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RESEARCH ARTICLE

Diversity of Femoral Diaphyseal Structure in East Asian Modern Humans During the Paleolithic–Neolithic Transition

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ABSTRACT

Objectives: During the Paleolithic–Neolithic transition, modern human femoral diaphyses underwent significant structural changes, primarily driven by shifts in subsistence patterns including decreased mobility and increased sedentism. However, femoral remains from East Asia during this period are inadequately reported and studied. This study investigates the femoral diaphyseal structures across East Asia during this transition, exploring their variation, evolutionary processes, and links to subsistence patterns reflected in the archeological record.

Materials and Methods: Human femora from Qihe Cave, Donghulin, and Taipinghu, representing South, North, and Northeast China during the transition, were analyzed. Midshaft cross-sectional shapes were compared with Early Upper Paleolithic (EUP), Late Upper Paleolithic (LUP), and recent sedentary agricultural (RSA) samples. Morphometric maps illustrating cortical bone thickness, external radius, and bending rigidity along the entire diaphysis were compared with Late Pleistocene early modern humans from South and North China and RSA specimens.

Results: Analysis of midshaft cross-sectional shapes revealed that DHL 4 and Qihe M2 align with the LUP group, whereas DHL M1 and TPH 45 show close affinities with the RSA group. Statistical analyses based on morphometric maps further reveal that DHL 4 and Qihe M2 share key features with Late Pleistocene early modern humans, whereas DHL M1 and TPH 45 fall within the RSA variation range.

Discussion: Two distinct femoral diaphyseal patterns are identified among East Asian modern humans during the transition, reflecting regional variations and intrapopulation divisions of labor, primarily associated with hunting and gathering strategies shaped by local environmental conditions and corresponding archeological cultures.

1 | Introduction

The transition from a Paleolithic hunter-gatherer lifestyle to a Neolithic production-based economy constitutes one of the most significant events in human evolutionary history. During this phase, the behavioral patterns and social organizations of modern humans underwent significant transformations, as evidenced by shifts in subsistence strategies, mobility, settlement patterns, resource acquisition, food production, technological innovation, and division of labor (Bar-Yosef 1998; Furholt 2021; Weisdorf 2005). This process manifested in diverse regional forms, interpreted through models such as indigenous Neolithic development, migration and replacement of indigenous populations by Neolithic colonizers, cultural diffusion, and various hybrid models (Ammerman 1973; Barbujani and Bertorelle 2001; Cavalli-Sforza et al. 1993; Pinhasi 2003; von Cramon-Taubadel and Pinhasi 2011; Whittle and Cummings 2007; Zilhão 2001; Zvelebil 1986; Zvelebil and Rowley-Conwy 1984).

Within the research framework concerning the Paleolithic–Neolithic transition in East Asia, the prevailing academic consensus situates this transitional period between approximately 20,000 and 8000 BP. The onset of this transition is characterized by the appearance of novel cultural elements that diverge from typical Paleolithic assemblages, including polished stone tools, pottery, and architectural remains. The culmination of this process—signifying the definitive establishment of the Neolithic period—is marked by the consistent, spatially clustered occurrence of diagnostic indicators, most prominently assemblages attesting to agricultural subsistence and sedentary lifestyles (Chen and Yu 2017a, 2017b; Cohen 2011; Gao 2025; Jing 2008; Lu 2006; Wu et al. 2012; Xia and Zhang 2025; Zhang 2024; Zhang and Hung 2010; Zhao et al. 2004). The Paleolithic–Neolithic transition broadly corresponds to the Mesolithic in other regions of the world (Bailey and Spikins 2008; Czarnik 1976; Price 1983). With East Asia widely recognized as a primary locus of early millet and rice domestication, diagnostic Neolithic markers—such as cultivated crops and ceramic production—emerge at a notably early stage in the archeological record (Lu et al. 2009; Wang and Sebillaud 2019; Wu et al. 2012; Yang et al. 2012; Zhang et al. 2024). The Paleolithic–Neolithic transition in this region was gradual and continuous, albeit marked by considerable regional variation, and no distinct Mesolithic age can be clearly identified (Gao 2025). The transformation of human physical characteristics, population genetic structure, and archeological cultures during the Paleolithic–Neolithic transition has been a central focus in East Asian archeological research (Chen and Yu 2017a, 2017b; Mao et al. 2021; Matsumura et al. 2019; Wang et al. 2021; Yang et al. 2020; Zhang et al. 2021).

The transition from Paleolithic to Neolithic is marked by substantial shifts in human subsistence patterns and habitual behaviors, including decreased mobility, increased sedentism, and intensified exploitation of local environments (Elston et al. 2011; Feng and Wang 2022; Tian et al. 2023; Yi et al. 2021). These behavioral changes are often reflected in the structural properties of human limb bone remains. As essential components of human locomotion, the structural properties of limb bones reflect behavioral patterns through the principle of "Wolff's Law" or "bone functional adaptation." According to this theory, bone tissue adapts to mechanical loads from the external environment, deforming in a feedback mechanism that maintains the bone at an "optimal customary strain level" (Ruff et al. 2006; Ruff 2018a).

The femur, crucial for walking, running, climbing, and body support, is closely linked to mobility and settlement patterns. Previous studies have documented notable changes in femoral structure from the Late Pleistocene to Early Holocene, including a more circular midshaft cross-section, a decline in anteroposterior bending strength, and decreased epiphyseal trabecular bone fraction (Chirchir et al. 2015; Holt 2003; Holt and Formicola 2008; Ruff et al. 2015, 2022; Shackelford 2007, 2014). These changes are generally attributed to declines in mobility associated with an increased degree of sedentism (Holt and Formicola 2008; Shaw and Stock 2013; Stock 2006; Wescott 2014). Research on European samples indicates that key indicators of mobility, such as femoral anteroposterior bending strength, initially declined with the onset of food production, and the transition to a more sedentary lifestyle was gradual, extending through agricultural intensification into the Iron Age (Macintosh et al. 2015, 2014, 2017; Ruff 2018b; Ruff et al. 2015).

Human femoral remains from East Asia, dating from the Late Pleistocene to the Early Holocene, provide valuable insights into femoral functional adaptations and behavioral changes among local populations. Notable examples include specimens from Tianyuan Cave (42–39 ka cal BP) and Zhoukoudian Upper Cave (38.3–35.8 ka) in North China, as well as Liujiang in South China (33–23 ka) (Ge et al. 2024; Li et al. 2018; Shang et al. 2007). These remains represent early modern humans in East Asia who lived before the Last Glacial Maximum (LGM) and exhibit structural features comparable to their European contemporaries, adapted for a highly mobile hunter-gatherer lifestyle (Ruff et al. 2022; Wei et al. 2023, 2017). In the post-LGM period, new structural variations appear in femoral specimens from Maomaodong (14.5 ± 1.2 ka) in South China (Wei et al. 2021). Intragroup variability is observed within the Maomaodong population, where the midshaft cross-sectional shape of specimen GM7508 exhibits a more rounded morphology compared to specimens GM7506 and GM7507. Notably, the pilastric index of GM7508 remains within the variation range of Upper Paleolithic specimens. This pattern may reflect intragroup variation, potentially attributable to factors such as sexual dimorphism (Ruff et al. 2022; Wei et al. 2021). In contrast to the relatively well-documented Late Pleistocene specimens, the femoral remains of Early Holocene modern humans in East Asia have not been as extensively reported or studied, though abundant evidence reflecting the shift from mobile to sedentary lifestyles, such as indications of crop cultivation and animal domestication, has been presented for this critical period.

