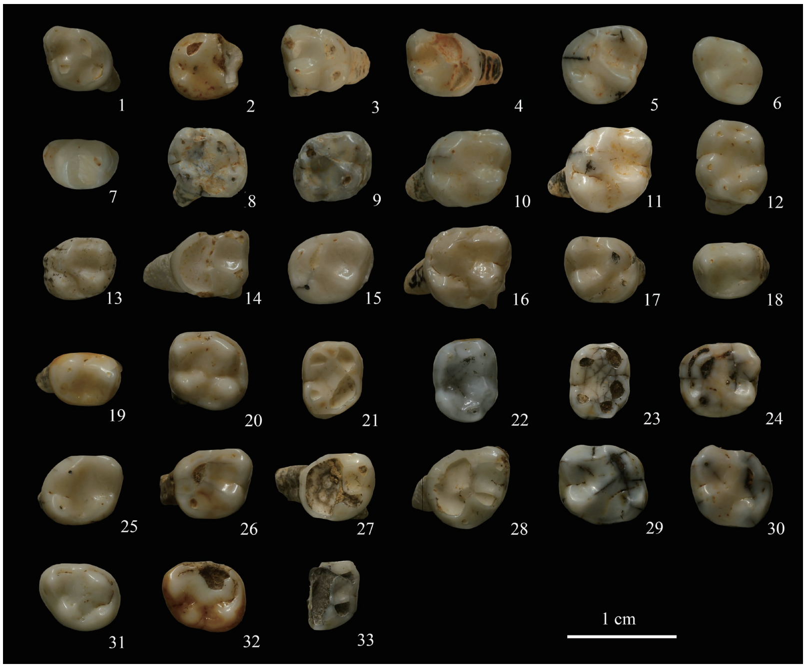

Fig. 2 Teeth of *Nomascus* sp. from the Chongzuo area in occlusal view
Baikong: 1. PA 1632, right M3, 2. PA 1633, left M3; Sanhe: 3. PA 1634, right M1, 4. PA 1635, right M1; Daxin Hei: 5. PA 1636, left M2, 6. PA 1637, right M3, 7. PA 1638, left P4; Yixiantian: 8. PA 1639, right M1, 9. PA 1640, left M1, 10. PA 1641, left M1 or M2; Shuangtan: 11. PA 1642, left M2, 12. PA 1643, left m2; Zhiren: 13. PA 1644, left M1 or M2, 14. PA 1645, left M1 or M2, 15. PA 1646, left M2; Yugong: 16. PA 1647, left M2, 17. PA 1648, right M1; Baxian: 18. PA 1649, right P4, 19. PA 1650, left P3, 20. PA 1651, right M2, 21. PA 1652, right m1 or m2, 22. PA 1653, right m3, 23. PA 1654, right m2, 24. PA 1655, left M2, 25. PA 1656, left M1 or M2, 26. PA 1657, left M1 or M2, 27. PA 1658, left M1, 28. PA 1659, left M2, 29. PA 1660, right M2, 30. PA 1661, right M2, 31. PA 1662, right M3, 32. PA 1663, right M3, 33. PA 1664, left M1 or M2

Isolated upper and lower first and second molars of hylobatids are difficult to discriminate from each other, and in these instances the fossils are described as M1 or M2 and m1 or m2 (see Table 1). In other cases, however, it is possible to assign molars, with reasonable confidence, to their appropriate serial position based on morphological criteria. Measurements of the specimens are presented in Table 1. Molar terminology follows Harrison and Gu (1999) (Fig. 3).

