Exploring the role of fibular extremities as indicators of mobility patterns and locomotor behavior in Homo sapiens from Mid-Late Upper Paleolithic to the modern age

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Abstract

The human fibular shape has been scarcely analyzed in anthropology. However, studies on athletes and human archaeological samples suggest the importance of including fibular structural properties to reconstruct mobility patterns in past populations. This study analyzes human fibular variation in relation to mobility patterns, environmental conditions, subsistence economies, and shoe use to further explore the role of this bone in reconstructing mobility patterns in past populations.

The sample consists of 173 individuals from archaeological and modern skeletal collections spanning the Mid-Late Upper Paleolithic to the 20th century and includes hunter-gatherers, agriculturalists, herders, and post-industrialists. Virtual three-dimensional models of left fibulae were acquired by computer tomography and surface scanning. Fibular proximal and distal epiphyseal morphologies were investigated through 3D semilandmark-based geometric morphometric methods and compared among populations and mobility categories.

Our analysis reveals a trend separating groups based on their subsistence strategy and chronology. Some fibular traits (e.g., horizontal proximal tibiofibular and tilted distal talofibular articular surfaces, robust interosseous membrane, broad malleolar fossa, projecting m. *biceps femoris* insertion) indicate greater mobility of fibular joints and load sharing during ankle and knee excursion in foraging groups, which are presumably highly active, frequently traversing uneven terrain with absent/minimalist foot coverings. Stiffer fibular joints (e.g., obliquely oriented tibiofibular and vertical talofibular articular surfaces) are observed in sedentary populations, which may suggest a restricted ankle excursion and limited lower limb loading and use, consistent with their sedentary lifestyle in plain urban settlements with hard-shoe coverings. Other fibular traits (e.g., shorter subcutaneous triangular surface, projecting and anteriorly-facing malleolus, concave peroneal groove and proximal peroneal insertion) might indicate for mobile groups a more everted foot posture with increased moment arm in eversion, more efficient for barefoot/minimal footwear running in a forefoot-strike gait and concurring in the stabilization of the first metatarsophalangeal ray. These results further stress the functional role of fibular morphology and its importance in studies investigating past population mobility patterns.

1. Introduction

Bone cortical and trabecular tissues are considered highly plastic, functionally adapting to mechanical loadings (Ruff, 2008; Stock, 2018) through the process of bone modeling and remodeling (Barack 2020). Although other biological factors (e.g., genetic expression, ontogeny, and aging) play an essential role in the process of bone remodeling (Pearson and Liebermann 2004; Ruff et al. 2006), many studies proposed a relationship between an increased behaviorally-mediated strain magnitude and increased mechanical performance of bone (Ruff et al. 2006 and reference therein).

In addition, numerous studies have shown that, due to the plasticity of cortical bone, the diaphyseal shape is also connected to bone mechanical performance and varies according to loading regimen (Burr et al. 1989; Currey 1984; Jones et al. 1977; Lanyon et al. 1982; Lanyon and Rubin 1984; Lanyon 1992; Martin and Burr 1989; Rubin et al. 1990; Ruff 1992; Ruff et al. 2006; Trinkaus et al. 1994; Woo et al. 1981). Indeed, several studies on long bones explored and affirmed the role of highly characterizing activities in shaping specific patterns of biomechanical rigidity and diaphyseal shapes in the upper and lower limbs of archeological populations and athletes (Haapasalo et al. 2000; Hagihara and Nara 2016; Nikander et al. 2006; Sparacello et al. 2014; Shaw and Stock 2009a, 2009b; Trinkaus et al. 1994; Wescott et al. 2014).

The diaphyseal shape of leg bones and their structural properties at cross-sectional level were vastly investigated. While tibial robusticity correlates to the level of mobility in a human sample of athletes, the tibial diaphyseal shape was also found to be an indicator of loading directionality: Shaw and Stock found that cross-country runners and field hockey players had significantly more robust tibiae than controls also reflecting different tibial shapes for each group linked to the loading regimen (2009b). The greater tibial robusticity and larger shape at the tibial midshaft were found to be linked to higher levels of terrestrial mobility also in bioarcheological samples (Ruff 1987; Ruff and Hayes 1983; Stock 2006). Shaw and Stock (2013) further highlighted the correspondence of tibial robusticity to mobility patterns by comparing bioarcheological samples, fossil hominins, and modern athletes. Other bioarcheological studies observed mixed evidence for a clear correspondence between tibial shape (I_{max}/I_{min} ratio) and changes in mobility levels (Holt 2003; Marchi 2008; Marchi and Shaw 2011; Marchi et al. 2011; Stock and Pfeiffer 2001;

Sladék et al. 2006), suggesting that considering the structural properties of the tibia alone, separated from the fibula, could be ambiguous in determining loading directionality.

The structural properties and shape of the fibular diaphysis relative to the tibia in response to different loading regimens were consequently explored. Rantaleinen and colleagues (2010) documented a higher robusticity of the tibia and fibula with high-impact activities but also suggested a different performance of the two leg bones, indicating that the tibia and fibula experience different loading responses despite their anatomical vicinity, depending on the amount of fibular weight-bearing. The authors hypothesize that this different response to loading is influenced by the complex interaction of tibiofibular kinematics at both proximal and distal tibiofibular joints (Rantaleinen et al. 2010). Similarly, Marchi and Shaw (2011) documented a progressive increase in fibular robusticity from sedentary to runners to field hockey players, possibly linked to a higher degree of ankle dorsiflexion and frequency of cutting movements in the latter groups. Greater ankle medio-lateral excursion modulated the fibula's mechanical load, resulting in higher fibular robusticity relative to the tibia. More recently, Auerbach and coworkers (2017) demonstrated that the cross-sectional properties of the tibia and the fibula vary with respect to their relative position to each other and that directional bending (I_{max} and I_{min}) and average bending rigidity (J) of the fibula is correlated to its distance to the tibia, further supporting the hypothesis that the two bones function both complementarily and in single units. Overall, the structural properties of the two leg bones respond to loading solicitations in terms of intensity and repetitiveness. However, their common interface following mechanical stresses and the link to other variables such as environment and behavior is still being investigated. Indeed, several studies considered fibular structural properties among human archaeological samples to explore its role and correspondence to mobility patterns in bioarcheological contexts, comparing habitual activities of different past populations and from different geographical regions (Hagihara and Nara 2016; Marchi 2008; Marchi et al. 2011; Sparacello and Marchi, 2008; Sparacello et al. 2014, 2018). Marchi and colleagues (2011) examined the impact of mountainous and uneven terrain on the fibular robusticity of the Italian Neolithic and Iron Age samples compared to medieval and modern populations inhabiting flat geographical areas. They tested the possible effect of habitual and repeated foot eversion/inversion movements, required by habitual weight-bearing activities on uneven terrains, on the mechanical loading of the fibula. The authors argued that fibular robusticity, either considered alone or paired with the tibia, is correlated with mobility levels, and is influenced by uneven terrain. Sparacello and colleagues (2014) further documented higher relative fibular robusticity in a mountain-dwelling archaeological sample compared to samples from regions with flat terrain. According to the authors, this difference indicates frequent directional changes occurring in uneven terrain during the exploitation of inland resources by Upper Paleolithic hunter-gatherers and Neolithic pastoralists. Sparacello and coworkers (2018) further examined the Mid to Late Upper Paleolithic – Mesolithic transition as documented by structural and shape variations in the tibiofibular complex correlating with mobility levels and types. They showed that individuals chronologically spanning this transition are comparable to modern athletes, documenting their high activity levels.

While the leg diaphyseal shape and cross-sectional geometrical properties have been quite well explored, less is known about the external morphology of their extremities, even though the shape and size of articular facets were found to strongly correlate with joint mobility and habitual movements (Currey 2002; Ruff 1988; Ruff and Runestad 1992; Ruff et al. 1994). However, little investigation has been performed on tibiae and fibulae epiphyseal and talar morphology and articular facets. Regarding the study of tibial epiphyseal shape and talar in skeletal samples, several investigations adopted a variety of methodological solutions to explore external shape morphologies for a variety of scopes (e.g., DeSilva 2009; Frelat et al. 2012, 2017; Latimer et al. 1987; Stevens and Vidarsðottir 2008; Sorrentino et al. 2020a, 2021, 2022; Turley et al. 2011). A squared talocrural joint shape was found in humans, uniformly distributing forces across the joint in bipedal locomotion with a perpendicular orientation to the long axis of the tibial shaft. In great apes, the joint is trapezoidal with an anterior tilt to accommodate the foot in extreme dorsiflexion during climbing (DeSilva 2008, 2009; DeSilva and Throckmorton 2010; Latimer et al. 1987; Sorrentino et al., 2020b; Turley et al. 2015; Venkataraman et al. 2013). While most of these studies focus on morphological comparisons among hominids, Brzobohatá and colleagues (2014) explored variations in the morphologies of tibial extremities of archaeological populations belonging to different socioeconomic living conditions (high vs. low economic status). However, they did not identify a statistically significant correspondence between tibial epiphyseal shape and socioeconomic category. However, a possible trend in distal epiphyseal shape was detected. Indeed, a complex interaction of genetic and non-genetic factors acts on external bone morphology, possibly challenging the reconstruction of finer details of behavior with functional significance (Kivell 2016; Lieberman 1997).

Similarly, Sorrentino and coworkers (2020a) examined the variations in talar morphology in highly mobile hunter-gatherers and more sedentary groups. They revealed that the former group exhibited laterally oriented talar trochleae with a flared lateral malleolar facet, linked to a more everted posture and a more robust and medially oriented talar neck/head, associated with long-distance walking performed barefoot or wearing minimalistic footwear along uneven terrains. On the other hand, individuals with a sedentary lifestyle showed a more parasagittal orientation of the trochlear axis and a less flared lateral malleolar facet linked to a neutral posture and less range of motion at the ankle joint. Sorrentino and colleagues (2020a) concluded that modern human talar shapes vary with locomotor and cultural behavior differences.

Several studies demonstrated that fibular morphology is linked to locomotor behavior in mammals (Barnett and Napier 1953; Carleton 1941). In *Homo sapiens* and primates, the degree of mobility of the fibula has been related to the degree of eversion/inversion and dorsiflexion/plantarflexion at the ankle joint (Marchi et al. 2007). Recent 3D geometric morphometric (3D-GM) studies revealed that proximal and distal fibular morphology are indicators of locomotor patterns associated with each extant hominid taxon (Marchi et al. 2022; Pietrobelli et al. 2023). The authors documented for proximal epiphysis a horizontal proximal tibiofibular joint (PTFJ), a superiorly flat fibular head, an anterolateral and inferior expansion of hamstring and peroneal muscles insertions area onto the fibular head, and a defined but shallower, more medially expanded m. *soleus* insertion in great apes compared to humans. Moreover, for the distal epiphysis the authors observed differences in the orientation of the lateral malleolus, proximal and distal fibulotalar articular facets (PAF and DAF, respectively), and subcutaneous triangular surface proportions, a wider peroneal groove and a deeper and broader malleolar fossa in great apes than in humans. Proximal and distal fibular epiphyseal shapes therefore vary according to locomotor behavior. However, to our knowledge, fibular epiphyseal morphologies were not tested as indicators of mobility and lifestyle within a *H. sapiens* sample to reveal finer behavioral aspects.

Overall, previous researches suggest that the transition from foraging to agriculture and finally to urban life seems to have entailed a reduction in activity and mobility, culminated in highly sedentary lifestyles in modern industrial populations that is reflected in the morphology of the bone (Ruff 2008; Ruff et al. 2015). These diachronic changes led to decreased mechanical stimuli to bone shafts and joints, resulting in generalized skeletal gracilization in more recent populations, in the form of reduced bone apposition in cross-sections, trabecular density and changes in bone and epiphyseal/joint shapes in recent *H. sapiens* (Ruff et al. 1993; Chirchir et al. 2015; Holt 2003; Ryan and Shaw 2015; Stock 2006).

In this study, we adopt a 3D-GM approach to explore shape variability of fibular proximal and distal extremities among Italian archaeological populations dated from the Mid-Late Upper Paleolithic to 20th century with subsistence strategies characterized by progressively declining subsistence-related activity levels (hunter-gatherers with high mobility, agro-pastoralists with intermediate mobility, and pre- and post-industrial groups with low mobility), from even to uneven substrate and with different shoe use.

