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Holocene cultural history of Red jungle fowl (*Gallus gallus*) and its domestic descendant in East Asia

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ABSTRACT

Nearly three decades ago, zooarchaeologists postulated that chicken husbandry was practiced in Northern China by ~8.0 ka calBP. Recently, ancient mitogenome analyses of galliform remains suggested that Red jungle fowl (*Gallus gallus*) was already present in the Yellow River basin several millennia earlier, shortly after the onset of the Holocene. If these conclusions are correct, the origins of chicken domestication and husbandry in the region may have been spurred by agricultural innovations in the lower Yellow River basin including millet cultivation, pig husbandry, and dog breeding. In addition, the dispersal of poultry farming from East Asia to Asia Minor and Europe could therefore date to the Neolithic along ancient trade routes across Central Asia rather than via South Asia and Mesopotamia. For this scenario to be plausible, the post-Pleistocene climatic conditions must have been favourable to allow for a northward extension of the native distribution of tropical Red jungle fowl currently not found north of ~25°N. This study combines Holocene palaeoclimate and archaeofaunal archives with new zooarchaeological insights alongside a discussion of methodological issues and cultural aspects in order to revisit the hypothesis of an early Holocene *Gallus* domestication and Neolithic poultry husbandry in Northern China. Our results regarding the natural and cultural history of Red jungle fowl and domestic chickens in East Asia, and the timing of chicken dispersal across the Old World suggest that an early Holocene domestication of chickens is problematic at best. We conclude by postulating an alternative model for the early exploitation of a key domestic species in present-day East Asia.

1. Introduction

Chickens are by far the most numerous domestic animal on earth and are of immense importance as a global food species. The domestication history of Red jungle fowl (*Gallus gallus*) and the spatio-temporal dispersal of chicken husbandry prior to the modern era, however, remain contentious. One hypothesis holds that middle Holocene[1] village economies in Northern China practiced poultry farming by at least ~8.0 ka calBP. Recently published mitogenetic signatures obtained by Xiang et al. (2014) from galliform bones collected at the early Neolithic site of Cishan that was inhabited ~8.0–7.7 ka calBP appear to substantiate a previous

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[1] Stratigraphic subdivision of the Holocene follows Walker et al. (2012). These authors advocate formal boundaries respectively at 8.2 ka calBP for the Early-Middle Holocene and at 4.2 ka calBP for the Middle-Late Holocene. Cultural phasing and dates of the Chinese Neolithic are according to Liu and Chen (2012), who defined a transitional/foraging period prior to ~9.0 ka calBP, which is followed by the Early Neolithic (9.0–7.0 ka calBP), Middle Neolithic (7.0–5.0 ka calBP) and Late Neolithic (5.0–4.0 ka calBP).

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zooarchaeological study published nearly three decades ago (West and Zhou, 1988). Both of these studies also conclude that since poultry farming had been established in the middle Holocene Yellow River basin ~8.0 calBP, efforts to manage Red jungle fowl must have started during the early Holocene.

In terms of geography, both Ho (1977) and Crawford (1984) argued for an autochthonous episode of *Gallus* domestication in Northern China, linked to the favourable climatic conditions of the Holocene that would have allowed Red jungle fowl to extend its native distribution (currently restricted to south of 25°N) much further north. West and Zhou (1988) disagreed, however, and pointed out that the late Pleistocene and early Holocene palaeoclimatic signatures documented in palaeosols of the Loess Plateau pointed to semi-arid and not tropical climate and vegetation required by Red Jungle fowl. The lack of conditions suitable to Red Jungle fowl thus obviated the potential for chickens to be independently domesticated in the north. Instead, West and Zhou argued that flocks must have been domesticated in the south and then transported to the north where they required human-assisted sheltering to survive the low winter temperatures and lack of vegetative ground cover characteristic of Holocene Northern China. More recently, this diffusion model has been challenged by a study of ancient chicken DNA (Xiang et al., 2014) which presented evidence supporting both the presence of Red jungle fowl in the early Holocene North China Plain and local chicken domestication.

If true, the occurrence of Red jungle fowl would thus imply the existence of suitable habitat for this thermophilic bird shortly after the onset of the Holocene. Xiang et al. (2014) argued that abundant remains of tropical animal and plant species at early Holocene Nanzhuangtou, with main occupation likely dated between 11.5 and 11.0 ka calBP[2] (Yang et al., 2012, Table S1), and middle Holocene Cishan (CPAM, Hebei Province Relics Preservation Station et al., 1981) suggest warmer and more humid conditions and a much larger forest cover. These conditions would have allowed *Gallus* to be present in areas where Red Jungle fowl do not exist today, thus facilitating their domestication.

With regard to the domestication status of *Gallus,* West and Zhou (1988) considered the chickens from middle Holocene Cishan and contemporary early and middle Neolithic sites in Northern China to be domestic birds introduced by humans based on both environmental arguments and because osteometrical comparisons demonstrated that the bones were larger than those of the wild ancestor *Gallus gallus,* but smaller than those of modern chickens. A zooarchaeological explanation posits that size increase in early domestic flocks results from regular and sufficient feeding and protection against predators, thereby reducing necessity to fly in birds kept in anthropogenic environments whilst converting energy intake more efficiently into meat and fat (von den Driesch, 1987).

Though the genetic analyses presented by Xiang et al. (2014) did not allow for a classification of individual bones as either domestic or wild, they concluded the bone finds from early and middle Holocene contexts represent the remains of a population ancestral to at least some of modern chicken mtDNA diversity. They based this conclusion on four arguments. Firstly, the remains were found in sites representing transitional foraging (Nanzhuangtou) and developed agricultural (Cishan, Wangyin) societies. Secondly, the chicken bones are present across several thousand years in the archaeological record of Northern China. Thirdly, these findings predate archaeological chicken remains from any other region in East and Southeast Asia by millennia. And lastly, all major modern chicken haplogroups and also one of the most common haplotypes were represented in their ancient DNA sequences.

The presence of domestic fowl in middle Holocene Northern China also necessitated revisiting the species' pattern of dispersal across Asia to Europe. West and Zhou (1988) postulated that the translocation of chickens occurred along East-West trade routes across Central Asia, rather than travelling from the jungle fowl's most western native distribution in South Asia, i.e. India across the Arabian Gulf to Mesopotamia and from there to Europe (Zeuner, 1963). At the time of publication, however, *Gallus* finds were remarkably absent in the assumed region of passage, which West and Zhou (1988) explained by Central Asia's poor archaeological coverage.

Thus, taken at face value, the historical zooarchaeological and recent genetic analyses published thus far suggest that chicken husbandry was being practiced by the Neolithic inhabitants of the Yellow River basin ~8.0 ka calBP. Recent ancient DNA data also imply the presence of an autochthonous *Gallus* population in the North China Plain since the beginning of the Holocene (Xiang et al., 2014). More recent and on-going zooarchaeological work, however, does not support the conclusions of either West and Zhou (1988) or Xiang et al. (2014).

One major concern is the fact that morphological comparison of specimens identified as *Gallus* and figured in Chinese archaeological literature revealed that they are not derived from chickens, but from pheasants (Benecke, 1994; Peters, 1998; Deng et al., 2013; Peters et al., 2015; Li et al., 2015; Eda et al., 2016). In addition, our current understanding of the early Holocene climate in Northern China suggests that *Gallus* could not survive in this region. This review, therefore, takes a closer look at final Pleistocene to middle Holocene climatic developments and associated vertebrate distribution patterns in Northwestern and Northern China, defined here as the region north of the Huai River – Qin Mountains line ranging between 33°03′N and 34°25′N. Against the background of Holocene climate and zoogeography, we reconsider the zooarchaeological record and related ancient DNA evidence alongside a discussion of methodological issues and cultural aspects relevant to the study of ancient poultry keeping in China. We close with an assessment of the Holocene cultural history of *Gallus* in northern China and adjacent areas.

2. Late quaternary climate, vegetation and fauna in Northern China

2.1. Palaeoclimate and vegetation

The modern climate in Northern China is controlled by the East Asian Summer Monsoon (EASM), associated with climatic features of the northern high latitudes, low latitude ocean and the southern hemisphere. Seasonal migration of the monsoon front causes prominent seasonality in Northern China, winters being cold and dry since dominated by air masses from the interior of Asia, whilst the moist and warm summer months are influenced by southeasterly winds from the western Pacific (An, 2000). Obviously, fluctuations in the EASM regime influenced settlement in Late Quaternary Northern China, with rapid cooling events causing major declines in human population density, as is illustrated by a study linking demographic fluctuations with records captured in loess, lake, palaeo-ocean and cave deposits as well as ice cores and stalagmites (Wang et al., 2014).

Of course, differences in temporal resolution and sensitivity of responses to changes in climate complicate detailing the magnitude of regional influence of the EASM (Chen et al., 2015), not to

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[2] Yang et al. (2012, Table S1) provided a series of seven radiocarbon dates from cultural deposits at Nanzhuangtou ranging between 12,798 ± 134 and 11,018 ± 163 calibrated years BP. Five of these cluster between 11.5 and 11.0 ka calBP. According to the authors, this strongly suggests that 11.5–11.0 ka calBP was the main occupational phase at Nanzhuangtou. The single radiocarbon date recently obtained on bone by Xiang et al. (2014, Table S6) is somewhat younger and dates ~10.5 ka calBP. Thus, site occupation possibly lasted until the middle of the 11th millennium calBP.

mention the nature and scale of the vegetation changes subsequently induced by these (Zhao et al., 2007; Stebich et al., 2009). Proxy data generated with different methods nonetheless agree that prior to the onset of the Holocene ~11.7 ka calBP, East Asia witnessed a severe climatic reversal compatible with the Younger Dryas event in the circum-Atlantic region. Signatures captured in for instance the stalagmites from Hulu Cave (32°05′N, 119°02′E) as well as peat deposits and lakes at the desert-loess transition belt in Northern China illustrate that this reversal brought about low temperatures, whilst humidity fluctuated (e.g., Zhou et al., 1998; Wang et al., 2001; Li et al., 2003; Xu et al., 2010; Chen et al., 2015).

Turning to the Holocene, pollen-based quantitative analyses of sedimentary sequences from Gonghai Lake (38°54′N, 112°14′E; 1,860m ASL) located on the NE margin of the Chinese Loess Plateau (Chen et al., 2015) and Daihai Lake (40°29′-40°79′N, 112°33′-112°46′E) situated ~200 km to the north of Gonghai Lake in arid North China (Xu et al., 2010) seem particularly relevant here. Both sequences show increasing arboreal pollen percentages in post-Pleistocene sediments indicative of more tree cover and a warmer climate. Assemblages in the Gonghai Lake core are dominated by temperate-forest (*Pinus, Picea, Betula, Quercus, Ulmus*) and temperate-steppe (*Artemisia*, Chenopodiaceae and Poaceae) pollen types (Chen et al., 2015). However, the EASM was clearly weaker during the early Holocene than during the middle Holocene, with lowered precipitation ~9.5–8.5 ka calBP. Maximum monsoon intensity occurred in the middle Holocene from ~7.8–5.3 ka calBP, with average annual precipitation ~30% higher than the modern value (Chen et al., 2015). At Daihai Lake, climatic conditions were essentially cool and dry ~11.7–9.0 ka calBP, annual precipitation being 50–100 mm lower than the present. Conversely, precipitation was 100–200 mm higher than today during the subsequent middle Holocene thermal optimum. During the latter, temperatures averaged up to 3 °C higher, whereas the preceding early Holocene witnessed on average 1°-2 °C lower temperatures compared to today (Xu et al., 2010).