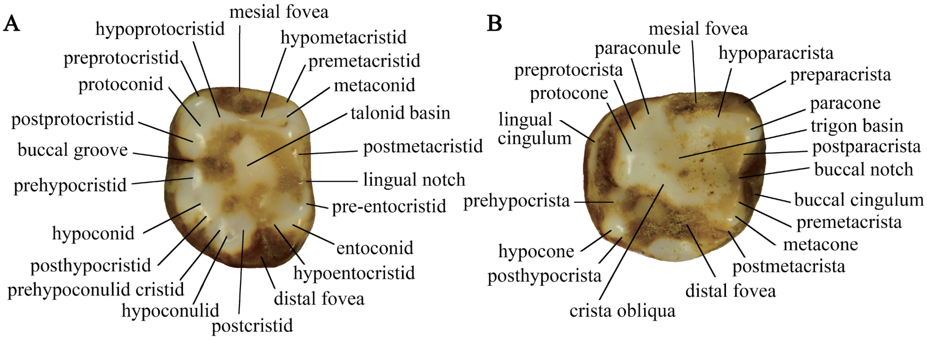

Fig. 3 Molar terminology used in this study
Left m2 (A) and left M2 (B) of *Nomascus concolor* (Kunming Institute of Zoology 024165)
Mesial is top, lingual is right on m2 and left on M2 (after Harrison and Gu, 1999)

Table 1 Dimensions of hylobatid teeth from Chongzuo, Guangxi (mm)

Age	Locality	Field no.	IVPP no.	Teeth	MD	BL
Early Pleistocene (~2.0 Ma)	Baikong	CLBBD201011-1040	PA 1632	RM3	5.8	6.5
		CLBBD201011-931	PA 1633	LM3	6.1	
Early Pleistocene (~1.2 Ma)	Sanhe	GCSD0605-1	PA 1634	RM1	6.5	
		GCSD0410-001	PA 1635	RM1	6.2	7.0
Middle Pleistocene (~380–310 ka)	Daxin Hei	DLZNH201206-30	PA 1636	LM2	7.0	8.1
		DLZNH201211-105	PA 1637	RM3	5.6	6.7
		DLZNH201211-820	PA 1638	LP4	4.7	6.9
Middle Pleistocene	Yixiantian	CFLSY201011-1115	PA 1639	RM1	6.4	7.5
		CFLSY201011-1113	PA 1640	LM1	6.2	7.4
		CFLSY201011-1112	PA 1641	LM1 or M2	6.9	7.7
Middle Pleistocene	Shuangtan	CMLST0911-37	PA 1642	LM2	7.9	7.8
		CMLST1005-11 (west)	PA 1643	Lm2	8.0	6.6
Late Pleistocene (~110 ka)	Zhiren	CLM0704-0116	PA 1644	LM1 or M2	5.8	6.8
		CZ0408a	PA 1645	LM1 or M2	6.2	7.8
		CZ0408g-13	PA 1646	LM2	6.4	7.9
Late Pleistocene	Yugong	CLBBG201112-350	PA 1647	LM2	7.4	8.0
		CLBBG201112-583	PA 1648	RM1	6.0	6.8
Late Pleistocene	Baxian	RTK201306-489 (RTK7)	PA 1649	RP4	5.2	6.6*
		RTK201306-490 (RTK7)	PA 1650	LP3	4.9	6.6
		RTK201306-391 (RTK6)	PA 1651	RM2	7.3	7.5
		RTK201306-502 (RTK7)	PA 1652	Rm1 or m2	6.8	5.8
		RTK201306-501 (RTK7)	PA 1653	Rm3	7.6	6.0
		RTK201306-500 (RTK7)	PA 1654	Rm2	7.2	5.6
		RTK201306-499 (RTK7)	PA 1655	LM2	6.8	7.4
		RTK201306-498 (RTK7)	PA 1656	LM1 or M2	6.4	7.4
		RTK201306-497 (RTK7)	PA 1657	LM1 or M2	6.5	7.0
		RTK201306-496 (RTK7)	PA 1658	LM1	6.2	7.1
		RTK201306-495 (RTK7)	PA 1659	LM2	7.2	7.9
		RTK201306-494 (RTK7)	PA 1660	RM2	7.2	8.2
		RTK201306-493 (RTK7)	PA 1661	RM2	7.0	7.9
		RTK201306-492 (RTK7)	PA 1662	RM3	6.1	7.5
		RTK201306-491 (RTK7)	PA 1663	RM3	6.3	7.9
		CXZB201211-32	PA 1664	LM1 or M2	6.2*	

Notes: Field numbers are abbreviations of either the locality name or the person name who numbered the specimens; BL. buccolingual dimension; L. left; MD. mesiodistal dimension; PA. IVPP numbers of the anthropological collection; R. right; * damaged, minimum dimension.

