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RESEARCH ARTICLE

A comparative study on the tibial morphology among several populations in ancient East Asia

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Human skeletal morphology is a dynamic system affected by both physiological and environmental factors, due to the functional adaptation and remodeling responses of bones. To further explore the adaptation of bone to the environment and the consequent subsistence strategies determined by the diverse natural contexts in the Anthropocene, this study presents a comparative study on the tibiae of seven ancient populations located in different regions of East Asia. Through the analysis of the tibial shaft morphology, a comparative analysis between the populations and genders was conducted to evaluate the differences in external morphology and sexual division of labor. The cnemic indices of the tibial shaft were selected to quantify the external shape. Results showed that different populations had different tibial morphology. Among males, those of Jinggouzi had the flattest tibia while those of Changle had the widest tibia. Among the females, females of Hanben had the flattest tibia, whereas tibia from females of Shiqiao, Changle, and Yinxu were among the widest. The sexual dimorphism was relatively larger in Shiqiao and Jinggouzi and smaller in Tuchengzi and Changle. Through a combination of previous archaeological findings, historical records, and ethnography of the aboriginal Taiwanese, it is concluded that the terrain and ecological environments laid basis for varied subsistence strategies. In addition, the mobility and social labor division under a particular subsistence strategy further contributed to the adaptation of the lower limb morphology to its context. The comparative analysis provides further insight on habitual activities, terrestrial mobility patterns, and subsistence strategies of the populations, which lived in different environmental contexts during the Bronze Age and early Iron Age, thus demonstrating the diverse interactions between human populations and natural environment in the Anthropocene.

Keywords: East Asia, Tibial morphology, Ecological environment, Subsistence strategy, Sexual dimorphism

Introduction

The interaction between humans and the natural environment and ecosystem is an important aspect throughout the human history. Humans settle down in areas that are suitable for their survival, and the diverse natural environment and ecological resources have varying degrees of impact on human lifestyle, diets, habitual activities, and social structure. Therefore, populations with different cultures and lifestyles in various areas contribute to the diversity of the world. With various geographic units and cultures, East Asia witnessed the diversity of human history in the past. From the steppe in the north to the coastal islands in the south, different ancient populations have adapted to the local natural environments and developed different subsistence strategies. To further explore the adaptation of humans to the natural environments and its effects on the populations due to the subsistence strategies and social patterns, the analysis of skeletal remains facilitates the clarification of the issues regarding the ancient relationship between human and earth. Skeletal morphology, especially the long bones, is affected by both physiological and environmental factors, due to the functional adaptation and remodeling responses of bones to the individual's habitual mechanical stimuli (Ruff et al., 2006; Carlson and Marchi, 2014). The Wolff's Law, which is developed by a German anatomist and surgeon Julius Wolff (1892) and the flowing researchers (Kummer, 1959; Pauwels, 1968, 1980; Amtmann, 1971), first states that bone is able to adapt to loads applied to it. As part of its biological properties, bone tissue has the ability to model or remodel its material properties, in response to a number of mechanical and nonmechanical factors throughout an individual's lifetime, which is termed as the "Bone Functional Adaptation" (Martin et al., 1998; Carter and Beaupré, 2001; Ruff et al., 2006). Therefore, the morphology and robusticity of bones are modified by genes, hormones, mechanical loading, habitual activities, body size, nutritional and health conditions, and even terrain and climate (Ruff and Hayes, 1983; Ruff, 1987, 1994; Feik et al., 2000; Pearson, 2000).

In the field of physical anthropology, with consideration of the cross-sectional shape and external