Similar climatic developments were noted east of Northern China across the Bohai Sea and Korea Bay. Until ~9.0 ka calBP winters remained cold preventing evergreen forests from prospering, higher mean annual temperatures compared to today (+2–3 °C) and warmer winters being evidenced during the middle Holocene in central South Korea, causing replacement of deciduous broadleaved forests by evergreen forests (Yi, 2011). In the Yangtze River delta (31°23′3″N, 121°58′59″E), middle Holocene temperatures were ~2–4 °C warmer than today (Yi et al., 2003).

Based on their results of arboreal pollen analyses, Yu et al. (2000) concluded that during the Holocene thermal optimum, the northern limit of the temperate deciduous forest, in which Northern China is presently situated (Liu, 1988), was located ca. 800 km north relative to today. This implies a northward shift of ca. 7° of the corresponding vegetation belts. However, even during the middle Holocene optimum climatic conditions were far from constant, with warm-humid periods alternating with cold-dry episodes and with corresponding effects on vegetation cover, fauna and human population density (e.g. Xu et al., 2010; Wang et al., 2014; Chen et al., 2015).

2.2. *Mammalian zoogeography*

Taxonomic composition and faunal distribution patterns place Northern China in the Palaearctic Region (e.g. Corbet and Hill, 1992; Hoffmann, 2001; Smith and Xie, 2008). Corbet and Hill (1992: 4, map 2) position the boundary of the Palaearctic with the Indomalayan Region slightly south of the lower Yangtze River. Between these two Regions, the authors defined three Divisions, i.e. (1) the Central China Division with predominantly Palaearctic taxa situated ~30–35°N, (2) the Southern China Division, where Palaearctic taxa form a minority and located between ~25 and 30°N, and (3) the Indochinese Division, with a mammalian fauna overwhelmingly Indomalayan in character and located south of ~25°N. Hoffmann (2001) further detailed the boundaries of the transition zone (Fig. 1) and confirmed that its mid-point should be close to 30°N.

Table 1 lists the mammalian taxa evidenced in early to middle Holocene archaeological contexts in Northern China. From this, we notice the rareness of tropical Indomalayan and the dominance of Palaearctic genera notably adapted to marked daily and seasonal variation in temperature and cool winters in particular. Even during the Holocene thermal optimum, the ubiquitous presence of Wild boar, Red deer, Sika deer, Musk deer, Chinese water deer, Roe deer, European hare etc. characterizes landscape and vegetation in the study area essentially as temperate, not (sub-)tropical.

In accordance with the warm-humid conditions of the mid-Holocene optimum evidenced in all East Asian palaeoclimate archives, sites located in Northern China however yielded remains of mammals classified to-date as Indomalayan (Hoffmann, 2001, Appendix), including Rhesus macaque (*Macaca mulatta*), Masked palm civet (*Paguma larvata*), Reeves's muntjac (*Muntiacus reevesi*), and Sambar (*Rusa unicolor*) (Table 1). Since specimen counts are missing in the respective faunal reports, their quantitative importance cannot be properly determined.

A similar picture emerges for the contemporaneous Ordos Loop region west of the North China Plain (Flad et al., 2007, Table 1; Wang, 2011, 93). Even in the ecologically favourable landscapes bordering the Wei River (the most prominent tributary of the Yellow River flowing eastward along latitude ~34°-35°N), specimen counts illustrate that Indomalayan taxa, if present at all, account for less than 0.2% (see Supplementary Table S1). Most interestingly, for four Indomalayan taxa identified in Neolithic Northern China and the Ordos Loop, i.e. *Macaca, Muntiacus, Hystrix,* and *Rusa*, their actual native distributions extend to the northern boundary of the Central Chinese Division ~35°N or slightly further north (Corbet and Hill, 1992, maps 79, 80, 109, 111, 137, 172; Smith and Xie, 2008, maps 10, 528, 531). As to the Masked palm civet (*Paguma larvata*), this Indomalayan taxon seems climatically particularly versatile, since it has been recorded to-date close to Beijing at ~39°N.

According to Xiang et al. (2014, 2015b), indicator species of warm-humid, tropical conditions and much more extensive forest coverage during the early Holocene are the Chinese alligator (*Alligator sinensis*) and the extinct Short-horned water buffalo (*Bubalus mephistopheles*). Until recently, the Chinese alligator was much more widely distributed across China and in the past possibly even lived in Korea (Groppi, 2006), underscoring its eurytherm rather than thermophile properties. As to *B. mephistopheles,* its remains have been identified at early Holocene Nanzhuangtou in the North China Plain and from several middle Holocene sites located near major drainages in Northern and Northwestern China (Table 1). Throughout its former range, however, Short-horned water buffalo was found associated exclusively with Palaearctic artiodactyls frequenting cool temperate deciduous and coniferous forests, such as Wild boar, Sika deer, Red deer, Roe deer, Thorold's deer, Musk deer, Chinese water deer, and Muntjac. Rather than implying a (sub-)tropical environment, the synecological context clearly shows that Short-horned (Chinese) water buffalo must have been much better adapted to low temperatures and cold winters than its thermophile (sub-)tropical relatives, the Asian wild water buffalo *Bubalus arnee* and its domestic descendant *Bubalus bubalis*. This distinctness is reinforced by DNA analysis which failed to establish direct genetic links between the domestic water buffalo *B. bubalis* and *B. mephistopheles* (Yang et al., 2008). In sum, climatic, synecological and genetic data show that *B. mephistopheles* differed markedly

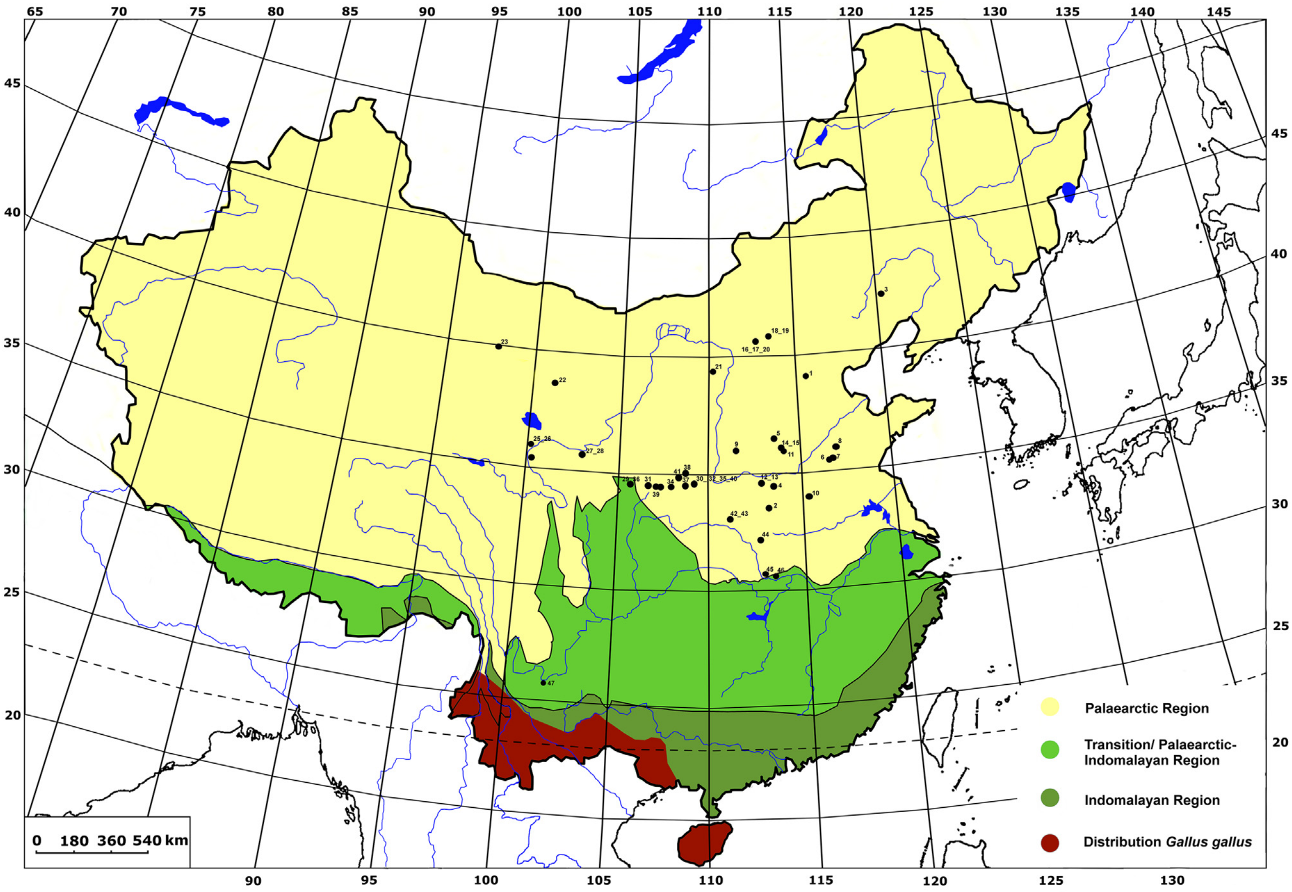

Fig. 1. Map of China indicating the geographic range and boundaries of the Palaearctic (yellow) and Indomalayan Regions (dark green). In between is the transition zone as defined by Hoffmann (2001, Pl. 1). Superposed is the modern distribution of Red jungle fowl *Gallus gallus* in China based on Cheng (1987, 160, Map 114) and McGowan (1994, 530). Sites mentioned in the text and tables are: 1 Nanzhuangtou, 2 Jiahu, 3 Xinglongwa, 4 Peiligang, 5 Cishan, 6 Yuhuangding, 7 Wangyin, 8 Dawenkou, 9 Taosi, 10 Shantaisi, 11 Baiying, 12 Erlitou, 13 Yanshishangcheng, 14 Yinxu, 15 Dasikongcun, 16 Daihai Region, 17 Shihushan, 18 Miaozigou, 19 Dabagou, 20 Wangmushan poshang, 21 Zhukaigou, 22 Donghuishan, 23 Huoshaogou/Ganguyan, 24 Zongri, 25 Yangqu shierdang, 26 Xiangnagou, 27 Dahezhuang, 28 Qinweijia, 29 Xishanping, 30 Baijiacun, 31 Guantaoyuan, 32 Lingkoucun, 33 Beishouling, 34 Anban, 35 Jiangzhai, 36 Shizhaocun, 37 Banpo, 38 Wayaogou, 39 Fulinbao, 40 Kangjia, 41 Zaoshugounao, 42 Xiawanggang, 43 Shenmingpu, 44 Jiuliandun, 45 Qujialing, 46 Dengjiawan, 47 Dadunzi. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

from present-day water buffaloes. Adapted to the cool temperate landscape and vegetation characterising Holocene Northern China, the Short-horned water buffalo clearly represents a Palaearctic, not an Indomalayan taxon.

