Reevaluation of early Holocene chicken domestication in northern China

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ABSTRACT

The chicken (Gallus gallus domesticus) is the most widespread domestic animal in the world. However, the timings and locations of their domestication have remained debatable for over a century. China, and particularly northern China, has been claimed as one of the early centers for the domestication of chickens, because many chicken remains have been discovered at a number of archaeological sites. However, the identification of archaeological domestic chicken bones from early Holocene sites in China remains contentious. In this study, we analyzed 1831 bird bones, which included 429 bones previously recorded as “domestic chicken” from 18 Neolithic and early Bronze Age sites in central and northern China. Although morphological species identification criteria for the bones of 55 modern Chinese Phasianidae species, including the domestic chicken and wild red junglefowls, have not yet been fully established, upon reanalysis none of the “domestic chicken” bones were derived from chickens. In addition, bones determined to be candidate chicken bones were found at only 2 of the 18 sites, suggesting that chickens were neither widely kept nor distributed in central and northern China during the early and middle Holocene period. Further studies that combine analyses of morphology, ancient DNA, and radiocarbon dating are required to fully reveal the origin and history of the domestic chicken in northern China.

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1. Introduction

Chickens (Gallus gallus domesticus) are the most widespread domestic animals in the world, providing meat and eggs on every continent and even some remote islands (Serjeantson, 2009). They appear to have been used for religious activities, cockcrowing and cockfighting at the earliest stages of their domestication. The domestic chicken principally originates from the red junglefowl G. gallus, which is distributed throughout Southeast Asia and China and is proposed to have been domesticated in multiple regions of the area (Akishinonomiya et al., 1994; Liu et al., 2006; Miao et al., 2013).

Some authors claimed that China, and particularly northern China, appears to be one of the early centers for chicken domestication because many alleged chicken remains have been recorded at a number of archaeological sites (Bellwood, 2005; Serjeantson, 2009; Xiang et al., 2014). To date, chicken bones have been discovered in at least 52 archaeological layers from 44 Neolithic sites and 18 layers from 12 Bronze Age sites in China (Deng et al., 2013; Li et al., 2015; West and Zhou, 1988). In addition, the oldest domestic chicken bones in the world have been discovered in northern China: at Cishan Site, Hebei Province, and Peiligang Site, Henan Province (Institute of Archaeology CASS, 1984; Zhou, 1981). Radiocarbon dating of the layers where chicken bones have been found has dated them to approximately 6000 BC. Furthermore, recent analyses of ancient DNA have discovered mtDNA haplotypes of G. gallus in samples from Nanzhuangton (Hebei Province), Cishan, and Wangyin (Shandong Province), suggesting that domestic chicken farming began approximately 10,000 BP in northern China (Xiang et al., 2014). However, some studies have challenged the discovery of early Holocene chicken bones in the northern China: Benecke (1994) and Peters (1997a, 1997b) pointed out that the purported chicken bones from Cishan are not in fact from

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chickens but rather are from pheasants, although they failed to explain how they identified the bones as such, while Yuan (2010) and Deng et al. (2013) indicated that the identification criteria for domestic chicken bones have not yet been fully established for northern China, and thus a reexamination of the early Holocene chicken bones is necessary. There are 55 Phasianidae species in China, including such as red junglefowl, common pheasant (Phasianus colchicus), Koklass pheasant (Pucrasia macrolopha), and brown-eared pheasant (Crossoptilon mantchuricum) (Zheng, 2011), therefore the criteria for discriminating the bones of chicken from those of indigenous birds in northern China are required.

To uncover the origin and early history of the domestic chicken throughout the world, a reevaluation of chicken bones from early Holocene China, especially northern China, is essential. Unfortunately, most of the recorded chicken bones are not fully available. Therefore, it is difficult or, in many cases impossible, to reanalyze them. However, many other bird bones have been found alongside these reported bones at Neolithic and Bronze Age sites in China. By studying them using clear identification criteria for chicken bones, it is possible to reevaluate the early Holocene history of domestic chickens in northern China.