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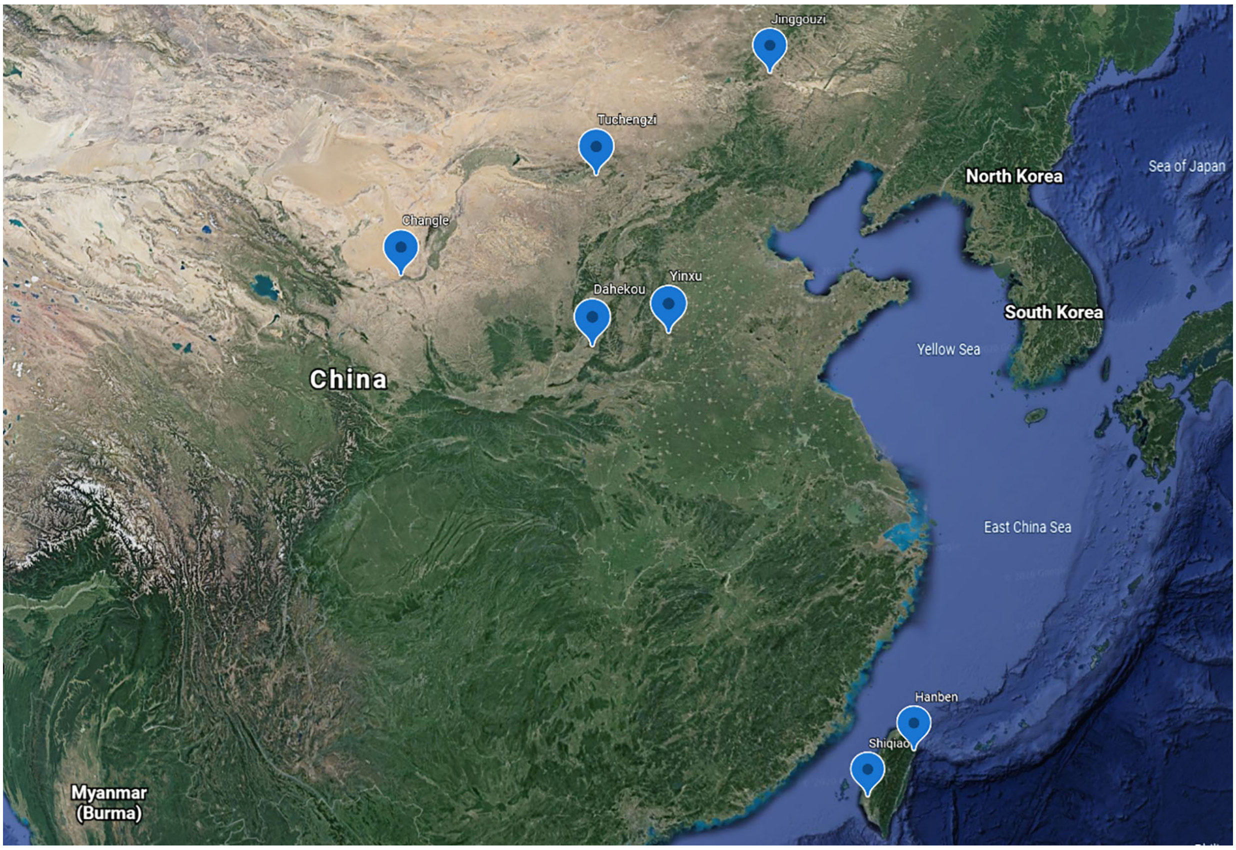

Figure 1. The location of the involved sites in East Asia. Seven archaeological sites located in East Asia are marked in the map with blue symbol. They distribute in different parts in East Asian continent and Taiwan Island with various terrains and ecological environments. DOI: https://doi.org/10.1525/elementa.2021.00071.f1

dimensions, the analysis of the upper and lower limbs diaphyseal morphology has been widely used to figure out the morphological differences among both archaeological and modern human populations (Brothwell et al., 1968; Lovejoy et al., 1976; Larsen, 1981; Senut, 1985; Ruff, 1987, 1994; Bridges, 1989; Collier, 1989; Ruff et al., 1993; van der Meulen and Carter, 1995; Abbott et al., 1996; Lieberman, 1997; Trinkaus and Ruff, 1999; Bridges et al., 2000; Pearson, 2000; Stock and Pfeiffer, 2001; Wescott, 2006, 2008; Wanner et al., 2007). Among these studies, researchers attributed the differences in populations' limb morphology to different subsistence strategies, varied social divisions of labor, and different geological regions. The present study aims to investigate the lower limb morphology and sexual dimorphism among different ancient populations in East Asia. To this end, the index calculated by external measurements of adult lower limbs was obtained to quantify the diaphyseal shape. It is important to understand that this study represents the first attempt at a comparative analysis of the lower limb morphological characteristics in ancient East Asian populations and, therefore, provides a unique way to deepen our knowledge of the diversity of the human adaptation to various environmental units in ancient East Asia.

Materials and methods

Seven populations from the East Asian continent and Taiwan Island were selected for this comparative study. These populations date back to the Bronze Age to the Iron Age with relatively specific subsistence strategies.

Shiqiao site (**Figure 1**) is located at 23°06′22"N, 120° 18′12"E at the river's alluvial fan in southwest Taiwan in Daying Village, Tainan County. The archaeological culture is characterized by red pottery, dating back to 1930–1370 years ago (Zhu, 2005; Yeh, 2009, 2010). The grave goods in this period consisted of pottery, earthen rings, earthen beads, earthen spindle whorls, earthen net sinkers, stone implements, iron tools, bone tools, accessories made from fish bone, and glass beads or rings. In addition, animal bones including mammals, amphibians, birds, fish, and a large amount of rice were unearthed (Chen, 2008; Chiu, 2009).

Hanben site (**Figure 1**) is located at 24°19′40"N, 121° 45′56"E in the subtropical mountainous east coast of Taiwan at the south of Yilan County. The dating indicated that the upper layer of archaeological remains could be dated to the Early Iron Age (1574–971BP), while the lower layer could be dated to the Late Neolithic Period (1992–1335BP). The archaeological remains consisted of a significant number of marine fish bones, coupled with several terrestrial animal bones (personal communications, unpublished reports by YC Liu). The skeletons discovered from the two abovementioned sites represented the early aboriginal Austronesians who lived in different regions of Taiwan.