South of the dividing line separating Northern and Southern China, the River Dan takes its origin in the Qin Mountains flowing southeast to join the Han River, a major tributary of the Yangtze River. On its left bank lies the Neolithic settlement of Xiawanggang (33°01′N, 111°21′E). Here Indomalayan taxa like Sumatran Rhinoceros (*Dicerorhinus sumatrensis)* and Asian elephant (*Elephas maximus*) have been evidenced as well as Giant panda (*Ailuropoda melanoleuca*) (Jia et al., 1977), pointing to warmer climatic conditions and extensive woodlands and bamboo vegetation near the site. The latter can therefore be considered suitable habitat for Red jungle fowl.

2.3. Holocene distribution of Red jungle fowl

The foregoing illustrates that only few Indomalayan taxa occurred in early and middle Holocene Northern China and that these are eurytherm rather than stenotherm. Conversely, not a single species typical of the Southern China (~25°-30°N) and Indochinese Divisions (south of ~25°N) has been identified in Northern Chinese transitional and Neolithic archaeofaunal assemblages. In its present-day tropical distribution range, Red jungle fowl are inhabitants of warm habitats at low and moderate altitudes and usually not exposed to any but slight changes in daily and seasonal temperatures. *Gallus gallus*, therefore, have no cause to make even limited seasonal migrations. However, wild fowl ranging up the valleys and southern slopes of the Himalayas will descend several thousand feet to warmer altitudes following the approach of cold weather (Beebe, 1921, 178).

Besides the availability of suitable habitat, another important but mostly overlooked aspect governing the natural dispersal of *Gallus* is the species' limited flight ability. Inhabiting forested habitats, ground-feeding jungle fowl needs only cover short distances, mainly to escape from immediate danger during daytime or to reach its roosting place a few metres above ground at sunset. However, *Gallus* dispersing to Northern China forcibly needed crossing vast East-West running water courses bordered by steep rock formations, extensive floodplains, swampy vegetation etc., raising the question how of the species coped with major ecogeographical barriers. Beebe (1921) and Delacour (1977) noted that jungle fowl avoid alluvial plains, turning many sections and particularly the lower reaches of the Yangtze and Yellow Rivers and their major tributaries into insuperable obstacles. Migrating jungle fowl along the Mekong River in Thailand illustrate this well: "*In the Chiengsen region the birds are apparently trying to cross the river eastwards, where it is about 700 yards* [=640 m] *across. In crossing, the birds fly up as high as they can go, and then attempt to glide across.*

Table 1

Mammalian taxa evidenced in Holocene sites dating ~11.5–3.0 ka BP in Northwestern and Northern China, based on data published in Bo (2011), Flad et al. (2007), Fu (2000), Hu et al. (2007), Li and Han (1963), Wang (2011), Wu (1993), Yuan and Li (2010), Zhong (2010) and Zhou (1981, 1983a, 1983b, 1992, 1994, 2000).

Region	Northern China																Northwestern China	
Subregion	North China plain										Arid north China						Hexi Corr.	
Sites	Nanzhuangtou (1)	Jiahu (2)	Peiligang (4)	Cishan (5)	Yuhuangding (6)	Wangyin (7)	Dawenkou (8)	Taosi (9)	Baiying (11)	Yinxu (14)	Daihai Region (16)	Shihushan (17)	Miaozigou (18)	Dabagou (19)	Wangmushan poshang (20)	Zhukaigou (21)	Donghuishan (22)	Huoshaogou/ Ganguyan (23)
Dates in ka calBP (ca.)	12.5–11.0	9.0–7.5	9.0–7.0	8.1–7.7	6.5–6.0	6.5–5.5	6.3–4.5	4.3–3.9	4.1–3.7	3.3–3.0	6.7–5.0	6.5–6.4	5.8–5.0	5.8–5.0	5.5–5.0	5.0–3.4	4.0–3.5	4.0–3.0
Taxa	*Palaearctic mammalian taxa*																	
Sus	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Bos		x	x	x	x	x		x	x				x	x		x		x
Bubalus	x	x				x					x				x			
Ovis (+*Ovis/Capra*)		x	x		x			x	x	x						x	x	x
Procapra												x	x	x				
Pseudois																		
Naemorhedus																x		
Gazella																		
Capricornis																		
Cervus																	x	
Cervus elaphus				x					x		x	x	x	x	x	x		
Elaphurus davidianus		x		x	x	x	x		x	x								
Cervus albirostris						x												
Cervus nippon	x	x		x	x	x	x					x		x				
Capreolus				x		x					x	x	x	x	x	x		
Moschus																	x	
Hydropotes		x	x	x	x	x	x		x									
Moschus/ Hydropotes	x																	
Muntiacus		x		x														
Camelus																x		
Equus									x	x				x				x
Canis	x	x	x	x	x	x		x	x	x		x		x	x	x	x	x
Nyctereutes		x				x						x						
Vulpes						x						x						
Cuon												x						
Meles		x	x	x	x	x						x				x		
Arctonyx																		
Mustela												x						
Martes		x																
Lutra						x												
Ursus/ Selenarctos						x						x		x		x		
Ailuropoda																		
Felis		x				x	x		x			x				x		
Panthera				x		x			x									
Marmota																		
Rhizomys																		
Myospalax				x	x							x			x			
Microtus								x										
Cricetulus																		
Sciurus																		
Castor																		
Spermophilus												x			x			
Ochotona												x						
Lepus	x	x		x	x			x				x						
Rhinopithecus																		
Taxa	*Indomalayan mammalian taxa*																	
Macaca				x														
Axis																		
Rusa								x										
Dicerorhinus																		
Paguma				x														
Hystrix							x											
Elephas										x								

	Northwestern China																	Southern China	
	Upper yellow river					Wei river												Dan river	Yunnan
	Zongri (24)	Yangqu Shierdang (25)	Xiangnagou (26)	Dahezhuang (27)	Qinweijia (28)	Xishanping (29)	Baijiacun (30)	Guantaoyuan (31)	Lingkoucun (32)	Beishouling (33)	Anban (34)	Jiangzhai (35)	Shizhaocun (36)	Banpo (37)	Wayaogou (38)	Fulinbao (39)	Kangjia (40)	Xiawanggang (42)	Dadunzi (47)
	5.6–4.0	5.6–4.0	5.6–4.0	4.1–3.9	4.1–3.9	8.0–3.9	7.5–6.3	7.3–6.9	7.0–4.8	7.0–4.5	7.0–4.3	6.8–4.0	6.8–3.9	6.7–5.6	6.5–6.0	5.5–5.0	4.5–4.0	5.0–2.7	3.2
Taxa																			
Sus	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Bos	x		x	x	x	x		x		x	x	x	x	x	x	x	x	x	x
Bubalus							x	x									x	x	
Ovis (+*Ovis/Capra*)				x	x				x				x	x	x		x		x
Procapra	x	x	x				x					x							
Pseudois	x										x								
Naemorhedus								x											
Gazella									x					x	x?				
Capricornis																		x	
Cervus				x		x						x	x						
Cervus elaphus	x	x	x			x	x			x					x	x			
Elaphurus davidianus								x	x										
Cervus albirostris																			
Cervus nippon								x	x		x	x		x	x	x	x	x	
Capreolus	x	x	x					x		x					x	x		x	

Table 1 (*continued*)

Northwestern China																	Southern China	
Upper yellow river					Wei river												Dan river	Yunnan
Zongri (24)	Yangqu Shierdang (25)	Xiangnagou (26)	Dahezhuang (27)	Qinweijia (28)	Xishanping (29)	Baijiacun (30)	Guantaoyuan (31)	Lingkoucun (32)	Beishouling (33)	Anban (34)	Jiangzhai (35)	Shizhaocun (36)	Banpo (37)	Wayaogou (38)	Fulinbao (39)	Kangjia (40)	Xiawanggang (42)	Dadunzi (47)
5.6–4.0	5.6–4.0	5.6–4.0	4.1–3.9	4.1–3.9	8.0–3.9	7.5–6.3	7.3–6.9	7.0–4.8	7.0–4.5	7.0–4.3	6.8–4.0	6.8–3.9	6.7–5.6	6.5–6.0	5.5–5.0	4.5–4.0	5.0–2.7	3.2
x	x	x			x		x	x	x		x	x		x	x		x	x
						x	x		x	x	x		x	x	x			
							x										x	x
			x		x		x					x		x				
x		x	x		x	x			x	x	x	x	x	x	x	x	x	x
						x		x	x	x	x			x		x	x	
							x		x				x	x		x		
											x					x		
								x	x		x		x				x	
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					x		x		x		x	x				x	x	x
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						x					x	x	x	x		x	x	
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x	x	x												x				
					x	x	x		x		x	x	x	x		x		x
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					x				x		x						x	x
																	x	
							x										x	x
							x										x	
								x		x							x	x
																	x	

A large number, however, fall in the river and are drowned" (Giles, 1932). Besides wide water courses, the fact that during the middle Holocene optimum Northern China also witnessed frequent, heavy flooding and large inundations (Liu et al., 2013) certainly imposed additional constraints on *Gallus*' northward dispersal and acclimatisation. Finally, physiological (cold, snow) and biotic barriers (availability of food species, predators, disease) would have taken their toll as well.

In sum, despite marked influence of the warm-humid East Asian Summer Monsoon on climate development in Northern China, Holocene high-resolution archives do not warrant the conclusion that the study area witnessed (sub-)tropical conditions with moderate variation in seasonal temperatures allowing for the continuous presence of Red jungle fowl (*Gallus gallus*). Moreover, given the nearly exclusive Palaearctic species composition in early and middle Holocene archaeofaunas from Northern China (Table 1), it is difficult to imagine that even at the height of the thermal optimum, wild fowl would have found suitable habitat north of ~35°N that allowed for its long-term exploitation and domestication. If true, these observations suggest that despite evidence to the contrary, purported chicken bones in Northern Chinese archaeological sites dated to ~11.5–4.5 ka calBP are instead derived from a different bird species.