3 Systematic paleontology

Order Primates Linnaeus, 1758

Suborder Haplorrhini Pocock, 1918

Hyporder Anthropoidea Mivart, 1864

Infraorder Catarrhini Geoffroy, 1812

Superfamily Hominoidea Gray, 1825

Family Hylobatidae Gray, 1870

Genus *Nomascus* Miller, 1933

Nomascus (crested gibbons) currently includes seven species, found today in China, Vietnam, Laos, and Cambodia (Mittermeier et al., 2013). Four species occur in the subtropical and tropical evergreen forests of southwestern China: *N. concolor* and *N. leucogenys* in Yunnan, *N. nasutus* in Guangxi, and *N. hainanus* in Hainan (Ma and Wang, 1986; Fooden et al., 1987; Groves and Wang, 1990; Ni and Ma, 2006).

The hylobatids from the Pleistocene cave sites of Chongzuo can be assigned to *Nomascus* based on the morphology of the upper and lower molars. The small sample of isolated teeth does not permit identification to species.

4 Description

Upper premolars are represented by one P3 and two P4s (Fig. 2). P3 is a broad ovoid tooth, with a length-breadth index of 74.2. The protocone is low and rounded, and less elevated than the paracone (the apico-basal height of the protocone is 86.0% that of the paracone). The paracone is pyramidal in shape. There is a low transverse crest connecting the paracone and protocone. The mesial fovea is short and relatively broad. The distal fovea is expansive, with slight wrinkling of the enamel surface. There is no lingual cingulum. P3 has two roots.

P4 has a broad ovoid crown, with a length-breadth index of 68.1. The two main cusps, the protocone and paracone, are relatively low. The protocone is only slightly less elevated than the paracone (the apico-basal height of the protocone averages 89.9% that of the paracone). The paracone is pyramidal in shape, whereas the protocone is more conical. The two cusps are situated transversely opposite to each other and are connected by a low and rounded transverse crest. There is no lingual cingulum. The mesial fovea is mesiodistally short, but relatively broad. The distal fovea is more expansive. A shallow median groove transects the transverse crest to connect the mesial and distal foveae. The floor of the distal fovea is smooth and lacks secondary wrinkling. A small rounded tubercle is present on the distolingual margin of the crown in PA 1649. The P4 has two buccal roots and one lingual root.

The fossil sample includes 26 upper molars (Fig. 2). M1 is broader than long and subrectangular, with subparallel mesial and distal margins, a distally receding buccal face, and well-rounded corners. The mean length-breadth index of the M1 is 87.1. The tooth is low-crowned with low and rounded cusps and crests. The protocone is the most voluminous cusp, but less elevated than the paracone and metacone. It occupies most of the mesiolingual quadrant of the occlusal surface. The paracone is a low pyramidal cusp with a bluntly rounded apex. The metacone is subequal in height to the paracone. The apices of the two buccal cusps are located close to the buccal margin of the crown. The hypocone is well developed, but considerably smaller than the protocone. A narrow C-shaped lingual cingulum passes around the mesial and lingual base of the protocone, but it does not continue around the hypocone. A lingual cingulum is present on all M1s, except in PA 1656. The preprotocrista is short and rounded and terminates at the mesial margin. Midway along its length, where it meets the hypoparacrista, there is a low swelling that corresponds to a paraconule. The postprotocrista is low and indistinct. A low, and often poorly developed, crista obliqua links the protocone and metacone. There is no metaconule. A fine groove transects the crista obliqua and passes obliquely from the trigon basin into the distal fovea. The preparacrista is represented by a short and sharp crest that passes mesiolingually from the apex of the paracone to terminate at the mesial marginal ridge. The postparacrista is also sharp and is subequal in length to the preparacrista. The hypoparacrista passes lingually from the paracone to meet the paraconule, where it forms the low distal margin of the mesial fovea. The mesial fovea is small and pit-like. The mesial marginal ridge is low and ill-defined. The premetacrista is sharp and passes mesially to meet the postparacrista. The latter two crests are separated by a fine groove that passes from the trigon basin through the buccal notch. A narrow ledge or tiny tubercle on the buccal face of the crown represents a trace of a buccal cingulum in 2/3 of specimens. The postmetacrista is low and arcs distally and lingually to become continuous with the distal marginal ridge. The trigon basin is shallow, but quite expansive, and slightly broader than long. It has traces of a barely discernable Y-shaped fissure pattern, of which the transverse arm passing through the buccal notch is the best developed. Otherwise, the floor of the trigon basin is smooth and has no crenulation. The prehypocrista is low and short and passes mesiobuccally to meet the postprotocrista. The distal fovea is a large triangular basin distal to the crista obliqua. It is about 2/3 of the size of the trigon basin. An oblique groove crosses the floor of the distal fovea from the distal margin of the metacone, passes between the prehypocrista and postprotocrista, to join the groove of the lingual cingulum. The posthypocrista is rounded and arcs distally and buccally to join the distal marginal ridge. M1 has three short roots.