Based on previous literature on the functional morphology and biomechanics on lower limb in hominoids and human archeological populations (e.g., DeSilva 2009; DeSilva and Throckmorton 2010; Holowka et al. 2017; Marchi et al. 2011, 2022; Pietrobelli et al. 2023; Sorrentino et al. 2020a; Sparacello et al. 2014, 2018) we expect that fibular extremities will vary in shape with decreasing mobility levels and mechanical stimuli (Chirchir et al. 2015; Holt 2003; Ryan and Shaw 2015; Stock 2006). Specifically, we hypothesize:

(a) that fibular morphology will account for the different functional requirements (e.g., frequent ankle and knee flexion, eversion, joint excursion) of the lower limb among the most and least active groups in relation to subsistence (foragers vs. sedentary city dwellers) (Barnett and Napier 1953; DeSilva 2009; Latimer et al. 1987; Stern and Susman 1983). Based on previous 3D-GM studies on the shape of fibular extremities in hominoids (Marchi et al. 2022; Pietrobelli et al. 2023), we expect that hunter-gatherers will display more horizontal proximal and more tilted distal fibular joints, more robust insertions, and uniquely oriented fibular processes, with significant shape difference from sedentary post-industrial populations. We expect that sedentary city dwellers, on the other hand, will display more oblique proximal and vertical distal fibular joints, less pronounced insertions, and distinctive fibular processes.

(b) that population with intermediate mobility (agro-pastoralists) would show a mosaic morphology, variably falling in-between extremes depending on their habitual frequency of other activities (e.g., military activity).

Moreover, we explore possible shape variations related to terrain type and shoe use to test fibular shape as a potential indicator of finer cultural aspects. We further expect:

(c) to find morphologies that are consistent with the requirements of frequent ankle flexion attained during traversing uneven terrain in mountain dwellers and a flexible ankle configuration in populations with no/flexible foot coverings, compared to the vertically loaded, static ankle configurations of city dwellers with hard-soled coverings. Fibular morphologies that are linked to frequent traversing uneven terrain may include specific joint orientations, features and orientation of fibular processes and more robust insertions.

2. Materials and Methods

2.1. Sample description and digital acquisition

The analyzed sample consists of human skeletal fibulae belonging to 173 individuals from 21 Italian archaeological sites and osteological collections, spanning Mid-Late Upper Paleolithic to the 20th century (Table 1) (Fig. 1a).

Table 1

Sample composition by population, chronology, subsistence, terrain and shoe use category and sex. UP = Mid-Upper Palaeolothic/Mesolithic populations; NEO = Neolithic populations; ODN = Bronze Age population of Olmo di Nogara; CER = Iron Age population of Casalecchio-Ceretolo; SUA = Roman population of Suasa; VCN = Late-Antiquity population of Vicenne; OR = Middle Age-Early Modern Jewish population of via Orfeo cemetery, Bologna; ROC = Late Modern population of Roccapelago; ER = contemporary 20th century population of Emilia-Romagna; SAR = contemporary 20th century population of Sardinia.

Population	Chronology	Subsistence	Terrain	Shoe use	F	M	ND	Tot
SAR (Sassari, Nuoro, Cagliari)	Contemporary Age (late 19th - early 20th century CE)	post-industrial, sedentary (low mobility)	flat	hard-sole	26	41	-	67
ER (Bologna, Parma)	Contemporary Age (late 19th - early 20th century CE)	post-industrial, sedentary (low mobility)	flat	hard-sole	19	18	-	37
ROC (Roccapelago)	Modern Age (17th -18th century CE)	agriculturalists/herders (intermediate mobility)	mountainous	hard-sole	-	-	10	10
OR (via Orfeo)	Early Modern Age (14th -16th century CE)	pre-industrial, sedentary (low mobility)	flat	soft-sole	4	4	-	8
VCN (Vicenne)	Early Middle Ages (7th century CE)	agriculturalists/military activity (intermediate mobility)	hilly	soft-sole	2	2	-	4
SUA (Suasa)	Roman Late Imperial Age (2nd -4th century CE)	agriculturalists (intermediate mobility)	hilly	soft-sole	5	3	-	8
CER (Casalecchio Ceretolo)	Second Iron Age (4th -3rd century BCE)	agriculturalists/military activity (intermediate mobility)	hilly	soft-sole	-	2	-	2
ODN (Olmo di Nogara)	Middle Bronze Age (1.550–1.300 BCE)	agriculturalists/military activity (intermediate mobility)	flat	soft-sole	2	5	-	7
NEO (Arene Candide, Grotta Pollera, Arma dell'Aquila, Bergeggi)	Neolithic (5.800–4.300 BCE)	agriculturalist/herders (intermediate mobility)	mountainous	soft-sole	3	10	2	15
UP (Arene Candide, Barma Grande, Grotta dell'Uzzo, San Teodoro, Grotta d'Oriente, Mezzocorona - Borgonuovo, Mondeval de Sora)	Mid-Late Upper Palaeolothic-Mesolithic (~ 28.000-4.700 cal BCE)	hunter-gatherers/fish foragers (high mobility)	mountainous	barefoot/minimalistic	4	11	-	15
Total					65	96	12	173

Individuals of both sexes are included, and age-at-death spans late adolescence/early adulthood to senescence. Sex-related differences in fibular shape were deemed insignificant by Procrustes ANOVA among sexes (SI Table 1) and primarily due to allometry (Pietrobelli et al. 2022a). Therefore, males and females were pooled in our analysis. In addition, the presence of a possible age effect was tested via linear correlations among PC scores and age-at-death and excluded as not significant (SI Table 2).

The Sardinia (SAR) and Emilia-Romagna (ER) sample is part of the Modern Identified Frassetto Collection housed at the University of Bologna. This osteological collection was assembled by Prof. Fabio Frassetto (Belcastro et al. 2017, 2022) and includes individuals from Bologna, Parma, Sassari, Cagliari, and Nuoro, located in Emilia-Romagna and Sardinia (Italy). These sedentary populations include males and females who died during the first two decades of the 20th century (1918–1932) and inhabited the urban area of these cities and their immediate rural surroundings. These individuals are primarily manual laborers, employed in the primary sector either working in the agricultural supply chain (such as in small cheese factories) or employed in small-scale artisanal business (such as in leather factories) (Belcastro et al. 2017; Brigaglia 2012; Milella et al. 2012, 2015). These jobs were moderately physically demanding but implied a low mobility level, limited within the sedentary context of the developing industrialized economy of a newly urbanized area and its province (Milella et al. 2015). Coherently, it is possible to hypothesize for this sample the use of leather or rubber, hard-soled foot coverings, such as shoes and boots (Sorrentino et al. 2020a).

Individuals from Roccapelago (ROC) lived in mountainous (> 1000m above sea level) settings in the Apennines within the Modena province (Italy) between the 17th – 18th century. Historical evidence and isotopic studies suggest that the pastoralist subsistence of this population is linked to seasonal transhumance, when shepherds conducted herds to Tuscany, transporting materials and goods for trade (Lugli et al. 2017; Traversari 2017). This occupation involved high levels of activity, as such activities required constant mobility. Consequently, shepherds preparing for the seasonal transhumance typically wore heavy leather boots with rigid soles nailed to the shoe leather upper (Calzolai 1998).

Individuals from the Jewish cemetery of via Orfeo (OR) (Bologna, Italy) were unearthed between 2012–2014 by the Soprintendenza Archaeologia, Belle Arti e Paesaggio of Bologna, Modena, Reggio-Emilia and Ferrara (SABAP-BO) and date from the late 14th to the mid-16th century (Belcastro et al. 2018; Curina and Di Stefano 2019; Di Stefano et al. 2018; Pietrobelli et al. 2020; Pini 1983). This population refers to the Jewish community of the Late Medieval - Early Modern Bologna, as it emerged from several archival and cartographical sources (Curina and Di Stefano 2019). Historical documentation vastly attests that this Bolognese community had sedentary, artisanal activities, involved in trading primarily as possessors of loan institutions and typographies or as merchants and artisans working on clothing, leather, and jewelry (Todeschini 2018; Muzzarelli 2019). This kind of occupation is only modestly physically demanding, with mobility restricted to the typical setting of a small urban town in the Early Modern Age. This population may have utilized soft leather coverings (Zallot 2018).

Individuals from the early medieval necropolis of Vicenne-Morrione (VCN) are dated to the 7th CE using relative dating methods, such as burial organization, numismatics, and weapon typology (Arslan 2004; Ceglia 2010; Ceglia and Marchetta 2012; Gasparini et al. 2022). These populations refer to a Germanic community that scattered into the hilly landscape centering around an inner plateau in Molise, in the central Italian Apennines, after the collapse of the Western Roman Empire. They carried cultural elements of provincial Roman (Pannonian and Norican) cultures, as well as of nomadic steppe peoples (Avars, Bulgars, Sarmatians, and Proto-Slavs) (Gasparini et al. 2022). This group was characterized by a highly hierarchized and gendered societal organization structured around military activity for males. They partook in high-intensity activity with heavy use of a weapon for defense and territorial control (Gasparini et al. 2022), as also documented by the abundant frequency of interpersonal violence (e.g., skeletal traumatic lesions) among males (Belcastro et al. 2001, 2002, 2005; Belcastro and Facchini 2004). Based on historical accounts (Paulus Diacunus, *Historia Langobardorum*) and archaeological parallels (Koncz 2015) for this population, it is possible to hypothesize the use of soft leather shoes, often completed with metal buckles and shoe fittings.

Individuals from the Roman necropoles of *Suasa* (SUA) (Marche, Italy) lived between the 2nd -4th centuries CE in the urban settlement of *Suasa*, established during the 3rd century BCE in a key hilly location to manage the Roman territories from the coast to the Apennine valleys after the Roman expansion into the area. This population is characterized by low mobility, mostly settled in the urban settlement, as attested by the chronologically continuous occupation and expansion of the town and funerary areas (Giorgi 2012). Epigraphic sources for this settlement attest to occupational activities mentioning a *collegium fabrii et centonarii*, a professional corporation in metal and clothing processing but also employed in fire brigades (Antolini 2000). However, the settlement mainly relies on agricultural activities, attested by the acquisition of productive land by illustrious families, and on the production of either building or domestic materials (Antolini 2000). Footwear included a variety of soft leather shoes and sandals with flexible leather soles, typically worn barefoot or with socks (Goldman 1994).

The population of Casalecchio-Ceretolo (CER) refers to a Boian Celtic community dating to the 4th -3rd century BCE and settled into the hilly river Reno valley, in the proximity of the Etruscan center of *Felsina*, the city of Bologna (Italy) (Ortalli 1995). The necropolis, discovered and excavated in 1991–1992, comprises 96 burials with 100 individuals and hosted a population referring to the "*La Tène*" culture, encompassing exclusively Celtic cultural elements (Brasili et al. 2000; Mariotti et al. 2005), with little to no influence of the Etruscan-Italic components, conversely typical of other surrounding Celtic settlements in the same area on the Apennines fluvial valleys (Vitali 1987, 1992). Based on the location of the selected individuals within the funerary area, pertaining to its early utilization (first half of 4th century CE), it is possible to hypothesize that such individuals belonged to Celtic populations who migrated into this landscape at the time, with a limited degree of admixture with local Italic communities (Belcastro et al. 2010). The societal organization was centered on a tribal community, based upon military activity. This is also attested by the presence of burials of warriors, which carried weapons as grave goods. At the same time, tombs of females had personal ornaments, indicating gendered divisions (Ortalli 1995). Based on coeval findings relating to similar groups in the surroundings, this population also benefitted from a subsistence based on agriculture, arboriculture, and farming of pigs and sheep (Grassi 1991). The use of soft leather shoes, usually worn with wool socks, is documented by other archaeological findings referring to Celtic cultures (Quillien et al. 2020).

The population of Olmo di Nogara (ODN) belonged to a community of the "*Terramare*," settled into the Northern Padania alluvial plain near the river Po valley of Western Veneto (Cavazzuti et al. 2019) during an advanced phase of Middle Bronze 2 (MB2) and Late Bronze Age 2 (LB2) (Canci et al. 2015; Pulcini 2014; Salzani 2005). In the case of Olmo di Nogara, we do not have direct evidence of these settlements associated to the cemetery. However, during the initial phases of the Middle Bronze Age, settlements belonging to this culture were typically small (1–2 hectares (ha)), with estimated 125/130 inhabitants per ha confined within substantial fortifications, later progressively enlarged to over 10 ha hosting 1000 individuals or more (Cardarelli 2015; Sabatini et al. 2018). The necropolis of Olmo di Nogara was excavated between 1987 and 2009 and comprised of ☒ 533 burials (471 inhumations and 62 incinerations) (Canci et al. 2015). The individuals in this study span the chronology of Middle Bronze Age 2 (BM2) and Middle Bronze Age 3 (BM3) (1.550–1.300 BCE), as established by burial typology, stratigraphy, and goods. All male individuals in this study had swords/daggers as grave goods (De Marinis and Salzani, 2005; Salzani, 2005). This population was structured in a chiefdom, articulated in structured parental ties and with strong warfare connotations and centered upon military *élites* and their activities (Cupitò and Leonardi, 2005a, 2005b). Biomechanical stress and paleopathological indicators, documented in the anthropological study of these individuals, revealed that this population engaged in a physically demanding activity (Cecchetto 2020; Canci et al., 2005, 2015; Pulcini, 2014), often connected to warfare (Beck Di Lotto 2010; Canci et al. 2009). Besides military activity, during these phases, hunting, fishing, agro-pastoralism, metallurgy, and textile production are documented in Northern Italy (Cocchi Genick 2009). Based on archeological evidence, it is possible to hypothesize the use of textiles (wool, animal skins, vegetal fibers) for cloth and shoe production (Harris, 2007; Sabatini et al. 2018).