Table 1. Sample composition of the femora and tibiae from each site. DOI: https://doi.org/10.1525/elementa.2021.00071.t1

		Tibia	
Population	**Subsistence Strategy**	**Male**	**Female**
Shiqiao	Agriculture/hunter-gathering	18	18
Hanben		36	16
Tuchengzi	Agriculture	22	12
Changle		29	27
Dahekou	Urban	70	78
Yinxu		29	19
Jinggouzi	Nomad	14	5

Tuchengzi site (**Figure 1**) is located at 40°27′25″N, 111° 45′57“E in the Tumote plain in Helingeer County, Inner Mongolia. Specifically, the area includes the piedmont alluvial plain and the Yellow River alluvial plain in north China. The site dating back to the Warring States period (2425–2171BP) was considered as one of the several troop stations along the ancient Great Wall. The unearthed burial items include pottery, bronze, iron, jade, and bone. The economic activities of the population were mainly farming, and grain crops such as millet and wheat were likely an important source of food for the residents of Tuchengzi (Gu, 2007).

Changle site (**Figure 1**) is located at 37°26′24“N, 105° 05′43″E in Ningxia. Specifically, it includes the second terrace of the southern bank of the Yellow River at the junction of the desert and the Loess Plateau in the middle and upper reaches of the Yellow River. The period of the site is from the early and middle period of the Western Han Dynasty to the early and middle period of the Eastern Han Dynasty (2152–1730BP). This population consisted of agricultural residents guarding the northern frontier in the Han Dynasty (Zhang, 2018).

Dahekou site (**Figure 1**) is located at 35°44′57“N, 111° 47′00″E in Yicheng County, Shanxi, right in the plain delta where the main stream and tributaries of the Hui River meet. Different types of tombs dating back to the early Western Zhou Dynasty to the early Spring and Autumn Period (2996–2720BP) were found and many of bronzes, pottery, and jade, lacquered items were excavated. The site is considered as the civilian cemetery of the Ba State of Western Zhou Dynasty, which consists of civilians and inferior nobles (Han, 2019).

Yinxu site (**Figure 1**) is located at 36°07′;21“N, 114° 19′24″E in Anyang, Henan, specifically the gentle slope of the eastern foothills of Taihang Mountain along the Huan River. The site was within the territory of the last capital of the late Shang Dynasty (3200–2996BP), and this region consisted of handicraft workshops, general residences, and civilian graves outside the tombs of kings. Most of the population should be civilians and inferior nobles. A large amount of bronze, gold foil, pottery, and jade was unearthed (Yuan, 2010).

Jinggouzi site (**Figure 1**) is located at 43°23′16“N, 118° 14′28″E on the gentle slope of the ranges of the Greater Xing'an Mountains in Linxi County, Inner Mongolia in Northern China. The cemetery was considered as nomad tombs dating back to 2485 ± 45 BP (Wang et al., 2010; Zhang et al., 2019). Livestock skeletons were abundantly found inside the tombs, and the main species were classified as horses, cattle, and sheep (Wang et al., 2010). No agricultural tools or swine bones were found in the cemetery, indicating that the population did not live an agrarian life (Zheng, 2004).

The data used in this study include tibial measurements from adult, nonpathological individuals of the above populations (**Table 1**). The measurements of the Shiqiao, Hanben, and Changle populations were taken by the authors, while the other measurements were extracted from published data. The preservation conditions of human remains vary in East Asia; the selected populations involved in this study are relatively large in sample size and representative of the populations in East Asia. The limbs are important indicators of human behavior patterns. Considering that the morphology of the lower limb largely reflects the daily activities and lifestyle, the tibia was chosen for analysis. The measurements of the right bones were preferentially used since the right side is considered as the dominant side in most populations (Auerbach and Ruff, 2006). The left counterparts were included when bones on the right were either absent or damaged.

Due to the poor conditions of the bones, two linear measurements related to the external shaft diameter were taken on the tibia at the level of the nutrient foramen to estimate the structural properties of lower limb. A digital sliding caliper, with accuracy of 0.01 mm, was used to obtain the measurements. To qualify the differences in bone shape, structural properties were derived from the external measurements (Ruff and Hayes, 1983; Ruff, 1984). The cnemic index of the tibia was calculated by dividing the anteroposterior (A-P) plane diameter by the mediolateral (M-L) plane diameter (A-P/M-L) at the level of nutrient foramina (Martin, 1928). Four types of tibia morphology based on the cnemic index were classified as shown in **Table 2** and **Figure 2** (Martin, 1928). Mean values for both sexes and the sexual percentage difference are presented. All the analyses were performed using IBM SPSS Statistics v. 25. To facilitate direct comparisons between genders and populations, the indices of the populations are plotted in **Figure 2**.