M2 is very similar in morphology to M1. It differs in being larger (the occlusal area is almost 30% larger on average than M1), the crown is mesiodistally longer in relation to its breadth (the mean length-breadth index is 90.9), the lingual cingulum tends to better developed, and the hypocone is relatively larger and separated from the trigon by a more pronounced groove. The lingual cingulum is present on all M2s, but in a few specimens it is rather weakly developed and not continuous around the protocone (e.g., PA 1642 and PA 1661). In PA 1651, the lingual cingulum continues distally onto the mesiolingual aspect of the hypocone. A trace of the buccal cingulum is present on 40% of M2s.

M3 has the same basic morphology as M1 and M2. However, it is more variable in shape and size than the other upper molars, and tends to have a relatively shorter crown (with a mean length-breadth index of 83.5), with strong distal tapering, and a hypocone and metacone that are reduced in size compared with the mesial cusps. A well-developed lingual cingulum is typically present, but it is absent in PA 1637. A trace of the buccal cingulum is present in half of the M3s. The crista obliqua is poorly developed or lacking. M3 has three roots, as in M1 and M2, but they are often fused together. M3 is subequal in size to M1, but has a mean area that is about 30% smaller than M2. The size differential between the upper molars (area of M1:M2:M3) is 77:100:77.

Lower molars are much less common than upper molars in the collection. Only four specimens are represented: one m1 or m2 (Fig. 2: 21, PA 1652), two m2s (Fig. 2: 12, PA 1643;

23, PA 1654), and one m3 (Fig. 2: 22, PA 1653). PA 1652 and PA 1654 are heavily worn, so details of the m2 and m3 are largely based on PA 1643 and PA 1653, respectively. The m2 is mesiodistally longer than broad (with a mean breadth-length index of 80.3), subrectangular in outline, tapering mesially, with well-rounded corners. The crown shows a moderate degree of buccolingual waisting (i.e., the crown narrows midway along its length). The buccal and lingual walls of the crown are convex and bulging. The five main cusps are arranged around the periphery of the crown. The protocone is low, rounded and conical. It has short but well-developed preprotocristid, hypoprotocristid, and postprotocristid. The size of the hypoconid is similar to the protoconid, and like the later cusp the hypoconid is low and rounded. The prehypocristid and posthypocristid of it are short. The hypoconulid is much smaller than the other buccal cusps. It is situated on the distobuccal margin of the crown, to the buccal side of the longitudinal midline of the crown. There is a slight trace of a buccal cingulid between the hypoconid and hypoconulid in PA 1643, but it appears to be absent in PA 1654. The metaconid and entoconid are pyramidal in shape, and are slightly more elevated than the buccal cusps. The premetacristid arcs mesially and buccally to become continuous with the elevated mesial marginal ridge. The hypometacristid is well developed, and together with the hypoprotocristid, forms the distal wall of the mesial fovea. The two crests are interrupted by a fine longitudinal groove that passes from the talonid basin into the mesial fovea. The mesial fovea is well defined and forms a broad lenticular-shaped furrow. The metaconid and entoconid are widely spaced, with a relatively long postmetacristid. The lingual notch, between the postmetacristid and pre-entocristid, is shallow. The talonid basin is shallow, but expansive. The floor of the basin is smooth and unwrinkled, but indistinct grooves separate the hypoconid from the protoconid and hypoconulid, and pass through the lingual notch, to form a weakly developed Y-shaped groove system. A low, but well-developed crest links the hypoconulid and entoconid to delimit the distal fovea. The D-shaped distal fovea forms a short heel to the crown that protrudes distolingually. The distal marginal ridge bears a prominent tuberculum sextum in PA 1643.

