



An examination of feeding ecology in Pleistocene proboscideans from southern China (*Sinomastodon*, *Stegodon*, *Elephas*), by means of dental microwear texture analysis



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ABSTRACT

It has long been thought that environmental perturbations were the key driving force behind the succession of three distinct mammal faunas in the Pleistocene *Ailuropoda-Stegodon* faunal complex (*sensu lato*) of South China: the lower Pleistocene *Gigantopithecus-Sinomastodon* fauna, the middle Pleistocene *Ailuropoda-Stegodon* fauna (*sensu stricto*) and the upper Pleistocene *Homo-Elephas* fauna. Here, we apply three-dimensional dental microwear texture analysis (DMTA) to three characteristic fossil proboscideans from these mammal faunas to provide preliminary tests for hypotheses of trophic ecology. Despite a few methodological caveats, this study demonstrates the potential of DMTA for understanding the diets of fossil proboscideans. The texture of microwear in *Sinomastodon* and *Stegodon* are more reflective of browsing, whereas that of *Elephas* is suggestive of mixed feeding. The results suggest a more complex process of Pleistocene faunal turnovers in South China. Rather than a unidirectional trend of climate-driven environmental deterioration, biotic factors might have played a more substantial role than previously thought.

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1. Introduction

It has been widely recognised that the evolution and turnover of megaherbivores during the Plio-Pleistocene was fundamentally governed by climate changes on local and global scales (Qiu, 2006; Wei et al., 2010; Wang et al., 2012; Fortelius et al., 2014). This is particularly evident in the Proboscidea, whose fossil record indicates a major decline in diversity throughout this period, eventually leaving only three extant species of a previously very diverse order (Shoshani and Tassy, 1996, 2005; Sukumar, 2003). With a comprehensive proboscidean phylogeny still a formidable task

(Shoshani, 1998; Adrian Lister, personal communication), it is crucial to understand their palaeobiology with respect to the environment, as the proboscideans are often deemed to be typical K-selected large mammal species, with sensitive responses to climatic and environmental fluctuations.

It may appear superficially that the proboscideans conform to the classic narrative of large herbivore evolution during the Cenozoic, of turning from browsing to grazing. As the global climate gradually deteriorated, forests and woodlands transformed into more arid grasslands towards the late Cenozoic (Janis, 1993, 2008), and many large herbivores evolved dentitions capable of processing more abrasive vegetation (see Damuth and Janis, 2011 for detailed review). The proboscideans saw the transition from the bunolophodont morphology of the molars in the broadly ancestral “gomphotheres”, to lophodonty in two families, Stegodontidae and Elephantidae, as shown in Fig. 1 (although the precise interrelationships remain weakly resolved: see Sanders et al., 2010, and references therein). Stegodonts retained the brachyodonty of

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gomphotheres, but the cusps and lophs which typify the bunolophodont morphology were multiplied to form enamel ridges more optimised for shearing (Fig. 1), similar to those seen in extant elephants (Saegusa, 1996; von Koenigswald, 2014). Evidence from morphology, geochronology and palaeobiogeography indicate that elephantids like *Elephas* evolved lophodonty in parallel with stegodonts such as *Stegodon* (Saegusa et al., 2005, 2014; Wang et al., 2015a; Ao et al., 2016). Elephantids have fused the transverse cusp pairs of the gomphothere molars into continuous loops of enamel, each filled with dentine and joined to its neighbours by cement (Rivals et al., 2015). In more derived elephantids, the tooth crown is also dramatically heightened (Maglio, 1973; also see Fig. 1).

The bunolophodont–lophodont transition in the proboscidean fossil record (Fig. 1), and the independent evolution of hypsodonty (increased height of tooth crown) among the different elephantid genera (Maglio, 1973), has long been linked with a transition from browsing to grazing (Savage and Long, 1986; Shoshani, 1998). However, recent application of more direct dietary proxies allow palaeontologists to decouple phenetic and behavioural inferences, in order to better interpret the evidence for evolutionarily adaptive responses in the fossil record (Lister, 2014). Cerling et al. (1999) demonstrated, using stable carbon isotope signatures of the dental enamel, that despite the C₄ signal of a grazing-dominated diet for the last 7 Ma, African proboscideans in the late Pleistocene showed a reversal to a signal of C₃ mixed-feeding, this is in spite of a continuing trend towards hypso-lophodonty (Maglio, 1973; Lister, 2013). Detailed corroboration of isotopic proxies for grazing and grassland domination with the African proboscidean fossil record suggests a time lag between emergence of grazing behaviour and subsequent morphological response in the appearance of a hypso-lophodont dentition (Lister, 2013). In fact, the gomphotheres remained the dominant grazing proboscideans for much of the late Cenozoic in Africa (Cerling et al., 1999; Lister, 2013).

The focus of this study is the proboscidean succession in the Pleistocene of South China. Proboscideans are good model organisms for the purpose of assessing the influence of environmental factors on faunal turnovers, not only because they are super-keystone species in their ecosystem (Fritz et al., 2002), but also because studies have shown that both fossil and extant proboscideans are highly generalist herbivores whose dietary composition reflects local environmental conditions more than

their “adaptive optimal” diet (e.g. Rivals et al., 2012, 2015; Lister, 2013, see discussion below). China has an enormous abundance and diversity of large mammal fossils from the late Cenozoic, including proboscideans (e.g. Owen, 1870; Hopwood, 1935; Colbert and Hooijer, 1953; Chow and Zhang, 1974; Han, 1987; Pei, 1987; Qiu et al., 2004; Qiu, 2006; Wang et al., 2013; Chi and Wei, 2014; Jin et al., 2014; Zeitoun et al., 2016): a long history of research of these materials has also provided an established literature for understanding the process of proboscidean evolution and turnover in the context of environmental change and faunal turnover (Maglio, 1972; Pei, 1987; Chen, 1999, 2011; Tong, 2007; Jin et al., 2009a,b; 2014; Wei et al., 2010; Wang et al., 2012; Button et al., 2013, 2014b).