In this study, we analyzed 1831 bird remains from 18 Neolithic and Bronze Age sites in central and northern China. Combining morphological identification with histological analysis of Phasianidae bones, we found that chickens and red junglefowls were absent, or at most very rare, during the early and middle Holocene in central and northern China. We discuss the large discrepancies between this study and previous studies.

2. Materials and methods

In total, 1,831 bird bones from 18 Neolithic and Bronze Age Chinese archaeological sites were studied (Table 1, Fig. 1). The time period for each sample was estimated from the layer in which it was found. Although bird bones from five sites at Wangyin (Zhou, 2000), Zhengpiyan (Yuan, 2003), Cishan (Zhou, 1981), Jiahu (Huang, 1999) and Nanzhuangtou (Hebei Provincial Institute of Cultural Relics et al., 2010) had already been recorded, all of the accessible samples were reevaluated as part of this study.

Taxonomic identification was conducted by ME with unaided eye observation of materials. For family-level identification, reference collections at the zooarchaeology laboratory in the Institute of Archaeology, Chinese Academy of Social Sciences, and the personal collection of ME were used. More detailed identification within the family Phasianidae was conducted on femora, tibiotarsi, and tarsometatarsi, according to the identification criteria by Eda and Inoué (Eda and Inoué, 2011), which focused on the discrimination of chickens and red junglefowls from Japanese indigenous pheasants (common pheasant and copper pheasant S. sommerringii). There are 55 Phasianidae species in China, including the red junglefowl and common pheasant (Zheng, 2011), therefore these criteria were not enough to distinguish chickens and red junglefowls from the other 53 indigenous Phasianidae. However, the criteria are effective for excluding the bones of non-chicken or non-red junglefowl and identifying candidate bones of chicken or red junglefowl. The presence or absence of pneumatic foramina of the greater trochanter (femur (Eda and Inoué, 2011)), a medial plantar crest (tarsometatarsus (Nishida and Hayashi, 1981)), and the shape of the posterior ligament of the tibiofibular joint (tibiotarsus) were recorded for each sample.

The development sites in central China (nestling or adult) and the presence or absence of medullary bone were recorded via unaided eye observation. We defined a nesting bone as a bone with at least one incomplete ossification. Although the production of glass slides and staining with Alcian blue is a reliable method for the identification of archaeological medullary bone, careful unaided eye observation is also useful for identifying stereotypic medullary bone with a developed woven bony structure (Eda et al., 2010).

3. Results

Of the 1831 bird remains, a total of 1215 Phasianidae bones were found at 18 Neolithic and Bronze Age sites in central and northern China (Table 1, Fig. 1). Except Phasianidae, the bones included at least nine other families: Anatidae, Podicipedidae, Ciconiidae, Ardeidae, Gruidae, Rallidae, Laridae, Accipitridae, and Corvidae. The discriminating characteristics of femur, tibiotarsus, or tarsometatarsus were observed in 280 of the 1215 Phasianidae bones and were used for further analyses.

Five tarsometatarsi from Cishan, which were exhibited at the Handan City Museum, Hebei, northern China, as “the oldest domestic chicken in the world” were analyzed (Fig. 2a). All of the tarsometatarsi had a medial plantar crest (Nishida and Hayashi, 1981), which was completely absent from the bones of chicken and red junglefowl, and were therefore identified as “non-chicken” bones. From Wangyin, 55 femora and 15 tarsometatarsi were reanalyzed (Fig. 2b). All of the tarsometatarsi had a medial plantar crest while all of the femora had pneumatic foramina of the greater trochanter (Eda and Inoué, 2011), which is absent from the bones of chicken and red junglefowl, and were identified as non-chicken bones. Among the bones from Nanzhuangtou, three tarsometatarsi, two femora, and one tibiotarsus were reanalyzed (Fig. 2c). All of the femora and tarsometatarsi had a medial plantar crest and pneumatic foramina of the greater trochanter, while the tibiotarsus exhibited a rounded posterior ligament of the tibiofibular joint similar to common pheasants and copper pheasants but different from chicken and red junglefowl (line-shaped) (Eda and Inoué, 2011). Again, all three skeletal parts were identified as non-chicken bones.