The Neolithic remains (NEO) belong to a sample from four caves (Arene Candide, Arma dell'Aquila, Grotta Pollera, and Bergeggi) near Finale Ligure in Liguria (Italy) with radiocarbon dates spanning 5209 – 4364 cal BCE (Marchi et al. 2006, 2011; Marchi 2008; Sparacello and Marchi 2008; Sparacello et al. 2011, 2014, 2019, 2020; Varalli et al. 2020). These sites were the object of early archaeological explorations since the mid-1800s. However, the archaeological, anthropological, and chronological study for the rational reorganization and characterization of this skeletal series was only recently undertaken, allowing for the recognition of human remains chronologically contemporary to Impresso-Cardial Complex and Square-Mouthed Pottery Culture (ca. 5.800–4.300 BCE) (Sparacello et al. 2018, 2019, 2020 and references therein). These sites are located in a mountainous area with very rugged terrain (Sparacello et al. 2014). Neolithic subsistence in the area relied on pastoralism (likely small-scale transhumance) and the exploitation of terrestrial resources (Macphail et al. 1997; Marchi et al. 2011; Rowley-Conwy 1997). This activity was facilitated by system of natural caves which contributed to controlling animals (Maggi and Nisbet 2000; Marchi et al. 2011). Animal skins to fabricate cloths and utilized for producing shoes are vastly attested in the Middle Neolithic Square-Mouthed Pottery Culture of Northern Italy (Harris 2014; Starnini and Voytek 1997a). Although the use of animal skin shoes is not directly documented in the context of the Finale Ligure caves, microwear patterns on stone and bone tools (including awls) at Arene Candide are indicative since they are considered compatible with the preparation and treatment of soft materials, likely animal skins for cloth making (Harris 2014; Maggi et al. 1997; Starnini and Voytek, 1997a, 1997b). In addition, other Middle Neolithic contexts in Northern Italy suggest evidence of basketry, which could also be employed for cloth and shoe making. However, no such traces were detected at Arene Candide (Harris 2014). Suggestive may be the attire of the "Iceman" (3.300 cal BCE) from the Alpine Italian region, the oldest direct finding of a shoe in the Italian territory, which comprises soles fabricated with *Ursus arctos* skin, padded with grass, uppers made with *Cervus elaphus* skin and sustained with a netting of lime bast (Groenman-van Waateringe 1993; Harris 2007; Lord and Wood 1999; O'Sullivan et al. 2016). Similarly, another parallel may consist of the oldest direct evidence of a leather moccasin-type shoe, found in the cave of Areni-1 (Armenia), dated to 3627 – 3377 cal BCE, with grass-padded soles (Pinhasi et al. 2010).

The Mid-Late Upper Paleolithic/Mesolithic sample (UP) groups includes individuals found in funerary contexts of the Italian peninsula, from the Ligurian caves of Barma Grande (Barma Grande 2, Barma Grande 5, Barma Grande 6: 28.903–25.731 cal BCE – referring to Barma Grande 6), Formicola 1988, 1989; Formicola et al., 2004) and Arene Candide (Arene Candide 2, 3, 4, and 12: all individuals are comprised between ca. 10,800 – 9.800 cal BCE; Sparacello et al. 2021 and references therein), the Sicilian cave sites of San Teodoro (San Teodoro 1: 13.283–12.177 cal BCE; D'Amore et al. 2009; Fabbri et al. 1993; Mannino et al. 2011; Garilli et al. 2020), Uzzo (Uzzo 1A, Uzzo 1B, Uzzo 2, Uzzo 5; 8.794–8.292 cal BCE; Borgognini Tarli 1993; Borgognini Tarli and Repetto 1985, 1986), and Oriente (Oriente B: 8.704–8.484 cal BCE; Catalano et al. 2020; Di Salvo et al. 2012; Mannino et al. 2012) and the rock shelters of Mezzocorona-Borgonuovo (ca. 5.600–5.400 cal BCE; Sparacello et al. 2023; see also Dalmeri et al. 1998, 2002; Gazzoni et al. 2021) and Mondeval de Sora (6429–6121 cal BCE; Alciati et al. 1992; Fontana 2006; Fontana et al. 2016, 2020; Gazzoni et al. 2021) located in Trentino and Veneto, respectively. Subsistence strategy for Late Upper Paleolithic-Mesolithic individuals varied based on the exploitation of different resources, comprising terrestrial (e.g., animal and plants) and occasional marine/freshwater elements. Both archaeological and biomechanical evidence suggest a subsistence based on hunting and foraging, which included highly intense activities based on seasonal availability (Gazzoni et al. 2021; Mannino et al. 2015; Sparacello et al. 2018), albeit with a decreased high mobility (involving walking and running) in comparison to Mid-Upper Paleolithic (Holt 1999; 2003), as also supported by data related to lithic raw material circulation (Bertola et al. 2018). However, Sparacello and colleagues (2018) suggested that these chronological groups were both highly mobile and shared a similarly high level of loads on the lower limb, as also attested by the entheseal robusticity (Sparacello et al. 2020). Moreover, all these sites are characterized by a moderate to marked terrain ruggedness (Gazzoni et al. 2021; Sparacello et al. 2014, 2020). The use of shoes among Mid-Upper Paleolithic and Mesolithic hunter-gatherers is debated due to the scarcity of direct archeological evidence (Sorrentino et al. 2020a, 2021). An interesting parallel within the same geographical region is represented by the ichnological record dated to 12.830-12.165 cal BCE from the Bàsura Cave, which documents the barefoot footprints of five individuals (Avanzini et al. 2021). Several material evidence of barefoot footprints in Paleolithic contexts are documented (Pastoors and Lenssen-Erz 2021). However, the use of minimalistic footwear (i.e., flexible foot coverings made of textiles, without arch support) for protection from rough substrate and insulation during colder climatic stages within this span (e.g., Younger Dryas cooling event: Sparacello et al. 2021 and references therein) are expected, as also attested in Mid-Upper Paleolithic by the use of soft shoes based on ichnological evidence as early as 26–29 ka cal BCE (Cussac Cave, France, Ledoux et al. 2021), as well as based on foot morphological considerations (Trinkaus 2005) and archeological indirect indicators (Soffer, 2004).

Based on historical sources, archaeological information, ethnographic accounts, and landscape data outlined above, we classified each population according to subsistence strategy (hunter-gatherers with high mobility, agro-pastoralists with intermediate mobility, and sedentary pre- and post-industrials with low mobility), terrain typology (flat, hilly, and mountainous; adapted following the protocol of Sparacello and colleagues (2014), considering the categories of “moderately hilly” and “hilly-mountainous” as a single one, here named “hilly”) and possible shoe use (hard-sole shoes soft-sole shoes and barefoot/minimalistic shoes) (Table 1, Fig. 1b).

The SAR and a subset of ER 3D surface models were obtained through computed tomography (CT), using a Revolution Discovery CT dual energy at Istituto Ortopedico Rizzoli (Bologna, Italy) (slice thickness and increment at 0.625 mm, voltage 100 kV, X-ray tube current 360 mA, reconstruction at 40 keV with "Detail" filter, voxel size ranging from 0.39 to 0.507 x 0.625 mm). The reconstructed DICOM (16-bit gray-scale, signed) images were then processed with Avizo 9.2 (Thermo Fisher Scientific) for image segmentation with half-maximum height (HMH) protocol outlined by Spoor and coworkers (1993) following Coleman and Colbert (2007). An isosurface was then generated for each segmentation.

ROC, OR, VCN, SUA, CER, and ODN samples were digitized with ARTEC Space Spider 3D (Luxembourg), housed at the BONES Lab in the Department of Cultural Heritage of the University of Bologna, a mobile and structured light laser scanner (point-accuracy: 0.05 mm; mesh resolution: 0.1 mm). The acquisition took place in two recording sessions for each specimen, then integrated with the scanner software (Artec Studio 9) after first cleaning and manual alignment. These aligned scans were globally registered. A single polygonal 3D mesh was created with the Sharp Fusion algorithm, finally generating the 3D surface model exported in stl (Little Endian) format (Artec Group 2013).

NEO and UP samples were digitized using the structured light scanner DAVID® SLS-2 (DAVID Group 2007–2015).

2.2. 3D Geometric morphometric analysis

A template of 142 landmarks and semilandmarks, created in Viewbox v. 4.0 (dHAL Software), captured both fibular extremities, covering major muscle, ligament, and tendon attachment sites and articular surfaces (Fig. 2, Table 2).

Table 2

Landmark and semilandmark template configuration for fibular proximal and distal epiphysis. For each landmark and semilandmark, name, definition and number are reported. See Fig. 2 for visual display and landmark positioning on the fibular ends.

Landmarks	**Definition**	
L1	Point where the *fibular anterolateral border* divides into two ridges: the proximal apex of the *subcutaneous triangular surface* (STS)	
L2	Most medial point of the medial border of the STS	
L3	Most lateral point of the lateral border of the STS	
L4	Most distal point of the *lateral malleolus* in anterior view	
L5	Most distal point of the posterior border of the *malleolar fossa*	
L7	Most anterior point on the anterior border of the *proximal fibular-talar articular facet* (PAF)	
L8	Point between the anterior border of PAF and the *anterior border of distal fibular-talar articular facet* (DAF)	
L9	Most distal point of DAF	
L10	Most proximal point on the posterior border of DAF	
L12	Most posterior point of the proximal border of PAF	
L13	Most proximal point of *proximal tibio-fibular articular facet*	
L14	Most proximal point of *interosseous tibio-fibular ligament* (ILA) insertion	
L15	Most proximal point on styloid process of fibular head in medial view	
L16	Most antero-proximal point on anterior border in medial view (above fibular neck)	
L17	Most postero-proximal point on posteromedial border in medial view (above fibular neck)	
L18	Most postero-proximal point on posterior border in lateral view (above fibular neck)	
Curves	**Definition**	**Number of semi-landmarks**
C_1->2	Medial border of the *subcutaneous triangular surface* (STS)	5
C_1->3	Posterior border of the STS	7
C_7->8	Anterior border of the *proximal fibular-talar articular facet* (PAF)	1
C_8->9	Anterior border of the *distal fibular-talar articular facet* (DAF)	1
C_9->10	Posterior border of the DAF	1
C_10->12	Posterior border of the PAF	1
C_8->10	Border between the PAF and DAF	1
C_13->13	Outline of *proximal tibio-fibular articular facet*	6
C_7->12	Proximal border of the PAF	2
Surfaces	**Definition**	**Number of semi-landmarks**
SSML_malleolar fossa	Surface of the *malleolar fossa*, attachment site of the *transverse tibiofibular* and *posterior talofibular ligaments*.	7

Landmarks	Definition	
SSML_ILA	Attachment surface of *interosseous tibio-fibular ligament* and part of *interosseous membrane* (ILA)	13
SSML_fibular groove	Groove for tendons of m. *peroneus longus* and m. *tertius* and attachment site of *posterior tibiofibular ligament*.	13
SSML_STS	*Subcutaneous triangular surface* (STS)	24
SSML_FiTal1Ar	Proximal *fibular-talar articular facet* (PAF)	4
SSML_FiTal2Ar	Distal *fibular-talar articular facet* (DAF)	3
SSML_head	Proximal *tibio-fibular articular surface*	5
SSML_prox_ep	Surface of *proximal epiphysis*	32

The template configuration was applied to all target samples in Viewbox v. 4.0. Semilandmarks were allowed to slide on curves and surfaces, minimizing thin-plate spline (TPS) bending energy between the targets and the template (Slice 2006) so that semilandmarks could be considered geometrically homologous among specimens (Gunz Mitteroecker and Bookstein 2006; Gunz and Mitteroecker 2013). The template repeatability (i.e., high intra-observer agreement) and applicability to 3D models generated with different scanning devices were assessed and confirmed by Pietrobelli and co-authors (2022).

Raw Cartesian coordinates were imported in R (version 4.0.3) (R Core Team 2020), and a further sliding of semilandmarks was performed against recursive updates of the Procrustes consensus while computing two separate Procrustes superimpositions via Generalized Procrustes Analysis (GPA), one for each epiphysis, after sub-setting the respective coordinates accordingly. A further GPA was carried out only on distal talofibular surfaces as previously studies have suggested its variation in humans with different subsistence strategies (Sorrentino et al. 2020a, 2022). Raw coordinates, separated for each epiphysis, were thus converted into standardized, scaled, centered, and oriented shape coordinates (i.e., Procrustes coordinates) (Slice 2006; Rohlf and Slice, 1990) using the *gpagen()* function in the R package "geomorph" version 3.3.2 (Adams et al. 2018). Outliers from Procrustes consensus were found utilizing the function *plotOutliers()* provided in this package and removed. The centroid size (CS) was also calculated and used as a proxy of the size of both fibular extremities separately (Slice 2006).

