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Biomechanics, behaviour dynamics and archaeology: Integrative attempts to study animal domestication and husbandry

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SUMMARY

The central historical problem this doctoral thesis deals with is the beginnings of livestock husbandry. Specifically, the management of mobility in the first domestic bovine herds is evaluated, emphasising whether the exploitation of animal power was an essential aspect in these economies. For this purpose, three emblematic sites of this chronology (early Neolithic) have been studied, allowing us to approach the subject from a diachronic and a synchronic perspective. The first site is Tell Halula, a location with continuous occupation for more than 2000 years, where we can observe the adoption of livestock farming of this species and its consolidation. The second site is the site of La Draga (Banyoles, Pla de l'Estany), a lacustrine site with perfect preservation of organic matter. Finally, the middle Neolithic site of Pixarelles (Tarvertet, Osona), located in a steep and abrupt environment, contrasts the lacustrine area of Banyoles, which is optimal for evaluating to what extent anthropic, ecological, and topographic variables influenced the biomechanical features of Neolithic bovines. Working with both sides of the Mediterranean has also allowed us to analyse a case of autochthonous domestication (Tell Halula) and a second case where the species arrives in its domestic form.In accordance with the historical subject addressed in this research, it has been considered appropriate to work with two of the animal species that played an important role in prehistoric husbandry practices, and which are key to the understanding of the Neolithic: cattle and pigs. The management of these species constitutes an important element of the Neolithisation process and contributed significantly to the economic, social, and ideological change during the Neolithic Revolution. Based on the analysis of the remains of *Bos taurus*, it has been addressed the issue of the origins of the exploitation of animal power. The use of animal power was a major innovation in terms of movement and tasks involving a significant amount of force. Economically, it was possible to increase productivity, apply more intensive agricultural techniques and move longer distances transporting loads. These innovations involved the application of powerful selective actions and pressures on animals, until animals fully specialized in these activities were obtained. In the case of pigs, a wild boar referential has been created for the research on the domestication and livestock breeding of this species. The reference collection includes 50 wild boars of known age, sex and origin, intending to examine the influence of sex and age on their morphological variance. As of now, this collection is the only one of its kind on the Iberian Peninsula. Its comprehensive characterisation based on geometric morphometrics constitutes an original contribution and an instrument of great value for archaeozoological research and research on the domestication of this species. During the early stages of domestication, it is notoriously difficult to distinguish between wild and domesticated forms. Size reduction is one of the most common approaches that has been used for this purpose, although there are numerous limitations that the published studies have highlighted. Moreover, it demonstrates the validity and efficiency of the instruments.

Complementary, and as a prominent part of this doctoral thesis, new analytical tools are designed and developed that facilitate analysing archaeological materials in all dimensions, contributing to methodological and technical advancements in archaeology. For this, it was deemed necessary to develop open-source software, ArchaeoToolbox, to conduct geometric morphometrics for the analysis of shapes in three dimensions. ArchaeoToolbox makes it possible to digitise landmarks, curve and surface semilandmarks, perform full and partial Procrustes analysis, perform principal component analysis on the Procrustes residuals, highlight the most important landmark of each morpho-space, and create exportable heatmaps for displaying morphological disparities.

The extent of geometric morphometrics, coupled with finite element analysis to investigate the unknown proportion of variance in zooarchaeological data, was tested through the presented research. The flexibility of geometric morphometrics to detect changes in morphological patterns, such as diminishing or exaggerating a structural asymmetry, was successfully used in the archaeozoological context to highlight human-induced changes in the *Bos* mechano-environment and separate it from the effects of anatomical factors. The contribution of finite element analysis to the study of cattle domestication in the Near East and Mediterranean was impeccable. Verifying observed disparities in Procrustes residuals and examining if the source of those disparities was rooted in husbandry-related activities was successfully achieved by finite element analysis.

RESUMEN

El problema histórico central que aborda esta tesis doctoral es el de los inicios de la ganadería. En concreto, se evalúa la gestión de la movilidad en los primeros rebaños domésticos de bovinos, haciendo hincapié en sí el aprovechamiento de la fuerza animal fue un aspecto esencial en estas economías. Para ello, se han estudiado tres yacimientos emblemáticos de esta cronología (Neolítico inicial), que permiten abordar el tema desde una perspectiva diacrónica y sincrónica. El primer yacimiento es el de Tell Halula, un yacimiento con una ocupación continuada durante más de 2000 años, donde se observa la adopción de la ganadería y su consolidación. El segundo yacimiento es el de La Draga (Banyoles, Pla de l'Estany), un yacimiento lacustre con una perfecta conservación de la materia orgánica. Finalmente, el yacimiento del Neolítico medio de Pixarelles (Tarvertet, Osona), situado en un entorno abrupto y escarpado, contrasta con la zona lacustre de Banyoles, óptimo para evaluar hasta qué punto las variables antrópicas, ecológicas y topográficas influyeron en las características biomecánicas de los animales neolíticos. El trabajo a ambas orillas del Mediterráneo también nos ha permitido analizar un caso de domesticación autóctona (Tell Halula) y un segundo caso en el que la especie llega en su forma doméstica (la Draga).

De acuerdo con la temática histórica abordada en esta investigación, se ha considerado oportuno trabajar con dos de las especies animales que desempeñaron un papel importante en las prácticas ganaderas prehistóricas, y que son claves para la comprensión del Neolítico: los bovinos y los suinos. El manejo de estas especies constituye un elemento importante del proceso de neolitización y contribuyó significativamente al cambio económico, social e ideológico durante la Revolución Neolítica. A partir del análisis de los restos de *Bos taurus*, se ha abordado la cuestión de los orígenes de la explotación de la energía animal. El uso de la fuerza animal supuso una importante innovación en lo que respecta al movimiento y a las tareas que implican una cantidad significativa de fuerza. Desde el punto de vista económico, permitió aumentar la productividad, aplicar técnicas agrícolas más intensivas y recorrer distancias más largas transportando cargas. Estas innovaciones supusieron la aplicación de potentes acciones y presiones selectivas sobre los animales, hasta conseguir animales plenamente especializados en estas actividades. En el caso del cerdo, se ha creado un referencial de jabalíes para la investigación sobre la domesticación y ganadería de esta especie. La colección de referencia incluye 50 jabalíes de edad, sexo y origen conocidos, con la intención de examinar la influencia del sexo y la edad en su variabilidad morfológica. Hasta el momento, esta colección es la única de estas características en la Península Ibérica. Su caracterización exhaustiva basada en la morfometría geométrica constituye una aportación original y un instrumento de gran valor para la investigación arqueozoológica y sobre la domesticación de esta especie.

Complementariamente, y como parte destacada de esta tesis doctoral, se ha diseñado y desarrollado nuevas herramientas analíticas que faciliten el análisis de los materiales arqueológicos en todas *Sus* dimensiones, contribuyendo a los avances metodológicos y técnicos en Arqueología. Para ello, se ha considerado necesario desarrollar un software de código abierto, ArchaeoToolbox, que permite realizar morfometría geométrica para el análisis de formas en tres dimensiones. ArchaeoToolbox permite digitalizar puntos de referencia, semipuntos de referencia curvos y superficiales, realizar análisis de Procrustes completos y parciales, efectuar análisis de componentes principales de los residuos de Procrustes, destacar los puntos de referencia más importantes de cada morfoespacio y crear mapas térmicos exportables para mostrar las disparidades morfológicas.

El alcance de la morfometría geométrica, junto con el análisis de elementos finitos para investigar la proporción desconocida de varianza en los datos zooarqueológicos, se ha puesto a prueba a través de la investigación presentada. La flexibilidad de la morfometría geométrica para detectar cambios en los patrones morfológicos, como la disminución o exageración de una asimetría estructural, se ha utilizado con éxito en el contexto arqueozoológico para destacar los cambios inducidos por la acción antrópica en el mecanoambiente de los bóvidos neolíticos y separarlos de los efectos de los factores anatómicos. La contribución del análisis de elementos finitos al estudio de la domesticación del ganado en Oriente Próximo y el Mediterráneo ha sido impecable. La verificación de las disparidades observadas en los residuos de Procrustes y el examen de si el origen de esas disparidades tenía su origen en actividades relacionadas con la cría se logró con éxito gracias al análisis de elementos finitos.

RESUM

El problema històric central que aborda aquesta tesi doctoral és el dels inicis de la ramaderia. En concret, s'avalua la gestió de la mobilitat en els primers ramats de bovins domèstics, posant èmfasi en si l'aprofitament de la força animal va ser un aspecte essencial en aquestes economies. Per fer-ho, s'han estudiat tres jaciments emblemàtics d'aquesta cronologia (Neolític antic), que permeten abordar el tema des d'una perspectiva diacrònica i sincrònica. El primer jaciment és Tell Halula, un jaciment amb una ocupació continuada durant més de 2000 anys on s'assisteix a l'adopció de la ramaderia d'aquesta espècie i la seva consolidació. El segon jaciment és el de la Draga (Banyoles, Pla de l'Estany), un jaciment lacustre amb una conservació idonia de la matèria orgànica. Finalment, el jaciment Neolític mitjà de Pixarelles (Tarvertet, Osona), situat en un entorn abrupte i escarpat, que contrasta amb la zona lacustre de Banyoles, òptima per avaluar fins a quin punt les variables antròpiques, ecològiques i topogràfiques van influir en les característiques biomecàniques dels bòvids neolítics. El treball amb jaciments dels dos extrems del Mediterrani també ha permès analitzar un cas de domesticació autòctona (Tell Halula) i un segon cas en què l'espècie arriba de forma domèstica (la Draga).

D'acord amb la temàtica històrica abordada en aquesta investigació, s'ha considerat oportú treballar amb dues de les espècies animals que van tenir un paper important a les pràctiques ramaderes prehistòriques, i que són claus per a la comprensió del Neolític: els bovins i els suins. La gestió d'aquestes espècies és un element important del procés de neolitització i va contribuir significativament al canvi econòmic, social i ideològic durant la Revolució Neolítica. A partir de l'anàlisi de les restes de *Bos taurus*, s'ha abordat la qüestió dels orígens de l'explotació de l'energia animal. L'ús de la força animal va suposar una innovació important pel que fa al moviment i a les tasques que impliquen una quantitat significativa de força. Des del punt de vista econòmic, va permetre augmentar la productivitat, aplicar tècniques agrícoles més intensives i recórrer distàncies més llargues transportant càrregues. Aquestes innovacions van suposar l'aplicació de potents accions i pressions selectives sobre els animals, fins a aconseguir animals plenament especialitzats en aquestes activitats. En el cas del porc, s'ha creat un referencial de porcs senglars per a la investigació sobre la domesticació i la ramaderia d'aquesta espècie. La col·lecció de referència inclou 50 senglars d'edat, sexe i origen coneguts, amb la intenció d'examinar la influència del sexe i l'edat en la variabilitat morfològica. Fins ara, aquesta col·lecció és l'única d'aquestes característiques a la Península Ibèrica. La seva caracterització exhaustiva basada en la morfometria geomètrica constitueix una aportació original i un instrument de gran valor per a la investigació arqueozoològica i la domesticació d'aquesta espècie.

Complementàriament, i com a part destacada d'aquesta tesi doctoral, s'han dissenyat i desenvolupat noves eines analítiques que facilitin l'anàlisi dels materials arqueològics en totes les seves dimensions, contribuint als avenços metodològics i tècnics en arqueologia. Per això, s'ha considerat necessari desenvolupar un programari de codi obert, ArchaeoToolbox, que permeti fer morfometria geomètrica per a l'anàlisi de formes en tres dimensions. ArchaeoToolbox permet digitalitzar punts de referència, semipunts de referència corbs i superficials, realitzar anàlisis de Procrustes completes i parcials, efectuar anàlisis de components principals dels residus de Procrustes, destacar els punts de referència més importants de cada morfoespai i crear mapes tèrmics exportables per mostrar les disparitats morfològiques.

L'abast de la morfometria geomètrica, juntament amb l'anàlisi d'elements finits per investigar la proporció desconeguda de variància en les dades zooarqueològiques, s'ha posat a prova a través de la investigació presentada. La flexibilitat de la morfometria geomètrica per detectar canvis en els patrons morfològics, com la disminució o exageració d'una asimetria estructural, es va utilitzar amb èxit en el context arqueozoològic per destacar els canvis induïts per les comunitats neolítiques al mecanoambient dels bovins neolítics i separar-los dels efectes dels factors anatòmics. La contribució de l'anàlisi d'elements finits a l'estudi de la domesticació animal al Pròxim Orient i al Mediterrani ha set impecable. La verificació de les disparitats observades als residus de Procrustes i l'examen de si aquestes disparitats tenen l'origen en activitats relacionades amb la ramaderia inicial s'ha aconseguit amb èxit gràcies a l'anàlisi d'elements finits.

1. INTRODUCTION: STRUCTURE AND OBJECTIVES

In order to gain a deeper understanding of human history, it is of utmost importance to study animal domestication and early husbandry practices. The foundations of today's economy were laid during this crucial period in prehistory, based on domesticated animals. More recent studies increasingly emphasize the spatial and temporal heterogeneity of the process of domestication rather than considering it as a single, linear event. In recent years, research has revealed that domestication trajectories were diverse and eventful responses to a wide range of historical needs. Even today, modern societies continue to domesticate various plants and animals to suit the interests of the modern world. Neolithic economies were based on animal husbandry, which was made possible by controlling animal biology and reproduction. In most countries, the main domesticated species in this period (sheep, goat, cattle, and pig) remain the most economically important species to this day. As with domestication, it is also being shown that animal husbandry during the early stages of the Neolithic was varied remarkably, contemplating diverse manifestations of concurrent exploitation strategies. On the one hand, these strategies depended on human needs and available technology, but on the other hand, they also depended on environmental factors. At the start of the Neolithic period, the first domesticated species changed their way of life; they had to adapt to the new conditions imposed on them by the environment and different groups of humans. These adaptations resulted in significant changes in their biology and aetiology, some of which were irreversible. Through a profuse study of these changes, archaeozoologists have understood the process of neolithization more thoroughly. However, some of the changes have also been extensively debated, implying that none of them can demonstrate domestication on their own.

There is growing consensus on integrating methodological approaches such as archaeozoology, paleo molecules, biomechanics and bone microstructure into an interdisciplinary study of animal domestication. Methods and high-resolution techniques are being developed within the said approaches to reveal phenomena and situations from archaeological faunal remains previously invisible to archaeologists. The paleogenomics, paleoproteomics and paleomolecules fields are currently opening up new opportunities that, in the near future, will provide essential information about the first domestication events, the function of involved genes, and the selective pressure that governed these changes going forward. More concrete results are being offered by stable isotope analysis. By making it possible to access information on the animal in a living state (when it was born, when it ceased to suckle, what it ate during its life, its movement, etc.), their application has revolutionised the study of the first husbandry practices. This field of study can also benefit from biomechanics and bone microstructure studies. Studies based on the shape and geometry of bones offer a novel approach that can provide insight into domestication and animal husbandry in the past. For instance, understanding the morphological consequences of different levels of activities or physical stress is crucial for comprehending processes involved in domestication and their impacts on animals' lifestyles and mobility. Breeding under such new conditions and exploitation undoubtedly affected bone biomechanics, which led to the development of new varieties of pathologies and side effects which are difficult to identify without the appropriate methods. From this point, new tools have been developed to study bone biomechanics and microstructure, such as geometric morphometrics. The quantification of the variation in the shape of the bones can provide evidence of evolutionary clues in response to domestication and the first phases of livestock breeding.

As a prominent part of this doctoral thesis, new analytical tools are designed and developed that facilitate analysing archaeological materials in all dimensions, contributing to methodological and technical advancements in archaeology. For this, it was deemed necessary to develop open-source software, ArchaeoToolbox, to conduct geometric morphometrics for the analysis of shapes in three dimensions. ArchaeoToolbox makes it possible to digitise landmarks, curve and surface semilandmarks, perform full and partial Procrustes analysis, perform principal component analysis on the Procrustes residuals, highlight the most important landmark of each morpho-space, and create exportable heatmaps for displaying morphological disparities.

Incorporating the concept of directional asymmetry in the context of archaeozoology, the next technical aspect of this research is to design an analytical approach to not only study the morphological responses of animals to the mechano-environment imposed by herd management or exploitation but also validate morpho-space components (principal components of Procrustes residuals) against finite element analysis results to ensure if the morphological differences in question are related to locomotion forces or not, and if they improve the ability of the bones to withstand the higher strain locally (a sign of more harsh mechano-environment), or in the opposite, the local morphological difference is making bones less robust (a sign of more mild mechano-environment).

Since its development, ArchaeoToolbox has been used to generate new knowledge about the central historical problem that this doctoral thesis deals with the beginnings of livestock husbandry. Specifically, in conjunction with the recent data and models proposed for the Mediterranean area, the management of mobility in the first domestic bovine herds is evaluated, emphasising whether the exploitation of animal power was an essential aspect in these economies. For this purpose, three emblematic sites of this chronology have been studied, allowing us to approach the subject from a diachronic and a synchronic perspective. The first site is Tell Halula, a settlement with continuous occupation for more than 2000 years, where we can observe the adoption of livestock farming of this species and its consolidation. The second site is the site of La Draga (Banyoles, Pla de l'Estany), a lacustrine site with perfect preservation of organic matter that has provided the most complete faunal collection of this species to date in the Iberian Peninsula. Finally, the middle Neolithic site of Pixarelles (Tarvertet, Osona), located in a steep and abrupt environment, contrasts the lacustrine area of Banyoles, which is optimal for evaluating to what extent anthropic, ecological, and topographic variables influenced the biomechanical features of Neolithic bovines. Working with both sides of the Mediterranean has also allowed us to analyse a case of autochthonous domestication (Tell Halula) and a second case where the species arrives in its domestic form.

A fourth aspect is assembling a reference population of 50 wild boars of known age, sex and origin, intending to examine the influence of sex and age on their morphological variance. As of now, this collection is the only one of its kind on the Iberian Peninsula. Its comprehensive characterisation based on geometric morphometrics constitutes an original contribution and an instrument of great value for archaeozoological research and research on the domestication of this species. During the early stages of domestication, it is notoriously difficult to distinguish between wild and domesticated forms. Size reduction is one of the most common approaches that has been used for this purpose, although there are numerous limitations that the published studies have highlighted. Therefore, this referential collection represents a significant betterment regarding the archaeozoology of *Sus* domestication. Moreover, it demonstrates the validity and efficiency of the instruments and procedures developed and designed within the framework of this doctoral dissertation.

1.1. Specific objectives

- Investigate if morphometrics approaches in conjunction with biomechanics (finite element analysis) can discriminate anatomical characteristics of *Bos* phalanges.

- Investigate if morphometrics approaches in conjunction with biomechanics (finite element analysis) can discriminate different animal exploitation strategies based on behaviour dynamics and locomotion.

- Investigate animal husbandry strategies in the Near East using the novel proposed methodology.

- Investigate animal husbandry strategies in Western Mediterranean using the novel proposed methodology.

- Using geometric morphometrics, differentiating sexual dimorphism in *Sus scrofa* mandible.

- Investigate how sexual dimorphism is advantageous for *Sus* males and females, food preference, shelter making or rooting.

2. STATE OF THE ART: ANIMAL DOMESTICATION AND ITS STUDY FROM ARCHAEOZOOLOGY

2.1. Definition of domestication and domestic animal

As the first step in documenting domestication, it is necessary to understand what an evolutionary process is. Biological processes are evolutionary if they satisfy the variation, heritability, and natural selection principles (Jensen & Wright, 2014; Tibell & Harms, 2017). The variation principle states that the output of a biological process can be unpredictable, singular, and asymmetric and have a long-lasting effect at the population level (Gould, 2002). The heritability principle implies that variation in a phenotype can be attributed (partially or entirely) to variations in genetic factors (Sanfilippo *et al.*, 2010). Finally, the natural selection principle indicates that in a population, the frequency of a heritable phenotype is subject to change (Tibell & Harms, 2017). The alteration of phenotype frequency was one of the key concepts that led Charles Darwin to formulate his groundbreaking theory of evolution based on the effects of artificial selection (he termed it unconscious selection) on domesticated animals.

In his influential work, The Origin of Species, Charles Darwin described domestication as an evolutionary process unconsciously initiated by man, which rapidly diversifies the phenotypic characteristics of species (Darwin, 1989). According to him, the morphological variability is a reflection of the differences in conditions of life to which each species has been exposed over successive generations, and the phenotypical traits (such as size, colour and shape) in those species will be subject to conscious (artificial by breeders) and unconscious (natural) selection pressures. Darwin also observed that domestic animals behave differently from their progenitors. In his subsequent publication, The Variation of Animals and Plants under Domestication (volume 1), he argued that the condition of life, or environmental factor as we refer to it today, was absolute and humans could not alter it in any way and that domestic species (animals or plants) were unintentionally exposed to various environmental conditions and then variability prevailed. While man does not cause variability, Darwin continued, he can select, maintain, and accumulate the diversity given to him by nature in any way he deems beneficial (Darwin, 1868). The first description of domestication in the archaeological context was provided by Zeuner (1963). He regarded domestication as a form of mutualism (*i.e.* a symbiosis relation in which both parties gain benefits), emphasised the importance of environmental factors for the process (contrary to Darwin) and argued that humans could also modify the environment to a substantial extent, *e.g.* by burning the fields, as they did during the Holocene epoch. Changes in the environment of this magnitude could significantly affect the natural selection process and disturb species' evolutionary pathways.