The majority of the other Phasianidae bones under scrutiny were similarly identified as non-chicken bones: 45 of 46 femora had pneumatic foramina of the greater trochanter, 25 of 27 tibiotarsi had rounded posterior ligaments of the tibiofibular joint, and 125 of 126 tarsometatarsi had medial plantar crests. Ultimately, only three chicken bone candidates were identified by the discriminating characteristics: one femur from Xiawanggang (found in the Longshan layer dating to between 3000 and 2000 BC, at Henan, Fig. 3a) and two tibiotarsi from Zaoshugou (dating from the Proto-Zhou culture, 1200–1050 BC, Shaanxi, Fig. 3b). An immature femur from Xiawanggang was found to have no pneumatic foramina of the greater trochanter and was thus recognized as a candidate chicken bone. The pneumatic foramina of the greater trochanter is evident in the immature femora of P. colchicus (Supplementary Data 1). Two tibiotarsi from Zaoshugou exhibited line-shaped posterior ligaments of the tibiofibular joint and were identified as candidate chicken bones. One of the two candidate chicken bones from the site included medullary bone. Apart from the tibiotarsus from Zaoshugou, the presence of medullary bone was rare but was also found in another tibiotarsus from Zaoshugou (Fig. 3c), a radius from Xiawanggang (Fig. 3d) and a tibiotarsus from Tengjiaogang (Bronze Age, Heilongjiang), although none had the characteristics needed to discriminate among chicken and indigenous pheasants and so be morphologically recognized as candidate chicken bones. An un-fused tarsometatarsus without a medial plantar crest was identified from Zhoujiazhuang (Taosi Culture, 2300–1900 BC, Shanxi). However, the tarsometatarsus was neither classified as a candidate chicken bone nor as non-chicken because the medial plantar crest is absent from a tarsometatarsus of nestling non-chicken Phasianidae birds (Eda and Inoué, 2011). Except for the femur from Xiawanggang and
Table 1
List of ancient Phasianidae bones analyzed in this study. Province, culture, period, number of identified specimens (NISP) of birds and Phasianidae, results of morphological analysis, and source of previous reports are also shown.

<table>
<thead>
<tr>
<th>Nos. in Fig. 1</th>
<th>Site name</th>
<th>Province</th>
<th>Culture</th>
<th>Period</th>
<th>Bird NISP (studied)</th>
<th>Phasianidae NISP</th>
<th>Femur Non-chicken</th>
<th>Candidate Non-chicken</th>
<th>Tibiotarsus Non-chicken</th>
<th>Tarsometatarsus Candidate</th>
<th>Reference</th>
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<td>13</td>
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<td>39</td>
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<td>Henan</td>
<td>Yinxi Culture (Late period of Shang Dynasty)</td>
<td>1250–1050 BC</td>
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<td>3</td>
<td>2</td>
<td>2</td>
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<td>Shandong</td>
<td>Late period of Shang Dynasty - Middle period of Western Zhou Dynasty</td>
<td>1200–900 BC</td>
<td>16</td>
<td>8</td>
<td>3</td>
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<td>22</td>
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<td>7</td>
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<td>Bronze Age</td>
<td>3000–700 BC</td>
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<td>356</td>
<td>24</td>
<td>16</td>
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<td>4500–3500 BC</td>
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</table>

Key characters for non-chicken and candidate chicken bone discrimination are the presence or absence of pneumatic foramina of the greater trochanter (femur) and a medial plantar crest (tarsometatarsus), and shape of the posterior ligament of the tibiofibular joint (tibiotarsus). * Bone of nestling.

the tarsometatarsus from Zhoujiazhuang, the discovery of immature Phasianidae bones was rare and only a humerus from...
Zaoshugounao was found (Fig. 3e).

