Modern human teeth from Late Pleistocene Luna Cave (Guangxi, China)

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ABSTRACT

We present two previously unreported hominin permanent teeth [one right upper second molar (M2), one left lower second molar (m2)] from Lunadong ("dong" = "cave"), Guangxi Zhuang Autonomous Region, China. The teeth are important because: 1) they were found in situ; 2) at least one (M2) can be confidently assigned to modern Homo sapiens, while the other (m2) is likely modern H. sapiens; and 3) the teeth can be securely dated between 126.9 ± 1.5 ka and 70.2 ± 1.4 ka, based on multiple MC-ICP-MS uranium-series dates of associated flowstones in clear stratigraphic context. The Lunadong modern H. sapiens teeth contribute to growing evidence (e.g., Callao Cave, Huanglongdong, Zhirendong) that modern and/or transitional humans were likely in eastern Asia between the crucial 120–50 ka time span, a period that some researchers have suggested no hominins were present in the region.

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1. Introduction

The origin of modern humans has been one of the most intensely debated topics in paleoanthropology over the past half century. Within the origin of modern humans debate a variety of topics have been deliberated, ranging from the hominin fossil record (e.g., Howells, 1976; Thorne and Wolpoff, 1981; Wolpoff et al., 1984, 2001; Stringer and Andrews, 1988; Lahr, 1996; Trinkaus, 2005; Gunz et al., 2009), to the genetics (e.g., Cann et al., 1987; Stoneking, 1993; Templeton, 1993, 2002, 2005; Relethford and Harpending, 1994, 1995; Stoneking and Krause, 2011), to the archaeology (e.g., McBrearty and Brooks, 2000; Henshilwood and Marean, 2003; Shea, 2003, 2011; Klein, 2008). The two primary models to describe the origin of modern humans are commonly referred to as the Replacement (or Out of Africa) Model and the Multiregional Evolution (or Regional Continuity) Model (for recent reviews published in the past decade see Pearson, 2004; Weaver and Roseman, 2008; Cartmill and Smith, 2009; Conroy and Pontzer, 2012). Many variations of these two models exist, with seeming increasing support for a scenario where modern humans first arose in Africa, but with their dispersal into Eurasia admixture with the indigenous populations taking place at least occasionally (Brauer, 1989; Smith et al., 1989; Pearson, 2004; Wu, 2004; Trinkaus, 2005; Weaver and Roseman, 2008). With the recent genetic evidence of some degree of modern human-Neanderthal admixture (Green et al., 2010), growing endorsement for some degree of interbreeding appears to exist (but see Hodgson et al., 2010).

The hominin fossil record has contributed significantly to the modern human origins question. Three decades ago a comprehensive volume edited by Fred Smith and Frank Spencer (1984) entitled The Origins of Modern Humans: A World Survey of the Fossil Evidence focused on the then state of the Old World hominin paleontological record and its contributions to the modern human origins debate. Follow up edited volumes appeared every few years after that also focused on the hominin fossil record or contributed the archaeological and/or chronometric records to the modern human origins debate. Follow up edited volumes appeared every few years after that also focused on the hominin fossil record or contributed the archaeological and/or chronometric records to the modern human origins debate (e.g., Mellars and Stringer, 1989; Trinkaus, 1989; Akazawa et al., 1992; Aitken et al., 1993; Clark

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The diversity of interpretations of the hominin fossil record in support of one or the other model suggests that there have been variable results from these studies. However, there seems to be growing support that minimally, modern humans and Neanderthals were morphologically different enough to be considered distinct species (e.g., Bailey, 2004; Harvati et al., 2004). The nature of modern humans and other archaic hominins (e.g., Neanderthals and mid-Pleistocene Homo) interactions (e.g., actual replacement or some degree of assimilation) remains a key area of research. Specimens assigned to “mid-Pleistocene Homo” are more or less the same fossils that are normally included in “archaic Homo sapiens” (e.g., Homo antecessor, H. heidelbergensis, H. rhodesiensis, H. soloensis, etc. and excluding H. neanderthalensis and modern H. sapiens), without the nomenclatural baggage associated with using the term “archaic” (for various discussion see Tattersall, 1986; Groves and Lahr, 1994; Rightmire, 1998, 2008; Cartmill and Smith, 2009; Bae, 2010, 2013; Xiao et al., in press).

One of the primary problems in addressing many of the questions raised by evaluations of the hominin fossils, genetics, and archaeological records to either support or refute the Replacement or Multiregional models has been the nature of the eastern Asian record. Bailey and Norton (2005a, 2008) have described the ZKD UC human calotte display little to no association. Another recent metric and morphometric analysis of a new set of hominin teeth from the Huanglongdong site in central China drew the conclusion that these teeth should be considered modern human because they “look gracile and lack the archaic features usually identified on Middle and Late Pleistocene humans” (Liu et al., 2010a: 40). The importance of the Huanglongdong human teeth is that they appear to date between 100 ka and 80 ka (Liu et al., 2010a; Shen et al., 2013), with clear implications for the modern human origins debate. These recent studies focusing on the Chinese record are clearly contributing to filling in empty spaces of what has traditionally been considered a relatively sparse hominin fossil record when compared to better known regions like Africa and Europe (Trinkaus, 2005; Norton and Jin, 2009; Bae, 2010; Norton and Braun, 2010; Liu et al., 2013).