Since then, biologists and archaeologists have observed domestication through two distinct but interconnected perspectives to simplify such a complex evolutionary phenomenon: 1- cultural and 2- biological viewpoints. In terms of the cultural perspective, the goal is to understand why breeders selected particular phenotypes and behavioural traits. The biological outlook, however, seeks to explain the selective pressure imposed by man and the consequent differences between populations of domestic species and their progenitors (Jensen & Wright, 2014; Russell, 2002; Russel, 2012; Saña Seguí, 2006; Zeder, 2012; Zeder, Bradley, *et al.*, 2006). Therefore, the term "domestication" and its related concepts can be defined in several ways to unriddle the cultural and (or) biological aspects of the evolutionary process. However, to apprehend different scientific portrayals of domestication, one must first understand what a domestic animal is.

2.2. Domestic animals and different perspectives

Domestic animals, such as dogs, sheep and goats, cows, pigs and others, are widely known to the public. These species have two typical features: They are social animals and, compared to wild species, have strong ties to humans. Although describing a comprehensive synopsis of “domestic animals” seems trivial, the sophisticated nature of human-animal interactions makes it surprisingly challenging. Terms such as tamed, free-range, feral, pet and even on-exhibit (*e.g.* zoo) animals exemplify different human-animal relationships, yet, all bear resemblances to what one might determine as a domestic species (Russel, 2012). It is worth mentioning that taming is the process of eliminating the flight distance or tendency to flee from humans (Hediger, 1950: Chapter 5). One way to deal with the problem is to conceptualise “domestic animal” broadly enough to cover the research subject (*i.e.* biological or/and cultural aspects) but not too general to make it impractical. Some researchers with a purely biological point of view observed the human-animal interactions as a symbiotic relationship (comparable to the ant-fungi association) and generalised the notion of domestic animals beyond the cultural boundaries, suggesting that a species is domestic if it can be exploited or harvested by another species (Rindos, 1984; Terrell *et al.*, 2003; Zeuner, 1963). However, this definition is too broad, not addressing the primary source of confusion in the cultural context, and it is also debatable if animals are beneficiaries of the relationship (Darwin, 1868; Docus, 1989; Clutton-Brock, 1994). Contrariwise, some researchers emphasised only the cultural-social aspects of domestication, stating that an animal is domesticated as soon as it integrates into human societies and becomes an object for ownership, trade and inheritance (Docus, 1989; Ingold, 1980, 1984, 1988). The cultural-centric definitions address the differences between wild, tamed and domestic animals by categorising the “productive” human-animal relationship into different morphologically distinct stages such as taming, herding and breeding (according to Ingold) or domestic and domesticated (according to Docus).

Apart from the two purely biological and cultural definitions of domestic animals, several middle-ground definitions were proposed combining both perspectives. They generally highlight man's regulatory role and suggest different reasons for a domestic animal to exist, from unintentional attempts to economic gain (Bökönyi, 1969, 1989; Clutton-Brock, 1981, 1989, 1994; Piggins & Phillips, 1998; Hale, 1969; Russel, 2012). Piggins & Phillips (1998) also mentioned the potential role of animal awareness as an influential factor. For example, an assortment of biological-cultural perspectives proposes that domestic animals have close ties to humans, who strongly regulate their breeding, feeding and territorial behaviour for beneficial gains. Consequently, these man-imposed restrictions propagate (physical and behavioural) uniform characteristics that, contrary to taming and pet keeping, are long-lasting and transfer through generations (Clutton-Brock, 1981, 1989, 1994; Russel, 2012). This description is broad enough to include the most known domesticated species (except the cat, which seemingly domesticated us, not the other way around!) while specific enough to exclude pets, free-roaming and feral animals.

2.3. Domestication: Definitions

The domestication process has also been illustrated in the same perspective-oriented way by taking a biological, cultural or both (biological-cultural) standpoint to simplify explaining one of the most complex events in human history. However, as Docus (1989) underlined, it is essential to note that Archaeozoology, similar to social science and statistics, is an observational field of science in which hypotheses are suggested based on empirical evidence (*e.g.* excavated materials) to provide a close-to-truth explanation of a non-replicable event or process. Therefore, such hypothesises can be verified only in the context or perspective of the provided evidence to reveal the so-called contextual truth (Massimi, 2018).

Biological perspectives on domestication tend to highlight the human-imposed selective pressures to explain how phenotypical and behavioural aspects of animal life evolve generation by generation. In Zeuner's (1963: chapter 2, 1974) biological model, domestication is a five-stage process developed naturally as a form of symbiosis without any motivation from the human associate, at least during the initial steps. In the earliest phase, according to him, domestic prototypes had a loose symbiotic tie with human societies and were phenotypically identical to their wild progenitors due to regular inter-breeding. During the second phase, however, the domestication process was completed, and humans took control over animals' breeding, *i.e.* inter-breeding was limited, and as a result, the morphological traits of domestic species emerged. He suggested that the first Neolithic settlers of Europe had completed the second stage before their arrival. In the next stage, economically motivated selective pressures (*e.g.* in favour of larger size and docility) were applied, and controlled inter-breeding with the wild progenitors was permitted to improve the profitable characteristics of domestic animals. This stage was critical since human societies began to take an active conscious role in the process. The fourth stage was marked by standardising the desirable phenotypical features and the total genetic isolation of domestic animals in which inter-breeding with the wild counterparts was deemed undesirable. Finally, in the fifth phase, wild progenitors lost all of their social significance to human societies; they were labelled as pests and nuisances, which could reverse the favourable attributes of highly specialised domestic herds, and eventually, they became the target of extermination.

According to a classic biological-cultural definition suggested by Bökönyi (1969), domestication is the separation of tamed or captured animals possessing specific behavioural characteristics from their natural population and environment and keeping them under controlled breeding conditions for beneficial pursuits, such as more accessible sources of food (Later in 1989, he noted that the said benefits are mutual). Domestication embodies two distinct phases, he continued, reflecting different levels of human control: animal keeping and breeding. Animal keeping comprises a primitive selective process in favour of smaller individuals (in the case of mammals, smaller individuals are easy to manage), incorporated with rudimentary or no intentional feeding control over so-called partially domesticated individuals, resulting in a single breed of animals per population. Contrarily, animal breeding includes purposeful selective breeding of now fully domesticated animals in favour of larger sizes (larger individuals are more productive compared to small ones) while imposing complete control over the quality and quantity of their food, resulting in diverse breeds of more productive animals living together in a population.

Like Bökönyi, Clutton-Brock (1989) described domestication as a biological-cultural process initiated by the proprietary integration of tamed animals into the human social structure for economic gain and imposing control over their breeding, territory and feeding habits. Then, after the initial integration and imposition of selective pressures on several generations of “founder population” (progenitors), the consequent phenotypic variations appeared, and gradually, the process concluded with the emergence of domestic breeds. Later (1994), she noted that domestication is a natural survival strategy, which evolved to overcome complex environmental pressures such as the food shortage crisis in the Holocene Near East. The said evolution was slow and gradual and propped up by the isolation of progenitors from their wild counterparts, which, along with inbreeding, poor diet and artificial selection in favour of small and docile individuals, promoted a significant decrease in the size of domestic animals. The Clutton-Brock point of view differs from Bökönyi in underlining behavioural changes in domestic animals. By portraying culture as the transference of knowledge from one generation to another (better known as the cumulative culture following Boyd & Richerson, 1996), she argued that domestication influenced the cultural aspects of animals population, similar to human hunters (Clutton-Brock, 1994). For more information about the cumulative culture in mammalians, readers are referred to Thornton & Clutton-Brock (2011).

Cultural perspectives on domestication tend to centre around the socio-economic evolution in hunter-gatherer societies to explain why and how domestication began. However, other factors, such as religious practices and ideological motivations, may have also played a crucial role (Hahn, 1896; Hayden, 2003, 2014; Hodder, 2010). Nevertheless, it was Karl Marx who first pointed out that economic motives and social structures are integral to the explanation of prehistorical narratives:

"*Relics of by-gone instruments of labor possess the same importance for the investigation of extinct economic forms of society, as do fossil bones for the determination of extinct species of animals.*" (Marx, 1906: chapter 7)

Materialist studies of human existence were the hallmark of Marxism during the nineteenth century, and eventually, it was integrated into the Soviet archaeological school of thought after Ravdonikas' publication in 1920 (Trigger, 2006). Influenced by Soviet research disciplines, Childe (1950: chapter 3) argued that cultural changes in hunter-gatherer societies that led to the Neolithic revolution (a term he coined earlier in 1936) were associated with both the technical knowledge of food production and the socioeconomic institutions, an idea which became the staple of many domestication culture-centric theories for decades to come. Accordingly, in the context of the pre-Neolithic to Neolithic transitional stage, the process by which socioeconomic institutions evolved is believed to be based on two premises: the necessity of securing a reliable source of food and the complexity of social structures, such as techno-economical specialisations, the existence of storehouses and social ranks (Lee & Devore, 1968; Sahlins, 1972; Zvelebil, 1986).

Masson (1971, 1972) complemented the previous takes on the economic transition and described three different models of societies that preceded the Neolithic revolution based on archaeological evidence excavated in the Near East (Zagros mountains), Central America, and Peru. 1) the Asia Minor model, which consisted of highly developed hunter-gatherers who eventually initiated farming and pastoral (cattle-rising) economies, 2) the Central American model consisted of highly developed hunter-gatherers who started a farming economy to evade the food crisis caused by the Palaeolithic climate change, and 3) Peruvian model, embodied fishermen and sea-hunters who ultimately commenced mainly agricultural economy. Unlike previous theories on the neolithic economic transition, Masson’s Asia Minor model excludes food shortages as an initiating factor. Instead, he argued that type 1 (Asia Minor) societies were advanced enough to maintain a high population growth rate, which motivated them to choose sedentary life and start to use pottery and at this point, their economy evolved into a more productive economy. It is essential to mention that in the context of Masson's research, highly developed hunter-gatherers were people who had a mixed appropriative-productive economy, where the appropriative was more than 50% of the total economy. Kabo (1985) inquired about the essence of the Neolithic revolution (*i.e.* transition of the food-based economy from appropriative to productive) by comparing pre-Neolithic hunter-gatherer societies and contemporary Australian Aboriginies. Influenced by Childe and Masson, he noted that the technical knowledge of food production, such as making essential tools (*e.g.* axe, hoe and grindstone), was necessary but not the leading motive for the transition to a productive agricultural economy. However, the societies themselves were the determining factor. He elaborated more on Masson’s Neolithic models by stating that strong motivation to make changes (*e.g.* food crisis) and enough social complexity were essential for people to start participating in the productive economy and practising domestication. Moreover, he outlined the third possible factor: the capacity for the gradual accumulation of knowledge (gnoseological or esoteric knowledge), which provides conditions for and ultimately pushes society toward drastic changes regardless of people's willpower. Masson’s type 1 model is an example of the third factor. Unlike the situation in Ice Age Europe, in which food was a strong motivation for socioeconomic change (Masson’s type 2), highly developed hunter-gatherers of the Near East did not experience ecological turmoils and food crises. Their soil was suitable for agriculture, the environment was fair for animal domestication, and after accumulating thousands of years of knowledge about their local animals and plants, they embarked on a productive economy.

Other scientists emphasised the social aspects of the said socioeconomic evolution and its impact on the process of domestication. Meadow (1984, 1989), for example, defined animal domestication, particularly in the case of the food species, as the gradual change in the human-animal relationship, encompassing not less than a shift of economic pull from dead animals to living ones: from acquiring and distributing dead animal products to securing and selectively preserving the animal offspring (progeny). This process changes the socioeconomic essence of living animals for humans, which exemplifies itself in the form of morphological and behavioural adaptations in the animals experiencing domestication, as well as the social transformations in human societies (*e.g.* the emergence of the social classes) due to the accumulation of materialistic wealth. Ingold (1980: chapter 2, 1984) similarly contemplated animal domestication as a period in the evolution of human resource exploitation. Resource exploitation and appreciation are regulated by the social structure, which eventually controls economic conventions. As mentioned before, he defined domestic (domesticated) animals as those “engaged” with and appreciated by human societies while alive, opposing wild animals, which have economic value only when they are dead. Therefore, domestication is best characterised by incorporating live animals and their offspring into human societies. He continued that the human-animal relationship can be categorised into three mutually exclusive forms: taming, herding and breeding. Herding differs objectively from hunting in the social context of resource production and distribution: hunting is sharing a collective resource (wild animal meat), whereas herding is protecting a private resource (living animals and their progeny) to which only the herder has access. Hunting is therefore based on collective access, while herding is based on divided access, which results in materialistic wealth accumulation due to the placement of control over resource reproduction. Saña Seguí (1999, 2006) also argued that animal domestication is a social transition of the human perspective regarding animals and their products, rendering societies to appropriate animals differently and legitimising other use of natural resources. As a result, humans perceive a domestic animal as a manufactured product mandating new techniques to be sustained and obtained.

In addition to the socioeconomic motives, the cultural stance on domestication also encompasses ideological incentives—for example, Ian Hodder (2010).

2.4. Domestication and its spectrums: The first step

Regardless of the perspective, all definitions of domestication share a common sentiment: it is a gradual multi-phased (cumulative) process involving various stages of animal-human interactions. To some, each stage can be mutually inclusive and succeeds the previous one very fast, hence the name of the Neolithic revolution (Childe, 1936; Masson, 1971, 1972) and to others, stages are mutually exclusive, and society cannot potentially be on multiple stages at the same time (Ingold, 1980: chapter 2). Nevertheless, defining what domestication is or what domesticated animals are, although crucial, is only practical by providing a stratified portrayal of the domestication process; otherwise, one might induce the converse fallacy in the context of zooarchaeological research. Simply put, the presence of domestic animal remains is not a sign of, for example, fully developed animal domestication practice (Meadow, 1984; Saña Seguí, 2006; Zeder, Emshwiller, *et al.*, 2006). Instead, despite different takes on domestic animals (biological or cultural outlooks), it is advisable to think of domestication as a spectrum of interactions between humans and animals, from wild to fully domesticated. The story begins with beasts becoming an integral part of man's life, and for a long time, it was challenging to explain how and why such a bond was formed. One of the earliest scientific attempts to demystify the starting stage of animal domestication was made by Galton (1865, 1907). He hypothesised that familiar farm animals were "reclaimed" during antiquity from the wilderness and have since been improved by generations of humans and that pet keeping was the cornerstone of domestication. Galton's theory on the origin of domestication has been advocated by many, especially regarding dogs, pigs, and poultry, to a lesser degree (Serpell, 1989). Harris (1978, chapter 3) theorised those old hunter-gatherers understood the implications of fostering sheep and goats as pets for economic gain and food stockpiling. However, they did not do so for a long time because they had a limited supply of food for both themselves and their flocks, and then, the cultivation of cereals removed the said obstacle, and animal domestication began. He continued that sheep and goats could be penned, consume scraps and non-edible agricultural by-products such as straw, and be milked and slaughtered selectively (*e.g.* aggressive, sick or underdeveloped individuals were slain before maturity). Serpell (1986: chapters 1 and 11, 1989) similarly argued that potentially all known domestic species, particularly dogs and pigs, started to accompany humans in a non-beneficiary manner as pet companions. He provided reasons for such species to be selected as pets, including expression of fondness toward people, playfulness, and loyalty, as well as physical attributes such as fluffiness, having a domed forehead and large eyes, which evokes parental emotions in humans. Unlike Harris, he believed that the emotional attachment of hunter-gatherers to their fellow pets was the major impediment to the onset of domestication. Eventually, the ever-increasing food crisis forced some Paleolithic hunter-gatherers and horticulturalists to change their non-beneficiary approach and undertake food or labour exploitation. Serpell (1986: chapter 11) described the coping mechanism or “distancing device” (coined by Hyam Maccoby) to deal with the cognitive dissonance caused by such a change of attitude toward animals, which includes concealment, misrepresentation, shifting the blame and most notably, detachment. For more information about this cognitive dissonance, readers are referred to Loughnan *et al.*, 2014.

Childe (1950: chapter 3) speculated that in certain places, such as the Near East, , cultivation of wheat and barley emerged spontaneously, and cereals complemented the diet of the hunter societies. Consequently, the unpalatable parts of cereals (*e.g.* grains husk) and the availability of water near human communities attracted certain animals, *i.e.* progenitors of pigs, goats and sheep and cattle, to hunter-cultivator settlements. Rather than killing those animals, hunters observed their behaviour, made them dependent and eventually tamed them. By observing the animals, they comprehended the usefulness of having tamed animals living around, and domestication and selective breeding in favour of specific characteristics were started. Childe described the benefits of keeping tamed animals as having “living larders and walking wardrobes”. In addition, he added cattle, goats, and sheep's wool and milk products to the list of motives for domesticating animals. Likewise, Ingold (1988, 1994: 2000 chapter 4) referred to the beginning of domestication and transition toward pastoralism or “the origins of food production”, as a change in hunters' perspective toward their prey animals. However, to describe such a transition, he portrayed the human-animal association beyond the philosophical canvas of the dualistic domain of nature and culture (for more information on nature and culture dualism, readers are referred to Haila, 2000; Ingold, 1990). By studying the arctic and sub-arctic hunter and herder societies, Ingold observed that, despite the general western dualistic perspective, hunter-gatherer communities do not envision themselves as separate entities beyond nature but as insignificant small parts of it. Their bond to their animal brethren is of the kind perceived as trust: by treating hunted animals respectfully (*e.g.* avoiding unnecessary killing, reducing the brutality, suffering and pain of butchering and not wasting the obtained products), hunters expect that as a payoff, prey hopefully returns to them (by their own free will) through a new cycle of life to be hunted again. Ingold then abstracted the fundamental requirements of the trust-based relationship (*i.e.* autonomy and dependency), stating that hunters do not strive for dominion over animals, and their weapons are not instruments of control but catalysts for acquiring personal "knowledge" and "revelation". Simply put, he supposed hunters desire to understand their relationship with nature rather than control nature itself.

Concurrent with this deterministic system of belief, Ingold continues, there existed a stochastic viewpoint among some hunters which questioned the absolution of natural consequences and the "trust" and considered the risk and probability of resources provided by nature failing to meet subsistence demands. The outcome of such a secular thought was the emergence of pastoralism: a transition in belief systems toward the tamed and decoy animals from "trust" to "dominance" to maintain the availability of subsistence resources. However, it is essential to accentuate that the said shift is confined to the human-animal bonds; therefore, herders, much like hunters, still conceive themselves as a part of nature, although not as insignificant as hunters since they gained some control over their association. During the transition, animals lost their reciprocal capacity to play a part in the relationship, and herders, took the role of executioner caretakers, making life-or-death decisions for and expressing dominance over all aspects of their proprietary animals. Unlike hunters, their tools (such as lasso and lash) portray control rather than revelation, as they desire to control their relationship with nature rather than understand it. Like Serpell (1986), Ingold also mentioned coping mechanisms, namely detachment, to overcome the cognitive dissonance caused by the transition in the human system of belief as the degree of control over animals increases. For example, he observed that Siberian reindeer ranchers, contrary to hunters and herders (to a lesser degree), totally abandoned the ritualistic appreciation of the mythical "big reindeer-man" and moderately benevolent butchering practice while showing ever-increasing levels of brutality toward reindeer to discourage them from escaping the ranch.

Zeuner (1963: chapter 2, 1974) hypothesised that domestication began with both keeping pets and taming wild animals; however, it was a natural socio-behavioural evolution bound to happen without any motivation rather than a cultural process inspired by socio-economic factors. He argued that Mesolithic hunters had too much leisure and economic stability to devote their effort to experimenting with new ways of life, such as taming and eventually domesticating animals. Their ecological niche, however, was a fertile medium for such a social evolution to thrive and reach the crucial stage portrayed as domestication. Before advancing further, it is necessary to clarify the terms Zeuner used to discuss his theory. Social behaviour is an adaptive multi-level evolutionary mechanism that ultimately increases an animal's fitness and survival rate by interacting with the members of its own or the other species. At one end of the social behaviour spectrum lies asocial species, which rarely interact with each other. The less primitive form of social behaviour is limited to intra-species interactions, such as a pack of wolves, whereas the most evolved form includes tight, interwoven series of interactions between different species, called mutualism. Corals-zooxanthellae and ant-fungus relationships are among the more well-known examples of divided-labour mutualism (McGlynn, 2010; Leigh, 2010). The long-term mutualism with the division of labour is called symbiosis. In theory, both partners could benefit equally from symbiosis; nevertheless, the inequality of gain and effort compels mutualism to develop and evolve (Trivers, 1971), and perfectly balanced symbiosis has rarely been documented. Extreme imbalance of gain, however, evolves the symbiosis to social parasitism. According to Zeuner (1963: chapter 2, 1974), the evolution of domestication can be traced back to mutualistic scavenging and social parasitism. He argued that scavenger progenitors of some domestic animals, such as dogs and pigs, used to roam settlements as pets and form a symbiotic bond with humans: disposal of human waste scraps was beneficial for both symbiont parties, human hosts and animal guests. There is another possible symbiotic scenario, Zeuner continued, in which the man role-played as the guest and gradually shifted the gain in his favour, so much so that the symbiosis evolved to social parasitism. Domestication of tamed reindeer is among the instances of social parasitism, in which, very similar to the other examples of parasitism, the guest (*i.e.* human) provides delicacy (*e.g.* salt, food scraps and urine) to entice the host to participate in a one-way exploitative relationship.