The m3 is subequal in size to m2, but larger samples and/or associated specimens are needed to confirm whether this is the typical pattern of size differential. The crown is subrectangular, narrowing slightly distally, with a moderate degree of buccolingual waisting, and a V-shaped distal heel. The five main cusps are low and rounded. They are peripherally arranged around the margin of the crown, with only a slight degree of buccal flare. The protoconid is the largest cusp. The preprotocristid is short and rounded, while the postprotocristid is longer and better developed. The hypoconid is slightly smaller than the protoconid. The prehypoctristid and posthypocristid are well developed. A fine groove separates the postprotocristid and the prehypocristid. There is a trace of a cingulid on the buccal face between the protoconid and hypoconid. The hypoconulid is small and situated almost in the midline on the protruding distal margin of the crown. The metaconid and entoconid are widely spaced. The metaconid is slightly more elevated than the protoconid, but it is not as voluminous. The premetacristid arcs mesially and buccally to join the mesial marginal ridge. The hypometacristid meets the hypoprotocristid to form a well-developed distal wall to the mesial fovea. The mesial fovea is broad. The postmetacristid is relatively long and bows lingually. The entoconid is relatively small, with rounded and poorly developed cristids. The pre-entocristid is separated from the postmetacristid by a transverse groove that passes through the shallow lingual notch. The talonid basin is shallow but extensive. Apart from a slight trace of a Y-shaped groove system, the floor of the talonid basin is smooth and lacks secondary wrinkling. The distal fovea is indistinct and restricted to a small pit-like depression on the margin of the crown between the hypoconulid and the entoconid. There is a single root, with mesial and distal lobes.

5 Comparisons

The isolated teeth from Chongzuo exhibit a marked degree of uniformity in both morphology and size that indicate that they all belong to a single species. The size variation in the upper and lower molars does not exceed the range of intraspecific variation seen in extant hylobatids (Table 2). Unlike some of the other hominoid taxa from the Pleistocene of southern China, such as *Pongo* and *Gigantopithecus* (Harrison et al., 2014; Zhang et al., 2015; Zhang and Harrison, 2017), the hylobatids do not appear to have undergone a change in overall dental size through time.

The fossils share a specialized suite of features of the molars that are characteristic of extant hylobatids. These include: low crowned molars; subrectangular in occlusal outline with rounded corners and buccolingual waisting, low and rounded cusps and crests; peripherally arranged cusps; expansive and shallow talonid and trigon basins; simple groove system with no secondary wrinkling; lower molars much longer than broad; buccal cingulid on lower molars weakly developed; relatively small and distally displaced hypoconulid; widely separated metaconid and entoconid; poorly defined distal fovea on lower molars; M1 and M2 only slightly broader than long; low and poorly developed crista obliqua; relatively small hypocone; moderate degree of size differential between M1 and M2; M3 relatively small.

Nevertheless, the dentitions of extant hylobatids differ in size and in a number of morphological traits that allow the genera to be discriminated from each other (see Frisch, 1965). These provide a basis for identifying the genus to which the fossils can be assigned. Extant hylobatids display a progressive increase in dental size in the order of *Hylobates*, *Nomascus*, *Hoolock* and *Symphalangus*. Based on the combined mean areas of the upper molars (the most commonly represented teeth in the fossil sample), the Chongzuo hylobatid is 29.9% and 32.9% larger than *Hylobates moloch* and *Hy. lar*, respectively, and 18.5% smaller than *Symphalangus syndactylus*. The fossil upper molars have a substantial overlap with the size range of *Nomascus concolor*, *N. leucogenys,* and *Hoolock hoolock*, but they are slightly larger on average (6.6% and 6.7% larger, respectively) than those of *N. concolor* and *N. leucogenys* and slightly smaller (4.0%) than those of *Ho. hoolock*. We can estimate, using

Table 2 Dimensions of upper and lower molars of the Chongzuo hylobatids compared with those of extant hylobatids (mm)