Procrustes coordinates for each epiphysis were then subjected to a Principal Component Analysis (PCA) to explore shape variations among populations and categories of subsistence strategy, terrain type, and shoe use (Schlager 2017).

Procrustes ANOVA was utilized to evaluate shape differences among different populations and categories of subsistence strategy, terrain type, and shoe use, calculating Procrustes distances among specimens using a residual randomization procedure (RRPP = T, iterations = 1,000), with the R package "geomorph" v. 3.3.2 (Adams et al. 2018).

3. Results

3.1. Proximal epiphysis

Figure 3. Shape space PCA plot computed for proximal fibular epiphysis (left). Mean shape (rhombus) for each population is displayed in the PCA plot. Extremes shapes warped on fibula model for PC1 (top right) and PC2 (bottom right) positive (+) and negative (-) scores; Morphologies highlighted in black represent features of sedentary, less mobile, recent populations; Morphologies highlighted in red represent features of mobile, highly active, oldest populations. UP = Mid-Upper Palaeolothic/Mesolithic populations; NEO = Neolithic populations; ODN = Bronze Age population of Olmo di Nogara; CER = Iron Age population of Casalecchio-Ceretolo; SUA = Roman population of Suasa; VCN = Late-Antiquity population of Vicenne; OR = Middle Age-Early Modern Jewish population of via Orfeo cemetery, Bologna; ROC = Late Modern population of Roccapelago; ER = contemporary 20th century population of Emilia-Romagna; SAR = contemporary 20th century population of Sardinia.

The first three PCs combined account for 45.48% of the total variance explained (PC1: 17.67%; PC2: 15.57%; PC3: 12.24%). Despite some overlapping, the plot shows a trend in separating populations according to chronology along the first two principal axes. Except for the modern pastoralists of ROC, most historic, sedentary populations fall within positive PC1 and PC2 scores. On the other hand, UP and CER lay within PC2 negative scores, while NEO and ODN fall within PC1 negative scores. Historic, sedentary populations with low-intensity activity are characterized by an oblique and diminutive PTFJ, a raised styloid process, and less projecting insertions of the *biceps femoris* tendon and *m. peroneus longus* (PC1 and PC2 positive shape extremes). Highly active prehistoric hunter-gatherers possess a horizontal and wide PTFJ, an absent styloid process, and projecting insertions (PC2 negative shape extremes). NEO and ODN agro-pastoralists clustering towards PC1 negative extremes, and show similar features compared to UP hunter-gatherers, except for a medial expansion of the fibular head. Significant shape differences among populations are confirmed by Procrustes ANOVA comparisons (Table 3), which shows that modern sedentary populations (SAR, ER, and OR) significantly differ from earlier active populations (hunter-gatherers UP, and agro-pastoralists NEO, and ODN). Interestingly, the two modern, sedentary city-dwellers of SAR and ER differ significantly from each other, and similarly, UP and NEO populations significantly differ.

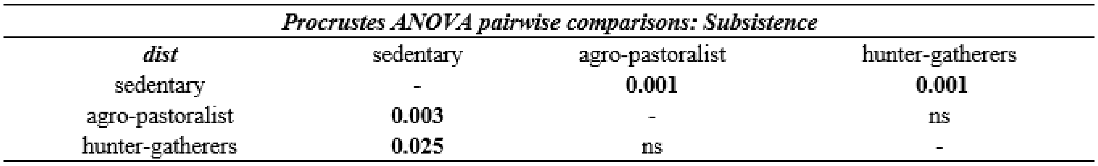
Table 3

Results of pairwise comparisons after Procrustes ANOVA test among populations, showing in bold significant shape differences. Below the diagonal are displayed comparisons for proximal epiphysis, while above the diagonal are displayed comparisons for distal epiphysis. UP = Mid-Upper Palaeolothic/Mesolithic populations; NEO = Neolithic populations; ODN = Bronze Age population of Olmo di Nogara; CER = Iron Age population of Casalecchio-Ceretolo; SUA = Roman population of Suasa; VCN = Late-Antiquity population of Vicenne; OR = Middle Age-Early Modern Jewish population of via Orfeo cemetery, Bologna; ROC = Late Modern population of Roccapelago; ER = contemporary 20th century population of Emilia-Romagna; SAR = contemporary 20th century population of Sardinia.ns = not significant, see Table 1 for abbreviations used for populations

	Procrustes ANOVA pairwise comparisons: Populations										
	Distal epiphysis	SAR	ER	ROC	OR	VCN	SUA	CER	ODN	NEO	UP
Proximal epiphysis	SAR	-	**0.001**	ns	ns	ns	ns	ns	**0.036**	**0.001**	**0.001**
	ER	**0.004**	-	**0.014**	ns	ns	ns	ns	ns	**0.002**	**0.005**
	ROC	ns	ns	-	ns	ns	ns	ns	ns	ns	ns
	OR	ns	ns	ns	-	**0.031**	ns	ns	**0.022**	**0.003**	**0.002**
	VCN	ns	ns	ns	ns	-	ns	ns	ns	ns	ns
	SUA	ns	ns	ns	ns	ns	-	ns	ns	ns	ns
	CER	ns	ns	ns	ns	ns	ns	-	ns	ns	ns
	ODN	ns	**0.052**	ns	ns	ns	ns	ns	-	**0.010**	**0.009**
	NEO	**0.007**	**0.001**	ns	**0.022**	ns	ns	ns	ns	-	ns
	UP	**0.012**	**0.049**	ns	**0.028**	ns	ns	ns	ns	**0.039**	-

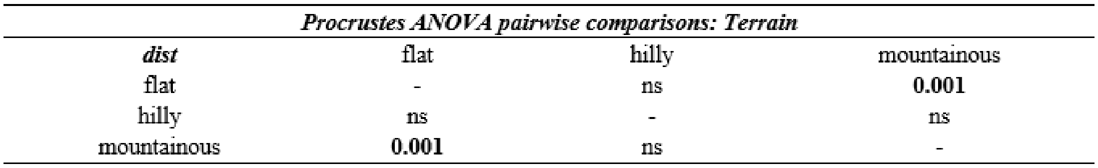
When population means are grouped by subsistence strategy, terrain type, and shoe use categories (Fig. 4), it is possible to detect a pattern determining variations among sedentary populations with low activity subsistence, living in flat terrain and using hard-sole shoes in comparison to other categories.

Procrustes ANOVA comparisons among categories confirm this pattern, with sedentary populations differing significantly from either agriculturalists and hunter-gatherers, populations living in flat terrain differing significantly from those living in mountainous areas, and populations using shoes differing significantly from those possibly not using any (Table 4–6).



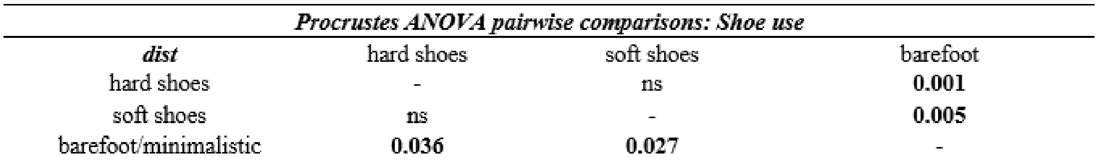
Procrustes ANOVA pairwise comparisons: Subsistence			
dist	sedentary	agro-pastoralist	hunter-gatherers
sedentary	-	**0.001**	**0.001**
agro-pastoralist	**0.003**	-	ns
hunter-gatherers	**0.025**	ns	-

Table 4. Results of pairwise comparisons after Procrustes ANOVA test among subsistence categories, showing in bold significant shape differences. Below the diagonal are displayed comparisons for proximal epiphysis, while above the diagonal are displayed comparisons for distal epiphysis. ns= not significant.



Procrustes ANOVA pairwise comparisons: Terrain			
dist	flat	hilly	mountainous
flat	-	ns	**0.001**
hilly	ns	-	ns
mountainous	**0.001**	ns	-

Table 5. Results of pairwise comparisons after Procrustes ANOVA test among terrain tipology categories, showing in bold significant shape differences. Below the diagonal are displayed comparisons for proximal epiphysis, while above the diagonal are displayed comparisons for distal epiphysis. ns= not significant.



Procrustes ANOVA pairwise comparisons: Shoe use			
dist	hard shoes	soft shoes	barefoot
hard shoes	-	ns	**0.001**
soft shoes	ns	-	**0.005**
barefoot/minimalistic	**0.036**	**0.027**	-

Table 6. Results of pairwise comparisons after Procrustes ANOVA test among shoe use categories, showing in bold significant shape differences. Below the diagonal are displayed comparisons for proximal epiphysis, while above the diagonal are displayed comparisons for distal epiphysis. ns= not significant.

However, some outliers are present for each category: CER is grouped outside the range for all categories and ODN is grouped outside the range of flat- terrain dwellers and soft-shoe users (Fig. 4).

Centroid size comparisons (Fig. 5) reveal little to no variation related to size (ANOVA: p-value > 0.05).

3.2. Distal epiphysis

Figure 6. Shape space PCA plot computed for distal fibular epiphysis (left). Mean shape (rhombus) for each population is displayed in the PCA plot. Extremes shapes warped on fibula model for PC1 (top right) and PC2 (bottom right) positive (+) and negative (-) scores; Morphologies highlighted in black represent features of sedentary, less mobile, recent populations; Morphologies highlighted in red represent features of mobile, highly active, oldest populations. UP = Mid-Upper Palaeolothic/Mesolithic populations; NEO = Neolithic populations; ODN = Bronze Age population of Olmo di Nogara; CER = Iron Age population of Casalecchio-Ceretolo; SUA = Roman population of Suasa; VCN = Late-Antiquity population of Vicenne; OR = Middle Age-Early Modern Jewish population of via Orfeo cemetery, Bologna; ROC = Late Modern population of Roccapelago; ER = contemporary 20th century population of Emilia-Romagna; SAR = contemporary 20th century population of Sardinia.

The first three combined PCs account for 57.12% of the variance explained (PC1: 27.32%; PC2: 20.01%; PC3: 9.79%). Despite some overlapping, the plot shows a trend in separating populations according to chronology along PC2. Most historic, sedentary populations fall within or towards positive PC2 scores, except for VCN. Agro-pastoralist ROC also cluster within this range. On the other hand, hunter-gatherers UP, agro-pastoralists NEO, ODN, and CER lay within PC2 negative scores. The latter prehistoric and protohistoric populations (either hunter-gatherers and agriculturalists) with high-intensity activity show that the talofibular articular surfaces are anteroposteriorly broad, with a projecting malleolus that is more anteriorly oriented in inferior view, a shortened STS and a robust interosseous tibiofibular ligament attachment (ILA) with marked rugosity. At the same time, the malleolar fossa and the peroneal groove are enlarged and more concave (PC2 negative extremes). Conversely, most historic and modern sedentary populations with low-intensity activity show narrow talofibular articular surfaces, a diminutive malleolus laterally oriented in inferior view, an elongated STS, and a less robust – even though elongated – ILA insertion and narrow and less concave malleolar fossa and peroneal groove (PC2 positive extremes).

When landmarks and semilandmarks covering only the talofibular articular surfaces are isolated and subjected to a separate GPA, with a PCA showing a similar separation among most and least mobile populations along PC1 (Figure S3), extreme shape reconstruction highlight an additional shape difference among active and sedentary populations concerning the orientation of the proximal and distal talofibular articular surfaces (PAF and DAF). In prehistoric and protohistoric populations (UP, NEO, ODN, either hunter-gatherers and agriculturalists) with high-intensity activity, the DAF is markedly more prominent than the PAF (with a markedly oblique superior margin) and highly flared and tilted. In contrast, in historic and modern populations with low-intensity activity, PAF (with a straight superior margin) and DAF have a similar vertical orientation (Figure S3).

Significant shape differences among populations are confirmed by Procrustes ANOVA comparisons (Table 3), which shows that modern sedentary populations (SAR, ER, and OR) significantly differ from earlier active populations (UP, NEO, and ODN). Similarly to proximal epiphysis, for distal epiphysis, comparisons among modern SAR and ER show a significant difference, making comparisons among UP, NEO, and ODN. In addition, ROC shows a significant difference from ER.