Hahn (1896) suggested that domestication began with successfully breeding (*i.e.* producing fertile offspring) captive pets and tamed animals. Even though hunter societies possessed much more diverse captive species, he emphasised that reproduction in captivity is rarely successful, which may explain why the number of domestic species we know today is so limited. According to him, the initial motivation for domestication was neither to enjoy accompany of pets (except in the case of the rabbit) nor to gain monetary benefit since the economically significant hoofed mammals (he called them “Wirtschaft lichen Haustiere”) were domesticated later and also there existed better economically justified choices to domesticate. Instead, ideological elements such as religiously significant species which were friendly toward and protected by humans played a crucial role in the dawn of animal domestication. Hayden's (2003, 2014) inquiries into the origins of agriculture led him to hypothesise, following Hahn (1896), that ideological/cognitive transformations inspired hunter-gatherers to initiate animal and plant domestication. Despite the lower and less stable productive return, higher labour effort and high risk associated with the early stages of domestication, he argued, ideological factors drove (pushed) humans to cultivate food. As the Epipalaeolithic hunter-gatherers evolved into more complex "trans-egalitarian" societies, economic rivalries emerged in pursuit of power and prestige, and no occasion better than a large and lavish banquet could serve as an arena for such competitions. The meat of desirable or exotic animals with digestible and delicious fat, dried fish, assortments of sauce, tobacco, alcohol and opium were among the luxurious items which used to be available on feasts to establish social status, impress allies and dissuade rivals. Domestic dogs (with some exceptions), hawks, eagles, geese, crows and magpies, wolves and foxes were also considered social status symbols since they had a high maintenance cost (consumption of up to 50-60% of household food resources, which is costly, even by our modern standards) while possessing no nutritional value. The preparation of banquets and feasts was planned for months or even years since fresh meat and vegetable sources could be spoiled. The initial preparatory measures incorporated salting, drying and smoking; however, Hayden suggested the alternative strategy of storing the surplus food resources in the form of living and breathing captured/tamed animals and serving them warm and fresh at the time of feast was a pivotal moment, eventually led to the animal domestication.

2.5. Documenting domestication:

Direct perception of the Neolithic transition, such as a scene contemplating animal husbandry or technological remnants reflecting farming or herding practices (*e.g.* yoke, saddle, harness, leashes, and hobbles, can be anointed as direct domestication markers), like any other prehistoric scenario, is a rare and ambiguous occasion. However, the only reliable alternative is to recreate the scenario and its cultural context based on information gathered from excavated archaeological materials, such as skeletal and hard tissue remains (Davis, 1978; O'Connor, 2000; Vigne, 2011). Regardless of the definition, animal husbandry emphasises two primary anthropogenic events: controlling animals' feeding, foraging and mating activities and inserting selective pressure on them to meet desirable behavioural, cultural or economic criteria. The conceivable responses of animals to these two events at the organismal or population level are called indirect domestication markers (or impact markers), which are theoretically traceable in archaeological records (*e.g.* skeletal remains) and can be used for the indirect documentation of the domestication process (Diamond, 2002; Zeder, 2006a, 2015). In practice, however, especially at the initial stage of domestication, the markers are vague, and their interpretation is difficult (Docus, 1989; Vigne, 2015; Zeder, Emshwiller, *et al.*, 2006), encouraging scientists to improve the existing methods or propose more reliable pipelines to comprehend the Neolithic transition. The indirect domestication markers (opposing the direct markers such as animal burial or husbandry scene in archaeological assemblages) fall into several categories, such as morphological (inheritable and plastic), behavioural, demographic and genetic attributes (Meadow, 1984; Zeder, 2006b, 2015; Zeder, Emshwiller, *et al.*, 2006). The characteristics of domestic animals have been extensively studied since 1868 when Charles Darwin wrote the first scientific commentary on the subject: The Variation of Animals and Plants Under Domestication. His groundbreaking natural selection theory was deeply rooted in the diversification of traits in domestic species due to the artificial selective pressure imposed by humans (Darwin, 1989). In the following decades, four principal strategies were pursued to study the divergence between domestic animals and their progenitors: comparative, longitudinal, hybridisation, and molecular (*e.g.* functional genomics) procedures (E. O. Price, 1984, 2002: chapter 3).

The comparative approach, the most conventional among the others, focuses on comparing domestic animals with their wild progenitors, usually providing no information regarding the mechanism behind the differences and assuming that the wild samples represent the ancestry linkage to the domestic ones. Although prevalent, the reliability of comparative results strictly depends on fulfilling the mentioned assumption, which is only sometimes achievable. For example, the uncertainty about some progenitors (Zeuner, 1963), their extinction at the time of the study (*e.g.* aurochs), the difficulty of accounting for temporal and spatial variation of wild species phenotypes (Pruett & Warner, 2021), and the possibility of wild and feral/free-range hybridisation (Schleimer *et al.*, 2022) are among the known issues that negatively affect the reliability of the comparative procedure. The longitudinal strategy, however, re-constructs the advent of domestication by keeping and breeding wild species in captivity for generations and monitoring the consequent changes. This approach provides an overview of evolutionary adaptations and the rate of resultant changes in response to the captive environment. It also can provide insight into the extent of adaptation by experimentally manipulating the environment or genetic pool of the target population (Connor, 1975; Dobney & Larson, 2006; E. O. Price, 1984). The silver fox experimental domestication (Belyaev, 1979), the DOMEXP project (Harbers, Neaux, *et al.*, 2020; Harbers, Zanolli, *et al.*, 2020; Neaux *et al.*, 2021, 2022), and the house mouse experimental domestication (Connor, 1975) are among the widely known examples of the longitudinal approach. The hybridisation and molecular approaches are beyond the scope of the present research, and for more information on those topics, readers are referred to E. O. Price, 2002.

Animals' morphological, behavioural and physiological traits encompass inheritable and plastic attributes resulting from two distinct mechanisms: genetic and environmental factors. The inheritable characteristics are derived mainly from selection pressures favouring genetic divergence from the ancestral lineage, whereas the plastic characteristics are nonhereditary responses to environmental changes to improve survival rate (T. D. Price *et al.*, 2003). In the same way, morphological domestication markers fall into two categories: inheritable (genetically driven) and plastic (Zeder *et al.*,, 2006a).

Since domestication is a gradual, cumulative event, its markers can also be thought of as highly temporal classifiers, necessitating the provision of a separate set of markers for each stage to differentiate the portrayal of the whole process into a stratified temporal perspective (Meadow, 1984; Saña Seguí, 2006; Zeder, Emshwiller, *et al.*, 2006).

Darwin listed several phenotypical and behavioural attributes that only are unique to domestic mammals across several species and not found in their wild counterparts. These attributes, also known as domestication syndrome traits (after Wilkins *et al.*, 2014) or the domestic phenotypes (after E. O. Price, 2002), have been updated since and include, among others, depigmentation (Belyaev, 1979; Darwin, 1868; Trut *et al.*, 2009), having floppy and small ears (Belyaev, 1979; Darwin, 1868), craniofacial (Darwin, 1868; Kruska, 2005; Neaux *et al.*, 2021, 2022; Zeuner, 1963) and skeletal (Harbers, Neaux, *et al.*, 2020; Harbers, Zanolli, *et al.*, 2020; Neaux *et al.*, 2022) disparities, having a curly tail (Belyaev, 1979; Darwin, 1868; Trut *et al.*, 2009), docility and tolerance toward humans and captivity environment (Arbuckle, 2005; Belyaev, 1979; Darwin, 1868; E. O. Price, 1984, 2002; Hale, 1969; Serpell, 1986), neoteny (Gariépy *et al.*, 2001; E. O. Price, 1999) and different sexual behaviours (Belyaev, 1979; Darwin, 1868; E. O. Price, 1980; Trut *et al.*, 2009). The molecular approach to domestication primarily centres around mapping genetic components responsible for the appearance of the domestication traits (Andersson, 2001) and determining their expression mechanisms (Jensen, 2006), or briefly, functional genomics (Gibson & Muse, 2009: chapter 5). Phenotypical/behavioural characteristics of animals, in the genetics context, can be organised into monogenic and polygenic traits. The monogenic traits follow the Mendelian inheritance and are controlled entirely by a single gene (sometimes two) or mutation (Wright, 2015). The polygenic traits, in contrast, do not follow the Mendelian inheritance and are controlled by multiple genes/mutations (Andersson, 2001).

2.6. Domestication from a geographical perspective

In a broader view, domestication is a spatial phenomenon. The participants, human societies, plants or animals, and possible external catalysts such as the environment are known to have substantial spatial variations. Therefore, to portray how societies and animal or plant species co-evolved at each stage of domestication and to reconstruct the dominant sociocultural background at the advent of the Neolithic transition, it is crucial to understand the geographical imprints of domestication. Vavilov (1926) was one of the first scientists to argue that plants were not domesticated randomly throughout the world but in eight specific regions, which he called the centres of origin. The argument was based on the law of homologous series in variation (established by himself six years earlier), assigning the region with the highest genetic diversity of a species to the centre of origin of that species. Although outdated, Vavilov’s centres of origin still overlap with some of the more recently proposed centres of domestication (Harlan, 1971; Hummer & Hancock, 2015; Roberts *et al.*, 1998). On a more extended worldwide scale, centres of origin fall into two categories: the primary centres, in which food production began independently via domestication of local crops and animals, and the secondary centres, where domestication of local species was limited and food production heavily depended on animals and plants, or so-called the “founder” species (since they founded local food economies), that were migrated or diffused from the said primary centres (Bogucki, 1996; Bulliet *et al.*, 2011; Diamond, 2002, 2017: chapter 5; Fuller, 2011; Mazoyer & Roudart, 2006; Zvelebil, 2001). At least during the earliest stages, a suitable geo-botanical/zoological background was an essential prerequisite for food production (Fuller, 2011; Kabo, 1985). Likewise, current archaeological and genetic data suggest that food production started independently at different periods (Early to Middle Holocene) across nine to eleven distinct regions, which are/were home to the progenitors of major domestic species. The early Holocene epicentres include Near East (the fertile crescent), China, Mesoamerica and Northwestern Lowland South America (Diamond, 2017: chapter 5; Larson *et al.*, 2014; Vigne, 2015). However, in the case of economically significant animals such as goats, sheep, cattle and pigs (around the same time, pigs were also domesticated in China(Cucchi *et al.*, 2011; Larson *et al.*, 2010)), the centres of origin were confined to the early Holocene Near East (Helmer *et al.*, 2005; Larson *et al.*, 2014; M. Price & Hongo, 2020; Roberts *et al.*, 1998; Vigne, 2011, 2015; Zeder, 1999, 2008).

As the agropastoralist societies or their ideas of the Neolithisation spread out from the primary centres of the Neolithic transition, they settled slowly down in exploitable territories around the globe or distributed their new economic knowledge and culture out in the world, and by doing so, they confronted more or less evolved pre-existing hunter-gatherer societies. Although the nature of the confrontations is disputable (direct violent or non-violent contact, transfer of knowledge and culture, et cetera), the indigenous hunter-gatherers, who also possessed some rudimentary farming skills, were convinced to start practising agriculture and passed the knowledge from generation to generation, so under the right circumstances, the secondary centres of domestication were established. Eventually, the new way of life spread to Egypt, the Iranian plateau and Europe (Bogucki, 1996; Mazoyer & Roudart, 2006; Zvelebil, 2001). Several models have described the Neolithic (agro-pastoral) expansion. The two oldest and simplest ones were proposed by Childe (1925, 1934), suggesting that farming spread because farmers migrated to new regions (also known as the folk migration model), and Edmonson (1961), supposing that the indigenous hunter-gatherers learned farming from their neighbouring farmers (also known as the cultural diffusion model). Decades later, Cavalli-Sforza revised the folk migration model by combining population genetic data and proposed the demic diffusion model. The demic diffusion model (DDM) has two sub-models and assumes that the Near East population growth in the aftermath of the Neolithic transition encouraged the early farmers to gradually spread (in several discontinuous waves over short distances, or the "wave of advance" sub-model) or colonise (the "colonization" sub-model) exploitable regions inhabited by semi-developed hunter-gatherers. Consequently, the genetic composition of the new territories, which once was dominated by the indigenous hunter-gatherers, changed in favour of the neolithic farmers due to their demographic superiority (Ammerman & Cavalli-Sforza, 1984: chapters 4 and 5; Cavalli-Sforza *et al.*, 1993). In sharp contrast, the cultural diffusion model (CDM) suggests that the Neolithic conception (ideas and culture, also called Neolithisation) was spread through the transmission of economic ideas and technology from the early Neolithic farmers to the indigenous hunter-gatherers; therefore, the population and genetic amalgamation of farmers and indigenous hunter-gatherers was inconsequential and negligible (Thomas, 1988; Whittle, 1996: chapter 3).

With the emergence of new archaeological evidence and more frequent use of diverse disciplines in pre-historical research (such as population genetics and the ancient DNA), it became clear that simple dichotomous models of the Neolithisation expansion, *i.e.* via immigration or cultural diffusion, are not sufficient to explain such a complex event. Hence several other theories were proposed, primarily by integrating DDM and CDM (Fernández-Domínguez & Reynolds, 2017; Zvelebil, 2001). Renfrew (1989: chapter 6), for example, proposed the “Elite dominance” model, describing the Neolithic expansion by the arrival of small groups of highly organised (“stratified”) and militarised elite agropastoralists in new regions and their domination over indigenous hunter-gatherers. The outcome of this dissemination, he continued, was a persistent demographic amalgamation (culture and gene pool) of immigrants and the indigenous population with various proportions; sometimes, the native culture died out, and other times, it retained its relevancy. Neústupný (1982) suggested the “Infiltration” model, depicting the Neolithic expansion by the arrival of small groups of skilled artisans in new vast contiguous territories to fill a niche economic role (*e.g.* farmer, herder or tinker) in the indigenous hunter-gatherer societies. However, the immigrants kept their ties with their homeland, and although their encounter with the indigenous population was peaceful, they did not mingle with them. Alexander (J. A. Alexander, 1984) introduced the frontier concept (the term coined by Turner (1893), referring to the temporary borderline of an expanding society) to archaeology and proposed the “advancing frontier” model. The advancing frontier explains Neolitisation as a small-scale dispersion of Neolithic agropastoralists within frontiers shared with native hunter-gatherers, which yielded sporadic contact between the two groups and even offered the possibility of mixed marriages, establishment of social networks and trading agreements. Arnaud (1982) and Zilhão (1993) suggested the “Leapfrog colonisation” model, portraying the Neolithic expansion as a four-phase process. Phase one is marked by the appearance of small groups (around 25 people) of expeditionary agropastoralist settlers in new regions already occupied by hunter-gatherers to establish enclave settlements, which made it easier to find new exploitable resources such as flint. Phase 2 is marked by gradual and sporadic contact between enclaved agropastoralists and local hunter-gatherers, followed by the same scenario described in the advancing frontier model. Phase three is characterised by sudden population growth in the agropastoralists communities, similar to the advent of the Neolithic transition. At the end of this stage, the advancing frontier was replaced by a gradual absorption of hunter-gatherers' culture. Finally, in Phase four, the already expanded (beyond the enclave) agropastoralist population reached its maximum capacity and, in the process, completely absorbed the surviving mesolithic hunter-gatherer societies.

2.6.1. Domestication from a geographical perspective: Near East

Southeast Asia has always been an emblematic area for studying the origins of agro-livestock economies. This interest is partly explained by the fact that it is the geographical area where animal and plant domestication is documented in the earliest chronologies. However, there are fewer and fewer researchers who no longer consider it as the single centre of domestication from which the processes and influences that led to the establishment of the first agricultural communities spread. Archaeological evidence analysed in recent years increasingly emphasises that these are not homogeneous or linear dynamics and that there is a significant variability of trajectories with multiple outcomes (Matthews *et al.,* 2020).

The last hunter-gatherer societies are at the base of these dynamics. With the development and implementation of longer-term food storage and preservation systems, these societies would have every so often lived through changes in mobility patterns. These changes could have had important consequences on settlement patterns and the intensification of subsistence activities, leading in some cases to sedentarism. In the Eastern Levant, following the criteria published by authors such as Price (1981), Hayden (1981), Testart (1982) and Ingold (1983), there has been a tendency to differentiate between simple and complex hunter-gatherer societies, attributing to the latter a greater degree of sedentarism, prioritisation of immediate versus deferred returns and a more pronounced tendency towards specialisation.

Various explanatory models of these historical changes have emphasised climate change as a causal factor (Bar-Yosef & Belfer-Cohen, 1989). Alternatively, authors such as Hayden (2020) propose that the basis of change in these Levantine Epipalaeolithic hunter-gatherer societies lies in the production of surpluses and the use of these in socio-political strategies to acquire power and wealth. According to the former, the decline in resources and the decrease in their predictability would have led to differentiated geographical developments. Some hunter-gatherer groups would have abandoned the arid southern areas and moved towards the Mediterranean area, reducing their mobility and making it exclusively seasonal. This resulted in an increase in the number of settlements, a greater territorial aggregation and a reduction of the exploited territories, favouring the development of storage practices. A significant concentration of settlements is documented in the semi-arid Levantine area with wild cereals (Cauvin, 1994), while in the Negev area, the sedentary character of the settlements is less evident. Some researchers (Maher *et al.,* 2012) note, however, that social interaction between communities during this period was intense and would have occurred on a larger scale than previously thought.

Animal and plant remains recovered from this Epipalaeolithic period point to a broad subsistence base, with a predilection for some animal resources such as gazelle and deer and the extensive use of plants in some settlements, including wild cereals. The trend towards intensification has been proposed mainly in terms of faunal resources, with an over-exploitation of gazelle and other large prey and an increase in small game, including prey that required specialised technologies for their capture (Maher *et al.,* 2012).

The more intensive exploitation of resources led to a reduction in the range of mobility and a greater degree of sedentarism (Moore, 1982), with a significant concentration of settlements in the semi-arid zone with wild cereals (Cauvin, 1994). This stage is historiographically defined as Natufian. The settlements increased in size and housed a larger number of people. In most cases, they are settlements with a uniform pattern, consisting of a group of circular huts dug into the ground (Molist, 1993). In some cases, storage structures have been documented, which is evidence of a growing interest in stored food plants (Watkins, 1992).

A key question at the centre of the debate for this chronology, is whether a broad-spectrum economy was practised during or not. As opposed to a diversified economy, Henry (1989) describes the economy practised during this time interval as specialising in the hunting of medium-sized resources. Moore (1982) had also proposed the intensive exploitation of certain animal and plant species with a significant degree of environmental management. Pre-domestication cultivation began in several areas simultaneously, although the species cultivated varied in different areas. Archaeobotanical data suggest that the transition from pre-domestication cultivation to the first appearance of domesticated phenotypes took several hundred years (Willcox, 2013). The domestication of plants would be the result of an evolutionary process that started with the systematic cultivation of morphologically wild cereals and legumes that would lead to the emergence of agriculture within 1000-2000 years (Arranz-Otaegui *et al.,* 2016).

Domestication is well attested during the Pre-Pottery Neolithic (PPN). The PPN was originally defined by Kenyon (1956) based on excavations at the Jericho site. He identified two distinct phases of the PPN, which have been redefined on the basis of subsequent research, with three main periods of the PPN generally accepted (PPN A, B and C), and three further sub-periods within the PPNB: Early PPNB (EPPNB), *between 8700 and 8200 cal BC,* Middle PPNB (MPPNB), *between 8200 and 7500 cal BC,* and Late PPNB (LPPNB), *between 7500 and 7000 cal BC* (Goring-Morris & Belfer-Cohen 1997; Garrard *et al.,* 1999; Aurenche *et al.,* 2001; Kuijt & Goring-Morris 2002).

The Pre-Pottery Neolithic A (PPNA) (10,000-8,700 cal BC) coincided with a change to a warmer and more humid climate. It has traditionally been divided into several sub-periods based on the technological and typological variability of the lithic assemblages, mainly based on the presence of microliths and el-Khiam points (Sultanian and Khiamian) (Kuijt & Goring-Morris 2002). Despite these cultural divisions, established on the basis of technological criteria and named after the site where they were first documented, the socio-economic dynamics observed for the whole Levant in this chronological interval present some common characteristics (Molist, 1993). The settlements generally acquired a more permanent character, reducing the radius of residential mobility. They consisted of circular, semi-subterranean huts. In some of them, the presence of fixed structures for the storage of products stands out (Kuijt & Finlayson 2009; Finlayson *et al.,* 2012). These structures occasionally show a significant investment of energy in their construction and care, with plastering and lining and internal compartments. Available evidence points to their collective management (Kuijt & Goring-Morris 2002). It is worth noting the recovery of sickle blades in some sites, which would have been used for the collection of wild cereals. The species mainly represented are wheat and barley

(Willcox *et al.,* 2008). The large amount of grinding tools, such as mills and mortars, documented in these sites is evidence that these cereals were intensively processed in the villages, where the presence of specialised areas in these work processes is noteworthy. Some authors see in this activity the basis for the later development of agriculture (Fuller *et al.,* 2011).

In the Tigris valley, some modalities of animal management during the PPNA reflect the change that is taking place in animal resources acquisition strategies, suggesting that these are the first livestock farming experiences, with direct control of animal populations (Bodet, 2009). One of the most relevant sites is Hallan Çemi, where there is a clear preference in consuming sheep juvenile males, between 2 and 3 years of age (Redding, 1981). This author interprets these results as the product of specialised hunting of the mouflon (*Ovis orientalis*), the wild ancestor of domestic sheep. We find the first clear evidence of size reduction resulting from the domestication of this species at sites in the upper Euphrates basin such as Nevalı Çori (Peters *et al.,* 2005) and in Anatolia, in particular at the site of Aşıklı Höyük (Stiner *et al.,* 2014). A close control of wild populations is also proposed for pigs at Hallan Çemi, as there is a high degree of selection of both the age of the animals and the skeletal portions destined for consumption Redding and Rosenberg, 1998). In this same geographical area, Çayönü (Ervynck *et al.,* 2001) is an example of intense human-pig interaction that testifies to a long and gradual evolution towards pig farming. The data from Çayönü show a slow process of size-reduction in pigs (Hongo and Meadow, 1998), highlighting the shift in pig acquisition strategies from hunting to free-range rearing. Extensive breeding would thus have taken place, facilitating feralisation and hybridisation processes (Price & Evin, 2019). These first populations of controlled animals were often small and retained wild phenotypes due to regular restocking from wild populations, which probably caused significant challenges for herders in terms of maintaining health, reproduction and stability (Peters *et al.,* 2017). Many of these early Neolithic communities continued to rely on wild game as an important food source (Arbuckle & Hammer, 2019).