Recently, chronologically well-constrained Pleistocene mammal fossil-bearing strata, have been reported from karst caves and fissures of the Guangxi Zhuang Autonomous Region in southernmost China. Systematic survey of biostratigraphy across areas in the vicinity of Chongzuo Ecological Park and the Buling Basin has enabled the definition and refined timescale of three key faunal stages making up South China’s characteristic *Ailuropoda–Stegodon* faunal complex (*sensu lato*, but see Zeitoun et al., 2016) during the Pleistocene: the early Pleistocene *Gigantopithecus–Sinomastodon* fauna, the middle Pleistocene *Ailuropoda–Stegodon* fauna (*sensu stricto*) and the late Pleistocene Asian elephant fauna, corroborated by an abundance of other Pleistocene fossils from Guangxi (Jin et al., 2007, 2009a; 2014; Wang et al., 2007, 2014a,b; Rink et al., 2008). The fossil proboscideans (*Sinomastodon*, *Stegodon*, *Elephas*) were always typical members of Quaternary faunas of southern China (Zeitoun et al., 2015, 2016).

Sinomastodon, the terminal and only brevirostrine Old World trilophodont gomphothere, possesses typical brachy-bunolophodont molars (Fig. 1) (Tobien et al., 1986; Chen, 1999; Wang et al., 2012, 2014b). The fossil record of *Sinomastodon* shows a northward shift during the latest Miocene to Pliocene (Wang et al., 2015b) but southward shift during Pleistocene, with Pleistocene *Sinomastodon* found only in South China (Tobien et al., 1986; Zong et al., 1989; Chen, 1999; Wang et al., 2012, 2014b). The same patterns appears to be repeated slightly later by *Stegodon*, with species found in both North and South China in the basal Pleistocene, but with the genus later also restricted to South China (Chen, 2011). It has been hypothesised that climate-induced vegetation shifts drove Chinese proboscidean turnovers in the Pleistocene. Namely, the southward dispersal of brachyodont

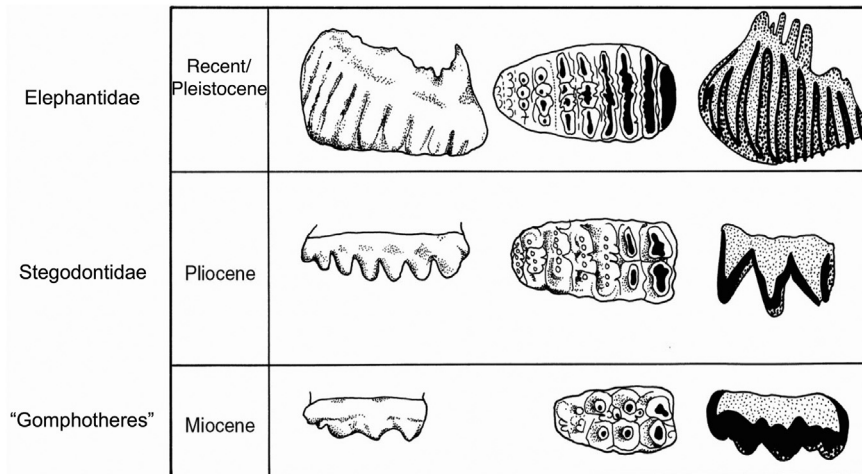


Fig. 1. Evolution of proboscidean molars in the late Cenozoic, with upper molars shown in lateral (left), occlusal (centre) and section views (right). The ancestral “gomphotheres” possessed low-crowned cheek teeth (brachyodont) typified by blunt, conical cusps arranged in transverse rows called lophs (upper molars) or lophids (lower molars) (bunolophodont), serving a grinding and crushing function during mastication (von Koenigswald, 2014). In stegodonts and elephantids, the cusps and loph(id)s have multiplied along with thinning of the enamel to form more incised ridges (lophodont) for shearing and cutting (Maglio, 1972; Saegusa, 1996; von Koenigswald, 2014). The dramatic evolution of hypsodonty in latter elephantids (Maglio, 1973; Todd and Roth, 1996) was complemented by highly developed cementum infilling between the enamel ridges. Enamel in black, cementum in heavy stipple and dentine in light stipple. From Benton (2015), after Savage and Long (1986). Reproduced with permission.