3. Zooarchaeology

Avifaunal specialists studying bird bones from prehistoric Asia are aware of the fact that pheasants in general and the ubiquitous Common or Ring-necked pheasant (*Phasianus colchicus*) in particular must have been a widely available food resource to Pleistocene and Holocene foragers and farmers inhabiting Central and East Asia. In China, for instance, 18 subspecies of *Phasianus colchicus* and an actual population counting tens of millions of birds have been reported (Cheng, 1987; McGowan, 1994). Based on published archaeofaunal accounts, however, it would seem as if the Holocene inhabitants of Northern China were far better acquainted with *Gallus* than with *Phasianus,* given the much lower frequency of the latter taxon in the archaeofaunal record of that region. The high population density of this species and the fact that Common pheasants are known to frequent anthropogenic environments and cultivated plots in search of food renders this situation counterintuitive.

3.1. Osteomorphology

Contrary to statements in the literature, different genera and species of galliform birds can be distinguished based on morphological criteria (e.g., Erbersdobler, 1968; Tomek and Bocheński, 2009; Eda and Inoué, 2011; Deng et al., 2013). Embedded in the tradition of vertebrate palaeontology, earlier zooarchaeological work in China figured single *'Gallus'* specimens, e.g. from middle Neolithic Banpo (Li and Han, 1963) and early Neolithic Cishan (Zhou, 1981). Morphological re-assessment of these bones showed that they represented exclusively pheasants (Peters, 1998; Deng et al., 2013; Eda et al., 2016; our Table 2). Relative to the key site of Cishan, this conclusion was reinforced by direct analysis of specimens housed at the Institute of Archaeology, Chinese Academy of Social Sciences, Beijing. Subsequently, we re-evaluated additional specimens depicted in the literature as well as bone samples from other Holocene sites, with a focus on Northern China. The results of our study are presented in Table 2 that incorporates key data published by other researchers. The overwhelming majority of Neolithic and Bronze Age finds identified originally as *Gallus* cannot be confirmed. Eda et al. (2016, Table 1) reached the same conclusion based on their analysis of selected Phasianid specimens (femur, tibiotarsus, tarsometatarsus) from 18 Holocene sites.

Medium to large Phasianid species distributed across Northern and Northwestern China include: Blood Pheasant (*Ithaginis cruentus*), Koklass Pheasant (*Pucrasia macrolopha*), Golden Pheasant (*Chrysolophus pictus*), Temminck's Tragopan (*Tragopan temminckii*), Reeves's pheasant (*Syrmaticus reevesii*), Brown Eared-pheasant (*Crossoptilon mantchuricum*) and the ubiquitous Common or Ring-necked Pheasant (*Phasianus colchicus*) (Cheng, 1987). One key morphological feature distinguishing *Phasianus colchicus* from *Gallus* is the presence of a *Foramen pneumaticum* at the greater trochanter of the femur (e.g. Tomek and Bocheński, 2009; Eda and Inoué, 2011). Except for a single specimen from Late Neolithic Xiawanggang (see below), all Neolithic and Bronze Age femora analysed by Eda et al. (2016) and those in this study exhibited this foramen.

A morphological analysis of modern comparatives, however, revealed that this foramen is missing in the genera *Pucrasia, Tragopan* and *Syrmaticus* as well, which excludes these taxa as possible identifications for Neolithic and Bronze Age femur specimens. Complementing this observation with other osteological criteria, for instance the morphology of the tarsometatarsus or the position, size and shape of the tarsometatarsal spur in male birds, we conclude that most archaeological specimens do not fit their homologues in the genera *Ithaginis*, *Chrysolophus* and *Crossoptilon*. In sum, a re-evaluation of early and middle Holocene specimens depicted in the literature and housed at the Institute of Archaeology, Chinese Academy of Social Sciences, Beijing (Table 2) excludes *Gallus* as possible identification while indicating that a high proportion of avifaunal assemblages from Northern and Northwestern China are made up of *Phasianus colchicus*.

In their study, Eda et al. (2016) noted a candidate chicken bone at Late Neolithic ~5.0–4.0 ka calBP Xiawanggang in the Yangtze River basin. These authors also mention two candidate chicken bones from the Proto-Zhou site of Zhaoshugounao (3.2–3.0 ka calBP) located in the Wei River valley. In the North China Plain, chicken appears present in a broadly contemporaneous context at Yinxu, the residential city of the late Shang Dynasty (1320-1046 BCE) (Deng et al., 2013).

3.2. Osteometry

Comparative osteometry can be useful for providing a secure morphological identification and confirming domestication status. Zhou (1981, Table 3) thus compared the Greatest Length of tarsometatarsi from Neolithic Cishan with metrical data from modern comparatives including Common pheasant (*Phasianus colchicus* subsp. *karpowi)*, Koklass pheasant (*Pucrasia macrolopha*) and Edward's pheasant (*Lophura edwardsii)*. The fact that the tarsometatarsi of modern *Phasianus colchicus* were significantly shorter than their homologues in modern *Gallus* reinforced the author's conclusion that the ancient finds from Cishan represented chickens.

Our analysis of the Greatest Length (GL) of the tarsometatarsus (according to von den Driesch, 1976) in 22 adult male *P. colchicus* collected in Germany[3] produced values between 69.5 and 81.0 mm (Table 3). Comparison with values obtained for *P.c. karpowi* by Zhou (1981, Table 3; 59.0–63.0 mm), however, illustrates birds with distinctly shorter legs. One possible explanation for this discrepancy is variability in size due to the species' wide distribution range across Asia, but this is not consistent with other lines of evidence. For instance, body weight in male *P.c. karpowi* (1000–1312 g; Cheng, 1978) overlaps considerably with that in its European relative (1145–1565 g; Glutz von Blotzheim et al., 1973). A closer look at Zhou's data revealed that his values were not obtained on macerated (dry) bone specimens but reproduced from the ornithological standard work edited by Cheng (1978). This compendium records the Tarsal Length (TL) in birds based on measurements of bird skins (Cheng, 1978, Pl. 6, no. 5). As such, TL values are often lower than GL measurements because small articular protrusions of the tarsometatarsus will not be included as they are ‘hidden’ in the joint.

Table 3 recapitulates the TL values published by Cheng (1978) for the major (sub-) species of pheasants confined to Northern and Northwestern China and compares this information with GL measurements from macerated specimens in modern collections. Our data confirm that TL and GL values can differ considerably and they illustrate that modern Chinese *P.c. karpowi, P.c. kiangsuensis, and P.c. torquatus* clearly overlap in size with European pheasants. Consequently, Zhou's assumption that the Cishan tarsometatarsi measuring between 70.0 and 86.5 mm fit male *Gallus* and not *Phasianus* must be rejected. As mentioned before, morphological analysis of the femora implied that the genera *Pucrasia, Tragopan* and *Syrmaticus* were absent from the assemblages studied. Metrical analysis of the tarsometatarsus allows extending this conclusion to the smaller and more slender-built genera *Ithaginis* and *Chrysolophus*. Because of its clearly larger size (Table 3), the genus *Crossoptilon* has been identified in the avifaunal record of the study area (Hou, 1989).

Finally, Zhou's conclusion that the remains pertained to *Gallus gallus domesticus* because the Cishan specimens were intermediate in size between larger-sized modern domestic chickens and smaller-sized wild fowl can no longer be maintained in view of the exclusive presence of pheasants in this assemblage (Eda et al., 2016; our Table 2).

3.3. Flock management and health status

Relative to Neolithic Cishan and Wangyin, *Gallus* has been considered domestic because agriculture was already practiced at considerable scale, including cultivation of millet (Lu et al., 2009) and pig husbandry (Larson et al., 2010; Cucchi et al., 2011). However, the premise ‘practicing agriculture’ does not allow reaching the logically certain conclusion that poultry keeping was part of it. According to us, postulating chicken farming presumes human management and should be reflected in the demographic profiles and particularly in the male to female ratio. In traditional poultry husbandry intended for local consumption, adult hens (laying, brooding) clearly outnumber cocks of the same age, surplus males usually being eliminated from the flocks prior to reaching sexual maturity in order to reduce aggressiveness in the coop. In this respect, human management mimics the situation in free-living Red jungle fowl during reproduction, with a reported ratio of cocks to hens of 1 to 3–5 (Raethel, 1988, 574).

To assess the males to females ratio in Phasianids, zooarchaeologists can consider (*i*) the pronounced sexual dimorphism expressed in the length of long bones, (*ii*) the tarsometatarsal spur present in mature cocks and absent in hens except in old birds (Peters, 1997), and (*iii*) the presence of medullary bone in the marrow cavity of long bones. The latter serves as calcium repository in egg-laying hens and is recognized easily in fragmentary specimens. In complete tarsometatarsi, however, the first two criteria allow sexing specimens securely, whilst the morphology of the articulations as well as texture of the bone surface and shape and

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[3] The earliest common pheasants introduced to Europe belong to the subspecies *P.c. colchicus* which occurs naturally in the Caucasus region. From the 18th century CE onwards, however, other subspecies were brought to Europe as well and crossed with *P.c. colchicus*, predominantly Central Asian *P.c. mongolicus* and East Asian *P.c. torquatus* (Glutz von Blotzheim et al., 1973, 326).

Table 2

Overview of Chinese sites with remains attributed to '*Gallus*' in literature that could be (re-)evaluated either by study of the literature and re-assessment of the specimens figured in these faunal reports and/or direct analysis of specimens curated at the Institute of Archaeology, Chinese Academy of Social Sciences (IA, CASS), Beijing[a,b]. Dating of the archaeofaunas is in calibrated ka before Present and based on published dates in Flad et al., 2007 (Table 1) and Liu and Chen (2012) as well as ^{14}C-dates in excavation and other reports. Column 3 provides information about the Galliform bones in the original publications and the site's cultural sequence. Column 4 summarizes the state-of-the-art. Site numbers as in Fig 1.