The Pre-Ceramic Neolithic B (PPNB) (8,800-8,600 cal BC) saw significant architectural innovations, with a shift from curvilinear to rectilinear constructions, the presence of plastered floors and permanent storage structures, now inside houses.

The record points to an increasing management of wild cereals that would lead to the domestication of wheat, barley and lentils (Asouti & Fuller, 2013). The first evidence of morphologically domestic cereals, with solid and resistant rachis, is documented. However, agriculture, understood as an economic system based on the cultivation of domestic species, developed later, during the middle and late PPNB (Peña-Chocarro & Arranz-Otaegui, 2019). A greater craft specialisation is also observed. Several authors have proposed rapid population growth and a certain demographic pressure in some areas, with a greater intensity of settlement in the drier areas compared to earlier times. These settlements usually consist of circular, semi-subterranean dwellings. In wetter areas, the more sedentary character of the settlements is well attested, with full exploitation of domestic resources (lentils, chickpeas, wheat, barley, flax, peas, figs, almonds and pistachios along with sheep and goats (Weiss & Zohary, 2011). The earliest records of cereal domestication have been recovered from the Late Epipalaeolithic levels of Abu Hureyra, where a small-scale cultivation strategy is represented. There is indirect evidence of agricultural practices at Jerf el Ahmar, Tell 'Abr and Dja'de, too.

Incipient pastoral practices involved the exploitation of sheep and goats for meat and, potentially, milk and wool, as at 'Ain Ghazal (Wasse 2002). Opposed to dryland occupations, these are settlements built on rectilinear architecture, with compartmentalised buildings often featuring a hearth in the central room and storage areas to the rear (Banning 2003). During the middle PPNB, the four main domestic species (sheep, goats, cattle and pigs) were documented throughout the eastern Levant. However, in contrast to the traditionally conceived model of a cohesive 'Neolithic pack', recent evidence shows that each species had its own history of origin and dispersal, with multiple areas of animal domestication documented (Zeder, 2008; Collony *et al.,* 2011). For the Euphrates Valley, the earliest experiences of animal domestication are documented at the sites of Dja'de, Jerf el Ahmar and tell Halula, while the proposal of ox proto-domestication for the site of Mureybet remains valid (Ducos, 1978; Gourichon & Helmer, 2008). The earliest evidence of domestic cattle comes from the Middle Euphrates Valley (Dja'de site) (Helmer *et al.,* 2005). Their use for carrying heavy loads is documented at Tell Aswad during the Middle PPNB (Helmer and Gourichon, 2008). In level 2 at Abu Hureyra 2 and at Tell Halula, animal and plant domestication are fully integrated with the economic practices of the site.

During the second half of the PPNB, agricultural practices and the gradual appearance of sheep, goats, pigs and cattle is evident at the sites of Nevalı Çori, Gritille, Akarçay and Çayönü B. Akarçay, Gritille, Hayaz, and Mezraa Teleilat confirm full domestication at the end of the PPNB. In the Zagros Mountains area, the earliest evidence is found at Zawi Chemi, with a significant presence of young sheep and goats as opposed to adults. At Asiab, the predominance of large adult males has been linked to selective hunting. Livestock husbandry practices are attested for the first time at Ganj Dareh (Hesse, 1978), where goats account for a significant proportion (90%) and there is evidence of captive breeding. Preceding this moment the animal economy in Ganj Dareh focused on managing goats with an intensive slaughter of young male goats. This practice has been linked to a desire to reduce the number of aggressive adult males in herds (Arbuckle and Atici, 2013). ADNA results provide evidence for the independent domestication of goats in the Zagros-Taurus highlands and its subsequent transmission eastwards (Luikart *et al.,* 2001; Daly *et al.,* 2018). Later evidence comes from the southernmost sites of Ali Kosh, Jarmo and Tepe Guran. Some authors argue that the introduction of sheep to the southern Levant may have been later due to their need to adapt to rising temperatures and aridity (Peters *et al.,* 2005). Domestic sheep suddenly appeared in the southern Levant in the 8th millennium, where there was no local mouflon hunting tradition (Martin & Edwards, 2013), coinciding also with their introduction to the island of Cyprus (Vigne *et al.,* 2011). From this time onwards, there is evidence of selective breeding of these species and their stabling in connection with the settlements. Examples of this can be found at Çayönü and Çatalhöyük.

During the Late PPNB (LPPNB) (7,400-6,700 cal BC), some of the sedentary settlements were abandoned, while those that remained occupied increased in size and number of settlers (Byrd, 1992). Some authors have proposed that there was some degree of environmental degradation during these chronologies, which would have influenced the availability of resources. Sheep, goats, pigs and cattle farming are fully established. The architectural characteristics of some sites point to a higher population density, the beginning of a more extended use of stone and more marked differences between private and communal space. In the El Kowm depression in central Syria, it is proposed that specialised nomadic pastoralism independent from the agricultural settlements emerged in the LPPNB (Stordeur, 2000). Domestic sheep were the dominant livestock, and herding practices consisted of culling large-size adults (Helmer, 2000). The sites of Qdeir and Umm el Tlel are interpreted as semi-nomadic camps that were periodically occupied.

The Pre-Pottery Neolithic C (PPNC) (6,700-6,400 cal BC) is mainly defined for the southern Levant (Rollefson & Köhler-Rollefson 1993). Changes in settlement patterns and architecture are documented. Settlements are characterised by less investment in buildings. The frequencies of sheep and goats, cattle and pigs during the PPNC vary greatly. One of the most emblematic sites of this period is 'Ain Ghazal, where sheep farming is attested as the main activity while hunting remains important (Kuijt & Goring-Morris, 2002).

During the pre-Halaf period, the architecture of the settlements shows a dispersed distribution of living units, with the generalised use of stone as a building material. In terms of subsistence strategies, agricultural and husbandry practices were fully consolidated in all of the eastern Levant, with complete domestication of animals and plants. For the south of the Levant, the intensification of the exploitation of the more arid areas has been proposed on the basis of pastoral nomadism. The first pottery was produced during this period. The transition between the Late Neolithic and the beginning of the Chalcolithic is then represented by the Halaf and Ubaid periods. The architecture of the Halaf period is characterised by the appearance of a new type of building, the so-called tholoi. It is during the Halaf when decorated ceramics are profusely made and circulated over great distances, especially in the northern area of the Levant. With animal domestication fully established, Halaf communities made widely differing decisions about the degree of dependence on domestic versus wild animals (Zeder, 1995), documenting the coexistence of a wide range of husbandry strategies. However, it is also relevant the relatively greater importance of hunting activities in settlements located in the more arid regions, where a mixed hunting and herding strategy was practised (Cavallo, 2000).

2.6.2. Domestication from a geographical perspective: Iberian Peninsula

Zvelebil (2001) categorised the European Neolithic expansion models into three archaeological schools of thought: the migrationist, indigenist, and integrationist perspectives. The migrationist school of thought holds the folk migration, demic diffusion, elite dominance, infiltration or/and leapfrog colonisation models accountable for the Neolithisation of Europe. However, from the indigenist perspective, migration played close to no role in the process, and Neolithisation expanded into Europe following the advancing frontier and cultural diffusion model (CDM) exclusively. Furthermore, by holding the middle ground, integrationists explain the Neolithic transition of Europe through the leapfrog colonisation, advancing frontier and the cultural diffusion models.

As far as the Iberian Peninsula is concerned, autochthonist proposals were formulated mainly in the 1980s (Olària, 1988; Acosta & Pellicer, 1990). The limitations to their testing have been mainly due to the lack of chronological precision of some dating and to stratigraphic and taphonomic problems at the sites (Bernabéu *et al.,* 1999). Exclusively diffusionist models do not explain some of the manifestations linked to the Neolithic colonisation of certain territories, although there is material evidence of maritime colonisation in some areas (Ammerman & Cavalli-Sforza, 1984; Zilhão, 2001). Currently, the dominant models are those that propose dynamics based on the interaction and transmission of knowledge and concepts, together with the arrival of external populations and territorial displacement (García Puchol, 2005; García Atiénzar, 2009). It should be noted that the sites excavated to date document discontinuity between the Mesolithic and Neolithic occupations, with a certain break or abrupt change being observed in most cases (García Puchol *et al.,* 2006). The results obtained from genetic analysis indicate a demographic contribution from the eastern Mediterranean (Gamba *et al.,* 2011). In short, everything seems to indicate that more than one mechanism must have been responsible for the dispersion of the Neolithic lifestyle in the different areas of the Iberian Peninsula, given the wide variability of climatic, geophysical and environmental conditions.

Due to its particular geographical situation, the Iberian Peninsula is an area of special relevance for the study of the dynamics of the process of animal domestication. The number of strategies of adoption of domestication recorded during the early Neolithic period is remarkable, with important contrasts between the different territories. Domestic resources range from 1.5% to 98%, with an average of around 70% (Saña, 2013). Differential exploitation dynamics have been documented for herds of cattle, pigs, sheep and goats. The species for which most homogeneity is documented is the domestic pig. Cattle have percentages around 30% in some settlements, but there is high variability and a higher relative presence in open-air settlements. The relative importance of cattle increases if we take into account the amount of meat that can be provided by one animal (250 kg), compared to that provided by goats and sheep (25 kg) or a pig (80 kg). The slaughter patterns of bovines show that they were exploited both for their meat and for their strength, and probably also as milk suppliers (Vigne & Helmer, 2007). Notwithstanding meat production dominates in the Iberian Peninsula (Saña *et al.,* 2020). as shown in Cueva de Chaves (Sierra, 2020), where individuals were slaughtered at an age of 18-27 months, or in Reina Amàlia (Navarrete, 2017), at an age of 2-3 years. For other Mediterranean areas, the specialised exploitation of cows for dairy has been proposed (Vigne & Helmer (2007). Already during the Middle Neolithic (4500-3300 cal BC) archaeozoological analyses show an increase in the percentage of bovine and suid remains (Martín Cólliga, 1992), while sheep and goats decrease relatively. The most represented wild species continue to be suids and cervids, as well as small carnivores, the latter more occasionally (Antolín *et al.,* 2020; Saña *et al.,*2021).

Various hypotheses have been put forward about the role that indigenous species may have played in early livestock farming. In the case of dogs, the first domestic species documented on the Iberian Peninsula, both its agriotype and its autochthonous domestication are well established. However, for the other species (cattle, sheep, goats and pigs) this relationship is more complex. For the domestic forms of sheep (*Ovis aries*) and goats (*Capra hircus*), cytogenetic studies show that the wild populations from which they originate (*Ovis orientalis* and *Capra aegagrus*, respectively) are limited to the end of the Pleistocene to the area of Southwest Asia (Saña, 1998). In the case of cattle (*Bos taurus*), the presence of their wild progenitor (*Bos primigenius*) is documented throughout the Iberian Peninsula. The same is true for pigs (*Sus domesticus*). The fact that a continuous evolution between the wild and domestic form has been found in several regions of Europe for cattle (Bökönyi, 1982; Kobryn & Lasota-Moskalewska, 1989) and pigs (Jonsson, 1986; Navarrete & Saña, 2017), would support independent domestication processes of these species, whether simultaneous or temporally spaced. As far as the northeastern peninsular territory is concerned, it is difficult to trace these dynamics due to the lack of continuous archaeological sequences corresponding to this chronology (Saña, 1998).

Recently published syntheses tend to emphasise the speed at which the expansion and adaptation of domesticated animals took place (Manen *et al.,* 2019). Sheep were first domesticated in southeastern Anatolia around 10500 cal BP (Peters *et al.,* 2005) and subsequently spread to Europe (Zeder, 2008) and abruptly introduced to the Iberian Peninsula on a Mesolithic substrate (Saña, 1998).

Biometric data show a clear size differentiation between *Capra pyrenaica* and *Capra hircus* from the Early Neolithic (Navarrete & Saña, 2017), which fits well with genetic studies. Archaeozoological data indicate that sheep and goats were adopted at the same time (Saña, 1998, 2013). The earliest dates of their adoption are found in the east, near the Mediterranean coast, at sites such as Nerja, Chaves, Cendres or Sarsa (Sierra, 2020). These sites are dated around 5600-5500 BC, but we can find domestic goats in almost all of the Iberia peninsula as soon as 5400 BC. In most sites, goats were a secondary species.

During the Neolithic, the relative importance of *Bos taurus* increased steadily. Although it will never completely displace the importance of sheep and goats in the overall assemblage, sites such as La Renke during the Early Neolithic, where cattle remains represented the 97% of the domestic animals, and Cova de les Pixarelles during the Middle Neolithic, where the remains of cattle represent 80% of the complete faunal assemblage (Alcàntara *et al.,* submitted), are clear examples of the economic importance that this species may have represented for Neolithic societies. Their percentages of representation among the domesticated animals are particularly low in the south (between 0.2% and 6%) and are more represented in the Levant (Saña, 2013). The northern areas show intermediate values, between 0.5% and 14% in the north and between 2% and 7% in the northeast. Although it is not homogeneously adopted throughout the Iberian Peninsula, its adoption is quite rapid in the Pyrenean and Mediterranean area (Saña, 2013).

Among domesticated animals, the pig (*Sus domesticus*) played an important role as a meat supplier during the Neolithic period in the Iberian Peninsula (Saña, 1998, 2013). Its relative abundance ranged from 4% to 23.9% of domestic animals in the early stages of its adoption. Wild boar was a widely exploited resource in the Mesolithic and continued to be hunted during the Neolithic. However, during the Early Neolithic the exploitation of wild boar decreased significantly, and in most sites it is not present in frequencies higher than 3% (Saña, 2013; Antolín *et al.*,, 2019). In those Early Neolithic sites where *Sus scrofa* and *Sus domesticus* are exploited simultaneously, the domestic form always predominates quantitatively (Saña 1998, 2013).

In short, the adoption of the four main domestic species took place rapidly and unevenly among the regions that make up the Iberian Peninsula, with a significant difference between the Eastern region and the North of the peninsula. The management methods practised also differed according to species. Some settlements such as La Draga (Saña, 2011) evidence the full-range exploitation of sheep, goats and cattle. Others prioritised meat production. However, hunting still played a significant role in some of them.

2.7. Bone remodelling and the Mechanostat Theory.

In 1892, Wolff proposed his idea that paved the way for future bone adaptation and simulation research. He observed that trabeculae of cancellous bone tissue are aligned with the direction of local principal stress. This observation led him to declare that “Every change in the function of bone is followed by certain definite changes in internal architecture and external conformation in accordance with mathematical laws” (Wolff, 1986). Bone is a metabolically active organ that constantly turns over and remodels based on the feedback of its mechanical environment. Remodelling in the context of musculoskeletal biomechanics describes how basic multicellular units, made of osteoblasts and osteoclasts, constantly renew bone tissue by resorbing and laying down bone. Bone volume increases when osteoblasts are more active than osteoclasts. Contrarily, when osteoclasts are more active than osteoblasts, bone volume decreases.

Bone remodelling alters the volume and density of the bone to reach the optimal mass needed to carry the loading it has been experiencing while preserving valuable minerals such as calcium. In the 1960s, Harold Frost provided a detailed theory regarding how load-bearing bones adapt to maintain mechanical competence in response to alterations in the mechanical environment. Frost suggested the existence of a homeostatic regulatory mechanism in bone responsible for sensing changes in the mechanical demands placed on the bone and subsequently altering the mass and conformation of bone to better meet these new mechanical demands (Frost, 2003). He postulated that several mechanical thresholds control whether the bone will be added or removed from the skeleton. He theorised that below a certain threshold of mechanical loading, the bone would be resorbed and, therefore, release excess mineral mass. Above the threshold, however, local bone formation will occur to increase bone strength. Thus, bone tissue has an intrinsic “mechanostat” which regulates bone functional adaptation.

Years later, Tommasini *et al.,* (2008) proved that the morphology of the bones significantly co-varies with the microstructure of the skeletal tissues. They suggested that remodelling is a biological process that co-adapts morphological and compositional traits, to make long bones (at the macrostructure level) robust enough to perform daily activities. The same adaptive trait is reported for the mandible (Anderson *et al.,* 2014).

Domestication can be defined as an adaptive dynamic process that encompasses social-behavioural development toward living in a man-controlled environment (Price, 1999). This concise definition of domestication highlights the role of behaviour dynamics of wild animals through their journey toward domestication. Considering the well-established relationship between the level of physical activity (which here is interpreted as animal behaviour dynamics) and bone morphology, this research establishes a robust approach to document morphological changes in the skeletal system while providing biomechanical explanations behind such changes.

2.8. Morphological variability in archaeological animal bone remains

Based on the principles of biomechanics, and excluding taphonomic factors that can affect the size and morphology of animal bones once deposited in archaeological sites, there are several causes that influence the size and shape of animal bones.

That is why the study of morphological and metric variability is an extremely complex issue to address from archaeozoology, since archaeological faunal remains are often fragmented and show high diversity in their conditions of preservation (Albarella, U., 2002). Variations in bone size and shape are highly informative of past animal lifestyles and uses. A distinction is usually made between pathological affectations, entheseal changes, and changes in bone geometry (Bindé, M. *et al.,* 2019; Hull, E. *et al.,* 2020; Sick and Kohut, 2022). The enthesal changes correspond to the morphological changes that muscles, tendons and ligaments cause in bone (also called *markers of musculoskeletal stress* in physical anthropology) (Villotte & Knüsel, 2013). These changes involve different degrees of bone modification resulting from the remodelling caused by the functional adaptation of the bone. Bone remodelling occurs by seeking the most effective distribution of mechanical loads (Wolff, 1986). A distinction is usually made between fibrocartilaginous entheses (located in the epiphyses of long bones) and fibrous entheses, typical of the diaphysis of long bones and not very representative of activity patterns (Bindé *et al.,* 2019).

Genetic and biological variables, such as gender and age of the animal, are among the causal factors that can influence bone morphology and size. Several factors can influence the dynamics of bone growth and skeletal maturation (genotype, health status, nutritional status, stress levels, climate, ...). Most of the work carried out with the aim of estimating bone size or skeletal proportions uses mainly bones that have already finished growing, in order to avoid errors in the comparisons. To estimate the age of the animals, both tooth wear and the fusion state of the bone epiphyses are used (Silver, 1969; Grant, 1982). The age of the animal is one of the factors that introduce variability when making comparisons of size and morphology between bones and assemblages. Body conformation and weight of the animal are related to physiological processes during growth. After reaching adult size, bone development continues to repair fractures and remodel to adapt to changes in lifestyle. Thus, bone development continues throughout adulthood (Davis, & Beckett 1999). Entheseal changes increase with age, due to a decrease in bone remodeling capacity as a result of reduced osteoblast activity (Milella *et al.,*, 2012; Thomas *et al.,* 2008). The gender of the animal can also influence morphometric variability. Sexual dimorphism is usually related to the size and body mass of the animal, being more pronounced in larger animals. Sexual dimorphism is well expressed in some species by measurements of the width of the medial part of the diaphysis. The body mass can also influence bone remodeling, with more affectations documented in the bones that support more body weight (Bartosiewicz *et al.,* 1997). All these physiological processes of growth and remodelling are also conditioned by the environment and climatic conditions in which they take place. Bone remodelling is highly influenced by geography and geology, with differences in size and proportions being observed between the same species according to climatic factors, altitude, latitude and, consequently, vegetation. Environmental variables influence the length of the limbs and overall size of the animal as a consequence of the energy regulation necessary to balance body temperature (Davis,1977). Bone growth and bone remodeling also depend on nutritional status. Low nutritional levels result in a slower growth rate and reduced size of the animal. The dynamics of bone growth in episodes of malnutrition have a greater effect on bone elements with a more delayed fusion age. Growth in thickness is more affected than growth in length. Diet-related changes also depend on whether malnutrition is punctual, seasonal or long-term (Huss-Ashmore *et al.,* 1982; O'Connor, 2000).

At the enthesis and pathological level, diet has a high influence also on bone disease and biomechanics. Changes in dental formula, dental morphology and tooth loss are related to environment, diet and behavior. Studies carried out in the Iberian Peninsula on 182 specimens of present-day wild boar from the Western Pyrenees and the Middle Ebro Valley have shown that damage to the mandible could be a consequence of rooting, as this bone is used as a shovel in the search for food underground. Interestingly, gender differences in rooting behavior were observed. Damage suffered by males is due to tree marking and fighting against other males. Females may spend more time rooting due to increased energy requirements related to gestation and rearing piglets (Granados-Rigol *et al.,* 2022). Changes have also been observed in this species at the entheseal level in the mandible, with bone remodeling in the areas involved in mastication (Neaux *et al.,* 2022). The plastic nature of the mandible has been demonstrated in several studies on populations of various animal species (sheep, lagomorphs, swine). In one of the recent studies carried out on a sample of 28 domestic pigs (Neaux *et al.,* 2022), a comprehensive and systematic evaluation of the influence of the characteristics of ingested food (hardness, degree of abrasiveness, size, density) on cortical bone remodelling and on mandibular morphology was carried out, showing that changes in the shape of the mandible are influenced by the hardness of the food (*e.g.* increased gonial angle, reduced corpus length). This study highlights, however, that other factors such as the geometrical properties of the food should also be taken into account, as they condition the strength and rhythm of the bite. The results showed a clear relationship between masticatory activity, an increase in the size of the masseters, and the establishment of a reduced gonial angle and a more upright ramus. The work concludes that food particle size and density, rather than hardness, play an important role in bone remodeling of the mandible. Studies on reindeer have also documented enthesal changes resulting from feeding, in addition to those caused by the physical activity levels of the animal (Hull, Niinimäki and Salmi 2020).