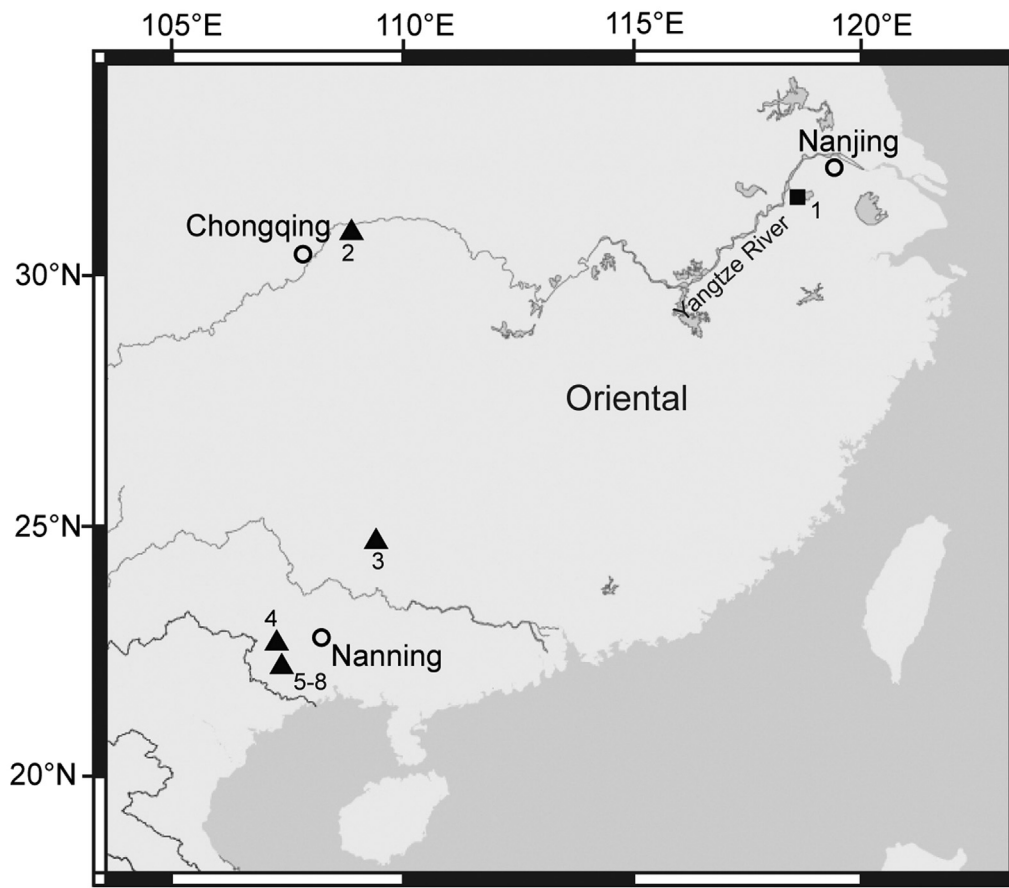


Fig. 2. A map of China highlighting geographical positions of the defined fossil localities concerned in this study: (1) Renzidong Cave; (2) Wushan; (3) Gigantopithecus Cave; (4) Baxian Cave; (5) Sanhe Cave; (6) Zhiren Cave; (7) Yugong Cave; (8) Nongbashan Cave. Also see Table 1.

proboscideans in the Plio-Pleistocene as forests and woodlands gave way to grasslands and steppes, and their subsequent replacement by more hypsodont elephantids (Jin et al., 2009a; Wei et al., 2010; Wang et al., 2012, 2014b) in this particular case. But so far, this hypothesis lacks quantitative testing.

In this paper, we present a first, preliminary analysis of dietary differences among fossil proboscideans using three-dimensional (3D) dental microwear texture analysis (DMTA) (Scott et al., 2005, 2006), applying the technique to *Sinomastodon*, *Stegodon* and *Elephas* from the Pleistocene of South China. We employ DMTA because it offers considerable advantages in terms of robustness, repeatability and comparability of studies over 2D approaches, including low magnification stereomicroscopy (Grine et al., 2002; Galbany et al., 2005; Purnell et al., 2006, 2012; Muhlbachler et al., 2012; DeSantis et al., 2013) and can detect differences in a small sample size (Merceron et al., 2010; Purnell et al., 2012).

2. Materials and methods

2.1. Material sampled

The bulk of materials for this study were collected from the karst caves and fissures in southern China, especially including the recent discoveries from Chongzuo, Guangxi. The fossils encompass all three major successive mammal faunas in South China during the Pleistocene. These sites include Liucheng *Gigantopithecus* Cave, Sanhe Cave, Zhiren Cave, Yugong Cave, Baxian Cave and Nongbashan Cave from Guangxi, as well as Renzidong Cave from Anhui and Wushan, Chongqing Municipality (Fig. 2). All the specimens are housed in the Collection of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences (CAS). Details of the specimens sampled are shown in Table 1.

Table 1
Summary of *Elephas*, *Sinomastodon*, and *Stegodon* specimens subjected to DMTA in this study. Specimen numbers without the “IVPP V” prefix are field numbers, with formalised collection access numbers yet to be assigned.

Species	Site	Age	Specimen number	Sample number	Tooth	Sampling locus	SSFA plot number
<i>Elephas kiangnanensis</i>	Nanning, Guangxi	Middle Pleistocene	IVPP V01945	194501	Lower m2	Posterior loph	1
<i>Elephas kiangnanensis</i>	Nanning, Guangxi	Middle Pleistocene	IVPP V01929	192901	Upper M2	Posterior loph	2
<i>Elephas kiangnanensis</i>	Nanning, Guangxi	Middle Pleistocene	IVPP V01966	196601	Upper M2	Posterior loph	3
<i>Elephas kiangnanensis</i>	Nanning, Guangxi	Middle Pleistocene	IVPP V10940	194001	Upper M2	Posterior loph	4

Table 1 (continued)

Species	Site	Age	Specimen number	Sample number	Tooth	Sampling locus	SSFA plot number
<i>Elephas kiangnanensis</i>	Liuzhou, Guangxi	Middle Pleistocene	IVPP V01961	196101	Upper M2	7th loph	5
<i>Elephas kiangnanensis</i>	Zhiren Cave, Chongzuo, Guangxi	110 ka (Early late Pleistocene)	CLMO704-008	400801	Upper M1/M2	8th loph	6
<i>Elephas maximus</i>	Baxian Cave, Chongzuo, Guangxi	Late Pleistocene	CXZB-E-02	BE0201	Lower m1/m2	8th loph	7
<i>Elephas maximus</i>	Guangxi	Middle Pleistocene	IVPP V01060	106001	M3 (upper)	7th loph anterior, central	8
<i>Elephas maximus</i>	Liuzhou, Guangxi	Late Pleistocene	IVPP V01959	195901	Left m3 (lower)	4th loph posterior	9
<i>Elephas maximus</i>	Bala Cave, Liujiang, Guangxi	Middle Pleistocene	IVPP V01981	198101	m2 (lower)	5th loph posterior, sinistral	10
<i>Elephas maximus</i>	Nongbashan, Chongzuo, Guangxi	30–20 ka (Late Pleistocene)	CSN0811-317	131701	Lower m3	7th and 8th loph	11
<i>Elephas maximus</i>	Baxian Cave, Chongzuo, Guangxi	Late Pleistocene	CXZB-E-01	BE0101	Lower m1/m2	5th loph posterior, central	12
<i>Sinomastodon jiangnanensis</i>	Renzidong, Anhui	2.4–2 Ma (Early early Pleistocene)	IVPP V18822.07	220701	Right m2 (lower)	1st loph posttrite	13
<i>Sinomastodon jiangnanensis</i>	Renzidong, Anhui	2.4–2 Ma (Early early Pleistocene)	IVPP V14011.03	110301 (011301)	Right m3 (lower)	1st loph pretrite	14
<i>Sinomastodon jiangnanensis</i>	Renzidong, Anhui	2.4–2 Ma (Early early Pleistocene)	IVPP V18222.02	220202	Right M2 (upper)	2nd loph posttrite	15
<i>Sinomastodon jiangnanensis</i>	Renzidong, Anhui	2.4–2 Ma (Early early Pleistocene)	IVPP V18822.08	220801	Right m1 (lower)	3rd loph pretrite	16
<i>Sinomastodon yangziensis</i>	Liucheng ("Gigantopithecus Cave")	Early early Pleistocene	IVPP V01723	172302	Right m3 (lower)	2nd loph posttrite	17
<i>Sinomastodon yangziensis</i>	Sanhe Cave, Chongzuo, Guangxi	1.6–1.2 Ma (Middle early Pleistocene)	IVPP V18220.01	200101 (200102)	Right m3 (lower)	1st loph posttrite	18
<i>Sinomastodon yangziensis</i>	Liucheng ("Gigantopithecus Cave")	Early early Pleistocene	IVPP V01723	172301	Right m3 (lower)	4th loph posttrite	19
<i>Sinomastodon yangziensis</i>	Wushan, Sichuan	Early early Pleistocene	IVPP V02399	239901	Right m3 (lower)	2nd loph posttrite	20
<i>Sinomastodon yangziensis</i>	Sanhe Cave, Chongzuo, Guangxi	1.6–1.2 Ma (Middle early Pleistocene)	IVPP V18820.02	200201	Right m3 (lower)	4th loph pretrite	21
<i>Stegodon huananensis</i>	Liucheng ("Gigantopithecus Cave")	Early early Pleistocene	IVPP V01752	175201	Upper M3	8th/9th/loph	22
<i>Stegodon huananensis</i>	Sanhe Cave, Chongzuo, Guangxi	1.2 Ma (Middle early Pleistocene)	CSD0704106	410601	Left m3 (lower)	7th loph	23
<i>Stegodon orientalis</i>	Liujiang, Guangxi	Late Pleistocene	V01767	176701	Upper M3	Fragmentary specimen, cannot determine locus	24
<i>Stegodon orientalis</i>	Liujiang, Guangxi	Late Pleistocene	V01777	177701	Left m3 (lower)	3rd loph central	25
<i>Stegodon orientalis</i>	Liujiang, Guangxi	Late Pleistocene	V01825	182501	Upper M2	Fragmentary specimen, cannot determine locus	26
<i>Stegodon sp. nov.</i>	Gongjishan	200 ka (Late middle Pleistocene)	CLBBG2012-S1	12S101		2nd loph	27