4. Discussion

Purported chicken bones have been recorded from 63.4% (52 of 86) of Neolithic layers at 58.7% (44 of 75) of Neolithic sites and in 56.3% (18 of 32) of Bronze Age layers at 46.2% (12 of 26) of Bronze Age sites in China (Deng et al., 2013; Li et al., 2015; West and Zhou, 1988). These records have led to China, particularly northern China, being considered one of the early centers of chicken domestication (Bellwood, 2005; Serjeantson, 2009; Xiang et al., 2014). However, according to our analysis, candidate chicken bones were only identified in 1 (Xiawanggang) of 12 Neolithic layers and 1 (Zaoshugounao) of 9 Bronze Age layers. Although direct radiocarbon dating of these bones are required to eliminate the possibility of their re-deposition or contamination from later deposits, the rarity of candidate chicken bone suggests that chickens and red jungle-fowls were not widely exploited throughout central and northern China at that time. Candidate chicken bones were not found at any of the other six sites (Cishan, Wangyin, Nanzhuangtou, Erlitou, Yinxu, and Zengpiyan) where chicken (Gallus sp.) or domestic chicken (G. gallus domesticus) bones have been reported in previous studies (Hou, 1989; Xiang et al., 2014; Yang, 2008; Yuan, 2003; Zhou, 1981, 2000). In particular, the samples taken from Cishan and Wangyin were originally recorded as being domestic chickens. Although further studies for the other bone elements, such as humeri and coracoids, applying identification keys for European Phasianidae birds (e.g. Erbersdobler, 1968; Cohen and Serjeantson, 1996; Tomek and Bochenski, 2009) as tools for discriminating candidate chicken bones from non-chicken ones might find out
some candidate chicken bones, it will be unreasonable to expect that the studies find out enormous chicken bones in other elements.

Therefore, the large discrepancy in the appearance of chicken bones between previous studies and the present study arises from the misidentification of chicken bones in some previous studies. As far as we are aware, there are no zooarchaeological reports that have used clear identification criteria for chicken or red junglefowl bones from the other 54 Phasianidae species in China (Deng et al., 2013; Yuan, 2010). For example, Zhou (1981) discussed “the oldest domestic chicken in the world” from Cishan but only mentioned that the specimens resembled wild red junglefowl in shape, and the criteria for discriminating the bones of chicken from those of indigenous birds in northern China, such as common pheasant, Koklass pheasant, and brown-eared pheasant, were not explained. Intriguingly, Zhou (1981) presented photographs of four tarsometatarsi with a medial plantar crest (Plate 9. 1–4) and a femur with pneumatic foramina of the greater trochanter (Plate 10. 2) as bones of a domestic chicken. However, no chickens or red junglefowl have a medial plantar crest or pneumatic foramina of the greater trochanter (eda and inoué, 2011). This misidentification of the tarsometatarsus is far more critical than those of the other skeletal elements because Zhou (1981) discussed chicken domestication at Cishan based on measurements and male biased sex ratio of the tarsometatarsus. The fact that all of the tarsometatarsi shown in the original zooarchaeological report of Cishan (zhou, 1981) and exhibited in a museum as “the oldest domestic chicken in the world from Cishan” were not in fact chicken bones suggests that a large number of non-chicken tarsometatarsi have been misidentified as chicken bones and that Zhou’s discussion of “the oldest domestic chicken in the world” is without proper evidence. Indeed, a photograph and drawing of a “chicken” tarsometatarsus with a medial plantar crest have also been reported from Beishouling (Shaanxi, Neolithic) and Dawenkou (Shandong, Neolithic) (deng et al., 2013). These types of misidentifications could also be present in other previous studies.