Nevertheless, two long standing problems with the eastern Asian record is the paucity of evidence dating between the Middle-Late Pleistocene transition and the upper limit of radiocarbon dating (i.e., between 120 and 50 ka) and the association of the hominin fossils with various relative and numerical dates (Norton and Jin, 2009; Bae, 2010; Shen et al., 2013). Jin and Su (2000) suggested that there is a complete absence of any hominins from China (and presumably the rest of eastern Asia as well) between 100 and 50 ka. Jin and Su (2000) subsequently used that evidence to support their argument that modern humans arrived in southern China after ~50 ka and spread north soon afterwards. However, as reviewed recently by Norton and Jin (2009) and Shen et al. (2013), there are a growing number of hominin fossils being reported in China that likely date to this important time period (e.g., Xuchang, Laishui, and see above, Huanglongdong). Furthermore, Mijares et al. (2010) recently reported a modern human 3rd metatarsal from Callao Cave, Luzon, Philippines, that has a direct U-series date of ~66.1 ka. Thus, there seems to be growing evidence that modern humans or at least mid-Pleistocene Homo were present in eastern Asia prior to ~50 ka.

Another problem that has weakened the potential importance of the eastern Asian hominin fossil record is that questions often exist about the relationship between the hominin fossils and the samples used to derive the chronometric dates (Shen et al., 2002). Nevertheless, a growing number of studies have focused on analyses of hominin fossils from Europe (e.g., Bailey, 2002, 2004; Bailey and Lynch, 2005; Martínn-Torres et al., 2006, 2012; Gómez-Robles et al., 2007, 2008, 2011, 2012), Africa (e.g., Wood and Engelman, 1988; Irish, 1988; Irish and Guatelli-Steinberg, 2003); and Western and Central Asia (e.g., Bailey et al., 2008; Martín-Torres et al., 2008; Hershkovitz et al., 2011). Fortunately, there are a growing number of studies that focus on or include data from eastern Asia (e.g., Brace et al., 1984; Turner, 1987, 1990; Liu et al., 2000, 2010a, b; Xing et al., 2009; Bailey and Liu, 2010; Xiao et al., in press)

Recent morphometric analyses of Chinese hominin fossil teeth are contributing to a better understanding of the variability of the late Middle and Late Pleistocene hominin fossil record of the region. For instance, Bailey and Liu (2010) analyzed a set of maxillary teeth from the Middle Pleistocene Chaoxian site in eastern China to determine if the hominin fossils could be allocated to H. neanderthalensis or whether they should be retained in the more inclusive mid-Pleistocene Homo group. Bailey and Liu (2010: 21) concluded that “no derived morphological characters link the teeth of Chaoxian … specifically with H. neanderthalensis.” Xiao et al. (in press) recently analyzed a set of previously unreported hominin teeth (and a partial mandible) from the Middle-Late Pleistocene Maba site in southern China, a site that is best known for the presence of a partial hominin calotte that at times has been assigned to mid-Pleistocene Homo, H. neanderthalensis, and even H. mabaensis (for review see Wu and Poirier, 1995; Bae, 2010). Xiao et al. (in press) concluded that the new set of fossils should be assigned to modern H. sapiens and were likely deposited at the site more recently. In other words, the new fossils and the Maba mid-Pleistocene Homo calotte display little to no association.
Besides the famous Zhoukoudian Upper Cave humans that have debated ages ranging between ~34 and 10 ka (Kamminga and Wright, 1988; Kamminga, 1992; Wu and Poirier, 1995; Norton and Gao, 2008; Norton and Jin, 2009), another well-known controversially-dated modern human fossil from China is the Liujiang skull (Wu and Poirier, 1995). Although the Liujiang human skull is often considered to date to around 20 ka and possibly 67 ka, Shen et al. (2002) conducted a U-series analyses on travertine from the cave and concluded the age of the Liujiang skull should date to between 139 and 111 ka and possibly older than 153 ka. Shen et al. (2002) concluded that the Liujiang skull could be as old as some of the oldest modern H. sapiens in Africa (e.g., Herto, Klasies River Mouth, Border Cave, but not Omo Kibish). Nevertheless, questions do exist regarding the exact provenance of the Liujiang fossil (Shen et al., 2002; Norton and Jin, 2009). Here, we hope to partially remedy these two long standing problems of the eastern Asian paleoanthropological record by presenting a set of newly excavated and previously unreported human teeth associated with a solid chronology from Lunadong, a Late Pleistocene cave site in Guangxi Zhuang Autonomous Region, southern China.

2. Background

Lunadong (“dong” = cave) (23°36’48”N, 106°58’11”E) is located in the karst mountains of the southeastern part of the Bubing basin in Guangxi Zhuang Autonomous Region, southern China (Figs. 1–2). The cave is about 30 m above the valley floor and 162 m above sea level. Lunadong was initially found by our paleoanthropological research team in March 2003. This cave is situated in Permian limestone, with its southern part sloping into the karst mountain area and the northern area facing the flat Bubing valley. The cave entrance, facing east, is 1.4 m in height and 5 m in width. The interior of the cave is flat, 3–4 m in depth, ~10 m in breadth (but possibly extending back further), and 1–4 m in height. The deposits are well preserved, about 0.5–2 m in thickness, and comprised primarily of light brown clay containing a few limestone breccia (Figs. 2–3).