Results

The differences between genders and populations in tibial morphology

For the cnemic index reflecting the flatness of tibia, the comparison between genders and populations were conducted respectively (**Table 3**, **Figure 3**).

Regarding differences between genders within the population, in the Hnaben population, the average of male was 65.71 and that of female was 65.06. As for the Shiqiao population, the average of male was 61.61 and that of female was 70.95. In the Tuchengzi population, the average of male was 68.20 and that of female was

68.56. In the Changle population, the average of male was 70.25 and that of female was 70.64. In the Dahekou population, the average of male was 66.31 and that of female was 68.34. In the Yinxu population, the average of male was 69.58 and that of female was 70.69. In the Jinggouzi population, the average of male was 59.54 and that of female was 68.23.

Among the males, the tibia of Shiqiao and Jinggouzi belongs to the platycnemic type, one of Changle belongs to the eurycnemic type, and the rest belong to the mesocnemic type. Among the females, the tibia of Hanben, Tuchengzi, Dahekou, and Jinggouzi are of mesocnemic type, while the ones of Shiqiao, Changle, and Yinxu are of eurycnemic type. The average of females was slightly greater than the males except for the Hanben population.

Table 2. Types of tibial morphology by index range (Martin, 1928). DOI: https://doi.org/10.1525/elementa.2021.00071.t2

Type	Index
Hyperplatycnemic	<54.9
Platycnemic	55.0–62.9
Mesocnemic	63.0–69.9
Eurycnemic	>70.0

Regarding differences between populations for the same sex, the average of the males in the Changle was the greatest and Jinggouzi was the least; the average cnemic index of females in the Shiqiao was the greatest and Hanben was the least, indicating that the tibia of the males in the Jinggouzi population and the females in the Hanben was much flatter.

The sexual dimorphism of tibial morphology in different populations

Sexual dimorphism exists in all populations regarding the tibial morphology. As for the flatness of the tibia, the sexual dimorphism in the Tuchengzi and Changle population is quite small, and the sexual percent difference is only 0.53 and 0.55, respectively. The sexual percentage difference in the Hanben, Dahekou, and Yinxu populations is between 1 and 3. However, the sexual dimorphism in the Shiqiao and Jinggouzi populations are particularly large as 13.16 and 12.74, respectively, demonstrating the existence of sexual division of labor and different habitual activity patterns.

Discussion

Comparisons of limb morphology between populations who lived in different regions of East Asia with different subsistence strategies could illustrate human history in the past and further clarify the interaction between