When population means are grouped by subsistence strategy, terrain type, and shoe use categories (Fig. 4), we highlighted a pattern determining variations among sedentary populations with low activity subsistence, living in flat terrain, and using hard-sole shoes in comparison to other categories. Procrustes ANOVA comparisons among categories confirm this pattern, with sedentary populations differing significantly from either agriculturalists and hunter-gatherers, populations living in flat terrain differing significantly from those living in mountainous areas, and populations using shoes differing significantly from those possibly not using any (Table 4–6). However, some outliers are present for each category: ROC is grouped outside the range of mountain-dwellers and OR falls outside the range of soft-shoe users (Fig. 4).

Centroid size comparisons (Fig. 5) reveal slight variation related to size emerging in pairwise comparison only between OR and UP (p-value < 0.05).

4. Discussion

In this study, we highlighted shape changes of fibular proximal and distal ends among Italian archaeological populations dated from the Mid-Late Upper Paleolithic to the 20th century through a 3D-GM approach. Fibular shape changes are especially evident when comparing hunter-gatherers to sedentary pre- and post-industrialists, documenting and paralleling the progressive decline of activity levels over time, as well as and variation in terrain properties and shoe use (Fig. 3–6; Table 4–6). The most and least active groups have different orientations of proximal and distal tibiofibular articular surfaces and degree of ligament and tendon insertion robusticity. These morphological changes likely reflect biomechanical differences in response to locomotor behavior among these groups, referring to the specific knee (Frelat et al. 2017; Sylvester 2013; Sylvester and Pfisterer 2012; Tardieu, 1999) and ankle (Barnett and Napier 1953; DeSilva 2009; Latimer et al. 1987; Stern and Susman 1983) kinematic and postures.

Regarding shape changes here documented in the proximal epiphysis, we found that the PTFJ is diminutive and obliquely oriented in historic/contemporary sedentary post- and pre-industrialist populations. On the other hand, highly active prehistoric hunter-gatherers possess a horizontal and wide PTFJ (Fig. 3; Figure S1). The PTFJ in humans shifts postero-laterally as the ankle dorsiflexes (Barnett and Napier 1953; Odgen, 1974a, 1974b). The orientation of the PTFJ in humans may range from 5° to 80° of inclination (Eichenblat and Nathan 1983). An oblique PTFJ is linked to the requirement for bipedal locomotion (Pietrobelli et al. 2022; Susman and Stern 1983). Ogden (1974a, 1974b) found an association among oblique joints (> 20°) with smaller articular surface areas and decreasing mobility, as the joints have a reduced ability to accommodate torsional forces, with a higher incidence (70%) of subluxation or dislocation. In contrast, the horizontal PTFJ enables greater mobility at the joint and is, therefore, less prone to injury (Alves-da-Silva et al. 2019). Therefore, sedentary humans with an oblique PTFJ are linked to a less mobile tibiofibular articulation (Eichenblat and Nathan 1983; Odgen 1974a, 1974b; Sarma et al. 2015) and associated with a reduced dorsiflexion axis inclination at the ankle (Barnett and Napier 1953; Odgen 1974a, 1974b). Indeed, humans with a sedentary lifestyle likely have a habitual neutral posture and less range of motion at the ankle joint (Barnett and Napier 1952; DeSilva 2009; Latimer et al. 1987; Parr et al. 2012; Sorrentino et al., 2020). On the other hand, hunter-gatherers, which engage in high intensity running and walking in uneven terrain were previously associated to morphological features at the ankle (i.e., trapezoidal talocrural joint) that allow a broader range of ankle excursion in the parasagittal plane (dorsal and plantar flexion) (Latimer et al. 1987; Oygucu et al. 1998; Trinkaus 1975). A horizontal PFTJ, as observed in this work in highly active hunter-gatherers (Fig. 3, Figure S1), would provide greater lateral knee stabilization through greater joint mobility in knee flexion (Chang et al. 2020; Huang et al. 2021), but ultimately leading to lateral knee osteoarthritis (OA) (Pietrobelli et al. 2022), as also attested by the higher incidence of OA in prehistoric populations compared to agriculturalists (Bridges 1989, 1991; Knusel 1996).

Our results showed that historic sedentary post- and pre-industrialists also possess a raised styloid process, while in highly active hunter-gatherers, the styloid process is markedly less pronounced (Fig. 3, Figure S1). A marked styloid process surmounting the fibular head sustains the lateral compartment of the knee in full extension (Tardieu 1999), as it is the attachment for the popliteus tendon through the popliteo-fibular ligament (Aiello and Dean 1990). In addition, the bony protuberance of the styloid process, associated with these soft structures at the postero-lateral corner of the knee, prevents posterior translation, varus angulation, and primary external rotation of the tibia relative to the femur (LaPrade et al. 2001, 2003). Conversely, highly mobile prehistoric hunter-gatherers, which travel large daily distances and home ranges (average 9.5 km for females and 14.1 km for males – modern hunter-gatherers: Marlowe 2005) and have an equally convenient energetic cost of barefoot running both in the forefoot and rearfoot strike (Cunningham et al. 2010), may be facilitated by a more mobile PTFJ in knee flexion during barefoot running, as increased knee flexion is more frequently attained (Hall et al. 2013). The correlation between barefoot/minimalistic shoe running and enhanced knee flexion, likely facilitated by the horizontal (and therefore mobile) PTFJ that we documented in hunter-gatherers (Fig. 3, Figure S1), may provide an explanation for the increased robustness and width of the *m. biceps femoris* tendon insertion on the fibula in the same group (Fig. 3 and Table 6). Additionally, experimental studies conducted on Jomon hunter-gatherers revealed a posteriorly elongated *linea aspera*, which is the site of femoral insertion for this muscle. This elongation parallelly suggests greater muscle mass and potentially increased utilization of the muscle (Mizushima et al., 2015).

Lastly, we found that in prehistoric, highly active hunter-gatherers, the *m. peroneus longus* proximal insertion is more concave and medially projecting (Fig. 3). Peroneal muscles activate in the support phase of locomotion (Jungers et al. 1993; Stern and Susman 1983), everting the inverted foot and laterally stabilizing the inverted ankle joint while traversing a medially inclined ramp (Bavdek et al. 2018). This mechanism may be crucial for hunter-gatherers traversing rugged terrains and further supports the results of Sparacello and coworkers (2014, 2018), which documented an increase in fibular robusticity with frequent directional changes occurring in uneven terrain of Upper Paleolithic-Mesolithic hunter-gatherers. In addition, this result is comparable to those obtained for the morphology and trabecular organization of the talus, reflecting an adaptation to uneven terrain that increases medio-lateral movement, thus requiring higher stability (Carlson et al. 2007; Sorrentino et al. 2020a, 2021, 2022). Sorrentino and colleagues (2020) also linked hunter-gatherers' more flexible talar configuration to barefoot/minimalistic shoe support, in contrast to individuals from post-industrial societies whose use of heavy leather shoes and boots may limit ankle excursions in eversion and inversion. This finding seems comparable to our results, where barefoot/flexible shoe- and hard-shoe-using populations are distinctly distributed (Fig. 4; Table 6).

As regards shape changes that we documented here for the distal epiphysis, hunter-gatherers with high-intensity activity have antero-posteriorly broad talofibular articular surfaces, with a markedly larger DAF, also highly flared and tilted than the PAF. In contrast, PAF and DAF have a similar vertical orientation in historic sedentary populations with low-intensity activity (Fig. 6; Figure S2-S3). Our result agrees with a hypothesized increased vertical component of the ground reaction force transmitted by the fibula through the talus in the ankle joint in mobile populations compared to sedentary ones, in parallel with observations in hominids (Stern and Susman 1983, but see also Latimer et al. 1987) and consistent with an increased degree of ankle dorsiflexion (Barnett and Napier 1953; DeSilva 2009; Marchi 2015; Marchi et al., 2022). In addition, the differences in the more oblique superior margin of PAF that we observed in hunter-gatherers compared to the straight margin seen in historic sedentary populations (Fig. 6; Figure S2-S3) were previously associated with a more plantarflexed ankle configuration (Stern and Susman, 1983). Comparably, this feature in great apes would suggest their greater ankle joint mobility compared to humans (Marchi et al. 2022). This fibular morphology, with larger, highly flared, and tilted DAF with an oblique superior margin, here seen in hunter-gatherers, may reflect a more "flexible" shape (i.e., a shape configuration sustaining greater talocrural joint motion range) as suggested by Sorrentino and colleagues (2020a), compatible with a more everted ankle posture of hunter-gatherers. Historic, sedentary populations, in our results, conversely have medially facing, vertical PAF and DAF, which may suggest a more "stable" shape (i.e., indicating limited talocrural joint motion range) referring to a more neutrally loading ankle (Sorrentino et al. 2020a).

Interestingly, the results of Sorrentino and colleagues (2020a) document the presence of markedly flared lateral malleolar facets in the tali of prehistoric hunter-gatherers, directly mirroring the downward-facing DAF of hunter-gatherers observed in our study. According to Sorrentino and coworkers (2020a), in addition, the stable, static configuration of the ankle, compatible with the vertical, medially oriented PAF and DAF, found here in sedentary populations, is compatible with a constraint in motion range using heavy leather shoes and boots (Fig. 4; Table 6). While these results are backed by theoretical studies on the loading patterns at the ankle (Preuschoft 1970), as well as empirical studies conducted on the fibula/tibia diaphyseal robusticity (Marchi 2007, 2015b; Marchi et al. 2019), a recent study (Venkataraman et al. 2013), however, could not identify any significant morphological changes of the habitual dorsiflexion of the foot in modern hunter-gatherers. Therefore, this mixed evidence suggests overall caution in this interpretation. Experimental kinetic and kinematic studies are needed to measure the impact of different ranges of motions with activity/terrain/shoe use among modern hunter-gatherers and controls on the morphology of the ankle bones.

Hunter-gatherers with high intensity activity were also found to have a shorter STS with a voluminous, projecting malleolus that is more anteriorly oriented in the inferior view. On the other hand, historic and modern sedentary populations with low-intensity activity show an elongated STS with a diminutive, laterally oriented malleolus in an inferior view (Fig. 6, Figure S2). A shorter STS in great apes than humans was previously linked to their more extended peroneal muscle bellies and shorter peroneal tendons (Marchi et al. 2022), which contribute to more potent and more precise eversion/inversion movements, as it is generally accomplished in mammals (Biewener 2016). A similar muscle-tendon unit dynamic in humans could hypothetically reflect a powerful inversion/eversion and plantarflexion of the foot. In addition, it could support the more everted ankle joint posture that our result on STS and malleolus shapes may indicate for highly mobile hunter-gatherers (Sorrentino et al. 2020a).

Furthermore, we may suggest that the projecting morphology and anterior orientation of the malleolus with a shortened STS here found in prehistoric highly active hunter-gatherers (Fig. 6, Figure S2) may provide an extended moment arm for the peroneal muscles in eversion (Hinterman et al. 1994), as their tendinous part (i.e., the peroneal tendon, comprising the *m. peroneus longus* and *brevis*) runs immediately posterior to this bony structure, partially covering it (Morgan et al. 2020). The peroneal tendon is one of the strongest everting structures, while the foot is plantarflexed (Hinterman et al. 1994). Given that the forefoot-strike pattern in barefoot endurance running, which among other factors, was linked to unshod human ancestors and modern groups (Hatala et al. 2013 and references therein), provides a greater degree of foot plantarflexion (Almeica et al. 2015; Hall et al. 2013), we may tentatively suggest that in prehistoric highly active hunter-gatherers a raised morphology of the malleolus with a conjoined shorter and anteriorly oriented STS is beneficial. Thanks to the positioning of the tendon of the evertors and its moment arm, this morphology may facilitate a powerful eversion. At the same time, the foot is plantarflexed and lateral ankle stabilization and involved in a unique biomechanical strategy for ground reaction force dissipation and injury risk mitigation (Liebermann et al. 2010).

Conversely, the elongated STS with a less projecting malleolus with lateral orientation that we found in historic and modern sedentary groups with low-intensity activity may be linked to a diminished eversion function of peroneal muscles in both plantarflexion and dorsiflexion, with relevant implications for the injury mechanism of lateral ankle sprains (Morgan et al. 2020). Connected to this hypothesized biomechanical dynamic for the peroneal tendon, we observed an enlarged, more concave peroneal groove hosting the peroneal tendon in prehistoric highly active hunter-gatherers. In contrast, in sedentary populations, we found that peroneal grooves are narrower and flatter (Fig. 6, Figure S2). The shape of the peroneal groove was evaluated in clinical studies, documenting that convex and flat grooves are directly associated with peroneal tendon dislocation/subluxation (Mabit et al. 1999; Cozzetto et al. 2014). This result would further strengthen the hypothesis of the reduced ankle mobility in sedentary groups due to narrower peroneal grooves, as on the contrary, the surgical deepening of this sulcus would provide a reduced pressure between the tendon-groove interface at different foot orientations (Title et al. 2005; Morgan et al. 2020). Following this interpretation, a thinner retro-malleolar area might suggest a thinner peroneal muscle with reduced muscle mass, as mentioned by Marchi and colleagues (2022). A thinner *peroneus longus* is implicated in a complex locking process of the first metatarsal against the medial cuneiform in individuals with pronating feet (Angin et al. 2014; Morgan et al. 2020). We may suggest that a thinner peroneal groove may be involved in a reduced medial stabilization of the first metatarsal-phalangeal ray of the foot in resisting motion by pulling it into plantarflexion (Morgan et al. 2020). Indeed, it was demonstrated that after transecting the m. *peroneus longus*, a considerable medial displacement of the transverse arch might occur (Bohne et al. 1997). The wider peroneal groove observed in mobile populations could be, therefore, consistent with a greater need for stabilization caused by an increased medial deviation of the first metatarsal in barefoot individuals and lateral deviation of the hallux in shod feet (Barnett 1962; Trinkaus 2005; Zipfel and Berger 2007). Indeed, studies describing the leg's muscular and tendinous structure (e.g., Marchi et al. 2018) with bone morphology associated with locomotor behavior in humans are needed to assess this hypothesis further.