The Natural History Museum of Guangxi Zhuang Autonomous Region conducted the first excavation in July 2004 and a second excavation in June 2008. Three 2 x 2 m squares were laid out in the western area of the cave and excavated down horizontally at 20 cm intervals. Squares A and B were excavated in 2004 and Square C was excavated in 2008. As a result of the excavations, more than one hundred mammalian teeth and bones, two hominin teeth, and one dozen stone artifacts were recovered. Most of the mammalian teeth and bones, including the two hominin teeth, were unearthed from Square B (Figs. 2–3).

2.1. Stratigraphy

The Lunadong deposits are mainly distributed in the western part of the cave, with an area of about 30 m² considered to be undisturbed. The sediment becomes thicker from east to west, varying in thickness from 10 to 130 cm. Five stratigraphic levels were identified (from upper to lower) (Fig. 3):
(1) Brown loose clay 0–5 cm;
(2) Yellow-brown sandy clay with occasional breccia, containing stone artifacts 5–30 cm;
(3) Light brown sandy clay with breccia, yielding abundant mammalian fossils and the hominin teeth 30–100 cm;
(4) Brown sandy clay, with occasional breccia and some mammalian fossils 100–140 cm;
(5) Large breccia filled by sandy clay 140–160 cm.

2.2. Dating

The mammalian faunas identified at Lunadong include Hylobates sp., Macaca sp., Stegodon sp., Cervus sp., Ailuropoda melanoleuca baconi, Muntiacus sp., Sus scrofa, Sus sp., Hystrix sp., and Bovidae. Because it is generally understood that Stegodon went extinct in eastern Asia during the early Late Pleistocene (Huang, 1979), the relative age of the deposits should be early Late Pleistocene.

With the intent to better constrain the chronology of the stratigraphic sequence, we collected stratigraphically significant flowstone and stalagmite samples from the eastern wall of Excavation Square B. A total of five speleothem samples (LN12-01-01, LN12-01-04, LN12-02, LN12-03, LN12-07), each consisting of carefully hand-picked small fragments, were submitted to the University of Queensland for U/Th dating using a Nu Plasma multi-collector Inductively Coupled Plasma Mass Spectrometer (MC-ICP-MS) following analytical procedures described in Zhou et al. (2011). The stratigraphic locations of these samples are presented in Fig. 3. Among these five samples, LN12-01-01, LN12-01-04 and LN12-02 are composed of impure calcite grains stained with clays. Their measurements show they contain elevated levels of detrital 232Th (with Th/U ratios ranging from 1.4 to 3.3, similar to silicate sediments), reflecting significant silicate sediment contamination, rendering them unsuitable for dating. Samples LN12-03 and LN12-07 are much purer, with measured Th/U ratios of 0.21 and 0.17, and corresponding 230Th/232Th activity ratios of 11.8 and 10.5. Ages derived from these two samples are reliable. As LN12-02 has a measured 230Th/232Th activity ratio of 0.62, the initial 230Th/232Th ratio in Lunadong cave must be < 0.62, otherwise LN12-02 will yield a negative corrected 230Th age (i.e. future age), which is unrealistic. Using this value for detrital 230Th correction, LN12-03 and LN12-07 give corrected 230Th ages of 126.9 ± 1.5 ka and 70.2 ± 1.4 ka, which are only slightly younger than their corresponding uncorrected 230Th ages of 130.6 ± 0.7 ka and 73.2 ± 0.4 ka; the uncorrected 230Th ages being considered as the maximum ages of the samples. Because the two hominin teeth were found in the horizon slightly above LN12-03 and slightly below LN12-07, the age of the teeth can be confidently placed within the age range between 126.9 ± 1.5 ka and 70.2 ± 1.4 ka. The biostratigraphy and numerical dates corroborate each other nicely; the Lunadong hominin teeth date to between the end of the terminal Middle Pleistocene and the middle Late Pleistocene (between marine isotope stage (“MIS”) 6-5 transition and MIS 4).

3. Materials and methods

3.1. Materials (Lunadong)

The Lunadong (“LND”) hominin fossil assemblage is comprised of one left upper second molar (“M2”) and one right lower second molar (“m2”). Both specimens are permanent teeth. These are described in more detail as follows with general mesial-distal and buccal-lingual dimensions presented in Table 2. We relied on Turner et al. (1991), Scott and Turner (1997), and White and Folkens (2000) for the morphological descriptions of the hominin teeth. Following standard paleontological practice (see author guide for the Journal of Vertebrate Paleontology), upper case “M” represents maxillary teeth, while lower case “m” represents mandibular teeth. We estimated the cusp sizes. We focused our analysis on the linear metric (size variation) and geometric morphometric (shape variation) aspects of the LND teeth. Although additional analyses (e.g., micro-CT study) could strengthen the evaluation of the LND hominin teeth, they are currently beyond the scope of the current investigation.

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**Table 1**
MC-ICP-MS U-series isotopic data for flowstone and stalagmite samples from Lunadong.