Our results also differ completely from those of the latest ancient DNA study by xiang et al. (2014), even where the samples originated from the same archaeological sites. In the present study, all of the studied Phasianidae bones from Cishan (N = 5), Wangyin (N = 70), and Nanzhuangtou (N = 6) were identified as non-chicken bones. In xiang et al. (2014), by comparison, a bone from Cishan (N = 7), two bones from Wangyin (N = 6), and three bones from Nanzhuangtou (N = 22) were identified as bones of gallus gallus and the remaining five bones were identified as bones of gallus; none of the bones were identified as being from any of the other Phasianidae species. The reason why all of the analyzed samples in that paper were identified as originating from chickens can only be explained if the authors had chosen to use morphology to identify them as such. However, they clearly disregarded the advice in their own paper, which stated: “isolated bones from different genera of the Galliformes are difficult to ascertain to genus level using morphological analyses alone. Therefore, we chose 39 presumed chicken bones...” (xiang et al., 2014). Conversely, judging by a photograph of “typical ancient chicken bones unearthed in northern China” (xiang et al. 2014; fig. 1 B), some of their samples also consisted of mammal bones: the two right bottom bones are clearly canids (peters et al., 2015), with more precision right metacarpi of canids (supplementary data 2; but see also xiang et al., 2015). The authors (xiang et al., 2015) insisted that they did not succeed in identifying the species of the two controversial bones and their identity has no bearing on the conclusions drawn in xiang et al. (2014). However, these types of bones have to be considered “typical” and representative of the reliability of xiang’s sample. In addition to some questions raised to xiang’s ancient DNA sequence data (peng et al., 2015; peters et al., 2015), it is important to note that the authors conducted replication experiments for five of their samples, but these results were not mentioned in their paper (xiang et al., 2014). Ancient DNA analysis is obviously a powerful tool for species identification of archaeological remains. However, reliable morphological analyses of archaeological remains and reproducible results from DNA analyses must also exist as the basis of the discussion.

One and two candidate chicken bones were identified from Xiawanggang and Zaoshugounao, respectively; the other analyzed Phasianidae bones were identified as non-chicken bones at those sites. This indicates that chickens and red junglefowls were uncommon in the Neolithic and early Bronze Age in central and northern China, and suggests that chickens were not widely kept and red junglefowls were not widely distributed throughout central and northern China during the early and middle Holocene. The non-wild distribution of red junglefowl in northern China during the early Holocene is consistent with reconstructed climatic and floral conditions in the region (peters et al., 2015; yuan et al., 2015; see also xiang et al., 2014, 2015).

It is important to note that some candidate chicken bones from Xiawanggang were from nestlings, and that other nestling Phasianidae bones have also been found at Zaoshugounao. However, the bones of nestling Phasianidae are rare at the other sites. These facts suggest that people from those two sites had an opportunity to exploit the nestlings of Phasianidae but people from the other sites did not. This difference could be explained by different hunting strategies, such as nesting bird hunting at the former sites. However, combined with the fact that candidate chicken bones were found at the former sites but were absent from the other sites, the rearing of chicken-like Phasianidae birds at Xiawanggang and Zaoshugounao would be a plausible scenario. The fact that bones containing medullary bone, a secondary woven bony tissue that is unique to breeding female birds (dacke et al., 1993; simkiss, 1961), were found in one of the candidate chicken bones from Zaoshugounao and in a Phasianidae radius from Xiawanggang, whereas bones including medullary bone were rare at the other sites, also supports this explanation. It is unreasonable to consider that people in northern China inherently possessed basic knowledge of hatching and rearing for an exotic subtropical bird, red junglefowl. Because of the scarcity of candidate chicken bones, and the simultaneous appearance of nestling Phasianidae and Phasianidae bones with medullary bone in northern and central China in the early and middle Holocene sites, chickens do not appear to have been originally domesticated in northern and central China but rather occasionally imported from other region(s) with some basic knowledge of hatching and rearing. Recent natural distribution area for the red junglefowl, i.e. tropical area in southern China and Southeast Asia, would be a reasonable origin of chicken domestication. Further studies using ancient DNA and radiocarbon dating are required to judge whether all of the candidate chicken bones are indeed chicken bones and from which cultural layers in the archaeology they originate, and thus when and from where chickens were imported to northern China.

Author contributions

M.E. and Y.J. designed research; P.L, Z.L. and F.L. arranged the samples; and M.E., Y.J., P.L and H.K. wrote the paper.

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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.jas.2016.01.012.

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