While regions across East Asia shared key features of the Paleolithic–Neolithic transition during the early Holocene, the specific manifestations of this transition varied regionally. Influenced by differences in climate, hydrologic conditions, and geological settings, archeological sites in South China are predominantly located in caves or rock shelters within small basins surrounded by low hills. In contrast, sites in North China are almost exclusively open-air and situated in river valleys. The warmer and more humid southern climate supported greater biodiversity, as evidenced by faunal assemblages that include terrestrial mammals, reptiles, birds, and a notably high proportion of aquatic species such as fish and shellfish. Conversely, the colder and drier northern environment offered relatively limited biotic resources, with faunal remains largely dominated by mammalian taxa—particularly, large herbivores (Zhao 2024). This environmental and ecological disparity between southern and northern East Asia persisted until the establishment of agricultural societies. In North China, the transition culminated in a sedentary agricultural economy primarily based on millet cultivation (Liu et al. 2012; Lu et al. 2009; Yang et al. 2012), whereas in South China, it gave rise to a sedentary agricultural economy centered on rice cultivation (Fuller et al. 2009; Gross and Zhao 2014; Zhang et al. 2024). In the northern part of Northeast China, a sedentary lifestyle developed based on a fishing–hunting–gathering economy, with the adoption of agriculture occurring relatively late, not until the Bronze Age (Li et al. 2020; Yuan 2016; Yue et al. 2022; Zhang 2024). These regional differences in ecological context and subsistence strategy were plausibly influential on habitual behaviors, which may in turn be reflected in the structural properties of the human femora.

To address gaps in the record of human femoral structures from the early Holocene in East Asia, and to elucidate the complex transitional processes of subsistence strategies across different regions, this study analyzed femoral remains from three early Holocene sites in various regions of China. The cross-sectional geometry (CSG), along with morphological and biomechanical properties along the entire diaphysis, was compared with those of Late Pleistocene early modern humans and recent sedentary agricultural (RSA) populations to provide a precise evaluation of their structural characteristics.

2 | Materials

This study incorporates human femoral remains from Qihe Cave in South China, Donghulin in North China, and Taipinghu in Northeast China to ensure representative geographic coverage across diverse regions of China (Figures 1 and S1). Key contextual information for the analyzed femoral specimens is summarized in Table 1.

2.1 | Donghulin

The Donghulin archeological site, located in Dongulin village, Mentougou District, Beijing, North China, was first identified in 1966 following the discovery of Early Neolithic burials and human skeletal remains, representing at least three individuals (Zhou and Zhu 1972). The first formal excavation of this site was conducted in 2001, leading to the discovery of the lower portion of a body, which some researchers designated as Donghulin 4 (DHL 4) (Xue and Hao 2010; Zhao 2006). Further excavations in 2003 and 2005 uncovered two well-preserved burials designated as Donghulin M1 and M2 (DHL M1 and M2) (Zhao 2006). Archeological investigations at Donghulin have yielded a substantial collection of pottery sherds, along with a variety of stone, bone, and shell tools, as well as rich animal remains (Zhao 2006). Plant remains found within the site's cultural deposits provide insights into the early domestication of millet in North China (Yang et al. 2012; Zhao et al. 2021).

For this study, the bilateral femora of the adult individuals DHL 4 and DHL M1 were analyzed, while the adolescent individual DHL M2 was excluded due to incomplete skeletal development. DHL 4 was assessed through DNA testing and radiocarbon dating of the femoral segments, which determined the individual to be male with an age of 9968–9400 cal BP (85.2%). Radiocarbon dating applied directly to the DHL M1 skeletal

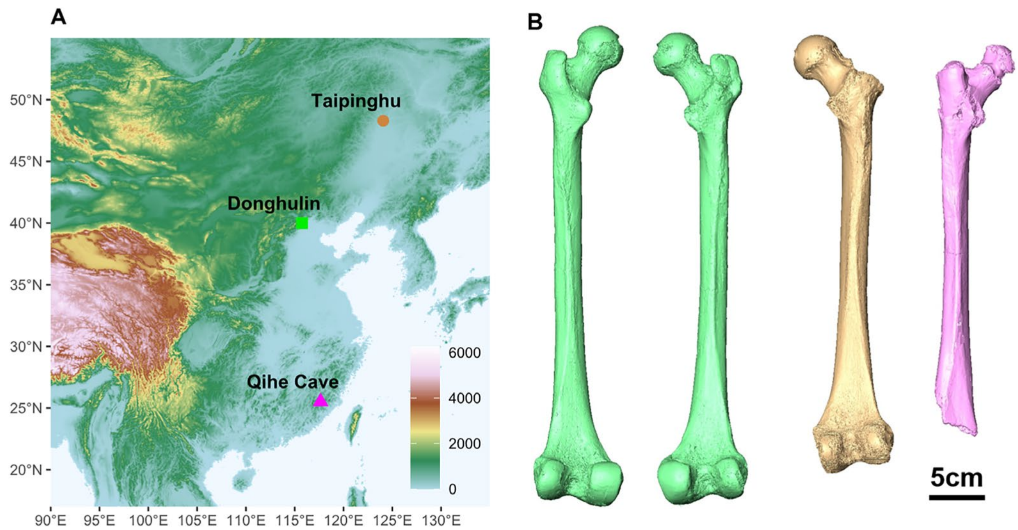

FIGURE 1 | Overview of femoral specimens from the Paleolithic–Neolithic Transition in East Asia. (A) Geographical distribution of archeological sites included in this study. (B) Virtual reconstructions of femoral specimens in posterior view. From left to right: the left and right femora of Donghulin M1, the right femoral specimen Taipinghu 45, and the left femur of Qihe M2. The fragmented femoral segments of Donghulin 4 are visualized in Figure S1.

TABLE 1 | Key information on femoral specimens from the Paleolithic–Neolithic Transition in East Asia.

	Donghulin 4	Donghulin M1	Qihe M2	Taipinghu 45
Location	Dongulin village, Mentougou District, Beijing, North China	Dongulin village, Mentougou District, Beijing, North China	Zaotou Village, Zhangping City, Fujian Province, South China	Gannan county, Qiqihar city, Heilongjiang Province, Northeastern China
Chronological age	9968–9400 cal BP	11,170–10,700 cal BP	8428–8359 cal BP	8170–7980 cal BP
Sex	Male	Female	Female	—
Stature	—	162 cm	160.3 cm	153.84 cm
Body mass	59.18 kg	59.2 kg	59.9 kg	55.69 kg
Biological age	—	40–50 years	26–35 years	—
Preservation	Subtrochanteric region to the midshaft	Completely preserved	Lacking distal epiphysis	Completely preserved
Biomechanical length	383.33 mm	397.46 mm (left) 389.92 mm (right)	364.63 mm	366.54 mm

material indicates an age range of 11,170–10,700 cal BP, corresponding to 9220–8750 cal BC (95.4%) as originally reported by Zhao (2006). DHL M1 has been identified as a female, aged 40–50 years, based on osteological indicators such as the morphology of the hip bones, skull, and symphysis pubis, as well as tooth wear, suture closure, and bone development. Her stature was reconstructed at 162 cm, and her body mass was estimated at 59.2 kg (He et al. 2021).

2.2 | Qihe Cave

Qihe Cave, located in Zaotou Village, Zhangping City, Fujian Province, South China, was discovered in 2008. Subsequent excavations conducted between 2009 and 2011 yielded a substantial assemblage of stone artifacts, bone tools, pottery sherds, mammalian bones, and the remains of three human individuals within the Neolithic cultural deposits (Fan et al. 2013). This site is critical for understanding the development of polished stone tools, the invention of early pottery, and the migration and cultural exchange of early Neolithic populations in southern China. The ancestral population of Qihe made significant contributions to the genetic structure of southern Chinese populations and Austronesians (Wang et al. 2021; Yang et al. 2020).

Based on the stratigraphic relationships, component assemblage, and ^{14}C dating data, three cultural phases were identified at Qihe Cave. The skeletal remains of three individuals were uncovered in the third phase with an absolute dating range of 10,000–7000 BP (Fan et al. 2013). Since only cranial remains were recovered from Qihe M1 and M3, this study focuses on Qihe M2 which preserved post-cranial elements including a nearly complete left femur. Qihe M2 is identified as a female based on both osteological indicators and DNA testing. She was estimated to have been 26–35 years old, with a stature of 160.3 cm and a body mass of 59.9 kg (Fang et al. 2015). Radiocarbon dating applied directly to the human bones indicates an age of 8428–8359 cal year BP (Yang et al. 2020).