<table>
<thead>
<tr>
<th>Sample name</th>
<th>U (ppm)</th>
<th>(^{230}\text{Th} (\text{ppb})</th>
<th>\left(\frac{^{230}\text{Th}}{^{232}\text{Th}}\right)</th>
<th>\left(\frac{^{234}\text{U}}{^{238}\text{U}}\right)</th>
<th>\text{Uncorrected} \left(\frac{^{230}\text{Th}}{^{232}\text{Th}}\right) \text{ age (ka)}</th>
<th>\text{Corrected age-I (ka)}</th>
<th>\text{Corr. Initial} \left(\frac{^{234}\text{U}}{^{238}\text{U}}\right)</th>
<th>\text{Corrected age-II (ka)}</th>
</tr>
</thead>
<tbody>
<tr>
<td>LN12-01-01</td>
<td>0.09197 ± 0.00006</td>
<td>207.4 ± 0.7</td>
<td>0.669 ± 0.006</td>
<td>0.4969 ± 0.0043</td>
<td>1.1841 ± 0.0035</td>
<td>58.4 ± 0.7</td>
<td>8 ± 32</td>
<td>Negative ge NA</td>
</tr>
<tr>
<td>LN12-01-04</td>
<td>0.10675 ± 0.00004</td>
<td>153.5 ± 0.3</td>
<td>0.809 ± 0.006</td>
<td>0.3834 ± 0.0030</td>
<td>1.1713 ± 0.0015</td>
<td>42.8 ± 0.4</td>
<td>13 ± 17</td>
<td>Negative ge NA</td>
</tr>
<tr>
<td>LN12-02</td>
<td>0.15826 ± 0.00007</td>
<td>522.8 ± 1.9</td>
<td>0.617 ± 0.003</td>
<td>0.6722 ± 0.0022</td>
<td>1.2466 ± 0.0013</td>
<td>81.9 ± 0.4</td>
<td>4 ± 59</td>
<td>Negative ge NA</td>
</tr>
<tr>
<td>LN12-03</td>
<td>0.11957 ± 0.00006</td>
<td>25.51 ± 0.02</td>
<td>11.88 ± 0.03</td>
<td>0.8356 ± 0.0021</td>
<td>1.1694 ± 0.0013</td>
<td>126.9 ± 1.5</td>
<td>125.4 ± 2.0</td>
<td>1.2564 ± 0.0073</td>
</tr>
<tr>
<td>LN12-07</td>
<td>0.11989 ± 0.00004</td>
<td>20.18 ± 0.05</td>
<td>10.50 ± 0.05</td>
<td>0.5825 ± 0.0022</td>
<td>1.1751 ± 0.0010</td>
<td>73.2 ± 0.4</td>
<td>70.2 ± 1.4</td>
<td>69.0 ± 1.8</td>
</tr>
</tbody>
</table>

Note: Ratios in parentheses are activity ratios calculated from the atomic ratios. Errors are at 2σ level for the least significant digits. The ages are calculated using Isoplot 3.0 Program of Ludwig (2003) with decay constants from Cheng et al. (2000). Corrected Age-I and Age-II were calculated assuming initial/detrital \(\frac{^{230}\text{Th}}{^{232}\text{Th}}\) activity ratio = 0.6 ± 50% (slightly lower than measured \(\frac{^{230}\text{Th}}{^{232}\text{Th}}\) activity for LN12-2) and 0.825 ± 50% (the bulk-Earth value, which is the most commonly used), respectively. For Luna Cave samples, Corrected Age-I should be a better estimate, because LN12-01-1, LN12-01-4, LN12-2 cannot have negative ages, as is the case if the bulk-Earth initial/detrital \(\frac{^{230}\text{Th}}{^{232}\text{Th}}\) activity ratio is used for correction. Only LN12-03 and LN12-07 are pure enough to return reliable age estimates. The other three samples are too dirty and severely altered, not suitable for dating. See text for discussion.

**Table 2**
Linear metric data of M2 and m2 teeth (see text for references). Measurements given in mm.

<table>
<thead>
<tr>
<th>Specimen/population</th>
<th>Buccal-lingual (s.d.)</th>
<th>Mesial-distal (s.d.)</th>
<th>Specimen/population</th>
<th>Buccal-lingual (s.d.)</th>
<th>Mesial-distal (s.d.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M2</td>
<td></td>
<td></td>
<td>m2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lunadong (LN0031)</td>
<td>11.83</td>
<td>10.65</td>
<td>Lunadong (LN0030)</td>
<td>11.11</td>
<td>12.05</td>
</tr>
<tr>
<td>A. afarensis (n = 8)</td>
<td>14.64 (0.76)</td>
<td>13.11 (0.70)</td>
<td>A. afarensis (n = 21)</td>
<td>13.39 (1.10)</td>
<td>14.03 (1.28)</td>
</tr>
<tr>
<td>A. africanaus (n = 11)</td>
<td>15.60 (0.76)</td>
<td>13.80 (0.71)</td>
<td>A. africanaus (n = 5)</td>
<td>14.10 (0.87)</td>
<td>15.22 (1.00)</td>
</tr>
<tr>
<td>P. robustus (n = 12)</td>
<td>15.84 (0.97)</td>
<td>14.73 (0.53)</td>
<td>P. robustus (n = 10)</td>
<td>14.90 (0.79)</td>
<td>16.23 (0.85)</td>
</tr>
<tr>
<td>P. bosei (n = 4)</td>
<td>18.38 (1.87)</td>
<td>16.05 (1.03)</td>
<td>P. bosei (n = 10)</td>
<td>16.80 (1.56)</td>
<td>18.51 (1.82)</td>
</tr>
<tr>
<td>Early Homo (n = 6)</td>
<td>14.82 (1.71)</td>
<td>12.77 (1.03)</td>
<td>Early Homo (n = 6)</td>
<td>13.53 (1.07)</td>
<td>15.08 (0.98)</td>
</tr>
<tr>
<td>H. erectus (n = 14)</td>
<td>13.09 (0.95)</td>
<td>11.86 (1.10)</td>
<td>H. erectus (n = 32)</td>
<td>12.55 (0.95)</td>
<td>13.30 (1.01)</td>
</tr>
<tr>
<td>Neanderthal (n = 17)</td>
<td>12.83 (0.85)</td>
<td>10.82 (0.89)</td>
<td>Neanderthal (n = 20)</td>
<td>11.29 (0.82)</td>
<td>12.34 (0.93)</td>
</tr>
<tr>
<td>Middle Paleolithic Modern Human (n = 3)</td>
<td>12.60 (0.40)</td>
<td>10.93 (0.75)</td>
<td>Middle Paleolithic Modern Human (n = 3)</td>
<td>11.53 (0.25)</td>
<td>11.27 (0.67)</td>
</tr>
<tr>
<td>Upper Paleolithic Modern Human (n = 128)</td>
<td>12.30 (0.77)</td>
<td>10.05 (0.79)</td>
<td>Upper Paleolithic Modern Human (n = 155)</td>
<td>10.97 (0.91)</td>
<td>11.13 (0.82)</td>
</tr>
<tr>
<td>Mesolithic Modern Human (n = 206)</td>
<td>11.81 (0.78)</td>
<td>9.62 (0.64)</td>
<td>Mesolithic Modern Human (n = 198)</td>
<td>10.49 (0.59)</td>
<td>10.65 (0.65)</td>
</tr>
<tr>
<td>Neolithic Modern Human (n = 148)</td>
<td>10.92 (0.88)</td>
<td>8.99 (0.61)</td>
<td>Neolithic Modern Human (n = 160)</td>
<td>9.79 (0.60)</td>
<td>10.11 (0.65)</td>
</tr>
</tbody>
</table>