2.1.1. Liucheng *Gigantopithecus* Cave

Liucheng *Gigantopithecus* Cave (= "Gigantopithecus Cave", Liucheng Juyuan Cave) is located on a vertical cliff 90 m above present ground level, characterised by two entrances (smaller upper entrance and the larger lower entrance) and three branches containing richly fossiliferous deposits, most likely of different Pleistocene stages (Pei, 1965; Jin, personal communication). Pei (1957) initially described the cave deposit bearing a mandible of *Gigantopithecus blacki* and other lower Pleistocene fossils as "yellowish red clay", sandwiched between a "bottom layer of violet sand and clay" and "hard breccia" on top. The entire cave deposit section intrudes into a limestone karst landscape. Jin et al. (2008) questioned the provisional amino acid date of 1.03 ± 0.25 Ma for this Cave, due to its apparent inconsistency from the archaic nature of the earlier faunal assemblage recovered from the Cave; but this age may be true for the younger deposits (Jin Changzu, personal communication), particularly given its greater proximity to an ESR/U-series age of 1.21–0.94 Ma for the *Gigantopithecus* Cave (Rink et al., 2008). Proboscidean materials from the *Gigantopithecus* Cave include molars of *Stegodon huananensis* (initially assigned under *St. preorientalis*, see Chen, 2011 for discussion) and *Sinomastodon yangziensis* (Wang et al., 2014b).

2.1.2. Sanhe Cave

Sanhe Cave is the largest tubular limestone karst cave within Chongzuo Ecological Park. The fossiliferous section includes an upper layer of calcareous sands with breccia, a middle layer of sandy silt and a much thicker lower layer of silty sand; these are located between a thick layer of argillaceous silt below and a much thinner calcareous stratum above (Jin et al., 2009b). Palaeomagnetic dating places the Sanhe section at 1.2 Ma (Sun et al., 2014), implying a middle Pleistocene affinity supported by biostratigraphy. However, more recent radiometric dating suggests a considerably younger age of 900–600 Ka (Shao et al., 2015). Several key megafaunal elements which resemble the classic *Gigantopithecus* Cave assemblage have been found, e.g. *Si. yangziensis*, *St. huananensis* and *G. blacki* (Jin et al., 2009b, 2014; Wang et al., 2014b), along side a more progressive chronospecies of giant panda (*A. wulingshanensis*) than specimens from older deposits (Jin et al., 2007, 2009b, 2014).

2.1.3. Zhiren Cave

Zhiren Cave (= "Homo sapiens Cave"; Zhirendong Cave) is located on the foothills of Mulan Mountain, 179 m above current ground level. A solid yellowish brown sandy clay cemented by

calcite with a few limestone breccia horizons, interbedded with interrupted calcitic beds marks the fossiliferous unit where an early modern human mandible was recovered alongside molars of *Elephas* (Jin et al., 2009a). ^{230}Th – ^{234}U series dating of associated depositional units yielded an upper Pleistocene age at 111–100 Ka, corroborated biostratigraphically by the presence of a *Homo* mandible with modern features (Liu et al., 2010) and two species of *Elephas*: the extant Asian elephant, *E. maximus* and the much more illusive fossil species, *E. kiangnanensis*. Genera such as *Megatapirus* and *Megalovis* are also present.

2.1.4. Yugong Cave

The mammalian fauna associated with a *Homo* tooth from Yugong Cave in Gongjishan Mountain recently discovered in Chongzuo area. The site is dated to be early or late middle Pleistocene based on biostratigraphy (Dong et al., 2014). In this fauna, *Elephas* and *Homo* are present, along with *Sus peii* (Dong et al., 2014) and a plesiomorphic type of *Stegodon*, which is possibly a new species (unpublished data), and will be referred to as *Stegodon* sp. nov. hereafter. A full description of this cave site and fauna will be addressed elsewhere.

2.1.5. Baxian Cave and Nongbashan Cave

Both Baxian Cave and Nongbashan Cave are from Chongzuo, *E. maximus* material has been recovered in both Caves. Both sites are biostratigraphically dated to the upper Pleistocene based on faunal assemblages (Takai et al., 2014; unpublished materials). At Nongbashan, the biostratigraphic date is corroborated by successful extraction of ancient DNA from *Sus scrofa* remains recovered at the site (Hou et al., 2014). Further description of both localities will be addressed elsewhere.