2.3 | Taipinghu

The Taipinghu human fossils were discovered along the upper reaches of the Songhua River, near Taipinghu in Harbin City, Heilongjiang Province, Northeast China. This area lies within the Songnen Plain, a region shaped predominantly by the alluvial deposits of the Songhua and Nen Rivers and characterized by an extensive network of wetlands and lakes (Mao et al. 2021). Over the past decades, numerous faunal and human fossils have been recovered from the riverbed near Taipinghu during sand-excavation activities. Between 2020 and 2023, approximately 20 human femoral specimens from this locality were submitted to research institutions for further study. The right femur specimen 20TPH-H-Fm45 (hereafter referred to as TPH 45), with a directly dated AMS ^{14}C age of 8170–7980 cal BP (95.4%), was analyzed in this study.

2.4 | Comparative Samples

Comparative samples for the cross-sectional shape analysis at the midshaft of the femoral diaphysis consist of three groups: Early Upper Paleolithic (EUP) modern humans, Late Upper Paleolithic (LUP) modern humans, and a RSA population. The EUP and LUP groups comprise Late Pleistocene early modern humans from geographically diverse regions, differentiated by the conventional 20 kyr BP chronological boundary established in prior research (Chevalier and Colard 2023; Holt 2003; Shackelford 2007). Data for the EUP and LUP samples were obtained from Ruff et al. (2022). Complete sample compositions for both groups are presented in Table S1.

The RSA group employs the Junzicun population as a representative sample. This population resided in Junzi village, Xinxiang city, Henan province, central China during the Qing dynasty (1736–1851 AD). The region features flat plain topography. Archeological evidence from burial relics and historical documentation indicates that this population maintained an intensive agricultural economy and a fully sedentary lifestyle, unaffected by technological developments of the Industrial Revolution (He and Tang 2015; Xing et al. 2018; Zhao 2023). Marked sexual dimorphism in humeral morphology reflects a sexual division of labor consistent with traditional Chinese agricultural societies, where males were more engaged in field cultivation and females in domestic tasks (Li et al. 2022; Zhao 2023). For the present study, we included a total of 38 femoral specimens, comprising 24 specimens from 12 males and 14 specimens from 7 females of the Junzicun population.

Comparative samples used for morphometric map comparisons include two Late Pleistocene early modern humans: Liujiang from South China and Tianyuan 1 from North China. Matrices storing characteristic values for plotting morphometric maps, which quantify structural properties along the entire femoral diaphysis of these samples, are cited from Wei et al. (2023). Although potential pathological abnormalities are present in the femoral pilaster region of Tianyuan 1, these features are unlikely to have compromised normal locomotor function (Wei et al. 2017). Instead, they appear to reflect an extreme reinforcement of femoral structure, comparable to that observed in other contemporary early modern humans and well adapted to intense physical activity. Accordingly, the intact diaphysis was incorporated into the morphometric mapping analyses. Junzicun specimens were included in morphometric mapping analyses to represent variation among recent modern humans.

3 | Methods

3.1 | Computed Tomographic Scanning and Virtual Data Processing

The femoral specimens of TPH 45, DHL 45, DHL M1, and Junzicun population were scanned using the Phoenix V|tome|x M microfocus CT cabinet system at the Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences (CAS). The scanning parameters included a voltage of 180 kV and a current of 140 μA, producing an isotropic voxel size of 74.312 μm. Additionally, the femur of Qihe M2 was scanned using a 450 kV industrial CT system developed by the Institute of High Energy Physics, CAS, also housed at the Key Laboratory of Vertebrate Evolution and Human Origins, IVPP, CAS. This scan was conducted with a voltage of 360 kV and a current of 1.5 mA, resulting in a voxel resolution of 160 μm.

The raw image stacks obtained from the scans were imported into VGStudio Max 3.0 for virtual reconstruction and positioning. The femoral specimens were volume-rendered and aligned to a standard orientation, following the protocol established by Ruff (2002) for physical specimens. Procedures specifically designed for digital environments were detailed by Xing et al. (2018). Virtual mesh objects of femoral specimens were then generated using Mimics 20.0 for landmark placement, cross-section extraction, CSG calculation, and morphometric mapping.

The R package "morphomap" was employed to achieve the accurate procedure of landmark placement (Profico et al. 2021; R Core Team 2022). Along the proximodistal section of the femur diaphysis, 100 cross-sections were extracted at equidistant intervals. Figure S2 visualizes cross-sections of the analyzed specimens at 20%, 35%, 50%, 65%, and 80% positions along the femoral diaphysis. The proximodistal section extends from 20% (distal) to 80% (proximal) of the femoral biomechanical length. At each cross-section, 360 paired landmarks were equiangularly positioned along both the endosteal and periosteal contours centered at the centroid of the cross-section. These landmarks collectively serve as inputs for calculating CSG properties and morphometric maps. For a visual representation of the landmark placement, refer to the schematic diagram presented by Wei et al. (2023).

3.2 | CSG Properties

The CSG properties of 100 cross-sections from 20% to 80% of femoral biomechanical length were calculated. These properties include total subperiosteal area (TA), cortical area (CA), medullary area (MA), second moment of area (SMA) about the mediolateral and anteroposterior axis (I_x and I_y), maximum and minimum SMA (I_{max} and I_{min}), polar SMA (J), section modulus about the mediolateral and anteroposterior axis (Z_x and Z_y), maximum and minimum section modulus (Z_{max} and Z_{min}), polar section modulus (Z_p), and theta. Definitions of these properties can be found in Ruff (2018a), while the calculation procedures are detailed in Ruff and Hayes (1983) and Trinkaus and Ruff (2012). Calculations were performed based on landmarks positioned on the cross-sections using the R package "morphomap" (Profico et al. 2021; R Core Team 2022). Table 2 presents commonly used CSG properties at the midshaft and subtrochanteric levels for the analyzed femoral specimens, while more detailed CSG data along the entire femoral diaphysis are provided in the Supporting Information.

The midshaft cross-sectional shapes of the femoral diaphysis of Qihe M2, DHL 4, DHL M1, and TPH 45 (Figure 2) were compared to those of the EUP, LUP, and RSA groups. The midshaft cross-sectional shape was evaluated by I_x versus I_y at the 50% cross-section, a measure that effectively reveals the development of linea aspera, the presence of medial or lateral buttress, and the anteroposterior or mediolateral reinforcement of the femoral diaphysis (Ruff and Hayes 1983; Trinkaus and Ruff 2012; Trinkaus et al. 2022). I_x and I_y were log-transformed before statistical analyses to normalize data distributions and control for allometric scaling effects (Trinkaus 1997).

Linear discriminant analysis (LDA) was employed to assess the reliability of using I_x and I_y to differentiate specimens classified within the EUP, LUP, and RSA groups, and to evaluate the affiliation of Qihe M2, DHL 4, DHL M1, and TPH 45 with these groups. To ensure the accuracy in posterior probabilities, the LDA calculations were repeated 1000 times until the mean posterior probabilities of all iterations stabilized. In each iteration, 75% of the dataset was sampled without replacement as the training set, while the remaining 25% served as the testing set. LDA was performed using the R package "MASS" (Venables and Ripley 2002).

TABLE 2 | Midshaft (50%) and subtrochanteric (80%) cross-sectional geometric properties of femoral specimens from the Paleolithic–Neolithic Transition in East Asia.