Northern China – North China plain			
Sites and their dating	Literature	Finds reported and stratigraphy of the sites	State-of-the-art
Nanzhuangtou (1) 12.5–10.5 ka calBP Hebei Province; site occupation mainly 11.5–11.0 ka calBP (Yang et al., 2012)	Baoding Prefectural Administration et al. (1992) Zhou (1992) Hebei Provincial Cultural Relics Institute et al. (2010)	*Bone specimens reported*: clavicula, humerus, radius, ulna, femur, tibiotarsus, tarsometatarsus. *Identification:* Wild fowl species, *Gallus* *Stratigraphy*: This is a multi-layered site with extensive historical occupation dating to the Warring States Period (476-221 BCE).	- Yuan and Li (2010) identified the bird remains from Nanzhuangtou only to the family level (Phasianidae). Contrary to earlier work, however, these faunal specialists did not confirm the presence of chickens at the site. - All specimens re-studied by Eda et al. (2016, Table 1, Fig. 2C) were classified as non-chicken.
Jiahu (2) 9.0–7.8 ka calBP Henan Province Peiligang Culture	Henan Institute of Cultural Relics and Archaeology (1999)	*Bone specimens reported*: 19 elements, including humerus, ulna, femur, tibiotarsus, tarsometatarsus. *Identification*: *Phasianus colchicus*; verifiable since specimens figured in the publication. *Stratigraphy*: Neolithic occupation covered with levels dating to the Han (202 BCE-220 CE) and Song (960–1279 CE) Dynasties.	- All specimens figured in literature are morphologically pheasants. - Analysis JP 2012: *Phasianus colchicus:* coracoid, femur - All femora, tibiotarsi and tarsometatarsi (n = 30) have been identified as non-chicken (Eda et al., 2016, Table 1).
Xinglongwa (3) 8.0–7.0 ka calBP Neimenggu Province Xinglongwa Culture	Neimeng Archaeological Team, Institute of Archaeology, CASS (1997)	*Bone specimens reported*: none. *Stratigraphy*: The Xinglongwa occupation is superposed by levels dating to the Hongshan (6.5–5.0 ka calBP) and the Lower Xiajiadian (4.3–3.6 ka calBP) Cultures.	- Analysis JP 2012: *Phasianus colchicus*: coracoid, several tarsometatarsi - Eda et al. (2016, Table 1) identified one tibiotarsus and 43 tarsometatarsi as non-chicken, whilst candidate chicken bones were absent from the site.
Peiligang (4) 9.0–7.0 ka calBP Henan Province Peiligang Culture	Henan Working Team, Institute of Archaeology, CASS (1984) West and Zhou (1988, Table 1)	*Bone specimens reported*: bones, tarsometatarsus. *Identification*: *Gallus*; not verifiable since specimens not figured. *Stratigraphy*: The Peiligang Culture occupation is located below top soil.	- In the original publication the remains were considered representing chicken because of their size. However, the use of size as distinctive criterion is problematic (Deng et al., 2013; see also text).
Cishan (5) 8.0–7.7 ka calBP Hebei Province Cishan-Beifudi Culture	CPAM, Hebei Provincial Relics Preservation Station et al. (1981) Zhou (1981) West and Zhou (1988, Table 1)	*Bone specimens reported*: clavicula, humerus, ulna, radius, femur, tibiotarsus, tarsometatarsus. *Identification*: *Gallus gallus domesticus;* verifiable in part because some humeri, femora, tibiotarsi and metatarsi have been figured. *Stratigraphy*: There is a Shang Dynasty (1600-1046 BCE) layer overlying the two Neolithic levels.	- Yuan (2010) and Deng et al. (2013) pointed out that the evidence presented by Zhou (1981) to claim the presence of *Gallus* is not tenable, necessitating revision of all Cishan finds. - Analysis JP 2012: *Phasianus colchicus*: humerus, tibiotarsus. In addition, we noted that the specimens figured on Plates 9 and 10 in Zhou (1981) exhibit the morphology of pheasants and are likely *P. colchicus* as well. - Five metatarsi displayed at the Handan City Museum, Hebei and labelled "the oldest domestic chicken in the world" were re-analysed by Eda et al. (2016, Table 1) and classified as non-chicken.
Yuhuangding (6) 6.5–6.0 ka calBP Shandong Province Beixin and Dawenkou Cultures	Shandong Cultural Relics Institute (2010) Zhong (2010)	*Bone specimens reported:* humerus, femur, tarsometatarsus. *Original identification: Gallus* sp.*;* not verifiable since the specimens have not been figured. *Stratigraphy:* The bones all originate from the late Beixin and early Dawenkou Culture levels. However, Yuhuangding also exhibits extensive Han Dynasty (202 BCE-220 CE) occupation.	- The faunal report states that the remains have been identified as chicken because most of the specimens pertain to male birds. Not only is this argument invalid (Deng et al., 2013), it is also counterintuitive (see text).
Wangyin (7) 6.5–5.5 ka calBP Shandong Province Late Beixin Culture and Dawenkou Culture	West and Zhou (1988, Table 1) Institute of Archaeology, CASS (2000) Zhou (2000)	*Bone specimens reported*: femur, tibiotarsus, tarsometatarsus. *Identification*: *Gallus gallus domesticus*; not verifiable since the specimens have not been figured. *Stratigraphy*: The Beixin and early Dawenkou Culture layers are located below an extensive, late Dawenkou graveyard.	- Zhou (2000) mentions the presence of domestic chicken at the site, but the evidence on which this is based is not presented (Deng et al., 2013). Prof. J. Yuan, Institute of Archaeology, CASS Beijing noted the presence of *Phasianus* at this site (pers. comm., 2015). - Analysis JP 2012: This site produced a large collection of pheasant bones

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Table 2 (*continued*)

Northern China – North China plain			
Sites and their dating	Literature	Finds reported and stratigraphy of the sites	State-of-the-art
			(mainly of *Phasianus colchicus*) including 36 humeri, 27 coracoids, ten carpometacarpi, 17 femora and twelve tarsometatarsi. - All femora and tarsometatarsi analysed by Eda et al. (2016, Table 1) were classified as non-chicken.
Dawenkou (8) 6.3–4.5 ka calBP Shandong Province Dawenkou Culture	Shandong Cultural Relics Institute (1974) Li (1974) West and Zhou (1988, Table 1)	*Bone specimens reported*: tarsometatarsus, bones. *Identification: Gallus;* verifiable in part because some specimens have been figured in the excavation report. *Stratigraphy*: The bones originate from a tomb.	- Li (1974) assigned the bones to *Gallus* but this identification must be rejected since the specimens figured in his contribution correspond to pheasants (Deng et al., 2013).
Taosi (9) 4.3–3.9 ka calBP Shanxi Province Longshan Culture	Shanxi Archaeological Team (1980) West and Zhou (1988, Table 1) Bo (2011)	*Bone specimens reported*: femur, tarsometatarsus. *Identification*: *Gallus*; not verifiable since specimens were not figured. *Stratigraphy*: Neolithic occupation is located partly below top soil and partly below levels of Western Zhou (1046-771 BCE) and subsequent Dynasties.	- Bo (2011) refrained from assigning the Phasianid remains from Taosi to either chicken or pheasant since she considered it hard telling the difference. - Eda et al. (2016, Table 1) did not find any candidate chicken bones in this small assemblage.
Shantaisi (10) 4.2–3.8 ka calBP Henan Province mainly Longshan Culture	China-US Joint Archaeological Team (2010)	*Bone specimens reported*: none. *Stratigraphy*: This is a multi-layered site with Late Neolithic and historical occupations dating to the Shang Dynasty (1600-1046 BCE).	- There is no mention of chicken bones in the excavation report - Analysis JP 2012: *Phasianus colchicus*: coracoid, tarsometatarsus - Eda et al. (2016, Table 1) only observed remains of pheasants in this small assemblage.
Baiying (11) 4.1–3.7 ka calBP Henan Province mainly Longshan Culture	CPAM of Anyang Prefecture of Henan Province (1983) Zhou (1983a) West and Zhou (1988, Table 1)	*Bone specimens reported*: femur, tarsometatarsus. *Identification*: *Gallus*; not verifiable since specimens were not figured. *Stratigraphy*: There is a Western Zhou Dynasty layer (1046-771 BCE) overlying the Longshan Culture deposits.	- Zhou (1983a) considered the remains pertaining to chicken simply because domestic chicken had already been evidenced at Baiying before (Deng et al., 2013).
Erlitou (12) 3.7–3.4 ka calBP Henan Province Erlitou-Erligang Cultures	Institute of Archaeology, CASS (1999) Yang (2008)	*Bone specimens reported:* 42 bones, including coracoid, humerus, femur, tarsometatarsus etc. *Identification: Gallus*; not verifiable since the specimens have not been all figured. *Stratigraphy:* The bones all originate from the Erlitou and Erligang Culture levels. However, besides Neolithic levels the site of Erlitou also exhibits a Han Dynasty (202 BCE-220 CE) occupation.	- Eda et al. (2016, Table 1) identified one tibiotarsus and ten tarsometarsi as non-chickens.
Yanshishangcheng (13) 3.6–3.4 ka calBP Henan Province Early Shang Dynasty (1600-1400 BCE)	Luoyang Hanwei City Ruins Team, Institute of Archaeology, CASS (1984) Du and Wang (2004)	*Bone specimens reported*: none. *Stratigraphy:* This is a multi-layered site with extensive historical occupation dating to the Ming Dynasty (1368–1644 CE).	- There is no mentioning of chicken bones in the excavation report. - Analysis JP 2012: *Phasianus colchicus*: tarsometatarsus - Amongst the femora, tibiotarsi and tarsometatarsi analysed, Eda et al. (2016, Table 1) identified only non-chicken remains.
Yinxu (14) 3.3–3.0 ka calBP Henan Province Late Shang Dynasty (1320-1046 BCE)	Hou (1989) Institute of Archaeology, CASS (1994a) Chen (1994)	*Bone specimens reported*: cranium, tarsometatarsi. *Identification*: *Gallus gallus domesticus.* *Stratigraphy*: Later levels overly the late Shang Dynasty occupation.	- Yinxu was the capital of the Late Shang Dynasty (1320-1046 BCE). Deng et al. (2013) identified a skull fragment as *Gallus* based on the specimen's comparably small *Condylus occipitalis* as well as its deep and large *Fossa occipitalis*. - Eda et al. (2016, Table 1) noted the presence of pheasants as well.
Dasikongcun (15) 3.3–3.0 ka calBP Henan Province Late Shang Dynasty	Ma et al. (1955)	*Specimens reported*: Two chicken skeletons in different tombs. *Identification*: *Gallus*; not verifiable since the specimens have not been figured.	- The cemetery of Dasikongcun is considered the burial ground of the Late Shang Dynasty kings (1320-1046 BCE). See text for discussion of these finds.
Northwestern China – Wei River Valley			
Baijiacun (30) 7.5–6.3 ka calBP	Institute of Archaeology, CASS (1994b) Zhou (1994)	*Bone specimens reported*: mandible, vertebra, scapula, femur. *Original identification*: *Gallus gallus*; not	- Zhou (1994) argued that the remains pertain to chicken simply because they look similar to the finds at that

Table 2 (*continued*)