2.1.6. Other Guangxi Cave

During the IVPP Guangxi expeditions of the 1950s, hundreds of fossils were purchased from local pharmaceutical firms (Pei, 1987), which include an abundance of *Stegodon* and *Elephas* materials. Mammalian fossil fragments have been established ingredients within traditional Chinese medicine, as addressed in *Ben Cao Gangmu* (= *Compendium of Materia Medica*) by Li Shizhen, the historically renowned traditional Chinese physician of the Ming Dynasty. Many of the pharmaceutical purchases lack accurate documentation of provenance. Therefore, their relative age can only be inferred based on established Pleistocene biostratigraphic relations. This unfortunately compromises the scientific value of the collection (also see Zeitoun et al., 2016).

2.1.7. Renzidong Cave

Renzidong Cave (= Renzi Cave) is located in Fanchang County, Anhui Province. It is situated 142 m above current ground level on the foothills of Laili Mountain on Triassic limestone bedrock (Yuan et al., 2009). In 1998, excavations began when lower Pleistocene mammal fossils were found in association with stone tools (Jin et al., 1999, 2000; Zhang et al., 2000). The *Si. jiangnanensis*-bearing deposit (previously identified as *Si. intermedius* and *Si. yangziensis*, in Jin et al. (2000) and Wei et al. (2009), respectively) is a breccia layer of red-brownish sandy clay matrix with poorly sorted limestone clasts, situated between an upper layer of limestone nodules agglutinated by a loose, brownish silt matrix (very few long bone fragments recovered) and a lower layer of red brownish silt with a very few well-sorted limestone clasts (fossils include the scimitar-toothed felid *Homotherium* and *Tapirus* among others, associated with a few stone tools) (Jin et al., 2000). 20% of the fossil species recovered from Renzidong represent Pliocene relict taxa: this biostratigraphic signal, and the absence of any microtine rodent remains, suggest that the fossiliferous deposits

should be older than 2 Ma (Jin et al., 2009c). This basal Pleistocene affinity is supported by provisional palaeomagnetic data (Wang et al., 2012). However, a systematic discussion over the absolute age of the Renzidong Cave materials awaits further address elsewhere. The current knowledge supports the Renzidong materials as the oldest Pleistocene *Sinomastodon* material, and *Si. jiangnanensis* is interpreted as ancestral to *Si. yangziensis* (Wang et al., 2012, 2014b).

2.1.8. Wushan

Chow (1959) reported the left upper M3 of a gomphothere from the karst fissure deposit of Wushan, Chongqing Municipality. On the basis of this tooth, he erected a new species, *Trilophodon yangziensis*. Tobien et al. (1986) then assigned this taxon and other similar materials across China to a new genus, *Sinomastodon*, as *Si. intermedius*. Later, Huang and Fang (1991) re-established Chow's (1959) "*T. yangziensis*" under *Sinomastodon*, using the original Wushan M3 as the holotype. This assignment is supported by Chen (1999) and Wang et al. (2014b). A robust absolute age for the Wushan holotype remains uncertain. However, the site of its original discovery lies in very close proximity to the fossiliferous Pleistocene deposits of the Longgupo Site (also within the Wushan region) where *Si. yangziensis* has also been recovered (Huang and Fang, 1991). Corroboration of palaeomagnetic, amino acid and electron resonance dating for the Longgupo fauna suggests an age between 2.58 and 1.95 Ma (Jin et al., 2008).

2.2. Data acquisition

To control for potential dietary difference across life stages, only specimens representing the second and third set of permanent molars from the above localities were sampled, with the exception of *Sinomastodon* (*Si. jiangnanensis*) due to extremely limited availability of materials (Wang et al., 2012). Specimens with extremely worn or with relatively unworn facets were rejected, as were those with apparent post-mortem damage. Reasonably complete teeth were chosen where possible in order to standardise the precise sampling loci over very large specimens. However, some fragmentary specimens with well-preserved wear facets were included to increase sample size (see Table 1). Sampling was optimised on the quality of preservation of worn tooth surfaces, and due to the constraints of time and material in this study we were unable to test the degree to which microwear textures vary over the surface of a proboscidean tooth, between different facets for example. All teeth sampled were isolated, rather than being from associated teeth within jaws. The possibility that two teeth are from the same individual is remote, but cannot be entirely excluded.

Due to the constraints of tooth size and location, analysis was based on replica surfaces, as is typical for DMTA, with moulding and casting following standard procedures. The occlusal surface of each specimen was cleaned using acetone-soaked cotton swabs. Moulds were made using President Jet Regular Body polyvinylsiloxane (Coltène/Whaledent Ltd., Burgess Hill, West Sussex, UK), recently demonstrated to produce replica surfaces that for almost all textural parameters, are statistically indistinguishable from original tooth surfaces (Goodall et al., 2015). An initial mould from each tooth was used to provide additional surface cleaning, and only second moulds were used for analysis. Epoxy casts were produced from each mould using EpoTek 320LV (Epoxy Technologies Corp., Billerica, MA, USA), mixed according to the manufacturer's instructions. In many studies of tooth microwear, transparent epoxy casting material is used, commonly EpoTek 301, but in order to optimise data acquisition using focus variation microscopy we used the black pigmented EpoTek 320LV, which in other respects has

similar properties to EpoTek 301. Epoxy surfaces were coated with gold (Emitech K500X sputter coater; 3 min) to optimise data acquisition and to standardise the optical properties of the surfaces.

Surface data capture followed standard laboratory protocols (Purnell et al., 2012, 2013; Goodall et al., 2015; Purnell and Darras, 2015), using an Alicona Infinite Focus microscope G4b (IFM; software v. 2.1.2, Alicona GmbH, Graz, Austria), equipped with a $\times 100$ objective to provide a field of view of $146 \times 100 \mu\text{m}$. Lateral resolution and vertical resolution were set to 440 nm and 20 nm respectively, as previous studies have extracted dietarily informative texture data from the same or similar-sized sample areas (Merceron et al., 2010; Purnell et al., 2012, 2013; Gill et al., 2014; Purnell and Darras, 2015). Point clouds were edited manually to remove measurements errors (e.g. single point data spikes) and to delete dirt and dust particles from the surface. Surfaces with evidence of post-mortem damage or with excessive adherent material were not subjected to further analysis.