We documented that a robust ILA insertion with marked rugosity characterizes mobile populations, while a less robust – even though elongated – ILA insertion is shown in sedentary populations (Fig. 6, Figure S2). This site contributes to the tibiofibular syndesmosis with the interosseous membrane attachment site through the interosseous ligament (Hermans et al. 2010). Given its function as a buffer, neutralizing forces during the heel-strike phase in walking and stabilizing the talocrural joint during loading, we suggest that its greater entheseal robusticity in highly active -gatherers may play a critical role in the load-sharing ability of the fibula relative to the tibia during loading (Skraba et al. 1984) and traversing uneven terrains (Sparacello et al. 2014, 2018) (Table 5).

Our results show that the malleolar fossa of mobile hunter-gatherers is broader and more concave, while in sedentary populations, it is less expanded and shallower (Fig. 6, Figure S2). This site provides insertion of the posterior tibiofibular ligament, which stabilizes the talocrural joint, prevents posterior talar translation, and dissipates internal rotation forces in the ankle joint (Ebraheim et al. 2006; Golanó et al. 2010; Hermans et al. 2010; Perrich et al. 2009); it also hosts the posterior/transverse talofibular ligaments, which restrict internal and external rotation, talar tilt, and dorsiflexion (Rasmussen et al. 1983). The spreading of the malleoli stretches these ligaments as they excurse over the wedge-shaped talar trochlea in ankle dorsiflexion (Barnett and Napier 1952; Close and Inman 1952; Hicks 1953; Trinkhaus 1975). Sorrentino and colleagues (2020a) found an expanded anterior mediolateral margin of the talar trochlea in hunter-gatherers and associated this feature with passive dorsiflexion extremes such as in frequent and habitual squatting. Thus, we suggest that the enlargement of the malleolar fossa in mobile populations may reflect a possible elongation of the ankle collateral ligaments and frequent tightness with prolonged pressure, such as in squatting (Viidik 1966; Trinkaus 1975). Similarly, a wider malleolar fossa in great apes was indeed associated with larger collateral ligaments in great apes due to the higher frequency and magnitude of dorsiflexion experienced during climbing (Marchi et al. 2022).

When comparing populations with less extreme differences in subsistence/mobility, shape variations are less marked. In addition, populations with intermediate levels of mobility clustered variably (Figs. 3 and 6).

Regarding the proximal epiphysis, Neolithic and Bronze Age agro-pastoralist populations exhibit a distinct distribution on PC1, clustering towards the negative extremes in Fig. 3. This is opposite to sedentary populations and different from hunter-gatherers. The morphological difference between hunter-gatherers and agriculturalists, as shown in Table 3, is primarily driven by a medially projecting PTFJ in agriculturalists, albeit with a horizontal orientation. Consequently, the mobility of this joint in agriculturalists can be compared to that of hunter-gatherers, with similar functional implications, despite the variable distribution in the plot. Other proximal fibular features are similarly comparable in these two groups. Bridges (1989) suggested that early agricultural life was hardly sedentary and perhaps more arduous than hunting and gathering (see also Cohen 1977), but this argument remains debatable, as according to Roberts and Manchester (2005), agriculturalist exhibited comparatively lower levels of physical activity compared to hunter-gatherers. The 17th -18th agro-pastoralist population of Roccapelago clusters towards Neolithic and Bronze Age individuals. Considering that this modern population may also have engaged in recurring transhumance, similarly to Neolithic populations (Marchi et al. 2011; Sparacello et al. 2018; Lugli et al. 2017), we may tentatively suggest that comparable physical demands on this joint may explain this similarity. Comparably, the Bronze Age agriculturalists/warriors of Olmo di Nogara may have similarly sustained intense physical requirements for military activity, attested by the presence of weapons in their grave goods. Karim and colleagues (1981) showed indeed that early agricultural labor created the same level of aerobic fitness of physically trained soldiers. Therefore, we suggest that all these three populations may have shared the necessity of dissipating tensile forces on the lower limb and accommodating the PTFJ excursion in knee and ankle flexion (Barnett and Napier 1953; Odgen 1974a, 1974b), potentially explaining the similar distribution that we observed for these groups.

At the same time, a different pattern emerges in the distal epiphysis for populations with intermediate mobility.

In this case, we observed a clearer gradient with declining mobility along PC2 (Fig. 6) with closely distributed hunter-gatherers and Neolithic agro-pastoralists, not far from Bronze Age agriculturalists, towards negative PC2 scores, and all sedentary modern and contemporary populations with low-activity level towards PC2 positive scores. Prehistoric hunter-gatherers and Neolithic agro-pastoralists share similar distal fibular features. However, Olmo di Nogara agriculturalists have a significantly different shape from hunter-gatherers and Neolithic populations (Table 3). This shape difference is mainly due to a different cranio-caudal elongation, more marked in the former group. Based on what was hypothesized for the STS shape difference among hunter-gatherers and modern sedentary groups, this would suggest that Bronze Age agriculturalist did not engage in an everted foot posture as frequently as hunter-gatherers and Neolithic populations did, possibly as a result of living in a flat area (Fig. 4). Contrary to the findings related to the proximal epiphysis, the 17th -18th century population of Roccapelago clusters more closely with sedentary modern populations for distal epiphysis. This result may suggest that the dynamic hypothesized for this population favoring knee and ankle flexion at proximal epiphysis, that could potentially contribute to its proximity to the Neolithic and Bronze Age agro-pastoralists, may manifest differently depending on specific joint (proximal vs. distal end) biomechanics, similar to what was observed for the tibia, although in early hominins and humans (Frelat et al. 2017). Furthermore, the population of Vicenne cluster towards active populations. This may be either explained by the peculiar social structure of this population, heavily focusing on physically demanding military activity or by other variables such as ancestry influencing bone morphology. Indeed, the population of Vicenne is of Avar ancestry (Gasparini et al. 2022). This interpretation may also be hypothesized for the population of Ceretolo, clustering towards active populations in both proximal and distal ends, as these populations may have trained and participated in combat actions and had Celtic ancestry (Ortalli et al. 1995). Nevertheless, neither of these historic groups has significant differences from the most and least active extremes, similar to other populations with intermediate mobility (Table 3). These results overall suggests that a more complex pattern of fibular shape emerges when populations in-between hunter-gathering and most sedentary subsistence extremes are compared, and that other factors such as military activity, transhumance and ancestry may play an important role (Bridges 1989; Karim et al. 1981).

Differences among contemporary, post-industrial city-dwellers also emerged (Table 3). Skeletal comparisons among the Sardinian and Northern Italian population of Emilia-Romagna already revealed occasional inter-population variability in tibial and fibular measurements (Calzoni 2021), the timing of skeletal maturation (Belcastro et al. 2019), sexual dimorphism (our unpublished data). Indeed, the reason for this microscale variation in fibular morphology may lie within the genetic diversity of Sardinia and Emilia Romagna and the emergence of unique regional-based traits (Chiang et al. 2018; Pelotti et al. 2008).

Another potential explanation for the morphological differences is related to age changes. For example, human peroneal muscles have also been reported to form concave furrows along the anterior fibular surface of the diaphysis in correlation with a combined effect of age and mechanical loading (Chevalier and Tignères 2020; Hagihara and Nara 2016). While the possible influence of sex and age was deemed insignificant in our work (SI Table 1–2), further studies using a broader sample are needed to assess whether other factors, such as skeletal development, age, diet, ancestry, and climate, could affect fibular shape (Betti et al. 2014).

A possible limitation of this study is the fact that our categories of subsistence, terrain and shoe use often overlap in the same population. For instance, the most mobile population of hunter-gatherers from the Mid-Late Upper Paleolithic is also likely barefoot/wearing minimalistic shoes and mountain-dwelling. Therefore, to better discern the influence of every single variable under study, including modern hunter-gatherers with more diverse environmental conditions (e.g., Venkataraman et al. 2013), would be beneficial. Furthermore, it is important to consider that changes in terrain topology during cooling phases could have influenced the patterns of habitual movement in mountainous regions in a periglacial environment, potentially posing obstacles to mobility (Djindjian 2016), influencing ankle posture and habitual movements.

In conclusion, the morphological investigation of fibular proximal and distal ends among Italian archaeological populations dated from the Mid-Late Upper Paleolithic to the 20th century through a 3D-GM approach revealed shape changes that are consistent with a decline of activity level in conjoint action of the type of terrain and shoe use, especially evident when comparing hunter-gatherers to sedentary pre- and post-industrialists. In addition, some fibular traits (e.g., horizontal proximal tibiofibular and tilted distal talofibular articular surfaces, robust interosseous membrane attachment, broad malleolar fossa, projecting m. *biceps femoris*) indicate greater mobility of fibular joints and degree of load sharing by the fibula during an anteroposterior excursion of the knee and ankle in highly active populations, compared to more rigid fibular joints in sedentary populations. These morphologies may be related to habitual and frequent ankle and knee flexion that is consistent with their foraging subsistence strategy in a combination of frequent traversing of uneven terrain with no/minimalistic foot coverings in the former and restricted ankle excursion by limited lower limb loading and use in plain urban settlements with hard-shoe coverings in the latter. Other fibular traits (e.g., shorter STS, projecting malleolus, concave peroneal groove, and robust proximal peroneal insertion) might indicate for mobile groups a more everted foot posture with increased moment arm in eversion, more efficient for barefoot/flexible shoe running in forefoot-strike gait and concurring in the stabilization of the I metatarsophalangeal ray. Our results agree with previous evaluations of proximal and distal fibular morphology (Marchi 2015; Marchi et al. 2022; Ogden 1974a, 1974b; Pietrobelli et al. 2022; Stern and Susman 1983) and add on the functional role of the fibula and its potential in inferring mobility patterns in *H. sapiens* (Sparacello et al. 2018). Furthermore, our findings align with previous studies conducted on the structural properties of the fibula in human archaeological specimens. These results reinforce the significance of this bone in distinguishing patterns of mobility within bioarcheological settings, enabling comparisons of habitual activities among diverse historical populations and across various geographic areas. (Hagihara and Nara, 2016; Marchi 2008; Marchi et al. 2011; Sparacello and Marchi 2008; Sparacello et al. 2014, 2018). Overall, these results reveal the potential of fibular morphology as an indicator of locomotion behavior and mobility patterns, further reporting on anatomical correlates to the role of physical activity in bone functional adaptation.

Declarations

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Data availability statements

Raw coordinates, sample lists and R scripts used for this analysis are available upon request addressed to the corresponding author.

Conflict of interest

The authors declare no conflict of interest.

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Authors contributions

AP: Conceptualization (equal); formal analysis (lead); investigation (lead); methodology (equal); validation (equal); writing – original draft (lead); writing – review and editing (equal). RS: Formal analysis (supporting); methodology (equal); validation (equal); writing – review and editing (equal). VSS: Writing – original draft (supporting): data curation (equal); Validation (equal); writing – review and editing (equal). EM: data curation (equal); writing – review and editing (equal). FF: data curation (equal); writing – review and editing (equal). LS: data curation (equal); writing – review and editing (equal). SB: Methodology (equal); resources (equal); supervision (equal); validation (equal); writing – review and editing (equal). DM: data curation (equal); investigation (supporting); resources (equal); supervision (equal); validation (equal); writing – review and editing (equal). MGB: project administration (lead); resources (equal); supervision (equal); validation (equal); writing – review and editing (equal).