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3.1.1. M2

The upper left second molar (LN0031, Fig. 4) is milky white in color and generally well preserved. The crown is well preserved, most of the neck is present, but the roots are absent. The crown of LN0031 has four well-developed cusps arranged in a rhombic shape, with the occlusal surface slightly worn. The four cusps are protocone > paracone > metacone > hypocone. The protocone and paracone are distinctly larger than the metacone and hypocone. The protocone is connected to the paracone by a gentle valley, separated from the hypocone with a fine lingual groove, and is linked to the metacone by a small ridge. The paracone is markedly convex mesially and buccally and is separated from the metacone by a buccal groove. The paracone extends in the mesial-buccal direction. Given the wear pattern, a chip on the distal-lingual side of the metacone probably occurred premortem (during chewing?) rather than postmortem.

3.1.2. m2

The lower right second molar (LN0030, Fig. 4) is milky white in color and heavily fossilized. However, the crown is well preserved. In occlusal view, the crown outline is square, with a fair degree of wear on the four intact cusps (metaconid, protoconid, entoconid, and hypoconid). The protoconid is the largest cusp. The entoconid and hypoconid are the smallest, but similar in size. A hypoconulid is present.

The lingual surface is rectangular, convex vertically and horizontally, with the lingual groove narrow and terminating in the middle. The mesial side is rectangular, with a fairly pronounced interproximal contact facet present that occupies half of the mesial surface. A transverse elliptical interproximal contact facet is present on the distal surface. The roots are mostly absent, with only the basal portion remaining. Evidence of rodent gnawing marks is present; thus, the roots were likely chewed off.

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Fig. 3. Plan and section map. Locations of speleothem and hominin fossils given (LN04-07; LN12-01; LN12-02; LN12-03; LN0030; LN0031). The unbroken horizontal lines in the bottom profile represent breaks in the stratigraphy.
absent. The buccal and lingual surfaces are slightly vertically convex, while the distal surface is vertical and horizontally convex. The mesial surface is flat due to heavy interproximal wear (a large interproximal contact facet is present at the upper edge of the mesial surface). The buccal and lingual grooves are short and weak because of wear. On the distal surface there is a smaller oval interproximal contact facet. The roots, relatively slender, divide into two branches, mesially and distally. The buccal-lingual dimension of the mesial branch is markedly larger than the same dimension of the distal branch.

3.2. Materials (comparative)

The comparative linear data for the mesial-distal and buccal-lingual measurements include Neolithic, Mesolithic, Upper Paleolithic, and Middle Paleolithic modern humans and Neanderthals. These data are from Voisin et al. (2012), while data from older hominins (e.g., H. erectus, H. habilis, gracile and robust Australopiths) were culled from published literature (Robinson, 1956; Tobias, 1967; Wood, 1991; Wu and Poirier, 1995; Kimbel et al., 2004; Kaifu et al., 2005; Bailey and Liu, 2010; Liu et al., 2010a; Macaluso, 2010, Table 2).

We conducted a two dimensional geometric morphometric (GM) analysis of the tooth occlusal surfaces on a fairly robust collection of hominin right M2s (N = 113) and left m2s (N = 87) (Tables 3a, b). The comparative samples for the GM analyses are from photographs of various hominins (e.g., Paranthropus, Australopithecus afarensis, Au. africanus, H. habilis, H. erectus, mid-Pleistocene Homo, H. neanderthalensis, etc.) contributed primarily by Eric Delson (“ED”) and Erik Trinkaus (“ET”) and their colleagues. In discussions with ED and ET, the images they provided were produced using fairly standard photographing methods in paleo-anthropology (see also Xiao et al., in press). Other hominin fossil teeth derive from publications that include high resolution images of tooth occlusal surfaces (e.g., Walker et al. 2008; Martínón-Torres et al., 2012). When possible, we collapsed various hominin taxa into more inclusive categories in order to increase sample size within that particular group (e.g., Au. afarensis and Au. africanus were grouped together, and H. antecessor, H. heidelbergensis, and archaic Homo sapiens were grouped into the more inclusive category of mid-Pleistocene Homo).