Northern China – North China plain			
Sites and their dating	Literature	Finds reported and stratigraphy of the sites	State-of-the-art
Shaanxi Province (Pre-)Yangshao Culture		verifiable since the specimens have not been figured. *Stratigraphy*: The bones all originate from Levels II and III. The pre-Yangshao Culture occupation phase is located below top soil.	time already excavated at Banpo, Cishan and Beishouling (Deng et al., 2013). However, this conclusion must be rejected because all specimens reported from Cishan, Banpo and Beishouling are pheasants (Eda et al., 2016; this Table).
Guantaoyuan (31) 7.3–6.9 ka cal BP Shaanxi Province Pre-Yangshao Culture	Shaanxi Provincial Institute of Archaeology et al. (2007) Hu et al. (2007)	*Bone specimens reported*: 12 bones + 47 bones of uncertain stratigraphic position. *Original identification*: *Gallus* sp.; not verifiable since the specimens have not been figured. *Stratigraphy*: This is a multi-layered site with extensive Neolithic inhabitation and historical occupation dating to the Ming Dynasty (1368–1644 CE). The 12 bones originate from Pre-Yangshao occupation Phases II and III.	- Hu et al. (2007) concluded that the remains pertain to chicken since they compare well with the figured specimens excavated at Banpo (Deng et al., 2013). However, the specimens excavated at Banpo represent pheasants (s. below).
Beishouling (33) 7.0–4.5 ka calBP Shaanxi Province Yangshao Culture	Institute of Archaeology, CASS (1983) Zhou (1983b) West and Zhou (1988, Table 1)	*Specimens reported*: Two skeletons in a pot. *Identification: Gallus gallus domesticus;* verifiable in part because some of the remains have been figured. *Stratigraphy:* An extensive Han Dynasty (202 BCE-220 CE) occupation superposes the Yangshao levels.	- The remains were assigned to chicken (Zhou, 1983b), but this identification must be rejected since the specimens figured in the publication correspond to pheasants (Deng et al., 2013).
Anban (34) 7.0–4.3 ka calBP Shaanxi Province Yangshao and Longshan Cultures	Dept. of Archaeology, Northwest Univ. (2000) Fu (2000)	*Bone specimens reported*: humerus, tarsometatarsus. *Identification*: *Gallus domesticus*; not verifiable since specimens were not figured. *Stratigraphy*: All *Gallus* finds would originate from Neolithic strata, but there are Zhou (1046-256 BCE) and Han Dynasty (202 BCE-220 CE) levels overlying the Neolithic occupation.	- The remains were considered representing chicken by Fu (2000) because the size of the Anban tarsometatarsus equalled that in similar finds from Cishan and Banpo (Deng et al., 2013). - Flad et al. (2007) had already expressed doubts about this identification since they addressed the finds as 'chicken (pheasant?)'.
Banpo (37) 6.7–5.6 ka calBP Shaanxi Province Yangshao Culture	Institute of Archaeology and Chinese Academy of Sciences (1963) Li and Han (1963) West and Zhou (1988, Table 1)	*Bone specimens reported*: femur, tibiotarsus, tarsometatarsus. *Identification:* tentatively as *Gallus* sp.*;* verifiable in part since two specimens have been figured by Li and Han (1963, Pl. 198).	- Banpo has an alluvial setting, which is hardly suitable for *Gallus* (see text). Although certainly not intended by the authors, their tentative identification likely paved the way for other *Gallus* finds in the Neolithic Yellow River basin. - The two specimens figured, i.e. one tarsometatarsus (Li and Han, 1963, Pl. 198, Figs. 8A, B) and one tibiotarsus (Figs. 9A, B) are morphologically pheasants, most likely *Phasianus colchicus*.
Fulinbao (39) 5.5–5.0 ka calBP Shaanxi Province Yangshao culture	Baoji Archaeological Team (1993), Wu (1993)	*Bone specimens reported*: bones. *Identification*: *Phasianus colchicus;* not verifiable, since specimens were not figured. *Stratigraphy*: There are historic levels overlying the Yangshao Culture occupation.	- Flad et al. (2007) reported the presence of *P. colchicus* at this site.
Zaoshugounao (41) 3.2–3.0 ka calBP Shaanxi Province Proto-Zhou Culture	School of Cultural Heritage, Northwest Univ. et al. (2013)	*Bone specimens reported:* none *Stratigraphy:* This is a multi-layered site with Neolithic and historical occupations dating to the Tang Dynasty (618–907 CE).	- Analysis by Eda et al. (2016, Table 1) of selected elements (femur, tibiotarsus, tarsometatarsus) showed that one femur and six tarsometatarsi represent non-chicken remains, whilst two tibiotarsi can be considered candidate chicken bones.
Southern China			
Xiawanggang (42) 5.0–2.7 ka calBP Henan Province Yangshao Culture till Western Zhou period	Jia and Zhang (1977) Henan Provincial Institute of Cultural Relics et al. (1989)	*Bone specimens reported*: none. *Stratigraphy*: This is a multi-layered site with extensive Neolithic and historical occupations dating to the Western Zhou Period (1046-771 BCE).	- There is no mentioning of chicken bones in the original report. - Eda et al. (2016, Table 1) identified a single candidate chicken femur from this site. The specimen was found in the Longshan layer dating to between 5.0 and 4.0 ka calBP.

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Table 2 (*continued*)

Northern China – North China plain			
Sites and their dating	Literature	Finds reported and stratigraphy of the sites	State-of-the-art
Shenmingpu (43) 2.2–2.0 ka calBP Henan Province Early Han Dynasty 202-141 BCE	Deng et al. (2013)	*Bone specimens reported*: Partial skeleton of chicken in a tomb. *Identification*: *Gallus domesticus*.	
Jiuliandun (44) 2.5–2.2 ka calBP Hubei Province Warring States Period 476-221 BCE	Hubei Provincial Museum (2007)	*Bone specimens reported*: several incomplete skeletons in Tomb 1. *Identification*: none.	- No report exists about the Jiuliandun fauna. - Analysis JP 2012: *Gallus domesticus*: coracoid, two humeri, femur and two tibiotarsi.
Quijaling (45) 5.0–4.6 ka calBP Hubei Province Quijaling Culture	Institute of Archaeology, CAS (1965) West and Zhou (1988, Table 1)	*Finds reported*: pottery figurines of fowl *Identification: Gallus*; only verifiable in part, since bone finds have not been figured. *Stratigraphy*: No post-Quijaling occupation.	- Plate LIV, Fig. 8 shows a bird figurine identified as *Gallus*. However, the absence of wattles and a comb (or any indication that these might have been broken off during excavation) makes this identification not very likely.
Dengjiawan (46) 4.5–4.0 ka calBP Hubei Province Shijiahe Culture	Wu (2001)	*Specimens reported*: Pottery figurines of fowl. *Identification: Gallus domestica* (Pl. 1, Fig. 12) and *Phasianus colchicus torquatus* (Pl. 1, Fig. 14).	- The assemblage of figurines depicted in Wu (2001, Plate 1) is rich in species and includes subtropical taxa including *Gallus, Bambusicola* and *Pavo*. Whether Gallus is domestic or not is difficult to decide based on the depiction (see text for discussion).
Dadunzi (47) 3.2 ka calBP Yunnan Province Dadunzi Culture	Yunnan Provincial Museum (1977), Zhang (1985), West and Zhou (1988, Table 1)	*Bone specimens reported*: tarsometatarsus, pottery figurines and a chicken-shaped pot. *Identification*: *Gallus*; the bone specimen is not verifiable since not figured. *Stratigraphy*: Two Late Neolithic occupation stages are located below top soil. A single ^{14}C-date comes from charcoal found in a post-hole of a dwelling associated with early occupation.	- Older publications considered domestic chicken to be present because of the chicken-shaped pot (Deng et al., 2013). However, Red jungle fowl (*Gallus gallus*) was distributed across Yunnan Province during that period as well. Thus, whether *Gallus* is wild or domestic birds is inconclusive. Detailed analysis of the Phasianid bones associated with this culture is crucial, since Yunnan Province could be a region of *Gallus* domestication.

[a] J. Peters compared bone specimens figured in the literature and housed at the Institute of Archaeology, Chinese Academy of Social Sciences (CASS) with reference skeletons from the Bavarian State Collection of Anthropology and Palaeoanatomy, Munich; H. Deng et al. (2013) verified identification of bone specimens with reference skeletons available at the Institute of Archaeology, CASS, Beijing.

[b] Apart from the sites listed here, 'chickens' have been reported from many other sites (e.g. Ren, 1996), but verification is impossible due to poor documentation (Deng et al., 2013). This applies for instance to the sites of Machengzi (Liaoning Institute of Cultural Relics and Archaeology, Benxi Museum, 1994), Beixin (Shandong Archaeological Team, Institute of Archaeology, CASS, 1984), Caiyuanzi and Mopandi (Yunnan Provincial Institute of Cultural Relics and Archaeology et al., 2003), Dongying (Hu, 2010), Shishanzi (Anhui Provincial Institute of Archaeology (1992)), Hougang (Anyang Archaeological Team, Institute of Archaeology, CASS, 1985), Kangjia (Liu et al., 2001), Longgangsi (Wu, 1990), Zaojiaoshu (Yuan, 2002), Zuojiashan (Chen, 1993), Qianbuxia (Kong, 2000), Xishanping (Zhou, 1999; Flad et al., 2007), Dadiwan (Qi et al., 2006), Yinjiacheng (Lu et al., 1990) and Zengpiyan (Yuan, 2003).

size of the spur enable distinguishing between infantile, juvenile, young-adult and mature birds.

Considering Early Neolithic Cishan once more, remains of adult male birds largely dominate the assemblage (Zhou, 1981, Table 2). This pattern has been observed in other Neolithic sites and interpreted as a conscious choice by flock keepers, with hens being

Table 3
Metrical comparison of medium to large-sized Phasianid species and several subspecies of *P. colchicus* confined to Northern and Northwestern China. Tarsus Lengths of ♀♀ and ♂♂ pheasants and *P. colchicus* subspecies from China according to Cheng (1978) and for *P. colchicus* from Germany according to Glutz von Blotzheim et al. (1973). Greatest Length values of tarsometatarsi were obtained with modern specimens from the Bavarian State Collection of Anthropology and Palaeoanatomy, Munich, Smithsonian Institution, Washington, Louisiana State University Museum of Natural Science, Baton Rouge, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, and Institute of Archaeology, Chinese Academy of Social Sciences, Beijing. Table S2 provides more detail about the modern comparatives. M. Eda (Hokkaido University, Japan) kindly provided measurements of pheasant specimens and of *P. colchicus karpowi* in particular.

Taxon		Tarsus length ♀	n	Tarsometatarsus GL ♀	n	Tarsus length ♂	n	Tarsometatarsus GL ♂	n
Blood Pheasant	*Ithaginis cruentus*	58–63	13	63.8	1	61–68	28	64.8	1
Koklas Pheasant	*Pucrasia macrolopha*	46–60	15	–		57–69	10	69.1–70.8	2
Golden Pheasant	*Chrysolophus pictus*	68–76	5	66.9–84.4	5	73–75	5	68.0–77.9	7
Temminck's Tragopan	*Tragopan temminckii*	58–66	5	65.9–69.8	2	71–76	5	80.2–90.7	2
Reeves's Pheasant	*Syrmaticus reevesii*	66	1	66.2–69.0	6	73–83	10	79.9–86.2	6
Common Pheasant	*Phasianus colchicus* (Germany)	56–64	13	56.3–70.2	31	64.0–77.0	58	69.1–81.0	22
	P. colchicus karpowi	46–55	8	60.2–62.7	2	59.0–63.0	10	69.2–74.3	5
	P. colchicus kiangsuensis	57–58	2	69.0	1	61.0–65.0	2	–	–
	P. colchicus torquatus	53–62	8	66.5	1	66.0–72.0	10	68.0–80.0	3
Brown Eared-Pheasant	*Crossoptilon mantchuricum*	89–97	8	84.6–95.8	3	92.0–101.0	8	97.6–101.5	2

raised for egg production and cocks for meat, whereby the latter may even have been used in religious rites (Ren, 1996). As mentioned above, keeping adult cocks in numbers is counterproductive, not only for behavioural reasons but also because feeding cocks predestined to meat consumption into adulthood is – economically speaking – not profitable. Moreover, meat production in early domestic *Gallus* (which was still close to the wild form) may not have been particularly rewarding, considering that brooding cycles and offspring per cycle number few. Furthermore, live weights in early breeds may still have been close to that in the wild form, ranging between 485–1050 g in females and 672–1450 g in males (McGowan, 1994). Contrary to Zhou (1981), Ren (1996) and other authors and independently of the galliform species dealt with in Northern China, the dominance of adult male birds in Neolithic assemblages does not support their conclusion of human-manipulated flocks. Rather, we consider such pattern indicative of fowling, male birds being easier targets due to their larger size, colourful plumage, and conspicuous courtship behaviour, whilst hens and chicks benefit from protective mimicry and hiding behaviour. Moreover, Northern China witnessed millet cultivation since the early Holocene (Yang et al., 2012), a highly nutritional staple attractive to ground-feeding birds including *P. colchicus*. High numbers of pheasant remains in archaeological assemblages can therefore be best explained by protection of agricultural plots against crop raiders.