Teeth	Measurements	Chongzuo hylobatids	*Nomascus concolor*	*Nomascus leucogenys*	*Hoolock hoolock*	*Symphalangus syndactylus*	*Hylobates agilis*	*Hylobates lar*	*Hylobates moloch*	*Hylobates klossii*
M1	N	6	8	6	17	36	16	26	11	8
	MD	6.1 (5.8–6.4)	6.1 (5.9–6.4)	6.3 (5.9–6.6)	6.7 (6.1–7.2)	7.6 (6.0–8.3)	5.9 (5.5–6.7)	5.7 (5.3–6.2)	5.7 (4.7–6.6)	5.4 (5.0–5.6)
	BL	7.1 (6.5–7.5)	6.8 (6.5–7.3)	6.7 (6.2–7.1)	7.0 (6.6–7.7)	7.2 (6.2–8.3)	6.3 (5.7–6.7)	6.2 (5.8–7.0)	6.3 (5.7–6.8)	5.9 (5.4–6.3)
M2	N	9	10	10	17	36	17	25	10	8
	MD	7.1 (6.4–7.9)	6.7 (5.7–7.2)	6.7 (6.2–7.1)	7.1 (6.7–7.5)	8.1 (6.9–9.0)	6.0 (5.7–6.5)	6.1 (5.2–6.7)	6.3 (5.9–7.3)	5.4 (5.0–5.8)
	BL	7.9 (7.4–8.2)	7.1 (6.5–7.7)	7.4 (6.7–7.9)	7.7 (7.0–8.1)	8.0 (6.9–8.8)	6.4 (5.8–6.8)	6.5 (6.1–7.0)	6.5 (5.7–7,2)	5.9 (5.4–6.3)
M3	N	5	7	3	13	26	17	24	9	8
	MD	6.0 (5.6–6.3)	6.3 (5.6–6.8)	5.9 (5.2–6.7)	6.4 (5.3–7.0)	7.2 (5.5–8.4)	5.4 (4.9–6.0)	5.3 (4.7–6.2)	5.3 (4.7–5.9)	4.0 (3.3–4.5)
	BL	7.2 (6.5–7.9)	7.1 (6.5–7.7)	7.1 (6.4–7.5)	7.3 (6.3–8.1)	7.7 (7.1–9.1)	6.1 (5.2–6.9)	6.1 (5.2–6.8)	6.2 (5.4–7.0)	5.6 (5.4–6.0)
m1	N		7	4	16	30	16	25	11	9
	MD		6.8 (6.5–7.2)	7.1 (6.7–7.5)	6.8 (6.5–7.3)	8.0 (6.9–8.7)	6.3 (5.6–6.8)	6.0 (5.7–6.5)	6.3 (5.7–7.2)	5.9 (5.7–6.1)
	BL		5.3 (5.0–5.7)	5.4 (5.2–5.7)	5.6 (5.0–6.2)	6.3 (5.4–6.9)	5.2 (5.6–6.8)	5.1 (4.6–5.7)	5.0 (4.4–5.8)	4.8 (4.2–5.8)
m2	N	2	9	6	16	30	17	23	10	8
	MD	7.6 (7.2–8.0)	7.2 (6.9–7.6)	7.2 (6.3–7.9)	7.6 (7.3–8.5)	8.7 (7.5–9.8)	6.3 (5.9–6.9)	6.2 (5.4–6.6)	6.5 (5.7–7.3)	6.0 (5.5–6.6)
	BL	6.1 (5.6–6.6)	5.8 (5.4–6.3)	6.0 (5.5–6.6)	6.6 (5.9–7.5)	6.9 (6.1–7.5)	5.6 (5.2–6.4)	5.4 (4.9–6.0)	5.6 (4.9–6.3)	6.0 (5.5–6.6)
m3	N	1	8	6	12	26	17	23	8	7
	MD	7.6	7.0 (6.5–7.6)	6.8 (6.2–7.2)	7.3 (6.5–7.9)	8.5 (6.5–9.8)	6.2 (5.5–6.8)	6.1 (5.3–7.0)	6.1 (5.7–6.5)	5.2 (4.4–5.6)
	BL	6	5.9 (5.6–6.3)	5.9 (5.4–6.2)	6.2 (5.5–6.8)	6.7 (5.3–7.7)	5.4 (4.8–5.9)	5.3 (4.8–5.9)	5.5 (5.0–6.1)	4.6 (4.1–4.8)
Data Source		This study	This study	This study	This study	This study, Hooijer (1960)	Hooijer (1960)	This study	This study	Swindler (2002)

Notes: BL. buccolingual dimension; MD. mesiodistal dimension; N. specimen number; means and range ( ) are given for MD and BL.

the Gingerich et al. (1982) formula for average m2 area, that the Chongzuo hylobatid had an average body mass of about 8.7±1.0 kg.