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Figures

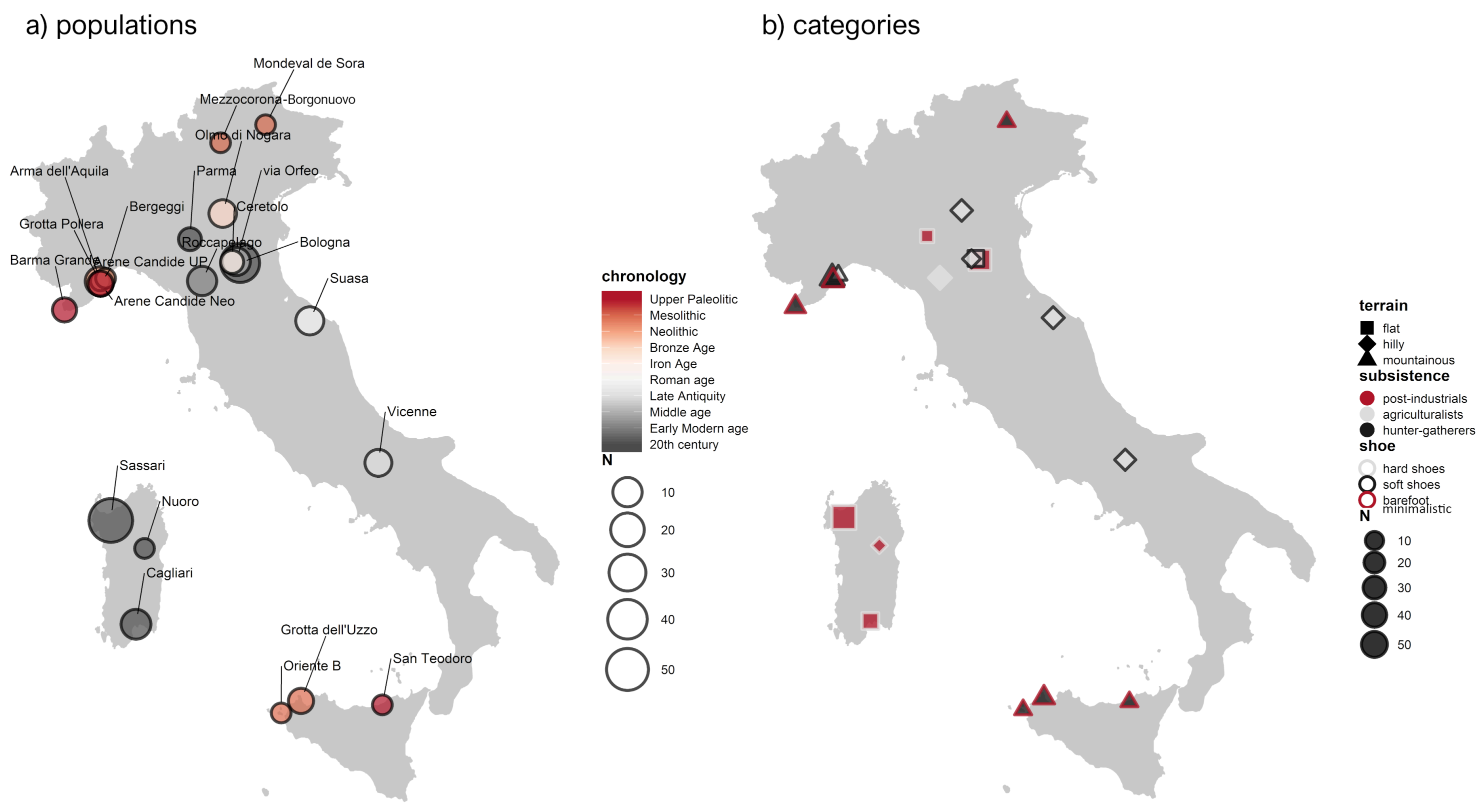

Figure 1

a. The archeological samples included in this study with respective provenance location, chronology and numerosity. **b.** the samples according to categories of subsistence (fill), terrain (shape) and shoe use (stroke).

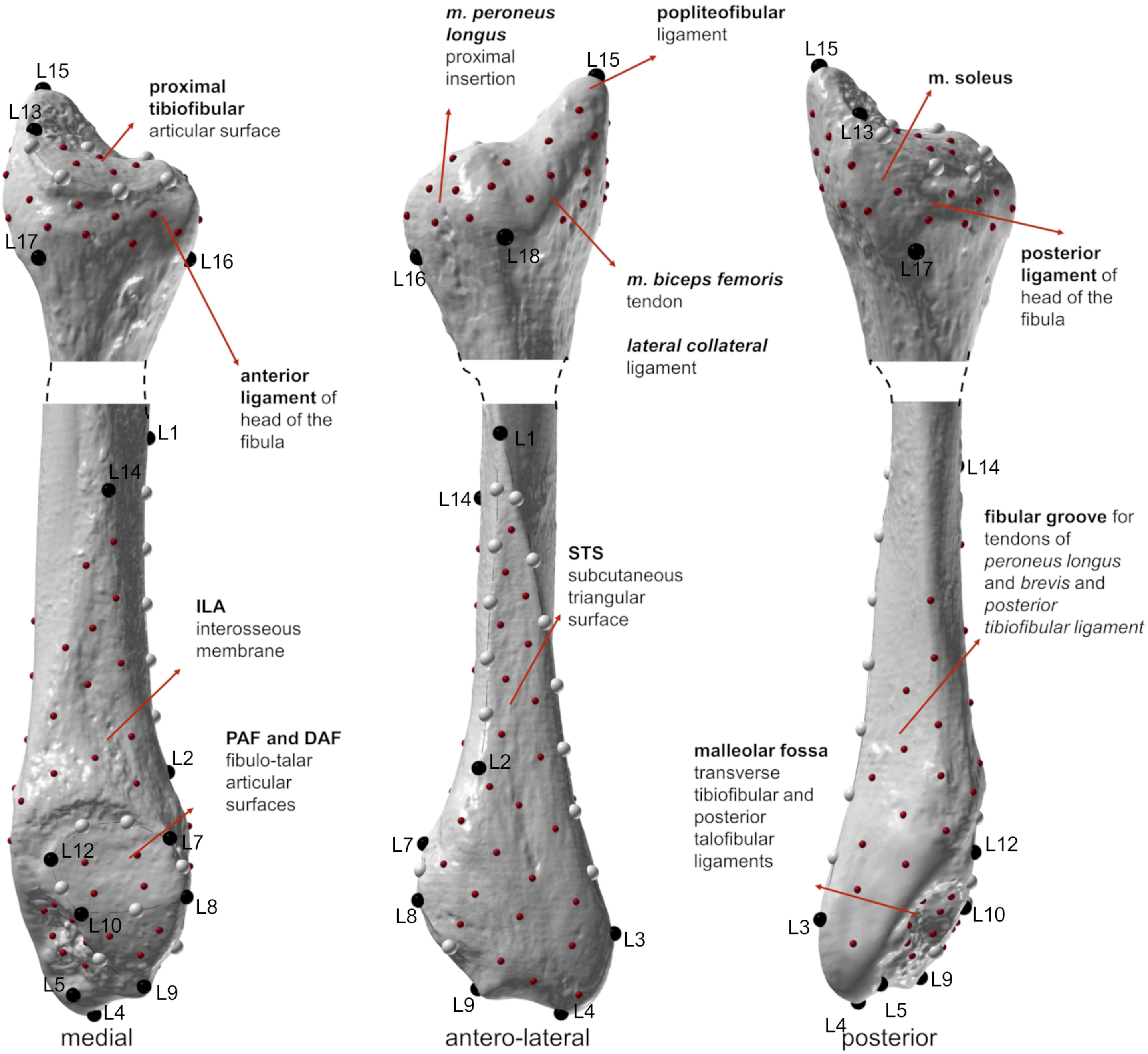

Figure 2

The template configuration on a human left proximal fibula in medial view (left), antero-lateral view (centre) and posterior view (right). Black dots are fixed landmarks, grey dots are curve semilandmarks and red dots are surface semilandmarks. See **Table 2** for definition of numbered landmarks and curve.

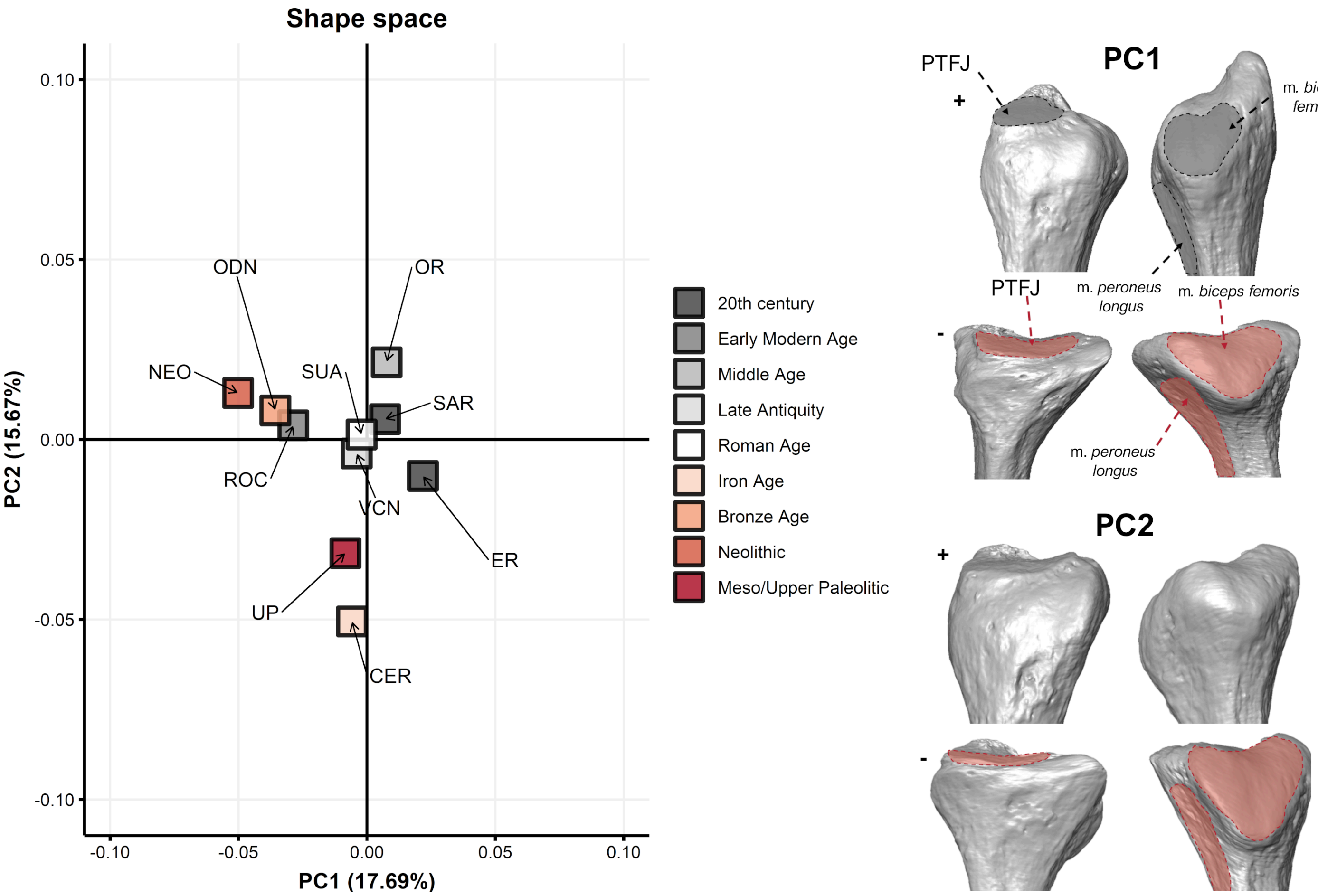

Figure 3

Shape space PCA plot computed for proximal fibular epiphysis (left). Mean shape (rhombus) for each population is displayed in the PCA plot. Extremes shapes warped on fibula model for PC1 (top right) and PC2 (bottom right) positive (+) and negative (-) scores; Morphologies highlighted in black represent features of sedentary, less mobile, recent populations; Morphologies highlighted in red represent features of mobile, highly active, oldest populations. UP= Mid-Upper Palaeolothic/Mesolithic populations; NEO= Neolithic populations; ODN=Bronze Age population of Olmo di Nogara; CER= Iron Age population of Casalecchio-Ceretolo; SUA= Roman population of Suasa; VCN= Late-Antiquity population of Vicenne; OR= Middle Age-Early Modern Jewish population of via Orfeo cemetery, Bologna; ROC= Late Modern population of Roccapelago; ER= contemporary 20th century population of Emilia-Romagna; SAR= contemporary 20th century population of Sardinia.