Physical activity, mobility, and animal overexertion has been an important topic of discussion from this perspective. Physical stress or animal work implies a greater overload of the organism. More extreme biomechanical overloads can derive from the activities performed by animals in farming regimes focused on labor. Riding, transporting, and pulling can produce diverse types of damage in bone tissues, since these are activities that require new biomechanical adaptations. In the case of cattle, for example, overexertion usually affects the anterior extremity because it supports a greater weight than the posterior (Bartosiewicz 2008). Resulting from this increased physical stress, the bone is broader and more robust, with a higher mineral density and thicker cortical tissue at the medial diaphysis (Bartosiewicz, Van Neer and Lentacker 1993; Sick and Kohut, 2022). Lesions such as exostosis, ankylosis, and eburnation also develop (Thomas *et al.,* 2021; Holmes *et al.,* 2021). The intensity, degree, and location of these lesions depend on the type of stress the bone receives. In the study on reindeer (Salmi, Niinimäki and Pudas, 2020) the distal limb elements most affected by sled pulling were the forelimb phalanges. In draft oxen, on the other hand, Bartosiewicz (2008) notes that the hind limb bones are usually more affected. Factors such as the weight of the animal are important, documenting an asymmetric distribution of bone mineral content in the medial aspect of the metapodials with increasing weight in working animals (Bartosiewicz *et al.,* 1993).

All this demonstrates that, with domestication and animal husbandry, the range of biomechanical affectations of animals increase and exhibit new features. These will be indicative of diverse states and selection actions that regulate animal behaviour. Some of these selective pressures may be at first unconscious. With time, communities introduce improvements in the technology used in these tasks in order to minimize the effects on animals. In the early 18th century, for example, loop yokes were attached to the necks of draught oxen in Hungary as a way of protecting the skeleton (Bartosiewicz 1995). Stabling also has an influence on the improvement of animal growth conditions, increasing the size of the animals as they are protected from environmental and climatic inclemencies (Higgins & Dodd 1989). Although there has been a tendency to relate the use of animal power to the exploitation of castrated animals, ethnographic studies show that animals of all ages and genders can be used as work animals. Castration delays skeletal maturity which allows a longer growth period and therefore results in longer limb bones. In some cases fusion may even be delayed for more than a year (Davis, 2000). The affectations caused by these works can be more or less severe depending on the quality of the soil and the rhythm, frequency and intensity of the works. Very prolonged or recurrent work could affect the auto-healing mechanism of the bone (Lin, 2022). In case of punctual works, sometimes the affectations are difficult to detect or can be confused with metabolic or inflammatory osteological processes (Bartosiewicz 2021).

Methodological approaches to their study are diverse, with important innovations in the last decade, increasingly applying quantification protocols using 3D technology (Nikita *et al.,* 2019). Finite element analysis is used to describe the biomechanical behavior of bones. Biomechanical analysis integrates biology and mechanical engineering to understand the behavior of biological materials. Finite element analysis studies have been applied mostly to human bone research and in Paleontology. Few examples are available applied to the study of animal bones and less still to the study of archaeological bones. In the case of animals, the most worked species are equines and canids, species of significant economic importance today. In the case of *Bos taurus*, a pioneering study has been carried out on the humerus (Bouza & Miramontes, 2014). This research is based on the principle that bone morphology can be predicted using a mathematical theory of bone adaptation to mechanical stress, combined with finite element analysis. Once the model was constructed, finite element analysis was applied to study the stress distribution in the humerus subjected to external loading forces. The results showed that the cortical bone layer undergoes the greatest mechanical stresses, and when moving from the cortical to the trabecular bone layer, the stresses decrease appreciably. The greatest concentration of stresses occurs in the distal diaphysis of the humerus, which is the area with the lowest section of the bone, and where a change in the bone material occurs. This area of stress concentration will be the most susceptible to fracture when the bone is overloaded. An increase in cortical thickness was observed in this zone, as a result of bone adaptation to minimize the maximum stresses generated in this zone. The bone will have experienced a remodeling process to reinforce the areas where high stresses occur in order to minimize them and adapt better to the mechanical stresses (Bouza & Miramontes, 2014). In another study, the hoof of cows has been analyzed with finite element analysis in order to compare the levels of mechanical stress experienced by the hoof on different types of soil. As a result, a clear distinction was detected between solid soil with full claw contact and grid soils, with solid soil being preferable in terms of stresses and loads (Hinterhofer *et al.,* 2005). Finite elements have also been used to study biomechanical adaptations of the jaw to feeding in ungulates (Fletcher, TM. *et al.,* 2010). Different ungulate mammals use foregut/ hindgut fermentation, with horses (which use the hindgut) being able to chew their food more thoroughly in the initial ingestion. The jaws of hindgut fermenters are generally more robust. Finite element analysis was used to corroborate this hypothesis, comparing cow and horse jaws. It was concluded that the robustness of ungulate jaws is correlated with digestive physiology. Hindgut-feeding species have jaws that show lower levels of muscle tension when equal muscle forces are applied. These jaws can be differentiated from the more gracile jaws of ruminants, a criterion that can be applied to the study of fossil remains to infer feeding patterns.

A second methodological approach to the study of bone biomechanics has been based on the study of the bony cortices of the diaphysis of long bones, assessing the resulting pressures on bone tissue from external loads (compression, tension, bending, torsion). The analysis is based on the examination of the geometric properties of the cross-section (Ruff, F., 2018). The number of studies carried out with this methodological approach to the study of animal domestication and initial animal husbandry practices is higher than with finite element analyses. Several studies have been published in recent years from this methodological perspective.

The animal species studied are also more diverse (reindeer, donkey, goat, cattle, pig...). The main issues addressed are captivity, use of animal power and animal mobility.

The issue of captivity has been addressed through the study of limb bones in modern reindeer populations (Pelletier *et al.,* 2021). These studies have shown that growth in captivity or the selection of individuals to perform domestic tasks induces significant changes in feeding and locomotor behaviour, which can affect body size, body mass and the shape and strength of the diaphyses of the long bones. More specifically, increased cortical bone thickness has been reported in individuals kept in total captivity (zoo), which has been related to better support of body mass and prolonged periods in static position (Salmi, Niinimäki, & Pudas, 2020; Pelletier *et al.,* 2021). Harbers *et al.,* (2020) have also worked on the establishment of bone morphological markers associated with human control in wild boar, based on the cortical thickness of the humerus diaphysis. The results showed that the captive stage induced a plastic change consisting of an increase in cortical bone volume and muscle strength, which is a useful criterion for studying the domestication of this species. Shackelford *et al.,* (2013) apply the same methodology to the study of donkey domestication. They start from the premise that the use of donkeys for transporting loads and managing captive herds led to a slower and steadier change of pace in this species. Bone remodelling of wild donkeys and donkey limbs was assessed using cross-sectional geometry to determine whether differences in loading or locomotion between wild and domestic forms were recognisable in cross-sections of the humeri, radii, metacarpals and metatarsals. The results showed that the forelimbs of wild donkeys have more cortical bone than domestic donkeys, with more cylindrical humeral diaphysis, indicating better resistance to a varied locomotor repertoire. Alcantara (2019) adressed using corss-sections of the humerus, tibia, metacarpal and metatarsal the domestication, mobility and management practices of goats throughout the archaeological sequence of Tell Halula. Results evidenced specific mobility patterns for wild goats, linked to their high mobility and freedomof movement. In the case of domestic goats the study evidence a clear tendency leading to a reduction of the relative cortical area and increasingly unidirectionallity in their usual movement. This was interpreted as the result of the intensification of husbandry practices that saw in the control of their mobility, a valid strategy to ensure the productive objectives of the herders. At the same time, Alcantara (2019) also focused on the study of bone phalanges of *Bos taurus*, which allowed to evidence the effects of different terrains (mountain and plain) in the distribution of forces on the animal’s body, as well as to suggest the potential use of some individuals as work animals because of their distinct mechanical properties. These studies are complementary to those based on the application of geometric morphometrics, which are numerous and have been used for a long time.The number of animal species is already wider here, as well as the historical issues addressed, although studies on domestication and initial captivity have also been the main focus (Owen,J. *et al.,* 2014; Pöllath *et al.,* 2019; Cucchi,T. *et al.,* 2021; Evin *et al.,* 2022). In recent years, geometric morphometrics has also been used as a marker of animal mobility, working with diverse bones of the limbs, especially the astragalus (Haruda *et al.,* 2019; Colominas, L., *et al.,* 2019).

These analytical advances are contributing to a new approach to the study of bone biomechanics, animal mobility and physical stress from archaeological faunal remains. Results obtained to date demonstrate the high potential of these methods. We also have access to more technological advantages to apply the principles on which these techniques are based non-destructively. However, there are still few investigations in which these analytical approaches are combined in an integrated manner. It is also evident that there is a growing need for reference collections where this kind of variables can be contrasted.These references are different in some way to the classic reference collection, due to its wide resolution capacity, which combines anatomical, morphological, biomechanical and paleomolecular data in the same skeletons. As stated in the objectives, this doctoral thesis integrates, in addition to biometry, for the first time geometric morphometry and finite element analysis with the aim of contributing to the methodological and technical improvement in archaeology, and generating new historical knowledge about animal domestication and initial husbandry, in the latter case, especially with regard to the role played by the use of animal power in the first Neolithic communities.

The use of animal power was a major innovation in terms of movement and tasks involving a significant amount of force. Economically, it was possible to increase productivity, apply more intensive agricultural techniques, move longer distances transporting loads .... These innovations involved the application of powerful selective actions and pressures on animals, until animals fully specialized in these activities were obtained.

Andrew Sherratt (1981,1983) developed the Secondary Products Revolution model to refer to these changes. This model placed the beginning of the exploitation of animals during their lifetime to obtain products such as traction, manure, milk or wool, once the livestock activity was fully consolidated, at the end of the Neolithic period. Methodological advances in the field of Archaeology demonstrated, however, that the exploitation of milk, and with it the Revolution of secondary products, was an element already documented at the beginning of the Neolithic and that it could have been one of the causes of animal domestication (Craig *et al.,* 2005, Helmer and Gourichon, 2008; Helmer *et al.,* 2018). From this point on, the debate opened up as to whether the exploitation of animal labor power could also have been contemporaneous with animal domestication, especially in relation to the domestication of *Bos taurus*. The exploitation of animal power had important repercussions at a historical level (Bogucki, 1993), representing a transcendental change in the economy during the Neolithic.

The earliest evidence of animal traction comes from Southwest Asia, with the earliest evidence dating back to the Middle PPNB at sites in the Middle Euphrates River Valley (Helmer *et al.,* 2018). In the Balkan area there is evidence dating back to the early Neolithic (c. 6100/6000 cal BC) (Gaastra *et al.,* 2018). In the eastern Mediterranean area, the oldest evidence corresponds to the Draga settlement (Banyoles, Spain) (Antolin *et al.,*, 2014; Lladó *et al.,* 2008). For northern and central Europe, the direct evidence is from the Middle Neolithic. Most of this early evidence has been established from the study of bone palaeopathology. Palaeopathology studies on archaeological cattle bones are a crucial source of information on this type of animal management. The works of Baker & Brothwell (1980), Higham *et al.,* (1981), Bartosiewicz (1993, 2008, *et al.,* 1997), Davies *et al.,* (2005) are highly interesting contributions on this subject. This doctoral thesis is based on the re-study of some of these sites where, using this method, it was possible to propose the hypothesis of the use of oxen as a workforce. It will be tested by means of the design and implementation of a novel methodology with a high resolution power.

3. MATERIALS

This chapter describes the criteria used in the selection of the case studies and the samples analysed, and provides sufficient data on their characteristics and context in order to provide the necessary information for the correct interpretation of the results. Particular emphasis is placed on the criteria which, in accordance with the objectives of this work, guided the selection of the archaeological sites, animal species and skeletal elements.

3.1. Selection of animal species: criteria

In accordance with the historical subject addressed in this research, it has been considered appropriate to work with two of the animal species that played an important role in prehistoric husbandry practices, and which are key to the understanding of the Neolithic: cattle and pigs. Cattle and pigs are important elements associated with the economic and social change that took place at the beginning of the Holocene, and which led to the domestication of animals and livestock farming. *Bos taurus* and *Sus domesticus* are species that derive from progenitors with a wide geographical distribution (*Bos primigenius* and *Sus scrofa,* respectively), present in different geographical areas, a fact that has often complicated their classification from archaeological faunal remains.

3.1.1. *Bos primigenius*, ancestor of *Bos taurus*

The wild lineages of Taurine and Zebu cattle diverged more than 800,000 years ago (Machugh *et al.,* 1997). Their habitat range included continental Europe (south Scandinavia), North Africa including the Nile's delta, the Near East (except the Arabian Peninsula), India, southern Siberia, and northern China (Lira, 2010). In Europe, aurochs arrived much earlier in the south than in more northern areas, around 700,000 years ago (Estévez & Saña, 1999). The distribution of aurochs has fluctuated with climatic change during the Pleistocene, being more dispersed in interglacial and interstadials. Aurochs became rare or disappeared entirely during the coldest periods in many areas of Europe (Neto de Carvalho *et al.,*, 2022). During the early Holocene, the species seems to have increased in numbers, probably due to progressively favourable mild and humid conditions. In Europe, its extinction was documented in 1627. In the northernmost parts of Europe, male aurochs were estimated to have a withers' height of 160-180 cm and females about 150 cm, with an unmistakable sexual dimorphism. The size of aurochs in southern Europe was smaller than in northern Europe (van Vuure T., 2014). This species mainly inhabited wooded areas along rivers, generally in low and plain areas rich in watercourses, and were absent from high and mountainous areas. They frequented swampy areas in summer and forests in winter. They fed mainly on grasses and herbs, which could be partly replaced in winter by tree and shrub branches. The gestation period of this species is nine months, and births are in spring (Boev & Boev, 2018).

The extent to which aurochs contributed to modern cattle through introgression is still a source of debate. Evidence of hybridisation with domestic cattle has been clearly documented (Troy *et al.,* 2001). The T3 mtDNA haplogroup is predominant in most European and North Asian breeds and is one of the four major haplogroups (T, T1, T2 and T3) in Southwest Asia. Meanwhile, the haplogroup T1 is dominant in Africa. Mitochondrial DNA analyses (Anderung *et al.,* 2005) show evidence that the ancestors of African and European cattle would have separated about 25,000 years ago and thus would have occurred before the domestication process started. These observations are consistent with the Southwest Asian origin of European cattle (Zeder *et al.,* 2006). A few exceptions are documented, however, which should be noted. The first is that the same mtDNA diversity is documented in 4 ancient Tuscan breeds as documented in Southwest Asia, suggesting a direct link (Pellecchia et al., 2007). The second is that haplogroup T1 has appreciable frequencies in several Spanish and Portuguese races (Ginja *et al.,* 2010, Bonfiglio *et al.,* 2012), indicating migration from Africa to the north. This may have occurred during the Neolithic or more recently. The documentation of haplogroup T1 in an analysed sample from the Early Neolithic site of La Draga (Banyoles, Girona) suggests the establishment of this variability already during the early Neolithic (Colominas *et al.,* 2015). Genetic analyses carried out on the remains of aurochs from the site of Mendandia show that one individual has the T3 haplotype, usually associated with domestic animals (*Bos taurus*) (Alday Ruiz *et al.,* 2012). Some studies show that *Bos primigenius* crossed with bovids from Southeast Asia in Europe. Cattle and aurochs coexisted in Europe for more than seven millennia. This coexistence could have made possible the introgression of the European aurochs in the formation of domestic breeds on the continent, either through auroch-cow hybridisation or through direct domestication (Alday Ruiz *et al.,* 2012). However, it should be noted that the data available on the genetic variability of the peninsular populations of *Bos primigenius* is currently scarce. Compared to *Bos taurus*, very few sequenced mitochondrial genomes are available, and more research on this lineage is needed to resolve the historical structure of the population (Lira, 2010).

In the Iberian Peninsula, remains of this species are frequently documented in the Palaeolithic, persisting during the Mesolithic and later periods. In Roman times, it has been documented at sites such as Amalda (Zestoa), dated to the 4th-5th century (Mariezkurrena, 1990) and at a Late Antiquity level of Iritegi (Oñati). It is also mentioned in a 4th-century text by the Latin author Servius Grammatius, who in his Georgics (2374) mentions that there are wild aurochs in the Pyrenees: "*silvestres uri qui in Pyreneo monte nascuntur inter Gallias. Uri autem boues silvestres, quos uulgo bobalos apellant*" (Altuna & Mariezkurrena, 2017). The study based on the biometry of bovine remains from Portuguese sites shows that Mesolithic aurochs were larger in size than those corresponding to the Chalcolithic. Based on this criterion, it has been proposed that the absence of large specimens after the Chalcolithic would be evidence that aurochs disappeared during or immediately after the Chalcolithic in the western part of the Iberian Peninsula (Castaños, 1991; Davis *et al.,* 2013).

3.1.2. *Sus* scropha, the ancestor of *Sus domesticus*

The wild boar's native range includes North Africa, Europe, southern Russia and China, the Middle East, India, Sri Lanka and Indonesia (Fernández-Llario, 2014). The large geographic range of wild boar populations is reflected in the great morphological and size variability that characterises this species (Albarella *et al.,* 2009). Suids are gregarious, disease-resistant animals with a fast production and reproduction rate. The high reproductive capacity of this species is based on three factors (Rosell *et al.,*, 2001): the precocity at which they reach sexual maturity, their relatively short gestation, and the high average number of offspring per parturition. Young males reach puberty at ten months (Mauget & Pépin 1985), although they are not really ready to compete for adult females until they are two years old. At the same time, females can become effective breeders between 8 and 10 months under suitable conditions of food availability. The life expectancy of the wild boar in natural conditions reaches 13 years.

The original habitats of the wild boar were warm deciduous lowland forests, but over time the wild boar has adapted to mixed and coniferous forests (Košinová K. *et al.,* 2022). It is a medium-sized mammal with not very marked sexual dimorphism (males are 5-10% larger than females). Sexual dimorphism is clearly observed in the canine teeth, which continuously grow in length up to 3 mm per year. It has been shown that dental molar measurements are not substantially affected by sexual dimorphism (Payne & Bull 1988), and the difference in sex ratio may be more significantly represented in bone measurements. The size of wild boar also varies for different reasons (Davis, 1981). Wild boars from colder climates are bigger than those from warmer climates. Weight is also highly variable according to geography. In the Iberian Peninsula, adult males have an average weight that varies between 75 and 85 kg and females between 55 and 65 kg (Fernández-Llario, 2014). Reproductively, it is an early, prolific, and short gestation species (120 days). The differences observed in the productivity of females are attributed especially to fluctuations in food availability. The basic unit is the matriarchal group consisting of one or more adult females accompanied by their young; other nuclei consist of young males. Adult males are solitary (Rosell & Herrero 2007).

The wild boar is an opportunistic omnivore with a broad trophic spectrum and markedly seasonal habits. Food supply depends on the size of the home range. The home range is determined by several factors such as population density, sex, and age of the animals, with males being more numerous than females (Košinová *et al.,* 2022). Its remarkable ecological plasticity allows it to use diverse food sources with a tendency to feed on a few abundant, digestible and nutritious resources. In agricultural areas, the home range of the pig is smaller than in forest-dominated areas. Annual home ranges of 12 to 15,000 ha for males and up to 6,000 ha for females have been described (Rosell & Herrero 2007).

Genetic analysis has shown that there was more than one domestication event, as the degree of genetic heterogeneity of the species suggests that individuals come from different populations. It has therefore been domesticated on multiple occasions and in various regions of Asia, the Middle East and Europe from local populations (Larson and Burger, 2013). Wild boar can hybridise with domestic pigs, especially in areas where pig farming is practised in its traditional extensive and free-ranging form. Unlike animals used primarily for transport, intentional crossbreeding of pigs with wild relatives does not confer any productive advantage. Gene flow is most likely due to the capture of wild animals as a herd-building strategy, or the chance crossing of domestic pigs with wild relatives (Marshall *et al.,* 2014). The level of hybridisation, and hence the biological distance, between domestic and feral populations depends in part on the domestic herd management strategies (Hadjikoumis, A., 2012). Feral populations of domestic pigs are currently distributed throughout the world (Albarella *et al.,* 2007).

Among the species domesticated during the Neolithic period, the wild boar is currently the most economically important in terms of food production and the most productive in terms of work investment, as the rate of return is relatively high while the investment in maintenance and feeding is less costly than in the case of herbivores. The limitation it may have compared to herbivores is that the only exploitable product of pig is meat (in addition to fur and hard animal tissues), all of which require the prior death of the animal.