The size difference between M1 and M2 is greater in the Chongzuo hylobatid (the average area of M1 relative to M2 is 77.2%) than the average in extant hylobatid taxa (84.4%–100.0%). It is most distinct from *Hylobates* spp., which have a small size differential between M1 and M2 compared to other genera. Sampling is a potential issue, but the M3 also appears to be relatively small in the Chongzuo hylobatid in relation to M2 when compared to extant hylobatids. The mean mesiodistal length of M3 is subequal to the mean mesiodistal length of M1 (with an index of 97.6). This is similar to the proportions in *N. concolor* (103.4), *Ho. hoolock* (95.5), and *S. syndactylus* (94.7). *Hylobates* spp. have a more reduced M3 (*Hy. moloch*, 93.0; *Hy. lar*, 93.0; *Hy. agilis*, 91.5; *Hy. klossii*, 74.1). Unfortunately, the sample of lower molars from Chongzuo is too small to analyze relative size.

The mean breadth-length index of the M1 and M2 (87.1 and 90.9, respectively) indicates that the upper molars of the Chongzuo hylobatid are relatively broad compared with those of extant hylobatids. Nevertheless, M1 is most similar in proportions to those of *N. concolor* (with a mean index of 89.7), while M2 is most similar in proportions to those of *N. leucogenys* (with a mean index of 90.5). The mean length-breadth index of m2 (80.3) in the Chongzuo hylobatid indicates that the lower molars are relatively narrow compared with those of most extant hylobatids, but are comparable to those of *S. syndactylus* (79.3), *N. concolor* (80.6), and *N. leucogenys* (83.3).

An important characteristic of the Chongzuo upper molars is the high incidence of a lingual cingulum and the occurrence of a trace of the buccal cingulum. A well-developed lingual cingulum is present in 81.8% (18 of 22) of upper molars. According to data compiled by Frisch (1965) for extant hylobatids, this high incidence of occurrence is comparable to that seen in *Nomascus* spp. (*N. gabriellae*, 87.5%; *N. leucogenys*, 72.2%) and *Hy. pileatus* (74.2%), whereas in other hylobatid species the cingulum is less fully developed and occurs much less frequently. A trace of a buccal cingulum is present on 52.4% of upper molars from Chongzuo (11 of 21). Frisch (1965) reported the occurrence of a buccal cingulum on the upper molars of *Symphalangus* (52.2%) and *Nomascus* (61.7%). A vestige of a buccal cingulid is present on three out of the four lower molars from Chongzuo. As noted by Frisch (1965), only *Nomascus* among extant hylobatids retains a trace of a buccal cingulid on the lower molars.

6 Discussion

Given the degree of metrical and morphological uniformity in the sample of hylobatid teeth from Pleistocene cave sites in Chongzuo, the specimens can all be attributed to a single species. Although sample sizes are small, there is no indication that there was any change in dental size through time. The teeth exhibit a suite of specialized features that are characteristic of extant hylobatids, implying that the fossils belonged to a crown member of the clade. The combination of features that the fossils share uniquely with *Nomascus* indicates that the

Chongzuo hylobatid should be assigned to this genus. As described above, these features include: upper and lower molars similar in size to *Nomascus* (also *Hoolock*); M3 subequal in length to M1 (also *Hoolock* and *Symphalangus*); upper molars relatively broad; high incidence of a well-developed lingual cingulum on the upper molars (also *Hylobates pileatus*); trace of a buccal cingulum on the upper molars common (also *Symphalangus*); lower molars relatively narrow; and presence of a trace of a buccal cingulid on the lower molars.

Unfortunately, the material from Chongzuo is insufficient to assign it to a particular species, so it is referred here to *Nomascus* sp. It can be distinguished from *N. concolor* and *N. leucogenys*, both of which occur today in southwestern China, in having slightly larger teeth and in the proportions of the molars. However, larger samples from Chongzuo, and more extensive comparisons with extant species of *Nomascus*, especially *N. hainanus* (from western Hainan) and *N. nasutus* (from northern Vietnam and western Guangxi), are needed to determine its species affinities.