Location	Specimens	Side	TA	CA	I_x	I_y	I_{min}	I_{max}	J	Z_x	Z_y	Z_{max}	Z_{min}	Z_p
50%	Donghulin 4	Left	461.02	394.13	20,910.14	13,570.94	13,509.52	20,938.13	34,481.08	1365.91	1166.96	1368.58	1158.08	2255.00
		Right	475.11	393.18	21,878.05	14,403.61	14,403.19	21,896.86	36,281.66	1379.92	1221.32	1382.02	1228.15	2295.94
	Donghulin M1	Left	415.68	326.26	11,831.53	14,726.52	11,795.73	14,782.41	26,558.04	972.74	1162.32	1173.08	971.81	2100.78
		Right	412.37	330.80	11,795.02	14,606.47	11,803.09	14,612.96	26,401.49	954.97	1153.83	1153.48	954.99	2081.08
	Qihe M2	Left	407.83	345.25	14,719.13	11,704.01	11,628.02	14,780.10	26,423.14	1063.99	1036.91	1086.91	1033.97	1902.83
	Taipinghu 45	Right	415.41	289.95	11,848.95	13,748.28	10,784.29	14,818.50	25,597.23	984.51	1105.96	1083.54	941.82	1877.86
80%	Donghulin 4	Left	497.65	390.21	17,062.67	21,310.73	16,133.98	22,243.81	38,373.41	1356.28	1497.78	1552.95	1301.27	2661.91
	Donghulin M1	Left	465.27	317.25	14,974.30	16,906.51	11,622.47	20,275.12	31,880.81	1165.33	1335.19	1435.41	1048.50	2249.97
		Right	466.59	328.16	15,545.96	17,810.44	11,161.31	22,178.50	33,356.40	1222.63	1371.22	1484.46	1047.02	2236.34
	Qihe M2	Left	485.72	360.02	18,418.31	18,090.89	13,230.81	23,289.73	36,509.20	1408.55	1370.20	1614.88	1194.13	2506.91
	Taipinghu 45	Right	568.33	322.23	22,830.92	22,825.04	13,169.52	32,478.67	45,655.96	1489.99	1544.91	1815.40	1104.83	2547.89

Abbreviations: CA = cortical area (mm^2); I_{max} and I_{min} = maximum and minimum second moment of area (mm^4); I_x and I_y = second moment of area about the mediolateral and anteroposterior axis (mm^4); J = polar second moment of area (mm^4); TA = total subperiosteal area (mm^2); Z_{max} and Z_{min} = maximum and minimum section modulus (mm^3); Z_p = polar section modulus (mm^3); Z_x and Z_y = section modulus about the mediolateral and anteroposterior axis (mm^3).

3.3 | Morphometric Mapping

Morphometric mapping was employed to quantify and visualize the spatial distribution of cortical bone thickness (CBT), external radius (ER), and SMA along the entire proximodistal section of the femur diaphysis. CBT quantifies the distance between paired landmarks on the endosteal and periosteal contours (Bondioli et al. 2010). ER measures the distance from landmarks on the periosteal contour to the centroid calculated from all landmarks within that specific cross-sectional plane (Morimoto et al. 2011). SMA is proportional to the bending rigidity along a specific neutral axis of a cross-section (Jashashvili et al. 2015), with its computation methodology adhering to Ruff and Hayes (1983).

These characteristic values are systematically arranged in a two-dimensional matrix based on their spatial coordinates. A chromatic scale, ranging from dark blue to light red, is employed to visualize this matrix and generate morphometric maps. For detailed procedures on generating CBT, ER, and SMA morphometric maps, refer to the schematic diagram provided by Wei et al. (2023).

All morphometric maps were standardized to account for body size, which directly influences the mechanical load applied to the locomotor skeleton. In accordance with previous studies, CBT and ER were standardized by bone length (Jashashvili et al. 2015; Wei et al. 2023, 2017), while SMA was standardized by body mass × bone length^2 (Ruff 2018a). Biomechanical length (length′) is adopted in the present study for standardization, measured parallel to the longitudinal axis from the average distal projection of the condyles to the superior surface of the neck at its deepest (most distal) point (Ruff 2002). Biomechanical length and body mass data, along with their sources and the methodology employed to estimate unknown biomechanical length and body mass, are comprehensively detailed in Supporting Information Text S1.

Morphometric maps depicting structural properties along the femoral diaphysis were compared among early Holocene individuals from China, early modern humans from North and South China, and RSA specimens. To quantitatively assess the relationships among different types of modern humans, principal component analysis (PCA) was conducted using the CBT, ER, or SMA values at all locations of the morphometric maps as variables. PCA was performed using the R package "stats" (R Core Team 2022). Neighbor-joining trees were constructed from distance matrices derived from the morphometric maps using the R package "ape" (Paradis and Schliep 2019).

4 | Results

4.1 | Cross-Sectional Geometric Analysis

The midshaft (50%) cross-sectional shapes of femoral diaphyses in Chinese early Holocene individuals were compared to those of the EUP, LUP, and RSA groups (Figure 3A). At the group level, the shape ratio quantified by log-transformed I_x and I_y exhibits a gradual decline from the EUP group to the LUP group, and further to the RSA group. The distribution areas of the EUP and

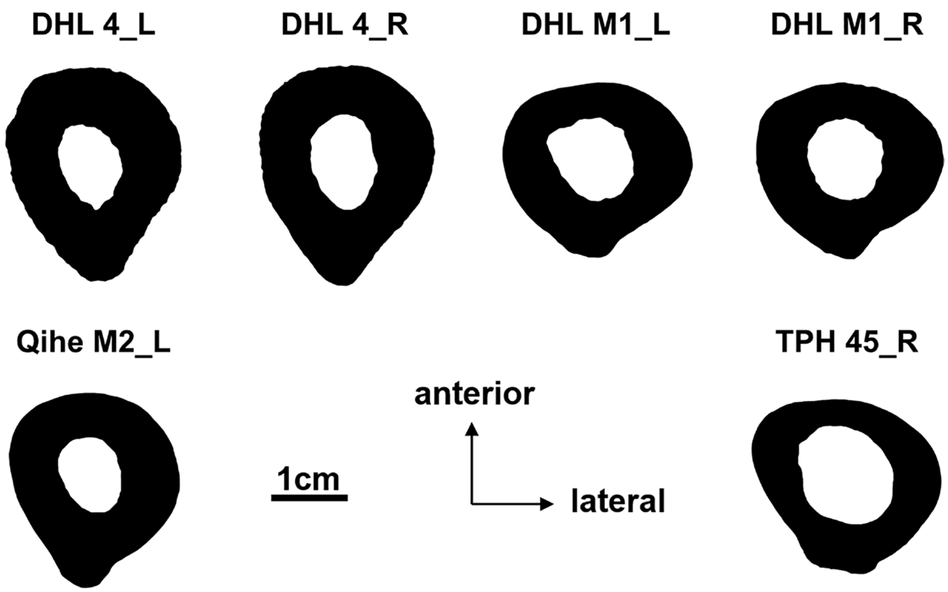

FIGURE 2 | Femoral midshaft (50%) cross-sectional outlines of specimens from the Paleolithic–Neolithic Transition in East Asia. DHL: Donghulin; L: left; Qihe: Qihe Cave; R: right; TPH: Taipinghu.

LUP groups, as well as those of the LUP and RSA groups, exhibit moderate overlap, while the EUP and RSA groups remain distinctly separate. DHL 4 falls within the region where the EUP and LUP groups overlap, whereas Qihe M2 closely aligns with the regression line of the LUP group. TPH 45 and DHL M1 are situated near the regression line of the RSA group.

Figure 3B presents the results of LDA performed on log-transformed I_x and I_y values obtained from the midshaft cross-section of the femoral diaphysis. The LDA was iterated 1000 times to ensure the stabilization of posterior probabilities (Figures S3 and S4). For specimens belonging to the EUP group, the posterior probabilities of classification are 50.49% for EUP, 44.27% for LUP, and 5.24% for RSA. LUP specimens show posterior probabilities of 30.55% for EUP, 44.92% for LUP, and 24.53% for RSA. RSA specimens show posterior probabilities of 2.1% for EUP, 15.82% for LUP, and 82.08% for RSA. DHL 4 exhibits high classification probabilities for both EUP (45.53%) and LUP (53.8%), exceeding those of LUP group members, with only minimal RSA probability (0.67%). Qihe M2 displays modest EUP (22.46%), very high LUP (72.5%), and low RSA (5.04%) probabilities. In contrast, TPH 45 revealed minimal EUP (0.72%) and low LUP (13.67%) probabilities but dominant RSA classification (85.61%). Similarly, DHL M1 exhibits near-negligible EUP (0.29%) and low LUP (7.15%) probabilities with near-complete RSA classification (92.56%).

Figure 3C presents the results of the comparison between Chinese Early Holocene specimens and sex-separated EUP, LUP, and RSA groups. Both the EUP and LUP groups exhibit clear sexual dimorphism, with males displaying higher I_x/I_y ratios than females at the group level. In contrast, the RSA males and females show broadly overlapping distributions of I_x/I_y ratios. Among the Early Holocene individuals, DHL 4 falls within the range observed in EUP and LUP males, lies near the upper limit of EUP females, and falls outside the range of LUP females and the RSA group. Qihe M2 falls within the range observed in the EUP and LUP groups, but outside that of the RSA group. In contrast, DHL M1 and TPH 45 fall within the range of the RSA group and lie outside that of the EUP and LUP groups. The DHL population exhibits a high level of sexual dimorphism, whereas the disparity between males and females is relatively limited in the RSA group.