3.1.3. Applied research on *Bos primigenius*/*Bos taurus* remains

The applied research developed in this work has been carried out on the remains of *Bos primigenius* and *Bos taurus*. The management of these species constitutes an important element of the Neolithisation process and contributed significantly to the economic, social and ideological change during the Neolithic Revolution. They are therefore considered a representative element of this dynamic of historical change and a representative element of the new way of life that was established, the new work processes, the new relationships with the environment and the new relationships between communities and also at an intra-community level. *Bos taurus* is initially documented in its domestic form in Southeast Asia and is subsequently distributed towards Europe via two main routes, via the Balkans towards Central Europe, and via the Mediterranean, becoming an important component of the Neolithic economy during the LBK, being the dominant species in the settlements of central and northern Europe between the sixth and fifth millennia BC (Gillis *et al.,* 2017). Increasing evidence shows that this species was exploited in a polyvalent way (milk, meat, labour force) from the beginning of its domestication (Vigne & Helmer, 2007; Saña *et al.,* 2020). Significant variability is documented in their initial modes of management and exploitation, both in Southeast Asia and in Europe, mainly due to the need to adapt to the environmental diversity that shapes this geographical area. The role that cultural traditions may have played in this variability has also been highlighted (Arbuckle *et al.,* 2014), in addition to their social and symbolic importance as an element of power and prestige (Cauvin, 1994). Several archaeological evidences show that during the Neolithic period this species played a role beyond the subsistence sphere, constituting a privileged resource in the actions involved in acts aimed at the social cohesion of communities. Systematic studies on archaeological remains of Neolithic cattle have shown that the labour force exploitation and castration of cattle are older practices than previously thought, and that this type of exploitation may have been one of the driving forces behind their domestication (Helmer *et al.,* 2018). Biometric and bone palaeopathology analyses have shown that animals of this species may have been involved in tasks such as ploughing, pulling and carrying loads. *Bos taurus* is thus a suitable species to assess the pace, intensity and direction of the various selective pressures that human groups applied on early domestic herd populations to adapt them to their needs, and to provide new elements to generate knowledge about the origins of the exploitation of animal labour and its social implications.

3.1.4. Constitution and study of the modern *Sus scrofa* referential

For the constitution of the modern referential and the morphometric study of its variability, we have worked with a population of contemporary wild boars, considering that the objective, in addition to advancing in the methodological area, is also to provide referentials to archaeozoology that serve as a basis for the study of animal domestication and early livestock practices. The domestication of *Sus scrofa* is an issue that has been approached from various analytical approaches, and the volume of data currently generated on this historical issue is significant. However, it is still difficult to find answers and contrast the status of this species in most contexts of recent prehistory. Recently published studies have also shown that the domestication of this species significantly increased the phenotypic variability of the wild form, sometimes making it impossible to differentiate between the domestic and wild populations using traditional biometric or osteometric methods. The increase in phenotypic variability may have been a response to the various forms of management in which wild boar and early domesticated pigs may have been involved. The exhaustive study carried out on the management of this species at Hallan Çemi (Zeder & Lemoine, 2022) provides an complete synthesis of the diversity of situations that may have occurred in these early times, contemplating various hunting strategies and taking into account both technical and organisational aspects. In this way, the authors differentiate between passive and active predation strategies, taking into account the different segments of a wild boar population (in terms of sex and age) that may be involved. They also differentiate between solitary hunting and social hunting. Solitary hunting favoured the capture of older individuals, with special emphasis on older males that are more likely to be found alone. Social hunting strategies, based on cooperation, generally involve the capture of several animals at once. About their capture and the beginning of their intentional control by human communities, several trajectories have also been proposed taking into account ethnographic work, from which their domestication would be feasible (Rappaport, 1968; Dwyer, P. 1996; Nakai 2012; Rowley-Conwy *et al.,* 2012). The various scenarios proposed envisage diverse degrees of human intervention. In the first, human intervention would be limited only to the appropriation of wild-bred infants or juveniles. In the second, there is continued control over breeding females, and in the last, males and females are entirely dependent on human action (Navarrete & Saña, 2017). Ervynck *et al.,* (2001) also propose commensalism as a possibility. Marshall *et al.,* (2014) highlights the possibility that flows between wild and domestic populations were common in these contexts. The work on traditional extensive pig husbandry practices in the Mediterranean region published by Halstead & Isaakidou (2011) and Hadjikoumis (2012) also demonstrates the diversity of rearing and feeding regimes to which this species may have been subjected in the early Neolithic period.

Differentiating between wild and domestic forms is therefore a complex question, but also crucial for the resolution of this historical subject. The constitution of high-resolution referentials is therefore a solution. The high resolution will be given, in this case, by the application to the references themselves, of a Geometric Morphometrics (GMM) methodological application also developed within the framework of this doctoral thesis that takes into account the changes, not only in size, but also in shape between wild and domestic pigs. Taking into account that shape is less affected by environmental factors than size, this methodological approach provides as a result algorithms that allow the classification of the pig remains using quantitative data, and also considering demographic variables (sex, age).

3.2. Selection of the skeletal elements: criteria

The skeletal elements selected have considered the mechanics of the skeleton and the plastic and adaptive properties of bones to be two basic aspects of animal life that can be highly informative of past livestock management: feeding and movement or physical actions.

3.2.1. Study of the phalanges of *Bos taurus*

The study of the biomechanical modifications that domestication and early husbandry practices may have caused on the bones of *Bos taurus* due to the new uses and husbandry regimes to which this species was subjected during Neolithic times, has been carried out on the first and second phalanges. The first and second phalanges of the forelimb and hindlimb were selected because most of the injuries related to physical stress and stabling are concentrated in the distal limbs. The weight of the animal is transmitted along the line from the second phalanx to the third phalanx. Under normal conditions, it is evenly distributed over the entire surface of the hoof. There are several factors that can influence the conformation and biomechanical affectation of the distal part of the limbs, including age, weight, feeding, growth, way of movement, environmental exposure or genetic factors. With the domestication and breeding of this species, we must add to these factors some others derived from the artificial pressure applied with the aim of utilising the animals of this species in tasks that require an investment in supplementary energy. The biomechanics derived from these new actions (*e.g.* pulling, traction or transport) can activate bone tissue remodelling due to the need to adapt the bone to these new pressures and stresses (Alcàntara, 2019). Complementary to the analysis of the potential involvement of early domesticated cattle in tasks requiring extra effort, it must be considered that various aspects linked to the animal biology itself, such as age and sex, may influence the variability of the first and second phalanges. In relation to age, ageing is an important factor affecting bone structure. The bone becomes thinner and loses minerals, the bone matrix weakens and the bone becomes more susceptible to fractures. Bone density analyses on bovine bones show that density values initially increase during maturity, but are balanced with the fusion (Telldahl, 2015; Costagliola *et al.,* 2016). Some limb injuries in cattle are usually due to chronic trauma caused by the activity performed but may also be due to the advanced age of the animal (Barbosa J. *et al.,* 2014). In general, females fuse their elements earlier than males, which affects bone size (Davis, 2000). Higham (1969) notes that width measurements tend to be more sexually dysmorphic than length measurements, while forelimb bones are more sexually dimorphic than equivalent hindlimb bones. He also points out, on a more specific level, that the dimensions that best reveal sexual dimorphism are those of the metacarpals, metatarsals and first anterior phalanges. For the phalanges, the separation between males and females is usually based on the ratio between maximum length and distal width (Stampfli, 1976). Another aspect that can influence variability is the presence of castrated specimens. Castration, especially if performed early in the life of males, delays epiphyseal closure, and increases the relative length of limb bones, mainly the distal ones (Shahin *et al.,* 1992; Davis *et al.,* 2018). The magnitude of the effect depends on the timing of castration. Early castration results in long-legged and long-horned steers, while late castration maintains bull-like conformation, assuming, from here, that the later the castration is performed, the lesser the effect (Rannamae *et al.,* 2022).

In addition to the biological variables of sex and age, anatomical features of the phalanges can also increase variability in a sample. The second phalanges are generally more homogeneous in size than the first phalanges (Bartosiewicz, 1993), with the posterior phalanges being somewhat thinner than the anterior phalanges. Recent work (Ocal *et al.,* 2004) confirms this trend, noting that between forelimb and hind limb differences in proximal and middle phalanges are observed in both length and width, with the difference in width being more prominent than in length. Another important variable considered when selecting this element for analysis is its high degree of adaptability. Species such as *Bos taurus*, with limbs of simple structure, tend to adapt very well to the terrain in which they feed and over which they habitually move. The high adaptability of cattle in adapting, for example, to soft ground has been highlighted in this regard (Qun Zhang *et al.,* 2017). Studies have also shown that the joints of the distal limbs of cattle destined to work regularly experience enlargement in response to excessive loads. This physiological reaction is represented in the morphometry of the joints (Lin, M., 2022).

From an archaeological point of view, the phalanges are an element which, due to their high bone density, are not affected by differential preservation, and are not usually fractured because they do not have consumable meat. This means that they are often recovered complete and can be studied morphometrically.

The study of the origins of the use of *Bos taurus* as a work force requires consideration of the complexity of the environmental and biological influences to which the growth and development of the bones of this species are subjected. Unravelling the causes of this variability using new analytical procedures will provide archaeozoological research with new diagnostic criteria and protocols with which to approach this problem. Finite element analysis modelling is of particular interest for the investigation of the functional mechanics of distal limb bone structures. The application of geometric morphometrics and finite element analysis on the first and second phalanges of this species is a novelty in archaeozoology.

3.2.2. Study of the mandible of *Sus scrofa*

The assessment of variability in the modern boar referential has been based on the jaw. The main variables influencing jaw shape and size are age, sex, weight, diet, climate, habitat, and geography (Owen *et al.,* 2014). Previous studies have also indicated that variability in jaw shape may be influenced by factors such as latitude and elevation (Endo *et al.,* 2002). In relation to sex, von den Driesch (1976) and Payne & Bull (1988) point out that the main difference between males and females is the shape of the canine, which is larger and more curved in males, and in females has a canal running along the anterior part of the tooth. In a recent study (Košinová K. *et al.,* 2022), significant sex differences were also found in BML (width of *caput mandibulae*), HG (height of the mandible from the bottom of *symphysis mandibulae* to the top of the *margo interalveolari*) and jaw angle in the incisor section, with values of measurements always higher in males, except for jaw angulation in the incisor section, where the difference is significant up to the age of 6 months, with higher values in females. Sexual dimorphism in the boar skull is conditioned by the different shape of the canines, which are larger in males and require more jaw space. Since tooth growth begins during embryonic development (Tucker, Sharpe 2004), it is possible to observe differences between males and females also in young animals.

In line with the objectives of the work, one aspect to consider when selecting this bone element is the marked difference between the feeding behaviour of wild and domestic pigs (Navarrete *et al.,*, 2017). Wild pigs have a diet rich in coarse foods, whereas domestic pigs can chew softer foods, and this characteristic influences the coordination of masticatory muscles and jaw movement, changing the tension pattern of the muscles involved in mastication (Herring & Liu 2001, Herring *et al.,* 2008). The masseter muscle exerts the key force in the whole mechanism triggered by the chewing process (Herring, 1992, Herring & Liu 2001). Bone tensions will vary according to mechanical regimes and therefore because of differential feeding (Herring *et al.,* 2000; Dino, 2009). Mechanical stress influences the volume and structure of jaw bone tissues by controlling bone remodelling. Sato *et al.,* (2005) conclude in their work that the adaptive functional response of the mandible to mechanical stress resulting from mastication occurs not only in the muscle insertion zone, but also in the mandibular alveolar bone of the molar region. Also, in relation to feeding habits, the published study by Neaux, D. *et al.,* (2021) mentions, for example, that it is possible to detect plastic changes in the jaws of juvenile and adult wild boars as a result of the captive condition, where access to food is controlled by humans. The modification of feeding and foraging behaviours thus influences jaw shape, documenting with captivity an increase in size and variation in some phenotypic traits (*e.g.* more vertical jaw branches). The characteristics of the food ingested, such as its hardness and size, also influence the force, direction and rhythm of the bite, provoking detectable plastic responses that can be of great interest for the study of ancient paleodiets from archaeological faunal remains (Neaux, D. *et al.,* 2022).

The morphology of the mandible may also be influenced by the type of landscape. Studies by Košinová K. *et al.,* (2022), considering the presence of wooded and agricultural areas in hunting areas, showed that individuals from localities containing at least 200 ha of forest had higher mandible values of the measurements, with a significant correlation between some measurements and the size of the wooded areas. These larger wooded areas probably offer better shelter possibilities than field areas, which is crucial during the first months of life, as calmness can positively influence the development of the young individual (Košinová K. *et al.,* 2022).

Most studies in which geometric morphometrics have been applied in archaeozoology are aimed at contrasting differences between wild and domestic populations (Evin *et al.,*, 2022). Skull and dental remains have been the most used bones, although few have focused on the jaw. However, some of the most recent studies highlight its great potential.

3.3. Site selection

For the selection of the sites, various historical, chronological, and environmental aspects have been considered, with the aim of ensuring that the sites analysed are representative of the historical actions studied. The sites (Figure 1) are La Draga (Spain, latitude: 42.126°, longitude: 2.763°), Pixarelles (Spain, latitude: 41.959°, longitude: 2.396°) and Tell Halula (Syria, latitude: 36.416°, longitude: 38.166°).

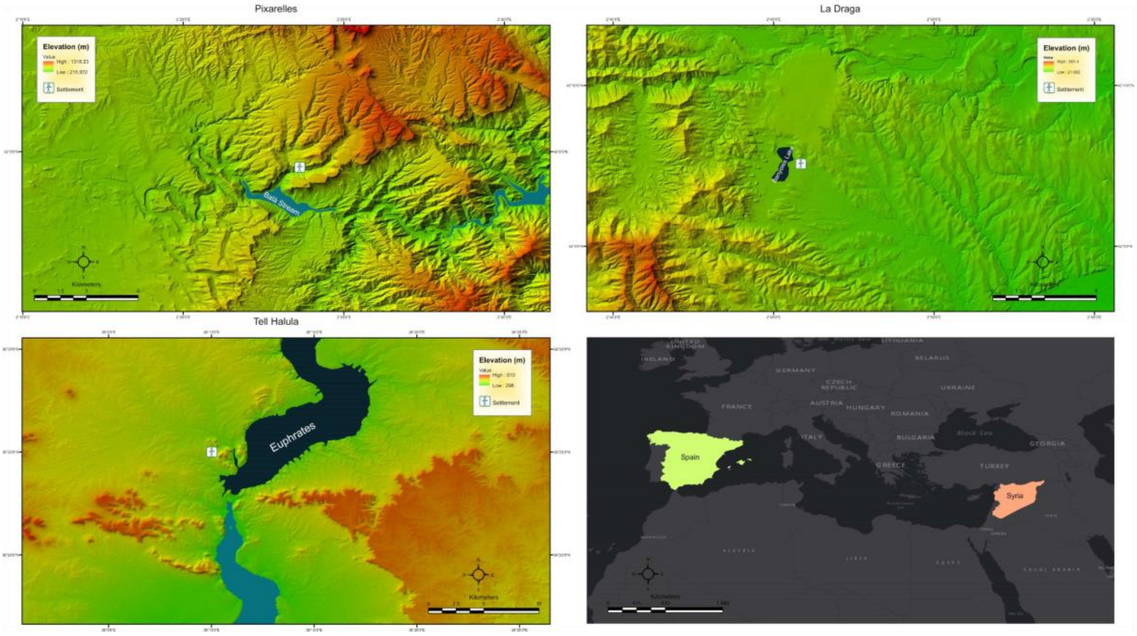

Figure 1 The geographical locations of the three archaeological excavation sites with the corresponding digital elevation maps.

Tell-Halula settlement, located at the western bank of the Euphrates river (east of Aleppo, Syria), is also a flatland which hosted a large Neolithic village occupied from the Middle Pre-Pottery Neolithic B (MPPNB) to the Halaf period (8800-6500 cal. BC) (Saña & Tornero, 2008; Peters *et al.*, 1999). Due to the long and continuous occupation phases, Tell Halula faunal records documented the initial emergence of the four major domestic species (cattle, pig, sheep, goat) and provided invaluable information to study the evolution of animal husbandry. In the present study, Tell Halula specimens are affiliated with the middle, late MPPNB and pre-Halaf period, when settlers mainly dined on aurochs (10.5% - 21.8%), gazelles (13.1% - 26%), swine (4.2% - 15.7%), cervids (3.6% - 14.4%), equines (0.3% - 3.2%) and domestic goat (26.3% - 39.5%). Domestic cattle (*Bos taurus*) became prevalent during the late MPNB and early LPPNB, whereas wild animal remains declined dramatically (Saña & Tornero, 2008).

Figure 2 Tell Halula excavation site (Source GRAMPO).

La Draga settlement is located at the eastern bank of Banyoles lake (Girona, Spain), a flatland hosting one of the earliest western Mediterranean Neolithic farming communities dating back to 5400 - 5000 cal. BC. The settlers lived mainly on intensive mixed agriculture and animal herding, complemented by hunting-gathering (Saña Seguí, 2011; Antolín *et al.*, 2014; Palomo *et al.*, 2014). The archaeo-faunal remains of domestic species mainly include *Bos taurus* (33.95%), caprines (42.82%) and *Sus domesticus* (22.4%). Regarding the archaeo-faunal remains of the wild species (3% of the total faunal remains), *Bos primigenius*, *Sus scrofa*, *Cervus elaphus*, *Capra pyrenaica* and *Capreolus capreolus* remains were documented more frequently (Saña Seguí, 2011).

Figure 3 La Draga excavation site (Source: AGREST)

Pixarelles specimens, on the other hand, were excavated from Pixarelles cave, located in a mountainous area close to Tavertet (Osona, Spain). Pixarelles archaeo-faunal records belong to the domesticated species and date back to the Iberian middle Neolithic (3930 - 3875 cal. BC). So far, there is no link connecting Pixarelles cave and any nearby Neolithic farming field, which makes it a peculiar case of possible temporary settlement tailored to serve as an animal reservoir or shelter (Alcàntara Fors, 2019).

Figure 4 A beautiful view of Pixarelles cave (Source: GRAMPO).

3.3.1. Chronological framework

At a chronological level, the studies developed within the framework of this thesis focus on the analysis of Neolithic sites, contemplating a sufficiently broad time interval to examine both the processes of animal domestication and the adoption and consolidation of livestock farming. Overall, the time interval covers from the Pre-Pottery Neolithic B (MPPNB), represented by the site of Tell Halula (7800-5700 cal. BC), through the Early Neolithic in Western Europe, with the site of La Draga (5430-4796 cal. BC), to the Middle Neolithic in the Western Mediterranean too, from the site of Cova de les Pixarelles (4250-4050 cal. BC).

Tell Halula is located on the right bank of the Euphrates River as it flows through Syria, near the town of Djerablus. The tell occupies an area of 8.3 ha and has 11 m of archaeological stratigraphy, composed of a succession of occupation-amortisation-continuous occupation levels. The settlement has been continuously inhabited from 7,800-5,700 cal BC, and 37 consecutive occupation phases have been identified, ranging from the Middle BPNB, Recent BPNB, Pre-Halaf, Halaf and Obeid (Molist, 1996, 2001).

The earliest occupations of Tell Halula are dated to between (MPPNB and LPPNB). During this period, the settlement is characterised by the agglutinated arrangement of multi-cellular rectangular dwellings (generally with 3-5 rooms) built in adobe and with lime-plastered floors, inside which some silos, ovens and hearths have been found. Production activities have also been documented in the open spaces between the houses. Towards the end of this period, a large wall was also built on the south-eastern side of the site, which seems to have been intended to protect the area (Molist, 2001; Molist *et al.,* 2004; Molist & Vicente, 2013).

The immediately subsequent occupation levels correspond to the pre-Halaf period. During this period the settlement reaches its maximum extension, with 7 ha of occupied surface area, and a change in the design of the houses can be seen. From an aggregated plan to a dispersed one (there can be up to 6 meters between dwelling units), so the increase in the occupied surface area is not necessarily related to an increase in the population (Molist & Vicente, 2013). During this period, circular constructions are documented for the first time, interpreted as domestic structures of complementary use, associated with production or storage tasks. The presence of pottery was also documented for the first time. Finally, the most recent occupation levels, corresponding to the Halaf and Obeid periods, have been excavated in a reduced area that does not allow for an exhaustive characterisation of the organisation of the settlement during this chronology.

La Draga is an Early Neolithic Cardial settlement, located on the shores of Lake Banyoles (Banyoles, Girona). The site is characterised by the preservation of organic remains such as wood and other plant fibres, due to the fact that part of the site is located in the water table (Bosch *et al.,* 2011). Through the analysis of radiocarbon dating, it has been possible to propose the possibility that the occupation of the settlement was continuous, except for a brief hiatus, which suggests the existence of two phases, although without implying an abandonment of the settlement. The earliest phase would comprise the period between 5,361 and 5,223 cal BC, while the most recent phase would be between 5,000 and 4,796 cal BC (Terradas *et al.,* 2017).

During the first phase the inhabitants of La Draga built their dwellings in the immediate surroundings of the lake, and two rows of eight huts have been documented perpendicular to the lake, raised above ground level by means of a series of posts to avoid damp, and prevent possible flooding, due to their proximity to the lake. These huts have a rectangular floor plan measuring 12 m long by 4 m wide with a gabled roof. Wood and other plant materials would have been the main construction material, along with clay, to cover the walls and some of the interior elements of the houses, such as the hearths. The higher, drier areas would have been reserved for agricultural and livestock activities and storage. The arrangement of some posts seems to indicate that there may have been a palisade around the living area, as well as a series of walkways linking the upper and lower parts of the settlement (Bosch *et al.,* 2011). The second occupation of La Draga has very different architectural characteristics, as the palafitte-type structures disappear and are replaced by structures built on travertine platforms. The presence of hearths and combustion features distributed throughout the site, seems to indicate that most of the production activities were carried out outside the huts (Bosch *et al.,* 2011). Although the construction characteristics change between the first and second phases, there are no changes in the material culture, which suggests that during both occupations the same community had settled in this place and must have changed their construction techniques, probably to cope with an increase in lake level (Palomo *et al.,* 2014).