Point clouds were exported as .sur files and imported into SurfStand (software version 5.0 Centre for Precision Technologies, University of Huddersfield, West Yorkshire, UK). Missing data were automatically restored during import. Surfaces were automatically levelled by subtraction of least squares plane.

2.3. SSFA analysis

Sur files were processed using Surftract and ToothFrax (www.surftract.com) following standard protocols (Scott et al., 2006). For length-scale calculations settings were: Min scale = 4.2, Max scale = 4.6, Intervals = 3; Run vector normalization checked and scale set to 4.4 (one order of magnitude higher than the sampling interval of $0.44 \mu\text{m}$ on the IFM). For area-scale calculations settings were: Min scale = 0.02, Max scale = 7200. SSFA generates five parameter categories: heterogeneity of area-scale fractal complexity (heterogeneity or Hasfc hereafter), area-scale fractal complexity (complexity or Asfc hereafter), scale of maximum complexity (Smc hereafter), exact proportion of length scale anisotropy of relief (anisotropy or EpLsar hereafter), and textural fill volume (Tfv). For all but one parameter we were unable to reject the null hypothesis that the data are drawn from a normal distribution (Shapiro Wilks; $P > 0.05$), so the analysis is based on untransformed data except for Smc (\log_{10} transformed). Analysis of variance (ANOVA) was performed to test for differences among fossil proboscidean taxa, with pairwise differences between taxa tested with Tukey's HSD and t-tests. Pairwise t-tests are likely to slightly inflate the probability of type 1 errors, but the more conservative Tukey HSD sometimes fails to detect which taxa differ where ANOVA yields a significant result. Where homogeneity of variance tests (Bartlett and Levene tests) revealed evidence of unequal variances, Welch ANOVA was used. Bivariate analysis of Asfc and EpLsar was used to make preliminary dietary inferences. This approach makes the explicit assumption that the relationship between diet and textural complexity and anisotropy that holds true across a broad taxonomic and size range of herbivorous mammals, both ungulates and macropods (Ungar et al., 2007; Prideaux et al., 2009; Scott, 2012; DeSantis et al., 2013; Merceron et al., 2014, 2016; Calandra and Merceron, 2016; DeSantis, 2016), and can therefore also be extended to proboscideans.

3. Results and discussion

3.1. Results

Although sample sizes are relatively small, this is taken into account when interpreting results; small sample sizes have

produced significant results in other DMTA studies (Purnell et al., 2012), and it is likely that where our tests indicate that we can reject the null hypothesis (particularly for EpLsar) the impact of small sample size, if there is one, will be to inflate the magnitude of the effect, not necessarily increase the likelihood that we have incorrectly rejected the null hypothesis (see Button et al., 2013, for a recent discussion of statistical power and sample size). ANOVA reveals three parameters for which the null hypothesis, that they do not differ between genera, can be rejected: EpLsar ($F = 5.8536$; $P = 0.012$, Welch), Hasfc 4×4 ($F = 4.4043$; $P = 0.0307$) and Hasfc 5×5 ($F = 3.545$; $P = 0.0448$). Pairwise testing indicates that *Elephas* differs from *Sinomastodon* and *Stegodon* in EpLsar (Tukey HSD and pairwise t-test), and Hasfc 4×4 (pairwise t-test). For Hasfc 5×5 , *Elephas* differs from *Stegodon* (pairwise t-test). Pairwise t-tests for a number of other Hasfc parameters yielded significant results, but in the absence of other significant test results we do not consider them further here.

Ecological interpretations of SSFA results are based on bivariate plots of complexity against anisotropy (EpLsar against Asfc; Fig. 3 and Supplementary Fig. 1). In herbivores, these plots can discriminate between taxa on an ecological spectrum ranging from obligate grazers, through generalists, to obligate browsers; anisotropy values increase and complexity decreases with increasing grass consumption in ungulates (Ungar et al., 2007; Schulz et al., 2010; Scott, 2012) and macropods (Prideaux et al., 2009); anisotropy decreases and complexity increases in both value and range with reduced toughness and increased brittleness of food (Scott, 2012; Calandra and Merceron, 2016; DeSantis, 2016). *Sinomastodon* and particularly *Stegodon*, exhibit low anisotropy values that are consistent with the hypothesis that they were primarily browsing

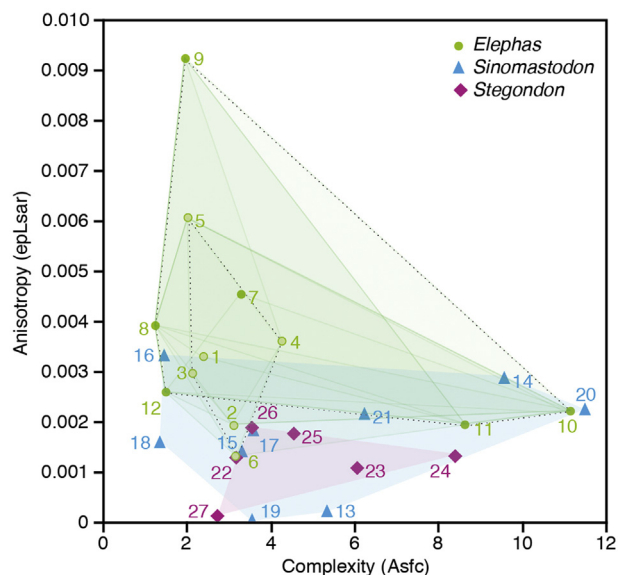


Fig. 3. Bivariate plot of anisotropy and complexity for *Elephas*, *Sinomastodon*, and *Stegodon*, with convex hulls (convex hull for *Elephas* reflects multiple random resamplings of data to $n = 6$; darker green shading indicates overlap of more than 6 hulls). Each data point represents a single sample and tooth; green = *Elephas* (*E. kiangnanensis* with paler centres), purple = *Stegodon*, blue = *Sinomastodon*. Absolute values for complexity cannot be compared with absolute values in published analysis due to differences in the field of view analysed and sampling resolution of data from the IFM instrument (which differ from those of Sensofar instruments upon which most previous analyses in the literature are based). However, preliminary results from ongoing analysis (by R. G. H. and M. A. P.) indicate a strongly correlated linear relationship between complexity values derived using Sensofar and IFM instruments, so the complexity-anisotropy relationship still holds. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