The modern human teeth used in the GM analyses are samples we were able to study directly. The modern human samples include a small skeletal collection from Dushandingong, a Neolithic burial cave site from Guangxi, China and excavated by some of the coauthors. The modern Korean samples are from Chosun Dynasty (1392–1897 A.D.) cemeteries, housed and curated at Hanyang University and Chungbuk University, and studied with the permission of Kidong Bae and Sunjoo Park, the principal curators of those respective collections. In cases (for both hominins and modern humans) where a right M2 or a left m2 was absent, but a left M2 or a right m2 was present, we mirror imaged the latter specimens. In no instance did we knowingly use two maxillary or two mandibular teeth from the same individual.

In general, we only used high resolution tooth images that had four cusps and intact occlusal surface outlines (see also Xiao et al., in press). Following many previous studies (e.g., Martínón-Torres et al., 2006; Gómez-Robles et al., 2007, 2008, 2011; Bailey and Liu, 2010; Xiao et al., in press), we excluded samples for a number of reasons. For instance, if the tooth was too worn or chipped and we could not easily locate the cusps and/or the outer edge of the occlusal surface, the tooth was not included in the subsequent analyses. Deciduous teeth and incomplete teeth were excluded. If the photograph was too grainy or of too low resolution, that particular specimen was also excluded from the study. Because it has been shown that photographs taken at an angle can skew the overall shape of the object (e.g., see Gharaibeh, 2005 for discussion of this effect on the analysis of crania), these specimens were also left out of the analyses. Although we admit that there may be some degree of error with using photographs of hominin teeth taken by others, the comparative database was created without any noticeable errors (see also Xiao et al., in press).

3.3. Methods

We took the linear measurement data using Mitutoyo digital calipers (model no. CD-20C). The mesial-distal and buccal-lingual measurements were taken at their widest points. The linear measurement data were graphed on bivariate scatterplots. In order to evaluate the degree of overlap among the different populations, convex hulls were created. Because of the large comparative samples of modern humans (Neolithic, Mesolithic, Upper Paleolithic), only the outline of the convex hulls are graphed for those respective populations. For the older hominins, each individual datapoint is graphed.

We collected digital images of the teeth occlusal surfaces using a Dino-Lite Digital Microscope [model AM413T Dino-Lite Pro...
(20–230 × magnification) with stand. The methodology follows closely many other recent dental studies (e.g., Bailey, 2002; Martinón-Torres et al., 2006; Gómez-Robles et al., 2007, 2008, 2011, 2012; Bailey et al., 2008; Bailey and Liu, 2010), except that instead of using a digital camera and macroslens, we used the digital microscope. In general, we found it easier to identify the tooth cusps and general outline of the tooth occlusal surface from the images produced by the Dino-Lite (see also Xiao et al., in press). In order to help hold the tooth level and parallel to the Dino-Lite, we used polyvinylsiloxane impression material (Exaflow Putty Type Catalyst and Base).

3.4. Geometric morphometrics

Geometric (landmark based) morphometrics (GM) methodologies is widely used to explore within- and between-taxon variation in paleoanthropology (for recent reviews of applications to anthropological research see: O’Higgins, 2000; Richtsmeier et al., 2002; Slice, 2005, 2007; Perez et al., 2006; Baab et al., 2012). The GM methodology employed here for the analysis of the Lunadong hominin teeth follows closely previous studies (e.g., Martinón-Torres et al., 2006; Perez et al., 2006; Gómez-Robles et al., 2007, 2008, 2011, 2012; Xing et al., 2009; Liu et al., 2010a, 2013; Xiao et al., in Press). Prior to beginning the digitizing process, each tooth was oriented in the same direction with the mesial side toward the top of the computer screen and the buccal side to the right (see Fig. 5 for example). The program MakeFan7 (Sheets, 2001) was used to create the centroid necessary to generate a series of equiangular fans. In order to create the centroid, four cusps on each tooth was digitized on the occlusal surface of the M2s [protocone (red), paracone (blue), metacone (green), hypocone (yellow)] and m2s [metaconid (red); protoconid (blue); hypoconid (green); entoconid (yellow)]. Because MakeFan7 generates a centroid from four data points, in cases where a fifth cusp may have been present it was not marked and included in the analyses (e.g., m2s hypoconulid). As described above, if the specimen did not have four cusps (e.g., M2s hypocone was absent), the specimen was excluded from the analysis. As with previous studies (e.g., Martinón-Torres et al., 2006; Gómez-Robles et al., 2007, 2008, 2011; Xiao et al., in press), the center of the dentinal facet of each cusp was chosen as the landmark location. If no dentinal facet was present, the highest point of the cusp was utilized. Once the centroid was calculated, 30 equiangular fan lines were created in MakeFan7 with an exaggeration of 3 to ensure that the fan lines crossed the edge of the tooth occlusal surface. Then, using TpsDig2, version 2.16 (Rohlf, 2010a), each of the 30 equiangular fan lines were digitized at the point where the fan line crossed the edge of the occlusal surface. The points were always digitized in the same clockwise order, with the first point digitized always the fan line that ran through the red landmark which occurred in every case (M2: protocone; m2: metaconid). In order to minimize the bending energy between each landmark and target form (Bookstein, 1997; Gunz et al., 2005) each of the 30 semilandmarks were then slid using TpsUtil and tpsRelw (Rohlf, 2010b, c). A Generalized Procrustes Analysis (GPA) was then performed in tpsRelw (Rohlf, 2010c) in order to remove the potential effects of translation, rotation, and scaling. The resultant shapes were then analyzed using the Relative Warps Analysis function in tpsRelw. In this context, the relative warp output is the same as the principal component output. TPS-grids were also evaluated to better observe the degree of variation at the edges of the different principal components (Bookstein, 1997). The TPS-grids and principal components plots were generated in tpsRelw and Microsoft Excel (for previous examples see Martinón-Torres et al., 2006; Gómez-Robles et al., 2007, 2008, 2011, 2012; Xiao et al., in Press). Minimum spanning trees were created using the program PAST (Hammer et al., 2001) to determine the closest links between the Lunadong teeth and the comparative samples.