The site of Cova de les Pixarelles has three different chronological stages, according to the stratigraphic seriation. The earliest occupation, covered in this work, corresponds to the Middle Neolithic (3930-3640 cal BC). The set of remains studied corresponds to level XXII (Molist and Rauret, 2017, 2016). Level XXII, in addition to faunal remains, contains pottery and lithic remains. The pottery remains include medium and small capacity vessels, intended for the consumption and transformation of foodstuffs. As for the tools, there are documented stone hammers and a polished cornubianite axe, as well as a bone awl. In relation to the archaeological structures, a hearth has been documented at this level, which could suggest that the cave functioned as a living area. The stratum corresponding to level XXII presents grey clays and is altered by the presence of organic remains, mainly coals and abundant ashes (Álvarez, 2019). The faunal remains were deposited in an area of 6m2, covered by a layer of travertine. After the abandonment of this area, the surface was quickly sealed by successive layers of calcium carbonate. It is probable that the abandonment was due to the immediate flooding of the site, which would have made this space impracticable.

3.3.2. Historical framework

In terms of historical issues, it has been considered relevant to analyse the subject from both a synchronic and diachronic perspective, bearing in mind that it is important to differentiate between the actions involved in animal domestication and those deriving from the initial stockbreeding. The selective actions may in some cases coincide, but the objectives do not necessarily. In contrast to domestication, animal husbandry contemplates all the work processes involved in the production and maintenance of animals, in obtaining their products or labour power, or the animal itself as a product. In this sense, while domestication is characterised by its eminently social component of appropriation of animal reproduction, livestock farming encompasses the technical procedures and strategies adopted to manage the maintenance, growth, and reproduction of animals (Saña, 1999). For this reason, we have selected a site with a long and continuous sequence of occupation, such as the site of Tell Halula. Although 2500 years of continuous occupation have been documented at this settlement, this thesis focuses mainly on the oldest ones, from the MPPNB to the beginning of the pre-Halaf period, taking into account the dynamics of *Bos taurus* representation throughout this sequence and the research objectives. The analysis of the variability of the phalanges of this species at a biomechanical level will make it possible to contrast whether their breeding regime or their use changes over time.

In the second site selected, La Draga, the study of variability has been oriented towards the analysis of a single herd, composed of completely domesticated animals when the community settled in this territory. As this is an *exnovo* settlement, with a relatively short duration (about 50 years), the perspective of analysis must be based on synchrony. Current evidence suggests that the domestic cattle at La Draga would have been imported. A highly complex question is to establish the number of imported animals that formed the basis of this herd. The notable importance of this species in this settlement (34,6%), which differs from the majority of contemporary sites in the Mediterranean and Pyrenean area, suggests that the founding population may have arrived with the new settlers. It is therefore interesting to analyse the degree of homogeneity of these animals and the possible causes of variability, considering both their management and exploitation and the new ecological adaptations that their rearing in this environment entailed as causal factors. The presence of remains of local aurochs, which would have been acquired through hunting activity (Saña, 2011), has not been ruled out at this site, adding the possibility of hybridisation. Recent studies have shown that domestication and initial stockbreeding are complex in nature, which makes it impossible to work only on the basis of the wild/domestic dichotomy (Saña, 1999). Wild forms would be subject only to natural selection. Captive animals, controlled directly by the groups in the wild, would be affected by a certain relaxation of natural selection because they are protected by humans, the latter being responsible for passive selection. In domestic animals, on the other hand, artificial selection is intensified by animal husbandry, although environmental factors such as climate and food availability still influence the variability of the species. The fact that domestication and early husbandry practices did not abruptly lead to stabling or enclosure, with animals living in free or semi-free-range conditions, means that contacts between wild and domestic forms can be common, leading to the presence of hybrids. Hybridisation can also be intentional, crossing both forms for breeding purposes and for the improvement of the species. The phenotypic characteristics of the hybrid specimens may be intermediate, with the traits of each of the parts varying widely.

The third site included in this doctoral thesis is the site of Cova de les Pixarelles. The occupation of Cova de les Pixarelles corresponds chronologically to the beginning of the Middle Neolithic, when livestock farming was already fully developed in the northeast of the Iberian Peninsula. The choice of this site has been determined, in part, by the results obtained from the genetic analyses carried out to date. The analysis of mitochondrial DNA has been carried out on 10 samples and is still awaiting publication. The remains have been analysed by Dr. Eva-Maria Geigl, Jacques Monod Institute (Paris) (Guimaraes *et al.,* In preparation). The study of the samples was based on the analysis of the hypervariable region with 33 single polymorphic nucleotides (SNPs) of the bovine mitochondrial genome. The data obtained indicate that the lineage present in the Cova de les Pixarelles corresponds to the T3 group, originating in Anatolia and predominant in the north-east of the Iberian Peninsula during the early Neolithic. The peculiarity of the herd from the Cova de les Pixarelles site is that this group of cattle stands out, compared to the rest of the bovine populations analysed so far, due to the presence of up to two additional SNPs (T3+1 and T3+2), showing a greater genetic variability in this site. This greater genetic variability could be the result of hybridisation, arrival or acquisition of new stocks, or different selective actions that demonstrate an increase in the genetic variability of the bovine populations between the Early Neolithic and the Middle Neolithic (Alcàntara, 2019).

Animal domestication is considered to initially lead to a loss of the genetic variability of the species. This loss would be a consequence of the genetic isolation of the wild population. Genetic studies have shown that domestication implied a reduction in the number of domestic animals relative to wild animals, a phenomenon known as a bottleneck (Pérez-Enciso, 2009). A bottleneck is defined as a drastic reduction in population size, followed by a recovery (Allaby *et al.,* 2019). According to Pérez-Enciso (2009), domestication also implied an increase in the phenomenon known as genetic drift (hazard). Genetic drift refers to the fact that the proportion of a genotype can vary due to hazard factors. The processes of natural selection and genetic drift occur naturally in wild populations, but when coupled with domestication and artificial selection, the speed and magnitude at which hazard can affect the genetic diversity of species changes. There are thus two main evolutionary forces conditioning the genetic variability of populations, selection, and genetic drift (Pérez-Enciso, 2009). Specialised animal husbandry can thus again contribute to increased variability. Once livestock farming is consolidated, selection actions would be more pronounced, with animals acquiring differentiated traits depending on their farming regime

(Helmer, 1992; Saña, 1999). With the aim of providing additional data to contribute to a better understanding of these dynamics and their respective genetic responses during the initial phases of cattle farming, it was considered appropriate to carry out an exhaustive characterisation and study of the sample of cattle recovered from the site of the Cova de les Pixarelles and to contrast whether, from the biometric and biomechanical analysis, this greater variability with respect to previous *Bos taurus* populations (early Neolithic) is also confirmed, thus establishing the possible correspondence between genetic and phenotypic variability.

3.3.3. Environmental framework

At the environmental level (geology, topography, ecology), the three sites mentioned represent environments with different characteristics. Echometric variables use morphological variation to understand the adaptability of an organism to a given environment and infer from this the environmental characteristics of their habitat (Adler *et al.,* 2022). Mammalian bones, depending on the weight, size, and proportions of the animal, can undergo changes in bone biomechanics and morphology depending on the characteristics of the environment. The bone anatomy of the locomotor system is highly adaptable to the ecological characteristics of the habitat frequented by the animals. Based on this principle, it has been considered important, when evaluating to what extent this aspect influenced the bone biomechanics of the first Neolithic cattle herds, to work with environments with different characteristics and to evaluate the weight of ecological versus anthropic adaptation.

Tell Halula is located on the right bank of the Euphrates River, 800 m from its present course. It is a large tell (8.3 ha), comparable in size only to the sites of Ain Ghazal (Jordan) and Tell Abu Hureyra (Syria), and much larger than other sites from the same period such as Jericho (Palestine) and Mureybet (Syria). The archaeological deposits are 11 m high, located on an ancient terrace surrounded by two small tributaries of the Euphrates River, in a small valley excavated by the erosion of the river into the limestone rocks of the Upper Eocene, at an altitude of about 300 m asl (Araus *et al.*,, 2001). The site is located at the confluence of two wadis, Wadi Nahr and Wadi Abu Gal Gal, which join at the site to form a single stream that flows 1 km into the Euphrates River. The ancient settlement is located at the interface of several natural ecosystems that allowed its inhabitants to exploit a wide variety of resources from the: alluvial plain (banks of the Euphrates valley and nearby tributaries) to the semi-arid steppe. At the beginning of the Holocene, with the improvement of the climate, the oak forest expanded, establishing an arboreal steppe around Halula, with higher water and rainfall conditions than today, which meant a much more extensive vegetation cover and a high proportion of grasses (Willcox *et al.,* 2009). Considering the environmental requirements of the animal species hunted, it is possible to reconstitute the environments frequented by the communities that inhabited the site. The presence of the equid-gazelle association is evidence of the exploitation of the open steppe, with semi-desert vegetation, while *Dama mesopotamica* and *Capreolus capreolus* indicate the parallel exploitation of a more wooded environment, with the presence of relatively abundant water. For *Sus scrofa* and *Bos primigenius* it is worth mentioning their wide ecological distribution, highlighting the high degree of ubiquity of the former species and a preferential distribution in more wooded environments with the presence of water for the latter. The proximity of the site to the Euphrates River should not be overlooked in this regard. While *Capra aegagrus* tend to live in rocky environments, with a predilection for cliffs (Helmer, 1992), *Ovis orientalis*, with a drier diet than *Capra*, prefers less mountainous habitats, and is well adapted to the vegetation of semi-desert steppe zones (Helmer, 1992). As far as the documented wild plant assemblages (Antolín & Buxó, 2000) are concerned, these show rather dry environmental conditions, in some cases even arid. However, taxa related to more humid environments have also been documented, which seems to suggest a richness and variety of exploited territories. The different chemical analyses carried out on the dental enamel of the gazelle remains recovered at tell Halula, dated between 7,800-7,000 cal BC, seem to indicate a wetter and colder climate than the present one, which is why the site's surroundings would have a very different appearance to the present one, characterised by a more dense vegetation cover (Saña & Tornero, 2008).

The stable isotope studies carried out have also made it possible to identify the dietary regimes of the main domestic species (Tornero, 2011). Goats and sheep show differentiated plant consumption patterns during the intermediate occupations of the settlement (late middle PPNB, early LPPNB). The sheep diet follows the natural dynamics, with no extraordinary food input. For this species, the sinusoidal oscillation of the carbon signal (related to the seasonal cycle) is correlated with the oscillation of the oxygen values and the variability or amplitude of the values (3-4 points) coincides with the natural one. Feeding is therefore based on natural availability (Tornero, 2011). In the case of cattle, it has been possible to document a different strategy for the oldest and most recent PPNB occupations, with natural seasonal patterns also dominating in the oldest ones. A low variability in O values between individuals is evident. However, C13 values show important differences. For gazelles, the distribution is more homogeneous than that obtained for *Bos*. In the latter species, a greater variability is observed, with an ordering of individuals according to chronology. Based on these results, it has been hypothesised that the changes in C13 values correspond to a change in the feeding patterns of the species, which may be related to its management. In relation to the suids, the study of dental enamel affectations is also evidence of a change in the management of this species that would have taken place at the beginning of the pre-Halaf occupations (Cabeza, 2017; Alcàntara, 2019). Dental hypoplasia is an important marker for detecting changes in breeding and feeding conditions based on the effects that these changes may have on the animal's physiology. The results obtained from the study of this condition show that important changes occur from the pre-Halaf occupations onwards, which are probably related to a modification of the pigs' living conditions. From this time onwards, the increase in the number of affections in animals of all ages shows that the animals of this species suffer more intensely seasonal changes, with more physiological stress, which could be linked to a change in the breeding regime of the species, increasing the management in captivity. Studies of bone biomechanics carried out on goat and sheep bones (Alcàntara, 2019) also show, for the most recent occupations of Tell Halula, a reduction in cortical mass and robustness linked to a reduction in physical stress and activity in general, and more homogeneous mobility patterns in terms of intensity and direction.

The site of La Draga is located on the shores of Lake Banyoles (Banyoles, Girona). The site is located 170 m above sea level on the eastern shore of Banyoles Lake. The lake of Banyoles is a formation of tectonic karstic origin and represents the largest continental mass of water in Catalonia. It is located in a geologically depressed area, surrounded by the reliefs of the Transversal Mountain range and the Catalan pre-coastal depression, and occupies the basins of the Fluvià river to the north and the Terri, a tributary of the Ter River, to the south. Although today part of La Draga is located inside the lake of Banyoles, during the ancient Neolithic period the settlement was located completely outside the lake. The lake of Banyoles would have had a very different appearance to the present day, with smaller dimensions and a much denser vegetation cover (due to a more humid climate than today), with riverside forests, deciduous forests, and taxa typical of Mediterranean forests. Pollen studies carried out at Banyoles lake (Pérez-Obiol, 1994; Pérez-Obiol & Julià, 1994; Burjachs, 2000; Revelles *et al.,* 2014; Revelles *et al.,* 2017) show that, around 9000 BP, the forest cover expanded considerably with the extension of oak and hazel forests in the area. Analyses of sediment samples taken from the archaeological site show that when La Draga was occupied, the forest cover was significant (around 85.3% tree pollen). The landscape around La Draga was densely wooded with riparian woodland (ash, willow, elm, and alder), with a predominance of oak (Caruso & Piqué 2014; López & Piqué, 2018). Coinciding with the first moment of occupation at La Draga, a quick decrease in tree pollen is documented (Burjachs 2000; Revelles *et al.,* 2016). This decline in tree pollen has been related to the massive felling of trees and the clearing of the forest related to the intensive agricultural system (Revelles *et al.,* 2015). The inhabitants of La Draga practised an intensive mixed farming model (Antolín *et al.,* 2014), with the cultivation of barley (*Hordeum distichum*), durum and soft wheat (*Triticum durum*; *Triticum aestivum*), emmer (*Triticum dicoccum*), small spelt (*Triticum monococcum*), a new type of wheat (*Triticum sp*.) and poppy (*Papaver somniferum*) on small permanent fields. Farming was combined with stockbreeding, leaving the crop stubble for the animals' consumption, thus facilitating the use of manure to fertilise the fields (Antolín *et al.,* 2014). Animal management at La Draga settlement focused primarily on domestic herds. It is a mixed husbandry strategy aimed at exploiting the different animal productions in an integrated manner (Saña, 2011). A certain variability in feeding strategies between domestic herds is documented, with the coexistence of different diets for sheep, goats, and cows, both in terms of diet composition and seasonal variability (Navarrete *et al.,* 2019). For sheep, carbon and oxygen values evidence a type of feeding based on the natural rhythms of plant availability in the wet meadows of the lakeshore. In contrast to sheep, significant seasonal variations are detected for goats and cows, a characteristic that probably indicates the extraordinary supply of forages in some seasons, possibly the most adverse or unproductive ones. From the C13 values, it has been possible to show, in the case of *Bos taurus*, that feed supplementation took place at the end of the dry season, coinciding with the oestrous cycle, possibly with the aim of reducing infant mortality rates or stimulating and maintaining milk production (Navarrete *et al.,* 2019). There is also evidence of animal stabling inside the settlement, both in terms of the presence of young individuals and the presence of parasites (Maicher *et al.,* 2017). The feeding territories would be for all animals near the settlement and would probably have similar topographical features. The proximity to the lake would imply the existence of a soft and nutrient-rich soil (Alcàntara, 2019), conditioned by the silt of the lake and the humus generated from the decomposition of organic matter.

The third site selected, the Pixarelles Cave, is located in Tavertet (Osona). The natural landscape of the area is part of the Collsacabra, a geographical area covering 142 km2. The cave is located in the middle valley of the river Ter, at a point of contact between different morphostructural units. The entrance of the cave opens onto the Les Balmes cliff, a limestone rock face with a vertical drop of about 70 meters. It is a landscape with an abrupt orography, with significant differences in altitude. The right side of the Balà stream has an abrupt orography with a staggered sequence of steep cliffs culminating in a flat upper platform. The last of these slopes has an average height, between the base of the risk and the flat top, of about 100 m (lower elevation 625 m and upper elevation 725 m). It could have been a strategic point of passage and communication between inland territories of Catalonia and the coastal plains of the area of the province of Girona today (Molist & Rauret, 2016, 2017). The current presence of different plant communities is very marked by anthropic action, because of the current presence of young forests of *Pinus Sylvestris* replacing the oak forest. On strongly carbonated soils, the vegetation is dominated by mountain holm oak, with residual oak groves and a large presence of boxwood. The exceptional feature of this site is its faunal assemblage, with exclusive presence of domestic species. Among these, *Bos taurus* represents a significantly high percentage (80%). The δ13C/δ15N isotope analyses carried out with the aim of studying the dietary patterns of this species show highly homogeneous results, like those of the aurochs' population from the Mendandia archaeological site taken as a reference (Viñas, in prep).

3.4. Selection of samples

Based on the research objectives, the selection of the samples has considered, on the one hand, the condition and taphonomic characteristics of the faunal remains and, on the other, the composition of the faunal assemblages and their variability at each site. For the selection of the collection of wild boar bones that make up the modern reference, we have taken into account their origin, age and sex, with the aim of analysing at a morphometric and biomechanical level how these variables are represented in the bone tissue.

3.4.1. Samples of bovine phalanges

Archaeological specimens constituted the first and second phalanges of cattle *(Bos taurus* and potentially *Bos primigenius*) from the three different excavation sites representing chronologically distinct Neolithic settlements, covering a range of different environments, and herding objectives.

3.4.1.1. Tell Halula (Euphrates Valley, Syria)

During the middle PPNB, which corresponds to the first nine first occupations of the settlement, the resources exploited came from hunting and the husbandry of goats, cattle, and pigs, with the introduction of domestic sheep being documented during Occupation Phase 8. *Bos primigenius, Sus scrofa, Equus hemionus, Cervus elaphus,* and *Capreolus capreolus* are the main hunted species, with the sporadic exploitation of tortoise, wolf, fox, small carnivores, birds and Leporidae. In the LPPNB, this hunting activity has declined in importance. Species previously represented, such as deer, ceased to be hunted and other wild species were no longer hunted. Equids. Leporidae, chelonians, small carnivores and birds are practically no longer represented. At the same time as this decline, sheep and goat farming became the central activity of animal management strategies. The exploitation of by-products, such as wool from sheep, becomes more important (Saña & Tornero, 2012). At the end of the LPPNB and during the pre-Halaf period, livestock farming continued to play an important role and intensified (Saña, 1997, 1999; Tornero, 2011). Bovids were the main source of meat supply, followed in importance by sheep and goats, which are managed in a polyvalent way to obtain meat, milk, and wool. Pig farming is based on the slaughter of individuals aged between 12 and 14 months to acquire meat (Saña, 1999; Alcàntara, 2019). Hunting plays a secondary role, focusing on the hunting of gazelles and, more specifically, deer, aurochs and wild boars. Significant changes in the management of animal resources are therefore evident throughout the sequence, notably: the incorporation of the four main domestic species, the consolidation and productive diversification of livestock strategies and the gradual decline in hunting activity. All these changes took place in a relatively short period of time.

Cattle husbandry is well attested at Tell Halula. Considering the percentages of representation, an increase in *Bos taurus* exploitation is observed from occupation one to occupation seven, occupation for which a maximum peak is recorded. From occupation phase seven onwards, there is a progressive decline (with some occasional increases) until occupation phase twenty-five. From this point onwards, the percentages stabilise and then gradually decrease again from occupation phase thirty-one to thirty-six. The presence of the wild form is also attested throughout the whole sequence. In terms of cattle management, the remains recovered in the oldest occupations (middle PPNB – beginnings LPPNB) mainly belong to adult individuals. During the most recent occupations (pre-Halaf and Halaf) there is a more balanced presence of adult and juvenile specimens. During these later occupations there is evidence for a greater control over the conditions of growth and reproduction of the resource, which favours a wider range of uses (Saña, 1999; Tornero, 2011). An interesting fact is that a progressive reduction in sexual dimorphism is observed throughout the sequence, probably because of these selective actions. Biometric studies have shown that the reduction in size over time is more pronounced in males than in females (Helmer *et al.,* 2005). In relation to the type of exploitation of this species, a recently published study (Helmer *et al.,* 2018) has shown, based on biometry and bone palaeopathology studies, the absence of castrated specimens, although some bone elements with a significant width of the medial diaphysis could be related to the use of these animals for obtaining supplementary energy.

From the 1912 remains of this species, a total of 48 first phalanges have been selected. An extra-scientific limitation to consider for this site is that most of the archaeological material from tell Halula is deposited in Syria, which is not currently accessible due to the war. Of these 48 phalanges, and due to taphonomic issues, a total of 11 could be used for geometric morphometrics analysis and modelling (Table 1). In the scatter diagram with the Gl and Bd measurements (Figure 5), it can be seen how the selected samples are distributed among the specimens of different sizes, with all sizes being represented among the set of selected samples.

code	Ant/Post	GL(mm)	SD(mm)	Bp(mm)	Bd(mm)	FO	Period
TH1FA13	Post	70,73	33,26	36,85	32,32	4	MPPNB
TH1FA15	Post	70,29	28,89	32,12	29,4	6	MPPNB
TH1FA10	Ant	73,95	32,48	39,23	35,58	8	MPPNB
TH1FA14	Post	77,18	32,19	37,08	31,72	8	MPPNB
TH1FA12	Post	78,91	32,31	38,65	39,96	8	MPPNB
TH1FA48	Ant	72,04	32,67	38,53	31,82	11	MPPNB
TH1FA16	Post	77,31	30,91	35,27	31,85	11	MPPNB
TH1FA46	Post	67	28,04	31,48	27,87	11	MPPNB
TH1FA11	Post	67,84	25,92	31,02	27,74	12	MPPNB
TH1FA45	Ant	76,45	35,45	43,1	35,06	14	LPPNB
TH1FA44	Ant	75,14	36,02	37,72	41,59	16	LPPNB

Table 1 Samples of first phalanges from Tell Halula. Tell Halula. Occupation phase, Period and anatomy of Tell Halula's first and second phalanges, after Molist (1996, 2001).