4.2 | Morphometric Mapping Analyses

Morphometric maps are employed to quantify and visualize CBT, ER, and SMA along the full length of the femoral diaphysis. Detailed results for the ER and SMA, as well as descriptions of the data structure and storage format, are provided in the Supporting Information (Text S2, Text S3, and Figures S5–S9).

Figure 4A illustrates the CBT distribution along the femoral diaphysis in modern humans from various chronological and regional backgrounds. Qihe M2 exhibits thicker cortices along the mid-proximal to mid-distal sections of the femoral diaphysis posteriorly, as well as near the posterolateral regions of the proximal diaphysis. In the preserved section of DHL 4's femoral diaphysis, a nearly identical distribution pattern is observed. TPH 45 and DHL M1 display similar patterns, with the thickest cortices located laterally from the proximal to middle diaphysis, while moderately thickened cortices are present medially along the proximal to middle diaphysis and posteriorly along the proximal to mid-distal diaphysis. In TPH 45, the posterior thickened region divides into two branches.

Among comparable specimens, Tianyuan 1 exhibits markedly thick cortices along the mid-proximal to distal femoral diaphysis posteriorly. Liujiang displays a pattern of thicker cortices posteriorly along the mid-proximal to mid-distal diaphysis, medially along the proximal to mid-proximal diaphysis, and posterolaterally in the proximal diaphysis. The mean morphometric maps of Junzicun males and females reveal similar patterns, with thick cortices distributed medially, posteriorly, and laterally along the proximal to middle diaphysis. In Junzicun males, these three

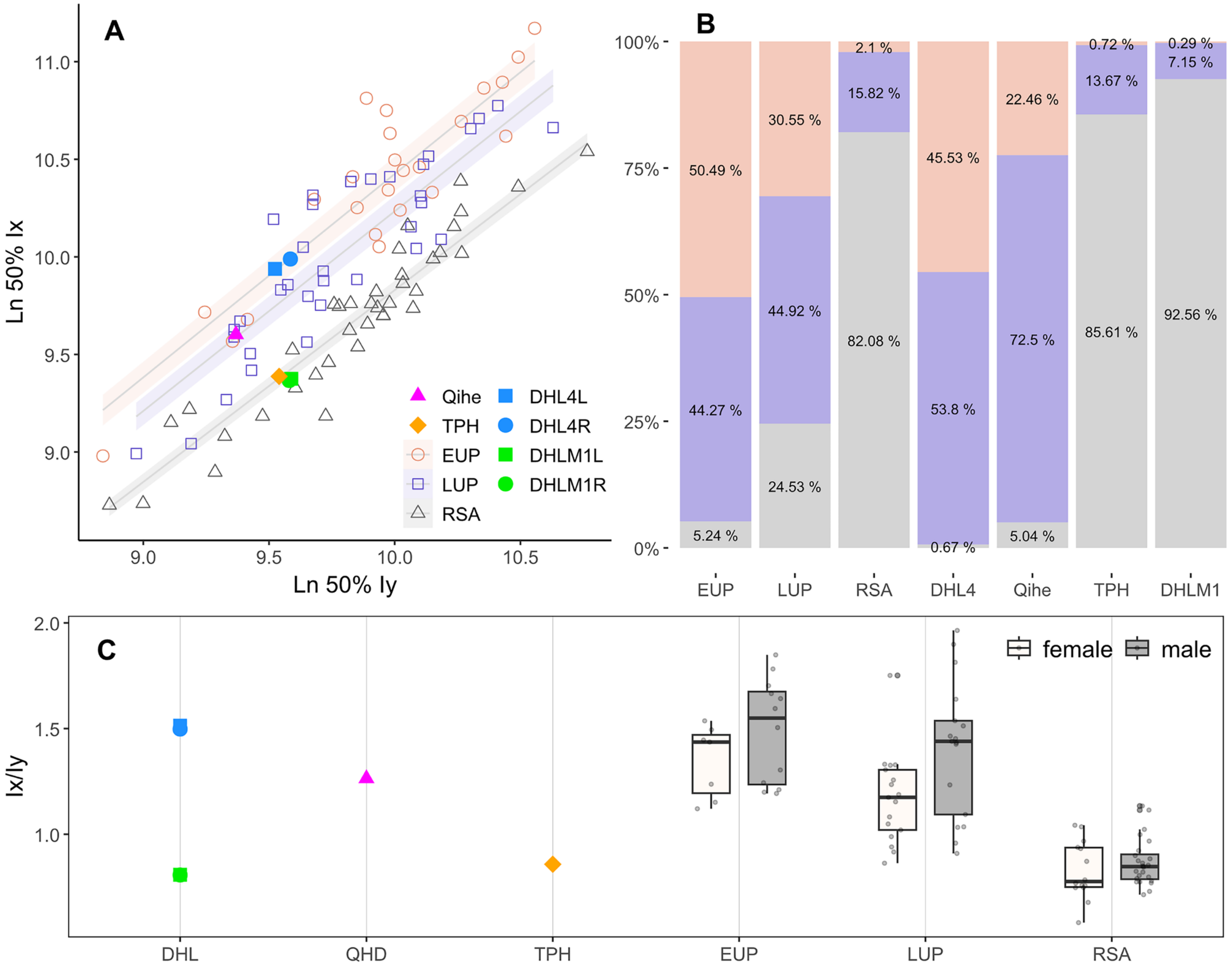

FIGURE 3 | Comparative analysis of cross-sectional shapes at femoral diaphyseal midshaft. (A) Bivariate plot of log-transformed anteropoterior (I_x) versus mediolateral (I_y) second moment of area. The shaded areas around the regression line represent the 95% confidence intervals of the fit. (B) Posterior probabilities for classification as EUP (red), LUP (blue), and RSA (GRAY) derived from linear discriminant analysis conducted over 1000 iterations. (C) Comparison of East Asian Early Holocene specimens with sex-separated comparative groups. DHL4L and DHL4R: Donghulin 4 left and right; DHLM1L and DHLM1R: Donghulin M1 left and right; EUP: Early Upper Paleolithic; LUP: Late Upper Paleolithic; Qihe: Qihe M2; RSA: recent sedentary agricultural population; TPH: Taipinghu 45.

regions of thickening are nearly identical, whereas in Junzicun females, the posterior thickening is less pronounced compared to the medial and lateral regions.

All individuals exhibit thinner cortices across the mid-distal to distal diaphysis (Figure 4B). The thickest standardized cortices are observed in the posterior aspect of Tianyuan 1. Additionally, DHL 4, Qihe M2, Liujiang, and Tianyuan 1 exhibit slightly greater overall cortical thickness along the entire femoral diaphysis when compared to DHL M1, TPH 45, and Junzicun specimens.

Figure 5A presents the results of the PCA based on CBT values along the entire femoral diaphysis. The first principal component (PC1) explains 50.8% of variance and primarily reflects overall CBT variation. As PC1 increases, the cortices of the entire femoral diaphysis thicken uniformly, while the distribution pattern of cortices remains stable, consistently showing three thicker regions in the medial, posterior, and lateral aspects. The second principal component (PC2) explains 10.01% of variance and mainly captures variations in the distribution pattern of cortices along the femoral diaphysis. At the PC2 minimum, the corresponding morphometric map exhibits notably thick cortices along the posterior diaphysis, whereas at the PC2 maximum, the corresponding morphometric map displays thicker cortices in the medial and lateral aspects.