animals (Fig. 3); previous work (Scott, 2012; in particular) indicates that browsers exhibit anisotropy values below 0.004 and this is true of all the *Sinomastodon* and *Stegodon* samples (Fig. 3; Supplementary Fig. 1). For *Elephas*, on the other hand, the broad range of values for both anisotropy and complexity indicate that it was not a dietary specialist. Comparison with Scott (2012; Supplementary Fig. 1) suggest it was more likely a variable feeder or generalist, with a more mixed diet, potentially feeding through both grazing and browsing. Considerable caution is required in interpreting these results, however, because the greater range of values for *Elephas* could in part reflect the larger number of samples for this taxon. In order to address this potential issue, the data for *Elephas* (and *Sinomastodon*) were randomly resampled to yield the same number of samples as *Stegodon* ($n = 6$; see Supplementary Fig. 2); the convex hulls for *Elephas* in Fig. 3 reflect this, with darker green shading reflecting overlap of convex hulls for multiple resampled datasets). In the majority of random subsamplings (6 of 10), results were similar to those obtained from the full dataset, with significant differences in anisotropy between taxa, and pairwise testing (Tukey HSD) in most cases finding differences between *Elephas* and both *Sinomastodon* and *Stegodon*. Pairwise t-tests found significant differences in anisotropy between *Elephas* and one or both of the other taxa in all resampled datasets. Interestingly, resampling in another way, by dividing *Elephas* data into separate species ($n = 6$ for each) also results in significant differences between taxa ($F_{Welch} = 3.69$, $P = 0.046$), with pairwise differences between *E. maximus* and *Stegodon* (Tukey HSD) or between *E. maximus* and both *Stegodon* and *Sinomastodon*. Further analysis is required but this result, and the distribution of the two *Elephas* species in the anisotropy-complexity plot (Fig. 3; Supplementary Fig. 2), is suggestive of dietary differences within the genus. This is not unexpected, and although very preliminary our analysis suggests that with larger sample sizes (and reduction in non-dietary noise in the data – see below) *E. kiangnanensis* might prove to show more tendencies towards grazing than the more generalist *E. maximus*.

There are further confounding factors with the potential to introduce non-dietary noise into the dietary signal of microwear texture in proboscideans, and these require investigation in future analyses. For example, with their large size and morphological complexity, the degree to which microwear textures vary over the surface of a proboscidean tooth is untested as far as DMTA is concerned, although low-magnification investigations of stereomicroscopy have found evidence for variations which might affect dietary interpretations (Palombo et al., 2005; Todd et al., 2007). This has implications for sampling strategies for collecting texture data, which typically analyses small fields of view at high resolution ($146 \times 110 \mu\text{m}$ for IFM at $\times 100$). The fact that different parts of the worn tooth surface are likely to be involved in different phases of the power stroke during food processing is also something that needs to be taken into account, as microwear from different phases of jaw movement is known to differ in proboscideans and other mammals, and to differ in its potential to discriminate among taxa with different diets (Todd et al., 2007; Calandra et al., 2008; Krueger et al., 2008). In particular, the way in which microwear signals are influenced by differences in masticatory mechanism between bunolophodont gomphotheres to lophodont stegodonts and elephantids (Maglio, 1972, 1973; von Koenigswald, 2014) needs to be clarified. More specifically, future analyses of the taxa investigated here should be conducted at species or population level (requiring more extensive sampling): although our analysis finds significant differences between genera, more subtle dietary differences between species (or populations) could be obscured by the lumping together of samples by genus. Sampling within species will require future research to establish much stronger chronological control for

the biostratigraphy of the Chinese Pleistocene (Turvey et al., 2013; Zeitoun et al., 2016).

Despite the caveats articulated above, our results indicate that the differences in microwear texture between *Elephas*, *Sinomastodon* and *Stegodon* cannot be explained as merely an artefact of the limitations of our analysis; they are thus likely to reflect dietary differences between the taxa. We predict that further texture analysis of tooth microwear based on larger numbers of samples, and taking other sampling issues into account, is likely to find more evidence for dietary differences between proboscidean taxa.

3.2. Proboscidean feeding ecology

Our results are consistent with the traditional linkage of evolutionary trends towards hypsodonty in proboscideans (among other large herbivorous mammals) with a transition from browsing to a more abrasive diet such as grazing (Janis and Fortelius, 1988; Shoshani, 1998; Damuth and Janis, 2011). The tooth microwear texture data suggest the brachyodont *Sinomastodon* and *Stegodon* were primarily browsers, whereas the tooth wear textures of the much more hypsodont *Elephas* species suggest more mixed feeding, potentially including some grazing. These interpretations are consistent with isotopic analysis suggesting that *Stegodon* from the Pleistocene of South China were C_3 browsers (Wang et al., 2007; Bocherens et al., 2017), and evidence from both isotopes and low-magnification stereomicroscopy that the extant *E. maximus* is a broad generalist (Sukumar, 2003; Rivals et al., 2012).

Given their apparently similar feeding preferences, there is some indication that *Stegodon* might have outcompeted *Sinomastodon* to become the dominant browsing herbivore in the middle–late Pleistocene of South China. From the late Miocene onwards, successive species of *Sinomastodon* and *Stegodon* showed highly coincident spatio-temporal distribution patterns over large areas of East Asia (Chen, 1999, 2011; Wang et al., 2012; Wang et al., 2015b). The interpretation of both *Sinomastodon* and *Stegodon* as browsers supports the shared preference for woodland habitat as a driver of their prolonged historical sympatry and their southward distribution shift in the Pleistocene (Wang et al., 2012, 2015b). But importantly, *Sinomastodon* remained bunolophodont throughout its evolutionary history (Wang et al., 2015b), whereas stegodont dentition evolved from late Miocene forms in which the plesiomorphic bunolophodont condition is clearly identifiable, to derived Plio-Pleistocene species with a high degree of lophodonty (Chow and Zhang, 1974; Saegusa, 1996; Saegusa et al., 2005; Chen, 2011). Lophodonty allows more efficient vegetation processing through shearing-dominated mastication, as opposed to crushing-shearing mastication in the bunolophodont gomphotheres (Maglio, 1972; Saegusa, 1996; Janis, 2008; von Koenigswald, 2014). Palynological evidence indicates substantial vegetational changes across China ca. 1.6–0.8 Ma, suggesting a cooler and dryer climate compared to the early Pleistocene conditions (Tong et al., 1999). Fossils from the Guangxi caves indicate a major faunal turnover during this period: *Sinomastodon* eventually became extinct in the Guangxi region alongside other Neogene relict taxa such as the terminal chalicotheres *Hesperotherium* and the short-faced hyena *Pachycrocuta* (Jin et al., 2014; Wang et al., 2014a; Xu et al., 2016). Other large mammals such as *Ailuropoda*, *Gigantopithecus* and *Tapirus* showed an increase in tooth size, which has been proposed as possibly an adaptation for feeding on tougher vegetation (Jin et al., 2014; Zhang et al., 2015). Recently, fossil materials identified as highly derived *Sinomastodon* have been reported from Thailand (Thasod and Ratanasthien, 2005; Thasod et al., 2011), said to be no earlier than middle Pleistocene in age (Jin Changzhu, personal communication). Alongside were the remains of *Stegodon* (Thasod et al., 2011). Further investigation into the new Thai materials may provide