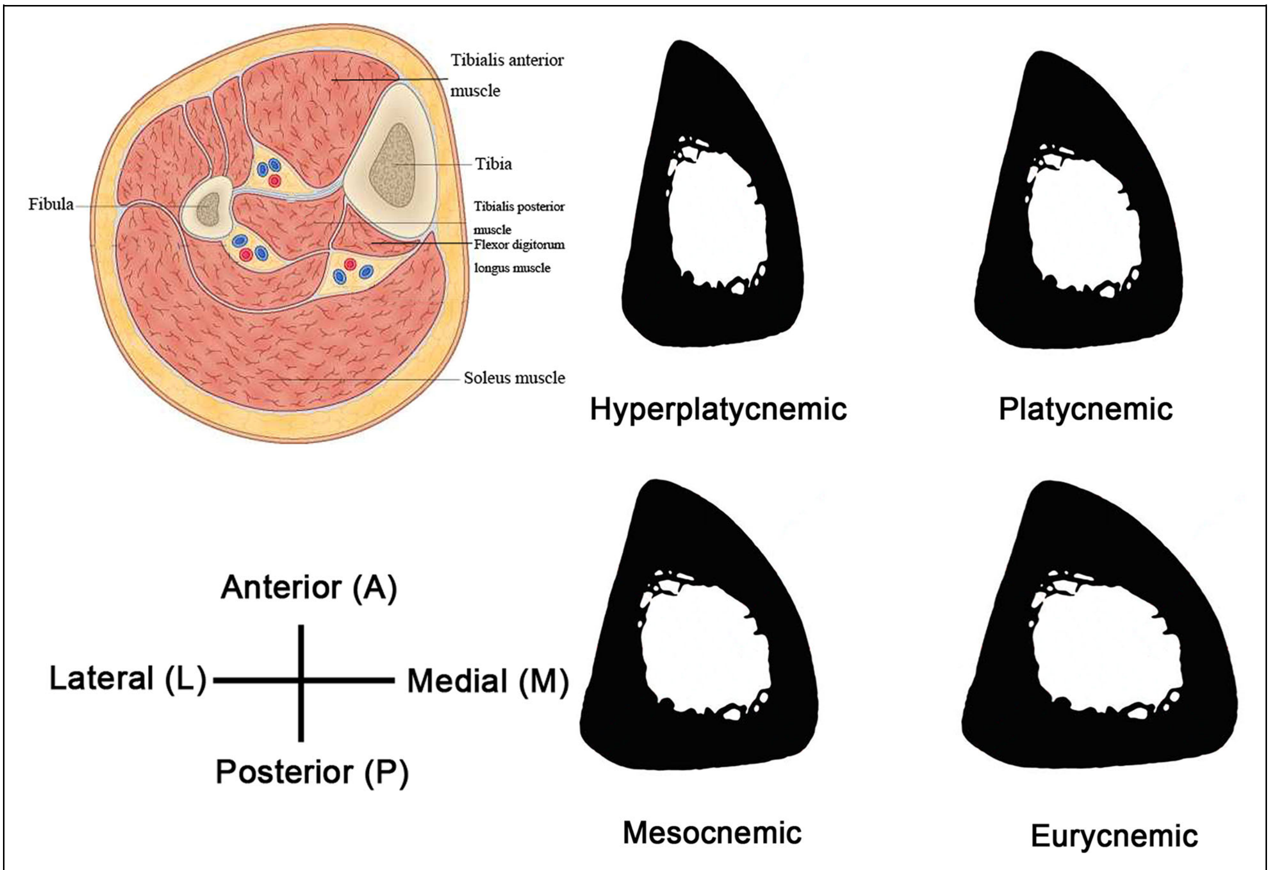

Figure 2. Types of tibial morphology at the level of nutrient foramen. Four types of tibia with different cnemic index are illustrated in the figure. The type with less cnemic index is flatter in the lateral-medial direction, while the one with greater cnemic index is wider. DOI: https://doi.org/10.1525/elementa.2021.00071.f2

Table 3. Statistic of the tibial cnemic index in Shiqiao and Hanben population. DOI: https://doi.org/10.1525/elementa.2021.00071.t3

	Male			Female			
Populations	***N***	**Mean**	***SD***	***N***	**Mean**	***SD***	**Percentage Difference**
Hanben	36	65.71	6.47	16	65.06	8.25	1.00
Shiqiao	19	61.61	5.70	19	70.95	6.98	–13.16
Tuchengzi	22	68.20	6.47	12	68.56	5.85	–0.53
Changle	29	70.25	4.64	27	70.64	4.87	–0.55
Dahekou	70	66.31	6.80	78	68.34	6.32	–2.97
Yinxu	29	69.58	5.82	19	70.69	5.60	–1.57
Jinggouzi	14	59.54	6.47	5	68.23	7.07	–12.74

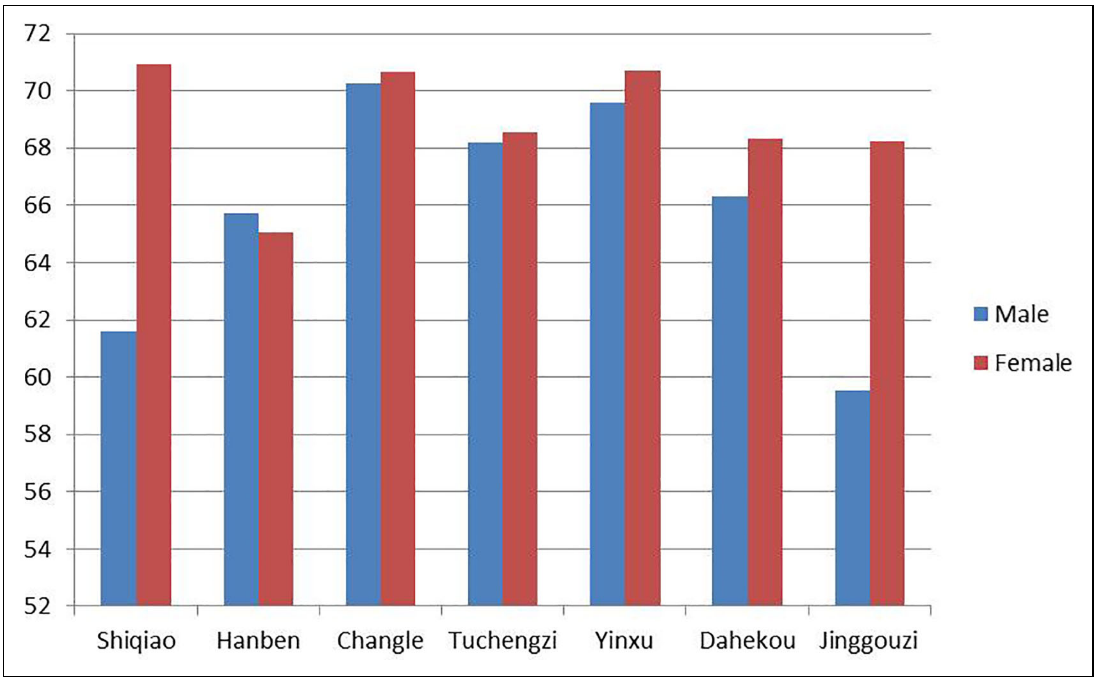

Figure 3. Cnemic index of the males and females in each population. The cnemic indices of each population are plotted by gender. The difference of cnemic index between populations and genders can be easily observed. DOI: https://doi.org/10.1525/elementa.2021.00071.f3