When combining the results of PC1 and PC2, Junzicun males and females are distinct, with males primarily located on the positive PC1 axis and females on the negative side. This suggests that Junzicun males tend to develop thicker cortices along the entire femoral diaphysis compared to Junzicun females. TPH 45 falls within the variation range for Junzicun females, while DHL M1 occupies the overlapping region between Junzicun males and females. They share similar overall cortical thickness and distribution patterns with Junzicun samples. Qihe M2 and

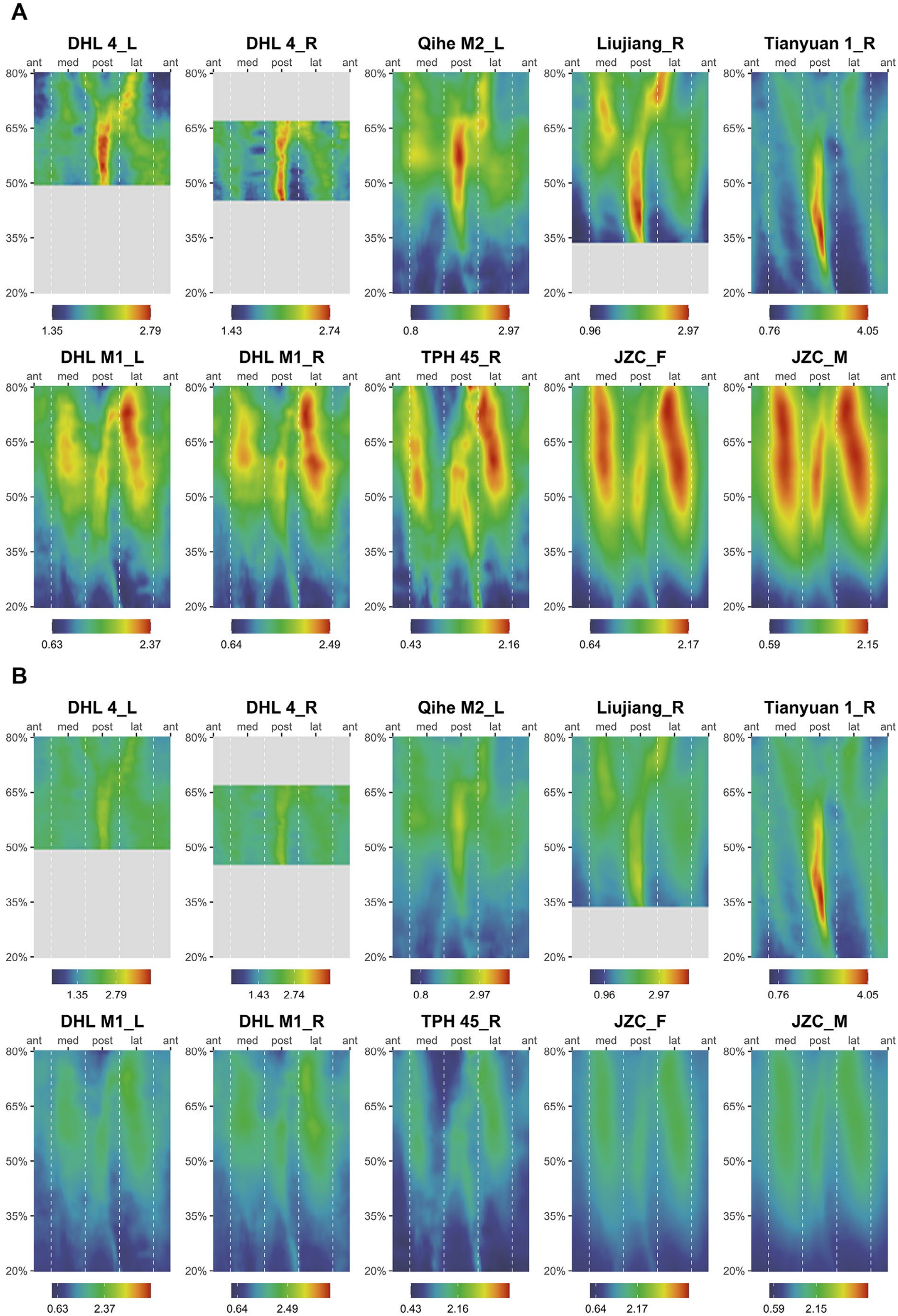

FIGURE 4 | Legend on next page.

FIGURE 4 | Morphometric maps of standardized cortical bone thickness along the femoral diaphysis. (A) Each morphometric map displays its own value range from minimum to maximum. (B) A global range with consistent minimum and maximum values is applied across all morphometric maps. Top *x* axis from left to right: anterior (ant), medial (med), posterior (post), lateral (lat), anterior (ant); Left y axis from bottom to top: distal (20%), mid-distal (35%), midshaft (50%), mid-proximal (65%), proximal (80%). DHL: Donghulin; F: female; JZC: Junzicun; L: left; M: male; Qihe: Qihe Cave; R: right; TPH: Taipinghu.

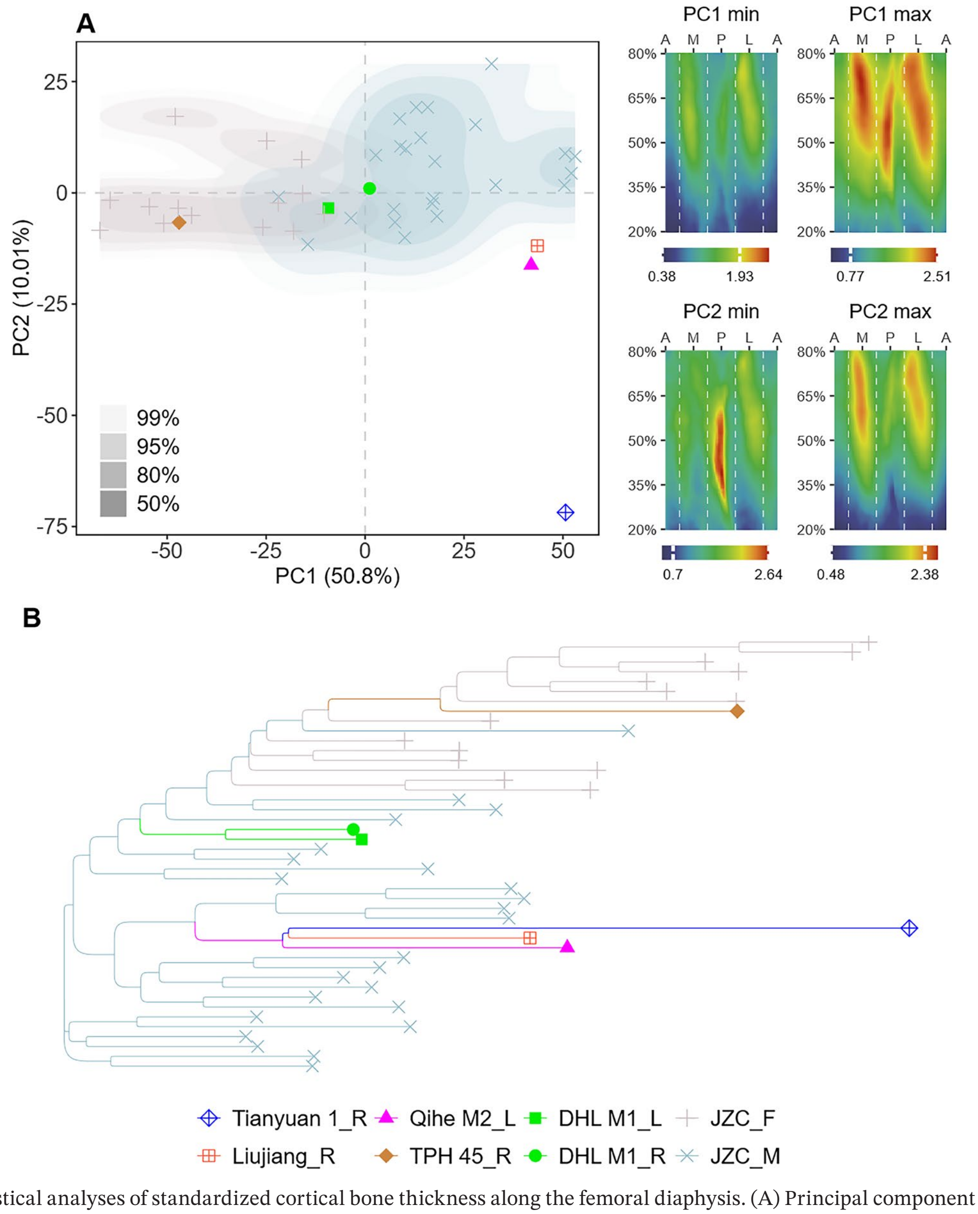

FIGURE 5 | Statistical analyses of standardized cortical bone thickness along the femoral diaphysis. (A) Principal component analysis. The shaded regions represent the confidence intervals for the distributions of the Junzicun population; (B) unrooted neighbor-joining tree.