crucial insight into the nature of ecological interactions between these two genera.

On the other hand, our analysis also suggests that niche partitioning between *Stegodon* and *Elephas* may have helped both survive from middle Pleistocene through to the very latest Pleistocene in South China (Pei, 1987; Saegusa, 2001; Tong and Patou-Mathis, 2003). Previous studies using tooth wear and isotopes indicate that niche partitioning and local environment had a substantial influence on the feeding ecology of fossil proboscideans, most of which adopted a fairly broad dietary niche. Low-magnification stereomicrowear suggests that the *Gomphotherium* from the middle and late Miocene of southern Germany was a mixed-feeder: with this diet it may have avoided competition with the exclusively browsing *Deinotherium* (Calandra et al., 2008, 2010). Isotopic signatures and mesowear (macroscopic tooth wear) suggest that late Neogene African gomphotheres and elephantids were quick to adopt grazing with the C₄ expansion in the East African landscape, despite being markedly more brachyodont than their modern relatives (Cerling et al., 1999, 2015; Lister, 2013; Saarinen et al., 2015). The gomphotheres *Anancus arvernensis* and early mammoths (*Mammuthus rumanus* and *M. meridionalis*; elephantids) were sympatric in several habitats across Western Europe in the early Pleistocene. Interpretations based on bivariate comparison of low-magnification stereomicrowear signals suggest that both were mixed feeders in a habitat of mosaic vegetation; and both showed a preference for browsing in forested habitats (Rivals et al., 2015).

When taking empirical data into account, a more complex picture of the mechanism behind proboscidean turnovers in the Pleistocene of South China emerges, where biotic and environmental factors might have interacted, as opposed to a process dominated by unilateral vegetation from forested to more open areas (Pei, 1987; Jin et al., 2009a, 2014; Wang et al., 2012, 2014b). Whereas Pleistocene spore and pollen assemblages in South China suggest environmental fluctuations (Tong et al., 1999), carbon isotope signatures from fossil tooth enamel strongly indicate the continual presence of C₃ forest-type vegetation throughout the early and middle Pleistocene in South China (Wang et al., 2007; Zhao et al., 2011; Qu et al., 2014; Bocherens et al., 2017; Supplementary materials). This indicates more limited direct impact of environmental fluctuations on the ecosystem. Reconciling this with results of the microwear analysis, one may thus propose interaction between vegetational changes and biotic competition as a possible mechanism for *Sinomastodon*'s extinction in South China and subsequent replacement by *Stegodon*. In contrast, reduced competition through niche partitioning might have played a role in allowing the coexistence of *Stegodon* and *Elephas* from the middle to the end Pleistocene, when a wide array of megafaunal components in South China, including *Stegodon*, became extinct (Tong and Liu, 2004; Turvey et al., 2013). *E. maximus*, alongside several other megafaunal elements that are still extant in other parts of Asia, survived into relatively recent historical times in South China (Turvey et al., 2013, and references therein). A thorough discussion of these extinctions is beyond the scope of this paper, as further studies are much needed to address the implications of feeding ecology and vegetational changes in understanding the demise of the megafauna. Like the end-Pleistocene megafaunal extinctions on other continents, much uncertainty and controversy surrounds the relative roles of environmental and early human pressures in causing the extinctions in East and Southeast Asia (Louys et al., 2007; Turvey et al., 2013; Stuart, 2015; Bartlett et al., 2015). In the absence of extinction chronologies and palaeoenvironmental proxies based on highly robust data, any proposed causal mechanism for the megafaunal extinctions in East and Southeast Asia, beyond tentative

suggestions, remains untenable (Louys et al., 2007; Turvey et al., 2013; Bartlett et al., 2015).

4. Conclusions

Dental Microwear Texture Analysis (DMTA) provides new evidence that the brachyodont proboscideans *Sinomastodon* from the early Pleistocene and *Stegodon* from the early to late Pleistocene were browsers, whereas the hypsodont *Elephas* species from the middle and late Pleistocene was a mixed feeder or more generalist herbivore, possibly engaging in both browsing and grazing. The suggestion that there are dietary differences between *Elephas* species requires further analysis, but *E. maximus* may prove to be more of a generalist than *E. kiangnanensis*. Our analysis also highlights the need for additional work required before DMTA can be used for robust investigation of diet in proboscideans.

The turnover from bunolophodont to lophodont proboscideans through the Pleistocene of South China has implications in terms of a transition from browsing to mixed feeding and grazing, as well as the record of turnovers in faunal assemblages, which supports the occurrence of continual environmental perturbations over this period. However, rather than the traditional view of environmental change characterised by a unilateral transition from forested to more open areas, our results and discussion suggest that biotic factors could also have had an important role to play. The evidence for browsing in both *Sinomastodon* and *Stegodon*, associated in the latter with a more efficient masticatory mechanism for processing vegetation brought about by more derived lophodont molars, may have allowed *Stegodon* to outcompete *Sinomastodon* and become the dominant proboscidean in the Pleistocene of South China. Differences in diet between *Stegodon* and *Elephas* suggest the possibility of niche partitioning as an explanation of *Stegodon*'s coexistence with *Elephas* right up to the end-Pleistocene.

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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.quaint.2016.07.011>.

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