human and the natural environment and ecosystem. By quantifying the tibial morphology, through the comparison between the populations and genders, the results from the external shaft shape and sexual dimorphism of the tibia facilitate our understanding of the differences in limb morphology and the patterns of sexual division of labor among the different ancient populations in East Asia.

The effect of terrain on the limb morphology among the populations

Considering that the geographic environment is similar, terrain could be an important factor in shaping the limb morphology. Shackelford (2014) has emphasized the terrain effects on populations that lived in relatively flat versus mountainous terrain. In another previous study on gender behavioral differences, it has been proven that the increased running and long-distance movement on uneven terrain could further modify the femoral and tibial midshaft from the basic circular cross-section to having an elongated morphology in A-P direction (Ruff and Hayes, 1983). Activities such as running or climbing could lead to the intensive contraction of the hamstrings and quadriceps muscles, which causes high A-P bending loads (Morrison, 1968, 1969, 1970). During running and other similar activities, the quadriceps, hamstrings, and gastrocnemius crossing the knee joint become more active and are capable of generating intensive A-P bending loads and very little M-L bending loads on the femur midshaft and the tibia midshaft (Alexander and Vernon, 1975;

Mann, 1982). Therefore, populations with low mobility are subjected to less directional loading on the lower limb and thus have a greater degree of femoral midshaft circularity, as compared to highly mobile populations.

However, among the seven populations, not all the populations living in the plains had a wide tibia shape, and not all the populations living in the hills and mountains could be characterized by a flat tibia. The Hanben site is located on the coastal sloping fields to the seashore in the east coastal of Taiwan, which is adjacent to the delta with limited plain; the Jinggouzi site is located on the gentle slope of the ranges of the Greater Xing'an Mountains; the Shiqiao site is located on the alluvial plain with numerous rivers; the Tuchengzi and Changle sites are located on the flat terraces or alluvial plains of the Yellow River Basin; the Dahekou site is located on the gentle sloping platform of the delta; and Yinxu is located in the alluvial plain of the river near the Taihang Mountain. Except for the Hanben and Jinggouzi sites located in the coastal mountains and continuous gentle slopes, all the other sites are located in relatively plain areas. Among the males, the cnemic index of Tuchengzi, Changle, and Yinxu is relatively greater, indicating a wider tibia shape, while the cnemic index of Shiqiao and Jinggouzi is smaller and indicates flatter tibias. Among females, Hanben population had the flattest tibias, while the tibial shape of Shiqiao, Changle, and Yinxu is much wider. The males of Shiqiao who lived in the plains have extremely flat tibias, even flatter than the Hanben males living in coastal mountains. The females of Jinggouzi who lived in the hillside fields have wider tibias, which are almost the same as those of Tuchengzi and Dahekou females living in the plain area.

Among these comparative studies, "mobility" (terrestrial logistic mobility) was considered as a measure/factor that resulted in different limb morphology (Cowgill, 2014; Wescott, 2014). Populations who lived in different geographic environments (e.g., terrestrial vs. marine, plain vs. mountainous) would have different levels of mobility (Kelly, 1995; Ruff, 1999; Binford, 2001; Stock and Pfeiffer, 2001; Stock, 2002, 2006; Weiss, 2003; Carlson et al., 2007; Marchi, 2008; Mazza, 2019). Indeed, the terrain has a certain influence on the mobility of the population. The people living in the mountains and hills often take part in more climbing, uphill, or downhill behaviors, while the people living in the plains have relatively less resistance in walking. In view of the seven populations living in different terrains, the shape of the human lower limb tibia is affected not only by the topographical factors but also by the diversification of the subsistence strategy and the social labor division.

The effect of subsistence strategy on the limb morphology among the populations

Different terrains and ecological environments do lead to different human subsistence strategies even within the same geographic unit. The first comparison of activity profiles at the population level is the one applied on the preagricultural and agricultural archeological samples of the Georgia Coast of North America (Ruff et al., 1984). It assessed the femoral cross-sectional properties and therefore initiated a framework for the subsequent analysis on the interpretation of the differences between populations (Ruff et al., 1984). Thereafter, limb morphology has become an increasingly popular field of studies to look into the bone functional adaptations in different populations characterized by various subsistence strategies (Ruff and Larsen, 2014). Among the populations that lived in the mountains and plains, farming and hunting with terrestrial resources is the main subsistence strategy. Long-distance running with high mobility results in greater A-P bending loads in the lower limbs. As the coastal populations were seldom involved in mobility over long distances, they can be characterized by more gracile lower limbs but more robust upper limbs (Stock and Pfeiffer, 2004).