Currently, *Nomascus* is not present in the Chongzuo area, but it does occur in nearby areas, including western Guangxi (*N. nasutus*) and Yunnan provinces, China, Vietnam, and Laos (*N. concolor* and *N. leucogenys*), as well as on the island of Hainan (*N. hainanus*) (Ortiz et al., 2015:fig. 7). In addition, historical records show that gibbons were more widely distributed in China in the recent past than they are today (van Gulik, 1967; Gao et al., 1981; Gu, 1989; Geissmann, 1995; Zhou and Zhang, 2013; Ortiz et al., 2015). Records of hylobatids south of the Xijiang River, are likely attributable to *Nomascus*, and suggest that the genus was previously widely distributed across southern China (Wang et al., 2000; Zhou and Zhang, 2013). Historical occurrences north of the Xijiang River in central and eastern China possibly represent *Bunopithecus*, an extinct genus of hylobatid most closely related to *Hoolock* (Ortiz et al., 2015).

7 Conclusions

Recent fieldwork in the Chongzuo area in Guangxi ZAR has led to the recovery of 33 isolated teeth of hylobatids from eight cave sites ranging in age from Early to Late Pleistocene. Morphological and metrical comparisons indicate that the teeth do not exceed the range of intraspecific variation in extant hylobatids, and that they can all be referred to a single species. A combination of features shared uniquely with *Nomascus* indicates that the Chongzuo hylobatid can be assigned to this genus. These features include relatively broad upper molars with a high incidence of a lingual cingulum and a trace of a buccal cingulum, M3 subequal in length to M1, and narrow lower molars with a vestige of a buccal cingulid. The molars are slightly larger on average than those of extant species of *Nomascus*. The material from Chongzuo is insufficient to assign it to a particular species of *Nomascus*. Unlike contemporary great apes from the Pleistocene of southern China, such as *Pongo* and *Gigantopithecus*, the hylobatids do not seem to have undergone a change in dental size through time. Although

Nomascus is not present in the Chongzuo area today, it is likely that the genus was widely distributed across southern China during historical times.

Acknowledgements We thank NI Xi-Jun and Nina JABLONSKI for comments on the manuscript. The authors are grateful to the collection managers at the following institutions for access to skeletal collections: American Museum of Natural History, New York; Smithsonian Institution, Washington D.C; Natural History Museum, London; Kunming Institute of Zoology, Kunming; Institute of Zoology, Beijing; Biology Museum, School of Life Sciences, Sun Yat-Sen University, Guangzhou. Research was supported by the Strategic Priority Research Program of Chinese Academy of Science (grant no. XDPB05) and National Natural Science Foundation of China (grant no. 41625005), and by the State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) (no. 173132), and New York University.

广西崇左更新世长臂猿化石新材料

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摘要：近年，在对广西崇左地区第四纪洞穴堆积调查的过程中，从年代贯穿更新世的8个地点采集到了33颗长臂猿游离牙齿化石。记述了这些新发现的长臂化石，并初步确定了其分类位置。形态和测量的对比表明，这些牙齿不超过现生长臂猿种内变异的范围，且都可以归入一个种内。它们与冠长臂猿属(*Nomascus*)共有的特征组合表明，这些化石可以归入该属。这些特征包括：上臼齿相对宽，舌侧齿带及唇侧齿带痕迹保留率高；M3长度几乎与M1相等；下臼齿狭窄，并保留唇侧齿带退化痕迹。崇左地区的化石长臂猿的臼齿平均比冠长臂猿属中现生种类稍显大。但是崇左地区的游离牙齿化石材料提供的证据并不足以支持将其归入该属中的某一具体种类。与中国南方更新世其他同时代的大型猿类猩猩(*Pongo*)和巨猿(*Gigantopithecus*)不同，长臂猿的牙齿大小并没有随时间发生变化。尽管冠长臂猿属在现今的崇左地区并没有分布，但是在历史时期该属曾经广泛分布于中国南方地区。

关键词：广西崇左，更新世，冠长臂猿属，分类学，游离牙齿，演化，牙齿大小

中图法分类号：Q915.879 **文献标识码：**A **文章编号：**1000–3118(2018)03–0248–16

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