4. Results

4.1. M2

4.1.1. Size variation

Fig. 6 plots the mesial-distal and buccal-lingual measurements of the upper second molars. In general, the older hominins have much larger teeth than the Holocene modern human samples and each group tends to cluster together. Homo erectus and H. neanderthalensis fall in between, overlapping somewhat at the upper range of the MP and UP modern H. sapiens and at the low end of the range of the Australopiths and early Homo populations. The LND M2 falls squarely in the middle of the Mesolithic and UP modern humans, at the upper end of the range of Neolithic modern humans, and at the low end of the range of H. neanderthalensis.

4.1.2. Shape variation

Results were obtained using the slid semilandmark configuration (tpsRelw). The results of the principal components analysis are presented in Figs. 7–8, with the first five principal components,
We evaluated the variation in the morphology of the tooth occlusal surface at the extreme edges of the buccal, lingual, mesial, and distal sides using the thin plate spline function in tpsRelw (Figs. 7–8). On the negative end of PC1 the occlusal surface is roughly rectangular shaped, while at the positive extreme of PC1 it is more squarish. The occlusal surfaces at the extremes of PC2 are rectangular. However, the negative end is longer on the mesial and distal sides, while the positive end has longer buccal and lingual sides. The extreme ends of PC3 are similar to those of PC2, with both extremes rectangular and longer on the mesial and distal sides (negative end) or buccal and lingual sides (positive end).

In Fig. 7 (PC1 vs. PC2), there appears to be substantial overlap among the modern human and hominin samples. In general, most of the older hominins (e.g., Australopiths, H. habilis, H. erectus) fall on the negative side of PC1 (the exception is OH 16). Mid-Pleistocene Homo and the Neanderthals display some degree of separation, with the former plotting on the positive side of PC2 and the majority of the latter specimens falling in the negative side of PC2. Modern humans (early, UP, and recent) generally fall away from the older hominins and overlap fairly extensively with mid-Pleistocene Homo and the Neanderthals. The LND M2 plots on the positive sides of PC1 and PC2 falling most closely to several Recent Modern Humans (Koreans), an Early Modern Human (Mumba XXI), and a Neanderthal (Amud). The minimum spanning tree connects LND M2 most closely to a Recent Modern Human (Korean).

The PC1 vs. PC3 chart (Fig. 8) presents a slightly clearer pattern. For instance, in Fig. 7 the mid-Pleistocene Homo and Neanderthals specimens display a great deal of variation, plotting in all four quadrants. However, in Fig. 8 the same specimens are much more tightly grouped, with the majority of them falling on the positive side of PC3 and displaying a good deal of overlap with each other. In the PC1 vs. PC3 chart, LND M2 falls closest to an Early Modern Human (Mumba XXI) and two Recent Modern Humans (Koreans). Not surprisingly, minimum spanning trees link LND M2 directly with those specimens.

4.2. m2

4.2.1. Size variation

Fig. 9 plots the mesial-distal and buccal-lingual measurements of the lower second molars. In general, the older hominins have larger teeth, particularly the robust Australopiths, and each group tends to cluster together. Although the older hominins generally have larger teeth, there does appear to be a substantial degree of overlap between the different populations. As with the M2s, the H. erectus and H. neanderthalensis populations generally fall in between, overlapping with the Mesolithic and Neolithic modern humans (falling at the upper range of those populations) and the older hominins (falling at the lower range of those populations). The LND m2 falls squarely in the middle of the Neanderthals and UP modern human convex hulls.

4.2.2. Shape variation

Results were obtained using the slid semilandmark configurations (tpsRelw). The results of the principal components analysis are presented in Figs. 10–11, with the first four principal components, totaling 81.40% of the variation, presented in Table 4. The first three principal components total 65.80% of the explained variance (PC1 = 28.95%; PC2 = 20.83%; PC3 = 16.02%). Because a great deal of overlap exists between the different hominin fossil samples, we evaluated two separate principal components charts [PC1-PC2 (Fig. 7), PC1-PC3 (Fig. 8)].