Among the seven populations involved in this study, archaeological and anthropological research results indicate that these populations can be divided into five categories in terms of their subsistence strategy: Tuchengzi and Changle are agricultural types (Gu, 2007; Zhang, 2018); Hanben is a coastal gathering and hunting type (personal communications, unpublished reports by YC Liu); Shiqiao is an agricultural and terrestrial hunting type (Chen, 2008; Chiu, 2009; Yeh, 2009); Dahekou and Yinxu are urban civilians (Yuan, 2010; Han, 2019); and Jinggouzi is a nomadic type (Wang et al., 2010). Both Tuchengzi and Changle are located on the flat riverside terrace at a relatively high altitude. A large amount of pottery was unearthed, and the populations were identified as immigrants from the Central Plains of China in charge of farming and guarding the frontier. The subsistence strategy should be agriculture with dominance of millet and wheat. Dahekou and Yinxu are urban civilians and inferior nobles in the metropolitan territory with relatively lower intensity of labor. The agricultural-based settlers Tuchengzi, Changle, Yinxu, and Dahekou males were mainly food-producing or urban settlers. There was a lower intensity of mobility required of the lower limbs, resulting in a relatively wide tibia.

However, the Shiqiao site is in the alluvial plain on the foothills. Animal bones including mammals, amphibians, birds, and fish and a large amount of rice were unearthed (Chen, 2008), indicating that the Shiqiao population made use of a territorial subsistence strategy based on agriculture and hunting. Jinggouzi is the nomad heading southward during the late Warring States period from the Eurasian steppe (Wang et al., 2010). The tombs are buried with many livestock bones, and the isotope results also are indicative of a meat-dominant diet (Zhang et al., 2008). There is greater daily mobility involved in gathering and hunting and nomadic populations. These activities, hence, involve the lower limbs to a larger degree, leading to a flatter tibia. The relatively greater A-P bending loads in males of Shiqiao and Jinggouzi population indicate the great mobility in these populations. The fairly flat tibias indicate that the males of these populations had more terrestrial mobile activities than the males in the other populations.

An exception would be the Hanben population. Although they lived in a coastal mountainous region with a hunting-gathering pattern, the tibial morphology is not as flat as the others. The Hanben site is located on the coastal sloping fields with limited plains. A large number of deep-sea fish bones, fish teeth, and shellfish were unearthed from the site, coupled with several skulls of wild boar and deer. In addition, exotic glass beads, agate, bronze, and gold foil were found here, indicating that the Hanben population were skilled in navigation and fishing. Thus, they relied on a marine subsistence strategy based on marine resources and trade (personal communications, unpublished reports by YC Liu). In the marine subsistence pattern of Hanben population, people were less likely to engage in long-distance activities. Males were more engaged in activities with less terrestrial mobility. Likewise, the females were more engaged in other activities than females of other populations. Such behavior is due to the lower proportion of settled agricultural production in marine-based pattern, reflecting the influence of ecological patterns on the habitual activities and subsistence strategy. The lower limbs of the Hanben males were less involved in activities than the terrestrial hunting populations, resulting to a medium shape of tibia. Compared with other females with terrestrial patterns, the tibia of Hanben female is the flattest due to their coastal subsistence strategy. The flattened tibia of the Hanben females is also due to greater mobility and greater involvement of lower limbs in coastal gathering and hunting activities.

The sexual dimorphism among the populations

Sexual dimorphism in bone morphology is pervasive as a result of physiological, genetic, and behavioral differences between the males and the females (Frayer and Wolpoff, 1985). Especially in lower limbs, sexual differences in morphology have long been noticed, which reflect the different patterns of mechanical loadings applied on the lower limb bones in daily life (Hrdlička, 1898, 1934; Parsons, 1914; Holtby, 1917; Pearson and Bell, 1919; Ruff and Hayes, 1983). Martin previously noted that among most of his archaeological and modern population samples, females generally had rounder cross sections morphology in the femur midshaft and proximal tibia (Martin, 1928). Generally, the lower limbs of males are adapted to relatively greater A-P bending load due to a greater participation of intense activities, while the lower limbs of females are adapted to a greater M-L bending load due to the relatively greater pelvic breadth and the consequent loads from the hip physiologically (Ruff, 1987). Besides the physical differences between the sexes, the existence of social division of labor in ancient society is another important factor that contributes to the sexual dimorphism. The previous findings for the femoral and tibial shafts strongly support the association between the subsistence strategy and sexual dimorphism in lower limb morphology (Armelagos and Van Gerven, 1980; Frayer, 1980, 1984; Hamilton, 1982; Collier, 1993; Wescott, 2005; Pomeroy and Zakrzewski, 2009). Ruff (1987) examined shaft morphology of lower limbs in different archaeological and modern populations and revealed the reduction in the degree of sexual dimorphism from hunting-gathering to agricultural populations due to the decrease in mobility and the degree of sexual division of labor.