Liujiang are positioned on the positive PC1 axis and negative PC2 axis, outside the range of Junzicun variation. They are characterized by overall thick cortices, with the thickest region located in the posterior aspect of the femoral diaphysis. Tianyuan 1 is positioned at the PC1 maximum and PC2 minimum, distinctly separated from all other samples, due to the pronounced thickening along the posterior diaphysis.

The neighbor-joining tree, constructed from the distance matrix calculated using CBT values along the entire femoral diaphysis, is shown in Figure 5B. Junzicun females exhibit a distinct clustering, diverging from Junzicun males. TPH 45 shows alignment with Junzicun females, whereas DHL M1 aligns with Junzicun males but is positioned closer to the female branch. Qihe M2, Liujiang, and Tianyuan 1 form a separate cluster, branching off from Junzicun males.

5 | Discussion

This study analyzed key structural properties of the femoral diaphysis in four individuals from Early Holocene East Asia, contextualizing their typical characteristics within a broader spectrum of variation that includes Late Pleistocene early modern humans and RSA populations. The results highlight varied trajectories in the transition of human limb functional morphology across East Asia during the Paleolithic–Neolithic transition.

The midshaft cross-sectional shape of the femoral diaphysis is recognized as a reliable indicator of terrestrial mobility and is commonly used to infer the degree of sedentism in populations during the Paleolithic–Neolithic transition (Holt 2003; Ruff et al. 2015; Shackelford 2007). The results of the present study indicate that, while distinctions exist between the midshaft cross-sectional shapes of EUP and RSA samples, the boundaries between EUP/LUP or LUP/RSA are not clearly defined. Adjacent groups differ at the group level, but individual specimens within these groups cannot be accurately classified based solely on the shape indicator I_x/I_y. Their posterior probabilities of being assigned to either their original or adjacent groups differ, but are not distinct (Figure 3). Among Chinese Early Holocene specimens, two shape patterns are observed: DHL 4 and Qihe M2 align closely with the LUP group, showing a posterior probability of classification as LUP that exceeds the group level probability for LUP specimens. Furthermore, DHL 4 demonstrates a noticeable possibility of being classified within the EUP group. In contrast, DHL M1 and TPH 45 closely resemble RSA specimens, with posterior probability distributions similar to those of the RSA group, although their posterior probabilities of being classified as RSA are slightly lower.

Morphometric maps provide deeper insights into femoral diaphyseal structure among modern humans from different regional and chronological contexts. Diverse patterns were detected among Chinese Early Holocene specimens. Qihe M2 exhibits a close relationship with Late Pleistocene early modern humans, particularly, Liujiang from South China, aligning with Liujiang in statistical analyses based on CBT and SMA morphometric maps. DHL 4 exhibits distribution patterns of CBT, ER, and SMA morphometric maps similar to those of Qihe M2, and is also comparable to Late Pleistocene early modern humans, though only in restricted diaphyseal sections can qualitative comparisons be made. Late Pleistocene early modern humans, represented by Liujiang and Tianyuan 1, exhibit similar patterns in CBT, ER, and SMA morphometric maps, characterized by thickened cortices and enlarged external radii in the posterior aspect, resulting in increased anteroposterior bending rigidity. These similarities are attributed to their pronounced and distally positioned femoral pilaster, a distinct crest rising from the posterior surface of the shaft where the linea aspera develops. This feature is one of the most typical characteristics of early modern humans (Trinkaus 2005, 2006; Trinkaus and Ruff 2012). Although a pilaster structure is present in the femora of DHL 4 and Qihe M2, SMA morphometric maps reveal that the anteroposterior diaphyseal reinforcement in Qihe M2 is less pronounced than in Liujiang and Tianyuan 1. In DHL 4, it is comparable to Liujiang but less developed than in Tianyuan 1. Additionally, both DHL 4 and Qihe M2 exhibit cortical reinforcement extending from the lateral aspect of the proximal diaphysis to the posterolateral aspect of the mid-proximal diaphysis, as primarily revealed by the CBT morphometric maps. This pattern corresponds to the development of the gluteal buttress, characterized as a clear ridge of bone on the lateral to posterolateral proximal diaphysis, which is commonly observed in Upper Paleolithic modern humans (Trinkaus 2006; Trinkaus and Ruff 2012; Trinkaus et al. 2022; Villotte et al. 2017; Xing et al. 2021). This morphological trait is also evident in Liujiang but absent in Tianyuan 1 (Shang et al. 2007; Wei et al. 2023, 2017).

In contrast to DHL 4 and Qihe M2, TPH 45 and DHL M1 exhibit closer affinities with RSA specimens. TPH 45 falls within the variation range of RSA specimens, particularly, RSA females, in statistical analyses based on CBT and SMA morphometric maps. DHL M1 aligns closely with RSA males in statistical analyses based on CBT morphometric maps, and with RSA females in statistical analyses based on ER and SMA morphometric maps. These findings suggest that both TPH 45 and DHL M1 share closer femoral diaphyseal structures with RSA specimens. The RSA specimens, represented by the Junzicun population, display distinct morphometric map patterns compared to early modern humans. Their femoral diaphyses typically exhibit prominent medial and lateral buttresses, leading to thickened cortices, enlarged external radii in the medial and lateral aspects, and reinforced mediolateral bending rigidity. The linea aspera is only moderately developed, with no pilaster structure present. Notably, TPH 45 displays extreme enlargement of external radii in the medial and lateral aspects, surpassing the range of RSA specimens in PCA based on ER. For DHL M1, the overall cortical thickness resembles that of RSA males, while the overall external radii and bending rigidity more closely match those of RSA females.

The Donghulin population exhibits pronounced sexual dimorphism in femoral morphology. The earlier female individual DHL M1 (11,170–10,700 cal BP) exhibits characteristics closely resembling those of RSA populations, whereas the later male individual DHL 4 (9968–9400 cal BP) retains traits indicative of highly mobile hunter-gatherers. Crucial evidence revealing the origins and development of millet domestication and dryland agriculture in North China has been uncovered at the Donghulin archeological site (Yang et al. 2012; Zhao 2014; Zhao et al. 2021). Charred seeds of foxtail millet recovered from the site have been identified as the domesticated species *Setaria italica* through morphological analysis (Zhao et al. 2021). However, the current archeological evidence does not support the hypothesis that a sedentary agricultural lifestyle was adopted by the Donghulin population or that it influenced the femoral structure of DHL M1. Most of the stone and bone tools found in Donghulin are classified as hunting tools, with no evident farming tools found, and all identified animal remains are wild rather than domesticated. Additionally, the charred seeds of domesticated foxtail millet, with a ^{14}C date of 8240–7820 cal BC, postdate the lifespan of DHL M1 and, therefore, cannot be considered direct evidence of agricultural production during her period (Zhao 2006; Zhao et al. 2021). The pronounced sexual dimorphism in femoral structures observed in the Donghulin population also parallels the pattern reported in Upper Paleolithic humans, Neandertals, and Native North American hunter-gatherers. In contrast, it differs markedly from the reduced levels of sexual dimorphism typical of agricultural populations, such as the Junzicun population and Native North American agricultural groups (Ruff 2005, 2018a).

A logically feasible hypothesis to explain the variation in femoral structures within the Donghulin population is that they practiced a hunter-gatherer subsistence pattern characterized by a "collector" strategy and a broad spectrum of resource utilization. The "collector" strategy involves a logistically organized population structure, where specific resources are procured through specially organized task groups. These task groups would leave the residential camp to obtain targeted resources (Binford 1980). This model accommodates the coexistence of both highly mobile and sedentary individuals within the same population. A division of labor, influenced by factors such as sex, may have contributed to this phenomenon. For instance, individuals like DHL 4 likely engaged in highly mobile hunting and gathering activities, often traveling far from the residential camp. In contrast, individuals like DHL M1 might have performed more sedentary tasks, such as processing plant resources within the residential camp. Evidence supporting sedentary behaviors includes the discovery of numerous pottery sherds and grinding stones at the Donghulin site (Liu et al. 2010; Zhao et al. 2003). The heavy and cumbersome nature of these items suggests that sedentary activities, such as processing plant foodstuffs and storing supplies, were important components of the subsistence strategies employed by the Donghulin population. Starch residues, particularly, from acorns found on grinding stones, along with molar macrowear patterns and dental pathology observed in both DHL 4 and DHL M1, suggest a broad-spectrum diet that included carbohydrate-rich plant resources (He et al. 2021; Liu et al. 2010; Xue and Hao 2010).