Table 4

<table>
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<th>Principal component</th>
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<th>m2</th>
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<tr>
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<td>35.38</td>
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<td>2</td>
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<td>27.64</td>
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<td>12.75</td>
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<td>4</td>
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<tr>
<td>5</td>
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<td></td>
</tr>
</tbody>
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totaling 81.40% of the variation, presented in Table 4; here and below only the principal components that can explain at least 5% of the variation are offered. The first three principal components total 65.80% of the explained variance (PC1 = 28.95%; PC2 = 20.83%; PC3 = 16.02%). Because a great deal of overlap exists between the different hominin fossil samples, we evaluated two separate principal components charts [PC1-PC2 (Fig. 7), PC1-PC3 (Fig. 8)].

We evaluated using MakeFan7 and tpsDig2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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Fig. 6. Scatterplot of mesial-distal length and buccal-lingual width for Lunadong and other M2s. Raw data presented in Table 3a (see text for references). Measurements in mm.

Fig. 7. Principal components plot (PC1-PC2) of LND M2 and other hominin M2s. Minimum spanning tree shows links to LND M2 as a solid black line. For comparative purposes, the branches between all of the other hominins are presented as light lines.

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Fig. 8. Principal components plot (PC1-PC3) of LND M2 and other hominin M2s. Minimum spanning tree shows links to LND M2 as a solid black line. For comparative purposes, the branches between all of the other hominins are presented as light lines.

Fig. 9. Scatterplot of mesial-distal length and buccal-lingual width for Lunadong and other m2s. Raw data presented in Table 3b (see text for references). Measurements in mm.

Please cite this article in press as: Bae, C.J., et al., Modern human teeth from Late Pleistocene Luna Cave (Guangxi, China), Quaternary International (2014), http://dx.doi.org/10.1016/j.quaint.2014.06.051
Fig. 10. Principal components plot (PC1-PC2) of LND m2 and other hominin m2s. Minimum spanning tree shows links to LND m2 as a solid black line. For comparative purposes, the branches between all of the other hominins are presented as light lines.

Fig. 11. Principal components plot (PC1-PC3) of LND m2 and other hominin m2s. Minimum spanning tree shows links to LND m2 as a solid black line. For comparative purposes, the branches between all of the other hominins are presented as light lines.
plot on the negative side of PC3, while most *H. erectus* plot on the positive side. The majority of the Recent Modern Humans fall on the positive side of PC3, while most of the mid-Pleistocene *Homo* specimens fall on the negative side. When compared to other members of their group, the only apparent outlier is one *H. erectus* specimen (Dmanisi D2735), which falls far away from the rest of the *H. erectus* specimens. LND m2 falls very close to the zero—zero point for both PC1 and PC3. However, unlike PC1-PC2 where LND m2 plotted almost directly on a Recent Modern Human, PC1-PC3 shows that the closest datapoints to LND m2 are a *H. erectus* (Ternifine 3) and a mid-Pleistocene *Homo* (AT 4147). Not surprisingly, the minimum spanning trees links LND m2 to Ternifine 3 and AT 4147.

5. Discussion

LND M2 metrically falls closest to the Mesolithic and Neolithic modern humans, though it does fall at the low end of the range of the Neanderthals. The LND M2 falls outside the range of the older hominin populations. In terms of the geometric morphometrics, LND M2 plots closely with Recent Modern Humans (Koreans in all cases) and an Early Modern Human (Mumba XXI) on both the PC1-PC2 (Fig. 7) and PC1-PC3 (Fig. 8) plots. The Minimum Spanning Trees for both plots indicate the closest relationship for LND M2 is to Choson Dynasty Koreans and Mumba XXI, corroborating the size analysis.

In general, the results for the LND m2 are not as clear as they are for the LND M2. There is clear distinction metrically between the older and younger hominin populations’ m2s (with the *H. erectus* and Neanderthal populations falling in between). The LND m2 does fall most comfortably within the UP and Mesolithic modern *H. sapiens* convex hulls. In reference to the geometric morphometrics, the PC1-PC2 plot (Fig. 10) and the PC1-PC3 plot (Fig. 11) present contrasting results. In the PC1-PC2 plot LND m2 falls almost directly on a Recent Modern Human, while in the PC1-PC3 plot LND m2 falls closest to Ternifine 3 (*H. erectus*) and AT 4147 (mid-Pleistocene *Homo*). The minimum spanning trees clearly link LND m2 to a Recent Modern Human (Fig. 10), but also to Ternifine 3 and AT 4147 (Fig. 11).

Overall, the metric and GM analyses of the LND M2 suggest it most closely aligns with modern *H. sapiens*. Although the results of the LND m2 are less clear, the metric and geometric morphometric analyses suggests likely affiliation with modern *H. sapiens*. The absence of a hypoconulid and relatively slender roots also suggest LND m2 represents a modern human. Nevertheless, given the relatively robust sample sizes utilized in this study, it is possible the m2 is more difficult to distinguish taxonomically than is the M2.

6. Conclusion

The Lunadong modern human M2 and the probable modern human m2 found *in situ*, given their chronometric age, have important implications for the modern human origins debate, particularly because some researchers (e.g., Jin and Su, 2000) have suggested there is a complete or nearly complete absence of hominin occupation in China during the first half of the Late Pleistocene. Simply stated, the Lunadong human teeth add to a growing list of modern and/or transitional humans that appear in this spatio-temporal point (e.g., Callao Cave, Huanglongdong, Zhirendon). The Lunadong human fossils can contribute to various aspects of the modern human origins debate.

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