Another issue in poultry farming is the health status in populations managed by humans. Although the life span in domestic chickens is comparably short and most health problems not expressed in their skeleton, bone specimens exhibiting pathologies are regularly encountered in *Gallus* assemblages (e.g. von den Driesch and Pöllath, 2000). Conditions observed mainly concern lesions due to traumas related to captivity and handling by humans, such as fractures, but ancient chicken populations also suffered from conditions like arthritis and avian osteopetrosis (or thick leg disease) caused by the Avian Leukosis Virus (ALV) (Peters, 1997). Most striking, therefore, is the fact that the galliform remains analysed by us (Table 2) revealed no bone lesions regularly encountered in domestic populations.

3.4. *Wild or domestic: the cultural context*

Like in most other species, difficulties arise in separating osseous remains of the wild from the domestic form if the finds originate from sites located in the native distribution of the wild ancestor (Dobney et al., 2013; Peters et al., 2013). One phenomenon indicative of a species' domestic status in the natural range of the wild ancestor, however, is animals deposited in funerary contexts. Indeed, to accompany the deceased on their last journey, farming communities have since the Neolithic selected mostly barnyard species as mortuary offerings ‘readily at hand’. The deposition of chickens *in toto* and sometimes even plucked in tombs and graves as well as the use of birds or parts thereof in offerings is a widespread custom as well, reported not only within the Southeast Asian native distribution of Red jungle fowl, e.g. at 3.0–2.0 ka calBP Thai Non Nok Tha (Higham, 1975) and Ban Non Wat (Higham and Kijngam, 2010, 2012) or Cambodian Phum Snay (2.2–1.7 ka calBP; O'Reilly et al., 2006), but also well beyond this range, e.g. in prehistoric and Roman Europe (Lignereux et al., 1995; Hochmuth et al., 2005).

Given the aforementioned absence of *Gallus gallus* in Northern China, birds intentionally deposited in funerary architecture and identified as chicken likely represent domesticates. This applies for instance to the finds recovered from the royal tombs at Jiuliandun and Shenmingpu dating respectively to the Warring States period and the Early Han Dynasty (Table 2). Of particular interest here is the fact that amongst the grave goods unearthed from the burial ground of the late Shang Dynasty Kings at Dasikongcun, two chicken skeletons dating ~3.2 ka calBP have been reported (Ma et al., 1955). Osteological details are lacking, but the archaeological context strongly suggests that we are dealing with *Gallus*, rather than *Phasianus*. Of course, considering the elite status of the persons interred at Dasikongcun, the possibility of Red jungle fowl being delivered to the royal household from (sub-)tropical China cannot be entirely ruled out, but this is not very likely given the distance. Moreover, other domestic animals including horses (with chariots) have been deposited in the royal tombs as well. Whether these birds were predestined as grave goods due to chickens at that time being particularly valued cannot be answered for the moment. However, the contemporaneity of these skeletons with isolated bone finds of chickens at the site of Yinxu allows postulating that Shang Dynasty farming communities played a role in the dispersal of *Gallus* in Northern China.

In summary, re-analysis of galliform bones depicted in publications and housed in archaeological collections at the Institute of Archaeology, Chinese Academy of Social Sciences, Beijing, suggest that all early and middle Holocene finds from Northern China hitherto classified as *Gallus* are instead derived from pheasants, and mainly *Phasianus colchicus*. Moreover, the predominance of adult males and the lack of bone pathologies usually associated with poultry farming in these assemblages contradict the hypothesis of chicken husbandry in Neolithic Northern China as well. Our re-evaluation suggests that the advent of poultry husbandry in this region postdates the middle Holocene thermal optimum and that chicken farming gained foothold in local food economies since the late Shang Dynasty (1320-1046 BCE).

4. Chickens in iconography and early writing

Apart from osseous remains in archaeological contexts, human interest in chickens is also expressed in iconography. Renowned early records comprise clay figurines in Late Neolithic contexts of the Shijiahe Culture at Dengjiawan (34°28′N, 109°43′E) on the middle Yangtze River. Found together with large amounts of slag and dating to ~4.5–4.0 ka calBP, these figurines are considered waste of local craft production (Liu and Chen, 2012, 245). Taxonomic richness in this assemblage is surprising (Wu, 2001, Plate 1). Besides domestic dog, pig, and sheep, Wu (2001) identified Daurian ground squirrel (*Citellus dauricus*), Siberian weasel (*Mustela sibirica*), Water deer (*Hydropotes inermis*), Rhesus macaque (*Macaca mulatta*), Asian elephant (*Elephas maximus*), Chinese soft-shell turtle (*Trionyx sinensis*), Chinese pond turtle (*Mauremys reevesi*), Chinese ring-necked pheasant (*Phasianus colchicus torquatus*), Chinese bamboo partridge (*Bambusicola thoracica thoracica*), green peafowl (*Pavo muticus imperator*), and chicken (*Gallus domesticus*). Classifying clay figurines to the subspecies level is questionable, though, since seldom detailed enough to separate closely related taxa. Even species identification is not always unequivocal, as is illustrated by a figurine classified either as Giant tapir (*Megatapirus augustus*) (Wu, 2001) or Asian elephant (Liu and Chen, 2012, Fig. 7.15).

If the habitus of dog, sheep and pig leaves little doubt about their domestic status, we consider the case of the chicken less clear in absence of features typical of domestic breeds, e.g. different body proportions. In this respect, chicken figurines are usually classified as representing domestic birds since found in (*i*) sites located outside the known native distribution of Red jungle fowl in southern China and (*ii*) archaeological contexts expressing ritual behaviour, for instance votive offerings. However, apart from *Gallus*, the species spectrum at Dengjiawan comprises other thermophile birds, such as bamboo partridge and green peafowl, as well as mammals confined to the (sub-)tropics, like the Asian elephant. It is worth noting that the faunal composition at the contemporaneous site of Xiawanggang mentioned afore possesses taxa adapted to warm-humid forests and bamboo vegetation as well, such as Asian elephant, Giant panda and (wild) fowl. From a spatio-temporal perspective, domestic chickens certainly arrived earlier in the Yangtze River than in the Yellow River Basin, but it remains to be seen if the candidate chicken found in levels dating ~5.0–4.0 ka calBP (Eda et al., 2016, Table 1) descended from a domestic flock.

Turning to the epigraphic record, the use of distinct characters for pheasant and chicken in early Chinese writing is noteworthy. At the late Shang Dynasty capital of Yinxu, an assemblage of oracle bones utilised in divination has been excavated. Usually written on flat bones such as plastrons of turtles and scapulae of mammals, these oracle texts mention pheasants and chickens, whereby the pictograph for chicken features a comb (Shen and Cao, 2001, No. 1921). In later writings such as The Book of Odes (*Shijing 诗经*), an anthology of 305 songs and odes collected during the Zhou Dynasty that provides insight into the life of ordinary people from the late 11th to the middle of the 6th century BCE (e.g., Ho, 1969), the crow of a rooster is mentioned (Yu Chong, pers. comm. 2016). Written during the subsequent Spring and Autumn period of the Eastern Zhou Dynasty (771-476 BCE), the narrative *Zuo zhuan (左传)* mentions six major domesticates: horse, cattle, sheep, pig, dog and chicken (Deng et al., 2013).

5. Genetics of modern and ancient chickens

Molecular genetic studies of modern jungle fowl and domestic breeds have confirmed the hypothesis of Red jungle fowl (*Gallus gallus*) being the primary wild ancestor of the domestic chicken. Obviously, several continental subspecies (*G.g. gallus, G.g. murghi, G.g. spadiceus, G.g. jabouillei*) contributed to the domestic chicken's genetic makeup (Fumihito et al., 1994, 1996; Hillel et al., 2003; Liu et al., 2006; Kanginakudru et al., 2008). Having said that, research conducted on the nuclear genome revealed that the yellow skin allele observed in domestic chickens did not originate from the Red jungle fowl (this characteristic being absent in the wild form) but rather from the Grey jungle fowl *Gallus sonneratii* (Eriksson et al., 2008), demonstrating that at least one other jungle fowl species had contributed genetic material to the domestic genome.

Investigations into mtDNA phylogeny by Liu et al. (2006) and Miao et al. (2013) revealed nine highly divergent matrilineal clades named clades A-I, whereby no breed pertained to a specific clade. Their distinct distribution patterns and expansion signatures suggest these clades may have originated in different regions. Clades A-G encompass both domestic chickens and Red jungle fowl; clade E is the most widely distributed matrilineal lineage while clades A and B are ubiquitously distributed across Eurasia but absent in Africa. Clades C, F and G are mostly identified in East Asia, Southeast Asia and South Asia. The geographical distribution of clade D is particularly interesting as it appears to mirror the dispersals of cultures practicing cockfighting. It is found in South Asia, Southeast Asia, East Asia and Africa with a frequency peaking in Southeast Asia and Oceania. Clades H and I, on the contrary, are much rarer and specific to domestic chickens; these are geographically restricted to East Asia and South Asia respectively. Finally, four additional clades named clade W-Z specific to Red jungle fowls were identified (Miao et al., 2013).