Previous studies have demonstrated that the subsistence pattern of Qihe M2 integrates elements of both hunting and plant resource utilization. Faunal and taphonomic analyses at Qihe Cave suggest a subsistence pattern predominantly focused on hunting, with gathering serving as a supplementary activity, as inferred from the species composition and quantity of animal bones (Fan 2014; Fan et al. 2013). Meanwhile, Qihe M2 and M3 exhibit multiple dental pathologies—including caries, periodontal disease, impacted third molars, and enamel hypoplasia—conditions rarely observed in other Chinese Neolithic individuals and that are generally associated with agricultural populations rather than hunter-gatherers (Fang and Fan 2015; Wu et al. 2014). Additionally, the humeri of Qihe M2 show a marked decline in bilateral asymmetry compared to the Late Pleistocene early modern human Tianyuan 1 (Zhao et al. 2022). A similar decline in humeral bilateral asymmetry has been documented in European populations from the Late Pleistocene to the Early Holocene, and that are generally associated with technological shifts in food processing, such as the introduction of two-handed saddle querns for early agricultural females (Shackelford 2007; Sládek et al. 2018; Sládek, Hora, et al. 2016; Sládek, Ruff, et al. 2016). These physical conditions, alongside other Neolithic indicators—such as pottery shards, polished stone and bone tools, livestock remains, and fire pits—suggest the presence of a subsistence pattern incorporating sedentary practices and plant resource utilization, similar to those seen in agricultural populations, within the Qihe population (Wu et al. 2014). The present study indicates that, although the femoral diaphysis of Qihe M2 exhibits affinities with Upper Paleolithic early modern humans, key structural features such as pilaster prominence and anteroposterior bending rigidity are already diminished compared to Liujiang and Tianyuan 1. Collectively, the evidence suggests that the Qihe population may have been in a transitional phase shifting from a highly mobile hunter-gatherer lifestyle to a more sedentary one with potential agricultural components.

Although TPH 45 lacks in situ archeological background information, nearby sites with close spatial and temporal connections provide valuable context. Taipinghu, situated in the Songhua River basin, is part of a plain region in northern Northeast China. This area began transitioning from the Paleolithic to the Neolithic in the late Pleistocene, eventually developing a unique subsistence pattern characterized by sedentary fishing–hunting–gathering in the early Holocene. The agricultural model of millet cultivation and livestock raising did not spread to northern Northeast China until the Bronze Age (Li et al. 2020; Yuan 2016; Yue et al. 2022). This study identifies a sedentary, agricultural-like pattern in the femoral diaphyseal structure of individuals from Early Neolithic northern Northeast China.

Environmental factors may also contribute to the variety in femoral structures among East Asian modern humans during the Paleolithic–Neolithic transition. The Donghulin population resided during a period of warming following the Younger Dryas. Vegetation analysis suggests that the climate had stabilized, with alternating coverage of dry temperate grassland and wet temperate meadow steppe. The Donghulin population typically inhabited the floodplain, a flat, warm, and humid environment rich in plant and animal resources, thus offering a favorable living environment (Xia et al. 2012). The abundance of local resources may have supported the hypothesized 'collector' subsistence strategies employed by the Donghulin population. Stratigraphical, faunal, and taphonomic analyses of the layer containing human remains from Qihe Cave indicate that, during the period of Qihe population habitation, the region supported a diverse and abundant faunal assemblage, reflecting an excellent ecological environment. This period corresponds to the Holocene climatic optimum, characterized by a warm and humid climate that supported the flourishing of forests in the mountainous ecological setting (Fan 2014). These environmental conditions, along with the mountainous topography of the Qihe Cave site, likely contributed to the femoral structures of Qihe M2. Mountainous ecological settings are hypothesized to biomechanically reinforce anteroposterior bending rigidity in the knee region. Traversing sloped terrain requires more flexed joint postures, which are expected to increase anteroposterior bending stresses on the lower limb bones as they flex posteriorly, due to an extended moment arm of the ground reaction force (Higgins 2014; Holt and Whittey 2019). In the regions surrounding Taipinghu, a warm and wet climate has developed since the Bølling–Allerød Interstadial. Rising temperatures facilitated the recovery of the vegetation landscape, increased the availability of aquatic resources, and enhanced the land's carrying capacity. Simultaneously, the formation of swamps and wetlands in low-lying areas reduced the amount of available land for habitation, thereby limiting the presence of large herbivorous mammals that require open landscapes (Mingram et al. 2018; Yue et al. 2022). These environmental changes ultimately contributed to the development of sedentary hunting-gathering-fishing subsistence patterns in this region, as well as the femoral structures observed in TPH 45.

Variation in body shape may also contribute to the structural differences observed in the femoral diaphysis among Early Holocene humans from East Asia. Individuals with relatively broader pelvises position their hip joints farther from the body's center of gravity, thereby increasing mechanical loading along the mediolateral axis during hip abduction. This, in turn, can lead to mediolateral reinforcement of the proximal femoral diaphysis (Burr et al. 1977; Davies and Stock 2014; Lovejoy et al. 1973; Pearson et al. 2014; Ruff 1987, 1995). Such biomechanical factors may partly explain the marked differences in femoral structure between DHL 4 and DHL M1. Although the lower limbs and pelvis of DHL 4 are not sufficiently preserved to allow a direct quantitative comparison of body shape with DHL M1, it is generally recognized that females tend to exhibit broader pelvic morphology (Burr et al. 1977; C. Ruff 1987). This consideration may also account for the extreme platymeric morphology observed in TPH 45. Although neither sex nor pelvic remains are preserved, estimates of body mass (55.69 kg), stature (153.84 cm), and pelvic (bi-iliac) breadth (26.4 cm) indicate a relatively stocky body build with a broad trunk (Text S1).

6 | Conclusion

Two distinct patterns of femoral diaphyseal structure are observed in East Asian modern humans from the Paleolithic–Neolithic transition period. The first pattern, represented by DHL 4 from North China and Qihe M2 from South China, exhibits femoral diaphyseal features adapted for a mobile hunter-gather lifestyle, showing close affinities with Late Pleistocene early modern humans, albeit with a reduction in characteristic traits. The second pattern, observed in DHL M1 from North China and TPH 45 from Northeast China, displays femoral diaphyseal structures closely resembling those of RSA populations. This study shows that human femoral diaphysis displays substantial structural diversity across different regions of East Asia during the Paleolithic–Neolithic transition. This diversity likely reflects variations in subsistence pattern transitions and intrapopulation division of labor, influenced by local factors such as environmental conditions. Other critical biological factors, including sex and body shape, likely also contribute to this observed diversity. This study, based on femoral structural analyses, offers supplementary behavioral insights that are difficult to discern from the archeological record alone.

Author Contributions

Yuhao Zhao: conceptualization, methodology, software, data curation, validation, formal analysis, funding acquisition, visualization, writing – original draft, writing – review and editing, supervision. **Jianing He:** conceptualization, data curation, investigation, supervision, funding acquisition, project administration, resources, writing – review and editing, validation. **Chaohong Zhao:** investigation, supervision, resources, writing – review and editing, project administration. **Jincheng Yu:** investigation, resources. **Yongming Yuan:** investigation, resources. **Tao Wang:** investigation, resources. **Jingning Guo:** investigation, resources. **Minna Wu:** investigation, resources. **Song Xing:** conceptualization, funding acquisition, supervision, project administration, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in the Supporting Information of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **File S1:** ajpa70146-sup-0001-Supinfo.pdf. **Table S1:** ajpa70146-sup-0002-DataS1.xlsx. **Table S2:** ajpa70146-sup-0003-DataS2.xlsx. **Table S3:** ajpa70146-sup-0004-DataS3.xlsx. **Table S4:** ajpa70146-sup-0005-DataS4.xlsx.