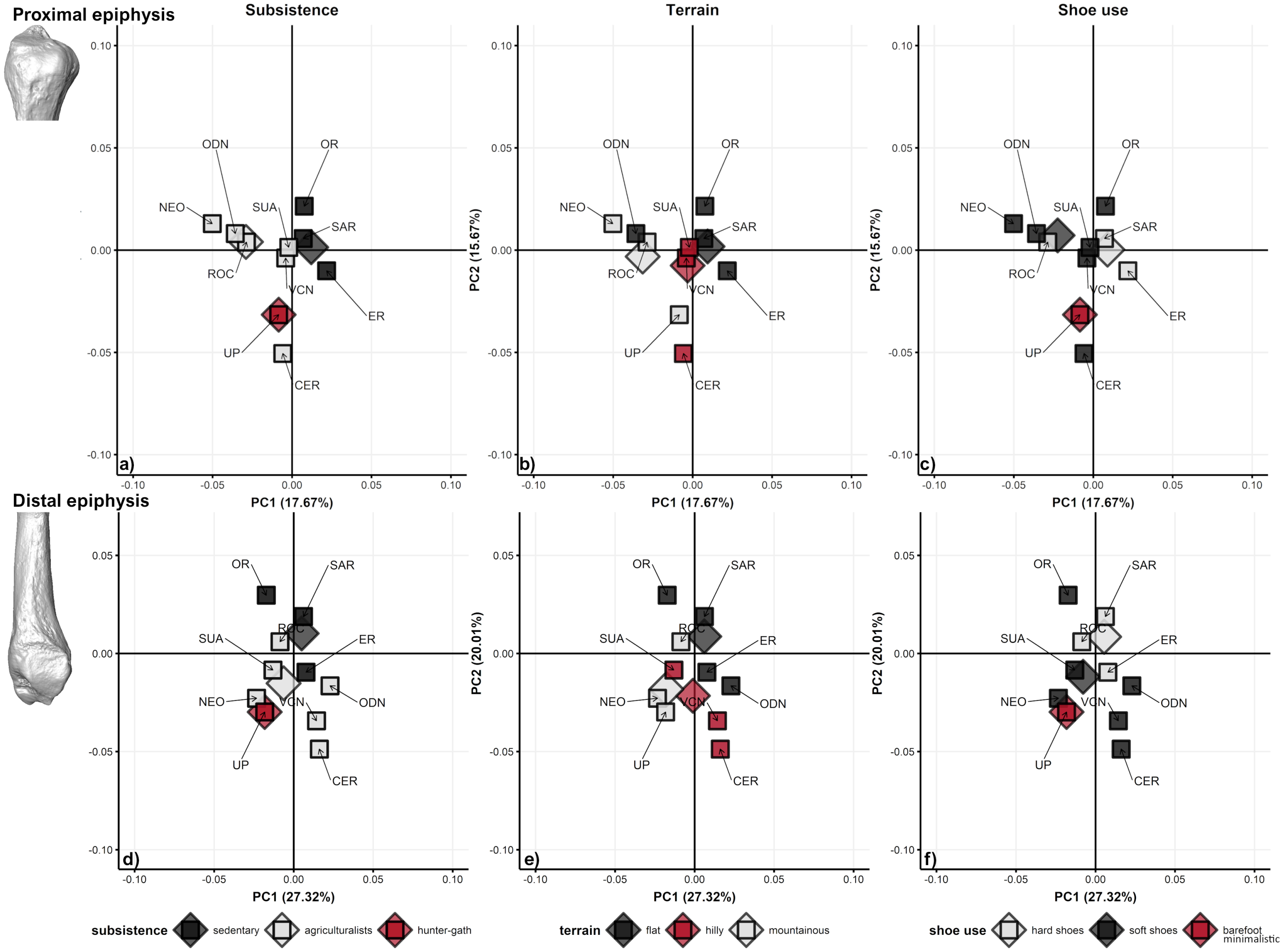

Figure 4

Shape PCA plots for proximal (top) and distal (bottom) fibular configurations displaying the distribution of each population (squares) represented according to subsistence (a;d), terrain typology (b;e) and shoe use (c;f) categories. Mean shape of each category (rhombus) is also depicted. UP= Mid-Upper Palaeolothic/Mesolithic populations; NEO= Neolithic populations; ODN=Bronze Age population of Olmo di Nogara; CER= Iron Age population of Casalecchio-Ceretolo; SUA= Roman population of Suasa; VCN= Late-Antiquity population of Vicenne; OR= Middle Age-Early Modern Jewish population of via Orfeo cemetery, Bologna; ROC= Late Modern population of Roccapelago; ER= contemporary 20th century population of Emilia-Romagna; SAR= contemporary 20th century population of Sardinia.

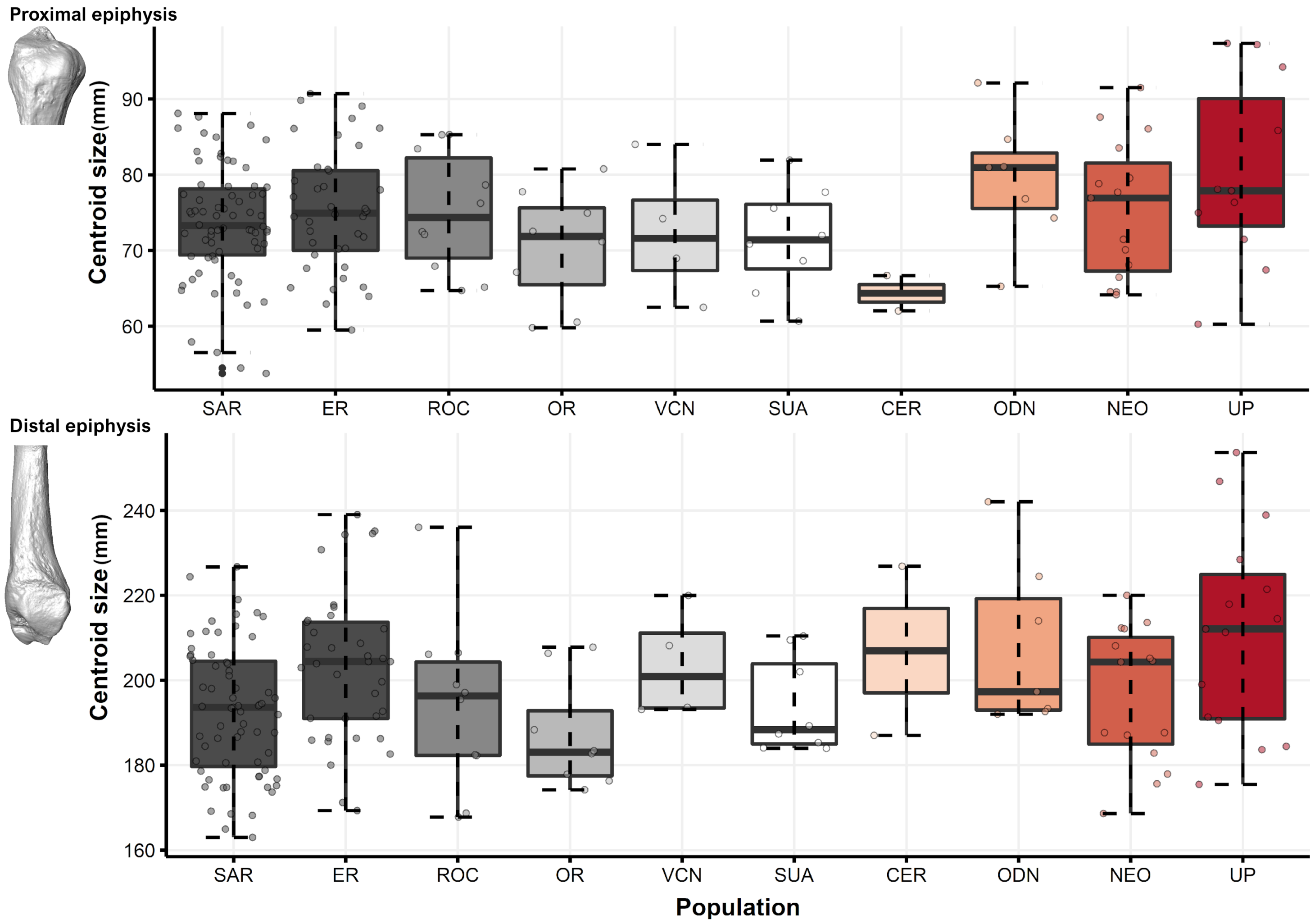

Figure 5

Boxplots for proximal (top) and distal (bottom) centroid size (mm) comparisons. Black lines are the medians, black boxes represent the interquartile ranges, whiskers the non-outliers range and black circles the outliers

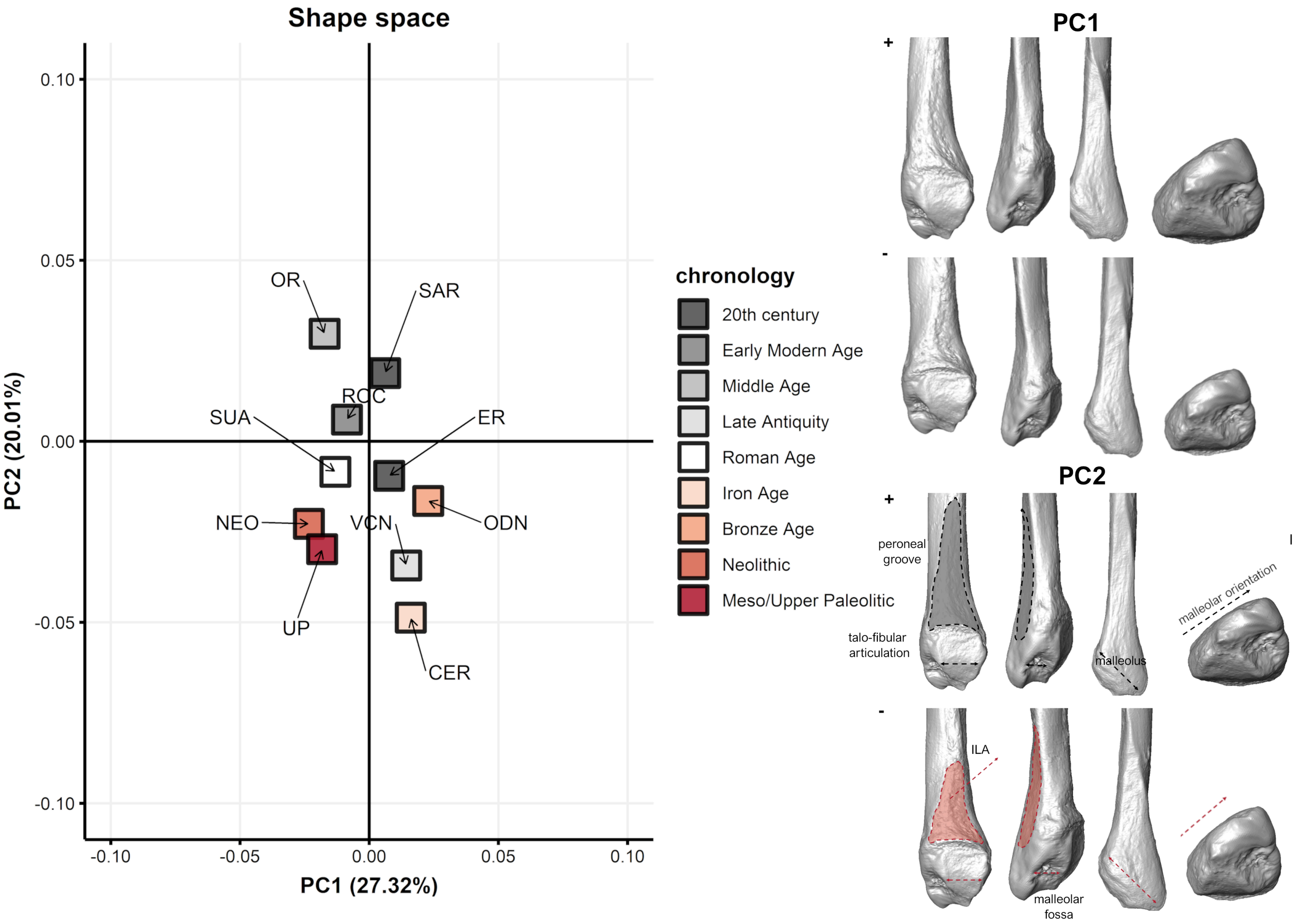

Figure 6

Shape space PCA plot computed for distal fibular epiphysis (left). Mean shape (rhombus) for each population is displayed in the PCA plot. Extremes shapes warped on fibula model for PC1 (top right) and PC2 (bottom right) positive (+) and negative (-) scores; Morphologies highlighted in black represent features of sedentary, less mobile, recent populations; Morphologies highlighted in red represent features of mobile, highly active, oldest populations. UP= Mid-Upper Palaeolothic/Mesolithic populations; NEO= Neolithic populations; ODN=Bronze Age population of Olmo di Nogara; CER= Iron Age population of Casalecchio-Ceretolo; SUA= Roman population of Suasa; VCN= Late-Antiquity population of Vicenne; OR= Middle Age-Early Modern Jewish population of via Orfeo cemetery, Bologna; ROC= Late Modern population of Roccapelago; ER= contemporary 20th century population of Emilia-Romagna; SAR= contemporary 20th century population of Sardinia.

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