Among the seven populations with different subsistence strategies, the gender differences are obvious. It is said that a higher degree of sexual division of labor is required in hunting-gathering populations than in the agricultural ones, which results in a greater degree of sexual dimorphism on the limb midshaft among hunter-gatherers (Ruff, 1987, 2000; Bridges, 1995; Larsen, 1997). The Shiqiao and the nomadic Jingouzi present the largest gender differences, indicating that their social labor division is quite obvious. The sexual dimorphism of the tibial morphology was quite great in the Shiqiao population, characterized by a much flatter tibia of males. Under the terrestrial subsistence strategy of the Shiqiao population, males were mainly responsible for the hunting that required long-distance running, while the females were more engaged in settled agricultural production, which is also reflected in the ethnographic records of the aboriginal Siraya people in this region (Zhou, 2005). In the Siraya society, females were mainly engaged in farming, wine making, and in charge of the domestic chores. Males were responsible for hunting and were skilled in rapid walking and running (Lv, 2006). This obvious sexual division was evident among the agricultural-hunting population that lived in the plain. While in Jinggouzi, the nomad grazed seasonally by chasing adequate rainfall and vegetation. Males in Jinggouzi generally undertook long-distance herding of cattle and horses, and females were engaged in milking, food processing, and production of fur products (Wuritaoketaohu, 2006).

However, the gender difference among the urban settlers Dahekou and Yinxu is as small as between 1.5 and 3, and the agricultural populations Tuchengzi and Changle have the smallest gender difference with only about 0.5. In ancient Chinese agricultural societies, especially in the garrison populations in the north like Tuchengzi and Changle, both males and females were involved in agricultural activities. It can also be verified from literature and historical research results that the garrison and females were mainly engaged in guarding and farming (Jia, 2004). As for the urban settlers Dahekou and Yinxu, historical records show that civilians in the Shang and Zhou Dynasties were both military and social units in urban organizations. Both civilian males and noble males became warriors in time of war. However, in times of peace, males were engaged in farming and handicraft such as casting, pottery, and jade processing, and females only acted as an auxiliary labor role in the family (Zhao, 2005).

The gender difference of coastal marine hunting population Hanben is also as low as 1. Ethnographic records documented that the ocean facing East Coast region, where the Hanben site is located, was mainly occupied by the aboriginal Amis/Pangcah people and the Kavalan people who relied on marine livelihoods. The marine hunting was well developed with the manufacturing and usage of bamboo boats (Dadangoyan; Zhang and Huang, 2011) and spearfishing (Mifisho/Mipacin; Qin, 1939). They engaged in a traditional maritime life, characterized by fishing and trading by canoes and sailboats, coupled with little farming and hunting (Shi, 2016). In the marine subsistence strategy of the Hanben population, where there was a small proportion of agriculture, both sexes were required to participate in different maritime activities. These maritime activities involved lesser terrestrial mobility, resulting in less sexual dimorphism in the lower limb morphology. The sexual division of labor with involvement of lower limbs was not obvious in these populations.

Conclusion

Through the analysis of differences in cnemic index between populations and genders, we further discussed the effects of terrain, ecological environment, human subsistence strategy, and division of labor on lower limb morphology among ancient populations in East Asia, demonstrating the functional adaptation and remodeling responses of bones to the environment in the Anthropocene. As for the tibial morphology, the females of Hanben had the flattest tibia; tibias of Shiqiao, Changle, and Yinxu populations were among the widest; the males of the terrestrial resource-based Shiqiao and Jinggouzi populations had flatter tibia with a greater degree of sexual dimorphism. However, agricultural and urban civilian and the marine resource-based Hanben population had wide tibial morphology with a lower degree of sexual dimorphism. Archaeological findings, historical records, and ethnographic records of the Taiwanese aborigines highlighted the influence of terrain and ecological environment on the subsistence strategy. These resources also clarified that the lower limb morphology was largely shaped by varied ways of resource utilization and degrees of social sexual division of labor in ancient populations.

Data accessibility statement

The raw data for this manuscript are available as a supplemental spreadsheet file.

Supplemental files

The supplemental files for this article can be found as follows: **Data S1.** Raw data. xlsx.

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Competing interests

The authors declare that no competing interests exist.

Author contributions

Contributed to conception and design: QZ, HY.

Contributed to acquisition of data: QZ, HY.

Contributed to analysis and interpretation of data: QZ, HY.

Drafted and/or revised the article: QZ, HY.

Approved the submitted version for publication: QZ, HY.

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