Patterning in modern and ancient mtDNA of chickens is increasingly used to tackle research questions, such as the Austronesian dispersals and the first introduction of the chicken in South America (e.g. Storey et al., 2007, 2010, 2012; Gongora et al., 2008; Thomson et al., 2014) or the origin and genetic signatures of early fowl in Europe (Girdland Flink et al., 2014). Recently, mitogenetic analysis was also applied to test the hypothesis of early chicken husbandry in Holocene Northern China (Xiang et al., 2014).[4] Specimens analysed originate from ~11.5–10.5 ka calBP Nanzhuangtou, ~8.0–7.7 ka calBP Cishan, ~6.5–4.6 ka calBP Wangyin and from a Warring States (476-221 BCE) tomb at Jiuliandun. Amplification of a 159bp fragment of the mitochondrial cytochrome c oxidase subunit 1 (COI) gene and comparison with 196 homologous sequences from *Gallus, Phasianus, Alectoris, Lophura, Tetraophasis and Syrmaticus* allowed the conclusion that the 13 ancient sequences obtained were closer to the genus *Gallus* than to any of the other genera considered (Xiang et al., 2014). Comparison with other taxa of the subfamilies *Perdicinae* and *Phasianinae* widespread in East Asia and available on GenBank confirms the partitioning between *Gallus* and other genera.

Xiang et al. (2014) also amplified a 326bp fragment of the mitochondrial DNA control region in eight samples and obtained eight different haplotypes belonging to clades A, C, and F. Though replies questioned aspects of their methodology (Peng et al., 2015) and the likelihood of DNA survival in ancient chicken bones (Peters et al., 2015), Xiang et al. (2015a,b) carried out a re-assessment of their data and concluded that their original findings remained valid.

Thus, taken at face value, the results of the ancient DNA analysis of early and middle Holocene galliform bone specimens (Xiang et al., 2014) directly contradict expectations based upon the climatic context and associated fauna as well as morphological reanalysis. More specifically, what we currently know about the Holocene climate and vegetation suggests that chickens should not exist in Northern China at this time, and the morphological analysis concludes that bone remains supposedly deriving from chickens are actually from pheasants. Based on a subsample of these, however, the ancient DNA data clearly demonstrates that the bones are in fact chickens and that *Gallus* must have been present in the study area since the very beginning of the Holocene. No obvious or satisfying reconciliation of these contradictory conclusions has been forthcoming.

One possible explanation might be that some specimens analysed represent late intrusives from superposing Bronze Age and/or historic layers (Table 2), but single radiocarbon dates on a galliform bone from Nanzhuangtou and Cishan each confirmed their respective archaeological ages (Xiang et al., 2014, Table S1). According to Xiang (2015b), additional finds also originate from secure early and middle Holocene contexts, but more data including the results of analyses of associated ceramics and lithics are required to substantiate this assessment. Unfortunately, no radiocarbon date is available for the galliform remains from Neolithic Wangyin, although archaeology reported an extensive late Dawenkou cemetery (~5.0–4.6 ka calBP) on top of the occupation layers attributed to the late Beixin (~6.5–6.3 ka calBP) and early Dawenkou (~6.3–5.0 ka calBP) cultures (Table 2). In sum, the fact that Northern Chinese sites often exhibit long stratigraphies explains why post-hoc human activities and bioturbation by burrowing taxa (*Rhizomys, Myospalax*, *Hystrix*, *Meles*) could have

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[4] In their paper Xiang et al. (2014, Fig. 1B) presented photographs of "*typical ancient chicken bones unearthed in northern China*". Peters et al. (2015) noted however that some of these finds represent mammal bones, more precisely from canids and possibly dogs. Upon reassessment Xiang et al. (2015b) excluded the mammalian origin of the specimens in question and affirmed their original identification specifying that "*… as these bones did not yield any chicken sequences, their identity has, in any case, no bearing on the conclusions drawn*". Recently, Eda et al. (2016, Suppl. Data 2) confirmed and substantiated our initial assessment by contrasting the archaeological specimens in question with modern dog metacarpals.

caused displacement of material culture (e.g. Horwitz et al., 2012), necessitating radiocarbon dating of key archaeological specimens. Lastly, a sequencing approach that does not rely on the amplification of PCR products from these bones but instead takes advantage of advances in massively parallel sequencing technologies will also help to verify the initial genetic results and resolve the current discordance between the genetic and all other lines of evidence.

6. Conclusions

Proxies generated with Holocene palaeoclimate archives agree that conditions improved under the influence of the East Asian Summer Monsoon, with higher average temperatures particularly during the middle Holocene thermal optimum ~7.8–5.3 ka calBP. Nonetheless, even during the latter warm-moist conditions alternated with cooler episodes. Despite the fact that temperatures were on average somewhat higher, the mammalian fauna in the study area remained essentially Palaearctic, complemented by few Indomalayan taxa exhibiting eurytherm properties. Arboreal pollen analyses confirm that during the thermal optimum, the northern limit of the temperate deciduous forest had shifted ca. 800 km further north (Yu et al., 2000). Ecological requirements and current distributions of the terrestrial mammalian taxa identified in the early and middle Holocene assemblages fit well into this picture. Contrary to assertions in the literature, however, habitat requirements of tropical Red jungle fowl precluded extending its native range into Northern China, the middle Yangtze River basin probably delimiting its northernmost boundary during the Holocene thermal optimum.

A zooarchaeological re-evaluation of avifaunal remains from Northern and Northwestern China (Deng et al., 2013; Eda et al., 2016, Table 2) confirms this assessment, since it could be demonstrated that the foraging and food-producing early and middle Holocene communities inhabiting the study area exploited exclusively pheasants, not chickens. Prior to this work, the Common or Ring-necked pheasant, unquestionably the most widespread and numerous galliform taxon in the study area was almost invisible in the archaeofaunal record of Holocene China, despite the species' ecological adaptability and high population density in temperate East Asia. Neolithic galliform bone assemblages also exhibited a strong bias towards adult males, which we explain by higher predation pressure by humans due to the pheasant cocks' conspicuous habitus and behaviour as well as larger size.

Paradoxically, the results emerging from this work are diametrically opposed to those based on ancient mtDNA analyses published by Xiang et al. (2014, 2015a,b). These authors obtained mitogenome signatures from *Gallus* exclusively and no sequences of the ubiquitous *Phasianus* at all. Is it possible that these ancient remains represent an extinct, less thermophile (sub-)species of *Gallus* once distributed throughout Northern China? Adapted to seasonal fluctuating climate, temperature and humidity, this hypothetical wild fowl population would have faced multiple challenges relative to heat, cold, plant cover, food sources, predators, photoperiodism and many other crucial factors, with corresponding effects on reproduction, growth, development, and possibly social and sexual behaviour likely resulting in a genetic make-up that differs from modern populations of wild and domestic fowl. The ancient mtDNA signatures, however, do not support this possibility, since the clades identified within the specimens (A, C and F) are widely distributed and recorded in both domestic chickens and present-day tropical Red jungle fowls.

According to Xiang et al. (2014), early chicken husbandry in Northern China would fit in as well in autochthonous agricultural innovations reported from the Yellow River basin, such as millet cultivation (Barton et al., 2009; Lu et al., 2009; Yang et al., 2012), pig husbandry (Larson et al., 2010; Cucchi et al., 2011) and dog breeding (Yuan, 2010). Since millet was being cultivated since the early Holocene (Yang et al., 2012), potential poultry keepers would have been able to feed their chickens on staples that remain appreciated for their nutritive value today. Moreover, since this chicken-crop combination would represent a cost-efficient subsistence activity, would one not expect it spreading readily in the wake of dispersal of millet (and later rice) cultivation throughout China and beyond?

As such, millets diffused from China to Korea in the 6th millennium calBP with secure direct dates from ~5.4 ka calBP, but whether domestic fauna, such as the pig, diffused at this time or significantly later remains unclear (Fuller et al., 2008). A Neolithic transfer of chickens, however, can be excluded, since it was noted that poultry farming in Korea started more than three millennia later ~2.0 ka calBP (M. Eda, pers. comm., June 2015). This date fits remarkably well with the beginning of fowl husbandry in Japan coinciding with the middle Yayoi Period ~2.2–1.7 ka calBP (Eda and Inoué, 2011). Obviously, chicken husbandry crossed the Yellow Sea together with other agricultural innovations known from mainland China, such as wet-rice farming. West of Northern China in the Wei River and Middle and Upper Yellow River valleys, the integration of chicken husbandry into local subsistence was a late achievement as well since securely identified remains of chickens seem absent from archaeological contexts pre-dating the Proto-Zhou culture (1200-1050 BCE) (Eda et al., 2016, Table 1). In summary, given that in the archaeological record of regions adjacent to Northern China chickens only show up in the later Bronze Age, it is difficult to conceive that beyond the study area, poultry husbandry passed unnoticed for nearly five millennia.

Finally, chicken husbandry in Neolithic Northern China would have facilitated an earlier dispersal to Europe across Central and West Asia (West and Zhou, 1988). However, the paucity of archaeofaunal analyses available for Central Asia in the 1980s precluded testing this hypothesis. Although this research gap is only being closed slowly, faunal studies published since then are consistent in that chickens represent a very late addition to the Central Asian barnyard. Extensive faunal assemblages from Iron Age South Kazakhstan dating 3.0–2.5 ka calBP, for instance, did not yield a single specimen attributable to *Gallus* (Benecke, 2003). Thus, early evidence comes from the 2.4–2.3 ka calBP fortification of Kurgansol in Bactria/Uzbekistan (Benecke, 2014). Erected during the military campaigns of Alexander the Great, it is therefore highly probable that the Kurgansol chickens were introduced from the army's region of origin in West Asia rather than being of East Asian origin. Conceivably, intensification of irrigation practices and increasing cultivation of cereals in the oasis landscapes of Central Asia promoted the adoption of poultry farming and its subsequent development into a sustainable activity.

Overall, the hypothesis of an autochthonous domestication episode of *Gallus* in Holocene Northern China is supported by the current ancient DNA results (Xiang, 2014), but not by any other evidence. The climatic context suggests that the habitat requirements for (sub-)tropical Red jungle fowl were not present in early and middle Holocene Northern China. The zooarchaeological re-evaluation of the avifaunal record available suggests that along the middle Yangtze River and its tributaries, the presence of (wild or domestic) *Gallus* seems possible ~5.0–4.0 ka calBP, as suggested by terracotta figurines associated with the Shijiahe culture and a single bone find from a late Neolithic context (Eda et al., 2016). However, even if chickens arrived in Central China towards the end of the Middle Holocene, the early stages of fowl husbandry further north in Northern China seem to post-date ~3.5 ka calBP, when bone finds and two skeletons of chickens from the late Shang Dynasty capital of Yinxu and the contemporaneous royal burial grounds at Dasikongcun have been discovered (Table 2). The presence of *Gallus* in Shang Dynasty times is also supported by contemporaneous early Chinese writing depicting distinct characters for pheasants and chickens on oracle bones (Shen and Cao, 2001).

In conclusion, the weight of evidence still suggests that in Northern and Northwestern China, the integration of poultry husbandry into food-producing economies was a comparably late development, resulting from human-mediated dispersal of domestic flocks originating from regions further south during the Bronze Age. Having said that, additional ancient DNA, morphometric and dating programs of purported chicken remains across China and East Asia generally will no doubt resolve the current paradox, and establish the spatial and temporal origins of the world's most numerous domestic animal.

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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.quascirev.2016.04.004.

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