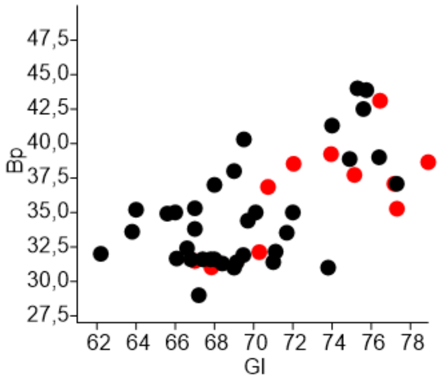

Figure 5 Dispersion plot of Gl and Bp measurements of the first phalanges of Bos of Tell Halula (in red the samples used for geometric morphometrics and finite element analysis).

The sample of second phalanges initially consisted of 107 individuals, with a total of 46 that allowed scanning and modelling (Table 2). The samples analysed (in red) are also distributed throughout the range of size variability of the second phalanges sample (Figure 6)

code	Ant/Posr	GL(mm)	Bp(mm)	Bd(mm)	SD(mm)	FO	Period
TH2FA63	Post	51,27	33,01	28,13	26,61	3	MPPNB
TH2FA52	Ant	52,96	38,09	33,2	32,21	4	MPPNB
TH1FA13	Post	50,9	34,31	30,32	27,96	5	MPPNB
TH2FA34	Ant	52,59	38,93	36	31,7	5	MPPNB
TH2FA41	Post	51,96	36,59	29,75	29,45	5	MPPNB
TH2FA58	Ant	44,86	32,57	27,62	26,28	5	MPPNB
TH2FA18	Post	45,03	30,91	26,56	25,39	6	MPPNB
TH2FA24	Post	53,59	38,66	35,34	33,07	6	MPPNB
TH2FA25	Ant	42,09	31,92	27,51	26,6	6	MPPNB
TH2FA32	Ant	52,07	39,2	35,74	32,4	6	MPPNB
TH2FA35	Post	51,05	33,44	31,21	28,07	6	MPPNB
TH2FA38	Post	52,68	35,3	29,92	28,18	6	MPPNB
TH2FA39	Post	46,31	30,77	27,61	25,32	6	MPPNB
TH2FA4	Post	46,54	29,1	25,4	22,46	6	MPPNB
TH2FA42	Ant	50,51	36,01	31,45	29,92	6	MPPNB
TH2FA50	Post	45,86	29,97	25,62	24,86	6	MPPNB
TH2FA51	Post	48,96	32,9	28,02	26,79	6	MPPNB
TH2FA57	Ant	46,96	33,67	29,16	26,93	6	MPPNB
TH2FA60	Ant	50,2	39,44	35,54	32,85	6	MPPNB
TH2FA7	Ant	47,49	36,12	31,49	29,72	6	MPPNB
TH2FA22	Post	46,65	29,88	25,99	24,83	7	MPPNB
TH2FA23	Post	50,5	35,3	29,03	27,73	7	MPPNB
TH2FA37	Post	50,96	32,31	27,67	26,44	7	MPPNB
TH2FA40	Post	52,02	34,51	29,61	29,05	7	MPPNB
TH2FA53	Ant	52,7	37,7	35,12	30,81	7	MPPNB
TH2FA54	Ant	46,7	33,45	29,53	27,39	7	MPPNB
TH2FA55	Post	43,31	30,67	25,5	25,57	7	MPPNB
TH2FA6	Post	54,73	35,43	31,57	29,15	7	MPPNB
TH2FA61	Post	52,18	38,55	33,31	31,33	7	MPPNB
TH2FA8	Ant	44,46	33,72	29,19	26,62	7	MPPNB
TH2FA19	Ant	49,46	35,95	30,3	28,06	8	MPPNB
TH2FA2	Ant	54,67	40,11	34,86	33,19	8	MPPNB
TH2FA26	Ant	50,37	37,63	34,06	30,37	8	MPPNB
TH2FA30	Post	46,16	30,69	25,24	25,88	8	MPPNB
TH2FA31	Post	49,72	35,59	29,73	29,55	8	MPPNB
TH2FA36	Ant	54,46	40,56	36,81	34,18	8	MPPNB
TH2FA5	Post	50,03	31,96	26,92	27,07	8	MPPNB
TH2FA56	Ant	41,43	29,86	27	25,66	8	MPPNB
TH2FA21	Post	56,39	37,91	31,65	30,17	13	LPPNB
TH2FA43	Post	51,46	36,3	31,09	30,52	13	LPPNB
TH2FA29	Ant	44,44	32,28	27,79	26,36	14	LPPNB
TH2FA59	Ant	49,71	38,64	32,76	30,52	14	LPPNB
TH2FA17	Post	55,01	35,57	30,87	30,81	20	LPPNB
TH2FA3	Ant	50,48	40,73	35,42	35,07	20	LPPNB

TH2FA33	Post	42,1	27,91	24,75	22,91	25	Pre-Halaf
TH2FA62	Post	47,4	33,43	27,7	25,51	27	Pre-Halaf

Table 2 Samples of first phalanges from Tell Halula.Tell Halula. Occupation phase, Period and anatomy of Tell Halula's first and second phalanges, after Molist (1996, 2001).

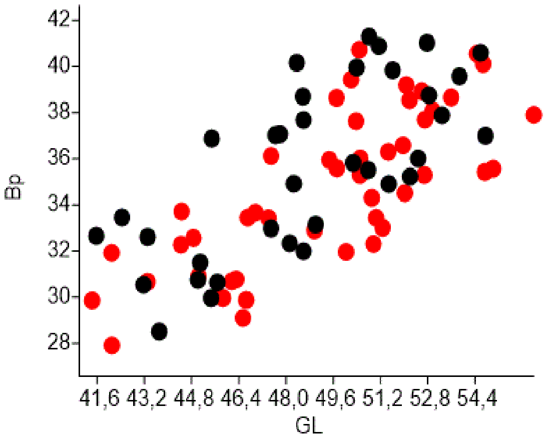

Figure 6 Dispersion plot of Gl and Bp measurements of the second phalanges of Bos of Tell Halula (in red the samples used for geometric morphometrics and finite element analysis).

3.4.1.2. La Draga (Banyoles, Spain)

The inhabitants of La Draga practiced a diversified strategy in terms of animal management. The large number of wild species documented (deer, wild goat, roe deer, fox, wild cat, badger, marten, and rabbit) is noteworthy, although herds of domestic animals for the supply and provision of foodstuffs were always important. The contribution of domestic species to meat production would have accounted for 85.11%, while wild species would have contributed, in relative terms, an amount proportional to 14.58 (Saña, 2011). The livestock farming practice was mixed, with herds of sheep, goats, cattle and pigs, which were exploited for different and complementary purposes at the same time. Based on the number of faunal remains classified from each species (NISP), cattle (*Bos taurus*) make up 34.6%, pigs (*Sus domesticus*) 23.4% and sheep (*Ovis aries* and *Capra hircus*) 41.8%. However, when using alternative units of quantification to NISP, the relative importance of the different taxa varies, highlighting the important weight that bovines had in terms of meat product supply (60.6%). On average, for every two sheep or goats slaughtered, one pig and 1.5 cattle were slaughtered proportionally. In any case, considering the reproductive cycles of each species, it is reasonable to think that the availability of animals was different either between species or during all the seasons of the year. A significant fact is that for all these species, the killing of animals of infantile and juvenile age is documented. In the case of *Bos taurus*, for example, an important presence of animals of a few weeks or months of age has been attested from the skeletal variability and the stage of development of the different bone elements. The stage of bone fusion shows that only a small number of animals of this species would have exceeded two years of age, documenting the significant death of animals before reaching 3 months of age, animals that would not yet have reached the theoretical meat optimum proposed by the species (estimated at between 2 and 4 years of age). The presence of remains of new-born and infantile animals has often been linked to dairy farming (Vigne & Helmer, 2007; Gillis *et al.,* 2016), although it should be borne in mind that, for this species, the presence of the calf is essential to stimulate milk production (Balasse *et al.,* 2000). More specifically, the age histogram obtained for *Bos taurus* shows that 45.3% of the animals of this species slaughtered were less than one year old, with 37.5% of animals slaughtered between one and two years old, 8.3% between two and three years old, 4.1% between three and four years old and 8.3% when they were over four years old (Saña, 2011). These data demonstrate their polyvalent exploitation, with a predominance of breeding for meat production. From the skeletal variability and ages, it has been possible to identify the presence of at least 23 *Bos taurus* specimens.

The specimens killed at adult age probably correspond to animals destined for reproduction (females) and exploitation of the workforce, animals that can normally be destined for consumption once the reproductive capacities are exhausted or when strength or energy begins to decline. The analysis of bone palaeopathology, following the criteria published by Bartosiewicz *et al.,* (1997) and De Cupere *et al.,* (2000), based on which the pathology index (PI) has been calculated, has shown that the animals of this species are generally in a good state of health. The pathology index is very close to zero (Tarrús *et al.,* 2006; Bosch *et al.,* 2008; Lladó *et al.,* 2008; Saña, 2011). The palaeopathologies documented on *Bos taurus* bones consist mainly of bone deformations (enlargement of the medial trochlea of the metapodials and lipping) and the formation of bony outgrowths with varying degrees (exostoses). These are mainly located on the articular surfaces (Antolín *et al.,* 2014). A series of 6 bucrania have also been recovered from this species, some with occipital perforations, although it has not been possible to relate them directly to the use of yokes (Lladó *et al.,* 2008). At this site, it has been possible to observe a high variability in the size of cattle. Between the large animals and the animals of relatively small size, there is not a clear break. When evaluating and interpreting this size distribution, it must be considered that cattle show a very pronounced sexual dimorphism, with significant differences in the degree of robustness between males and females. The study carried out on bone cross-sections attested the similarity between males and females in terms of loads received and mobility habits (Alcàntara, 2019).

Of the 1598 faunal remains of this species classified so far, a total of 134 first phalanges have been selected for this study, of which it has been possible to scan and model 25 (Table 3). The scatter diagram of the Gl and Bp measurements (Figure 7) shows a relative degree of homogeneity in the size of this bone, with a clear continuity between the largest and smallest specimens. The 25 more exhaustively worked samples cover the whole range of size variability.

code	Ant/Post	GL(mm)	SD(mm)	Bp(mm)	Bd(mm)
LD1FA53	Ant	63,7	26,26	30,3	25,28
LD1FA50	Ant	64,7	27,47	34,42	28,96
LD1FA52	Ant	62,1	26,69	31,17	22,62
LD1FA28	Ant	64,4	25,79	31,32	27,89
LD1FA44	Ant	59,6	25,89	30,1	28,59
LD1FA51	Ant	59,8	27,01	31,58	26,59
LD1FA29	Ant	68,2	30,6	35,36	32,71
LD1FA54	Ant	63,4	26,13	30,78	26,79
LD1FA35	Ant	62,2	25,82	32	27,08
LD1FA47	Ant	58	25,18	31,06	26,26
LD1FA40	Ant	61,6	25,52	29,49	25,93
LD1FA36	Ant	65,9	25,28	28,59	27,16
LD1FA43	Ant	64,7	25,57	30,21	26,44
LD1FA37	Post	68,5	21,65	27,62	23,71
LD1FA41	Post	57,6	22,4	26,93	24,8
LD1FA42	Post	74,2	24,93	29,77	27,38
LD1FA39	Post	59	23,64	28,46	24,4
LD1FA55	Post	63,9	23,33	28,95	24,85
LD1FA34	Post	64,5	20,77	26,92	23,76
LD1FA48	Post	71,7	24,9	31,49	28,27
LD1FA49	Post	63,5	22,18	25,25	23,46

LD1FA38	Post	63,3	25,03	31,33	27,76
LD1FA56	Post	67	23,27	26,81	23,27
LD1FA46	Post	65,2	23,28	28,15	24,54
LD1FA45	Post	69,7	23,46	28,51	25,37

Table 3 Samples of first phalanges from la Draga.

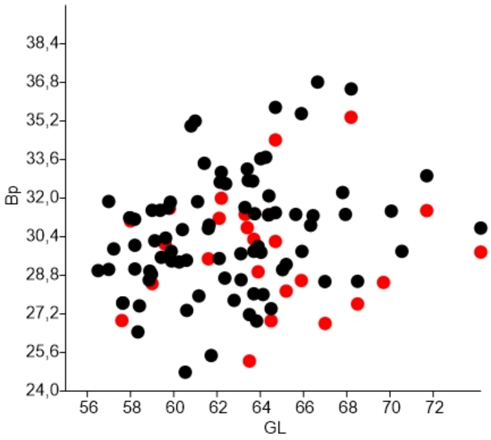

Figure 7 Dispersion plot of Gl and Bp measurements of the firts phalanges of Bos taurus of la Draga (in red the samples used for geometric morphometrics and finite element analysis).

In the case of the second phalanges, 31 samples out of the 71 recovered were used to develop this study (Table 4). The scatter diagram of the Gl and Bp measurements also shows how the samples that could be recorded and analysed cover the whole range of metric variability of the cattle from La Draga (Figure 8).

code	Ant/Posr	GL(mm)	Bp(mm)	Bd(mm)	SD(mm)
LD2FA1	Post	41,7	28,58	23,15	21,6
LD2FA10	Post	42,18	28,58	23,42	22,07
LD2FA11	Post	41,99	26,82	22,09	19,98
LD2FA12	Post	43,51	27,84	22,76	21,64
LD2FA13	Ant	41,6	31,28	27,74	25,78
LD2FA14	Post	45,08	30,03	25,63	23,99
LD2FA15	Post	42,02	28,38	23,58	21,49
LD2FA16	Post	46,39	32,3	27,25	26,43
LD2FA17	Post	42,38	26,47	22,95	21,6
LD2FA18	Ant	42,6	28,61	24,82	22,7
LD2FA19	Ant	44,77	32,65	27,26	26,57
LD2FA2	Post	41,17	26,9	22,08	20,19
LD2FA20	Ant	38,37	27,82	24,3	22,69
LD2FA21	Ant	41,37	29,49	25,87	23,73
LD2FA22	Ant	46,93	35,43	31,34	28,3
LD2FA23	Ant	41,77	29,6	25,42	23
LD2FA24	Ant	41,25	29,28	24,28	23,49

LD2FA25	Ant	41,26	28,79	23,23	21,6
LD2FA26	Post	45,46	30,45	28,25	25,32
LD2FA27	Post	41,34	28,84	23,72	23,74
LD2FA3	Ant	42,96	27,78	22,64	21,69
LD2FA30	Post	47,03	34,6	28,83	28,07
LD2FA31	Post	42,5	29,19	24,06	22,92
LD2FA32	Ant	42,92	29,24	26,05	24,26
LD2FA33	Post	42,92	32,02	26,6	26,85
LD2FA4	Ant	42,05	31,12	27,89	25,69
LD2FA5	Post	45,13	29,82	25,63	24,01
LD2FA6	Ant	42,04	28,38	23,59	21,73
LD2FA7	Post	46,57	32,18	26,99	26,04
LD2FA8	Ant	42,37	26,54	22,92	21,26
LD2FA9	Ant	42,56	28,45	24,64	22,69

Table 4 Samples of second phalanges from la Draga.

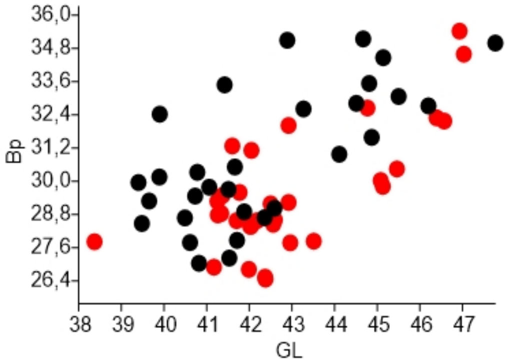

Figure 8 Dispersion plot of Gl and Bp measurements of the second phalanges of Bos taurus of la Draga (in red the samples used for geometric morphometrics and finite element analysis).

3.4.1.3. Cova de les Pixarelles (Tavertet, Spain)

A total of 465 faunal remains were found in this site, of which 375 could be classified at the anatomical and taxonomical level (Alcàntara *et al.,* 2017). At level XXII, a total of 302 remains were identified as belonging to *Bos taurus*, a species that represents 80% of the recovered assemblage. Next in order of quantitative importance are the caprines (*Ovis aries and Capra hircus*), with 18%, and finally the pig (2%). This large concentration of *Bos taurus* remains is an exceptional case in the Neolithic period in the northeast of the Iberian Peninsula. This collection has a high concentration of bones from the distal extremities, forelimbs and hind limbs, with the humerus-radiusulna and pelvis-femur-tibia being the most represented. There is therefore a clear selection of the skeletal portions with the highest meat content. These skeletal elements correspond mostly to juvenile and subadult specimens. The most represented age range is from 18 to 24 months, when the animals are at their optimal meat production (Alcàntara *et al.,* 2017; Alcàntara, 2019). The type of animal husbandry practiced indicates an intensive production that could be linked to the storage of meat.

Two specific research studies have previously been carried out on this assemblage. The first focused on the study of the pathological affectations on *Bos taurus* bones (Tonda, 2019). The results obtained showed that the group of animals with pathologies is made up of both males and females, with a slight tendency for males to be more affected. The predominant conditions are traumatic, infectious and those resulting from the use of the animals. Among the traumatic ones, 40% belong to the axial skeleton and, more specifically, to the rib section. The identification of overosifications can be closely linked to traumatic situations related to blunt shocks, blows or falls of the animal in life, which are much more likely and frequent if we take into account the orographic nature of the context, defined by steep and difficult to access terrain. In relation to the infectious ones, two pairs of connected ribs evidence a very accentuated growth of the bone mass around the point of fracture of this bone. While the process of ossification of the fracture never got to conclude it is evident that the affected animal (or animals) lived long enough to develop a large exostosis. In a similar sense, one of the hemimadibles documented exhibits a ossification of the alveolus of the first molar, meaning that in spite of the conditions of the trauma that probably caused this loss, the individual survived and lived long enough to suture the wounded mandible bone, even if not without a slight deformation in the shape of the mandible. At the same time, a first phalange evidences an exacerbated exostosis on all of its surface which might be related to either an infectious process or the result of abnormal development of bone tissue usually linked to ageing or overexertion. Finally, 46% of the affections are derived from the use made of these animals. These are located in the distal extremities and are related to the use or the mobility to which the animals had been subjected during their lifetime. In this case, there is a tendency for the bones of the posterior distal extremities to be more affected than the anterior ones, characteristic that could result from the differential non-physiological stress caused by loading and pulling work. In loading situations, the joints, especially those of the limbs, are subjected to additional stress. In tensile activities, the posterior section is subjected to excessive stress. This is the case with the metatarsals and the hip joint, which are most frequently deformed, whereas almost no anomalies are recorded in the scapula (Bartosiewicz, 2008).

The second research work carried out on this assemblage (Alcàntara, 2019) focused on the biomechanical study of the phalanges through cross-section analysis. The results obtained showed a greater relative robustness of the posterior phalanges, a characteristic that was linked to habitual movement on steep slopes, which would require the animal’s weight to be shifted onto the posterior skeleton when moving towards new pastures. However, it should be noted that there were differences in mobility between male and female specimens. These differences are especially significant in the case of the value of cortical mass, with females showing a significantly higher relative amount. Females would be more resistant to torsional stresses than males, while their mobility would be more oriented towards the anteroposterior axis.

A distinctive feature of the Cova de les Pixarelles herd is that, compared to the other bovine populations analysed to date, this group stands out due to its presence of two additional SNPs (T3+1 and T3+ 2), which indicates a more significant level of genetic diversity at this site. Higher genetic variability of Pixarelles bovine populations could be attributed to hybridisation, the arrival or acquisition of new stock, or different selective pressures between the Early Neolithic and Middle Neolithic.

The processes of natural selection and genetic drift occur naturally in wild populations; however, their combinational effect with the process of domestication and artificial selection can influence the possibility and frequency of a genetic bottleneck. Thus, two main evolutionary forces conditioning the genetic variability of populations are selection and genetic drift (Pérez-Enciso, 2009). Specialised animal husbandry can thus furthermore contribute to increased genetic variability. Once livestock farming is consolidated, selection actions would be more pronounced, with animals acquiring differentiated traits depending on their farming strategy (Helmer, 1992; Saña, 1999). With the aim of contributing knowledge for better comprehension of the domestication dynamics and their respective genetic responses during the initial phases of cattle farming, it was decided to carry out a detailed characterisation and examination of cattle specimens collected from the Cova de les Pixarelles and investigate if, similar to the earlier Neolithic *Bos taurus* population, the increase of genetic variability can be confirmed using morphometrics, biometry and biomechanical procedures.

From this site, a total of 10 first phalanges (Table 5) have been selected from the 29 recorded (Figure 9), and a total of 8 second phalanges (Table 6) from the 24 available (Figure 10).

code	Ant/Post	GL(mm)	SD(mm)	Bp(mm)	Bd(mm)
PX1FA10	Ant	57,47	24,56	29,87	26,72
PX1FA16	Ant	60,54	26,75	32,11	29,21
PX1FA17	Ant	55,96	23,55	27,41	25,8
PX1FA18	Ant	57,79	35,59	37,1	32,99
PX1FA9	Post	59,96	24,83	30,13	28,44
PX1FA11	Post	59,79	26,69	29,66	25,29
PX1FA12	Post	58,83	24,79	28,25	25,62
PX1FA13	Post	58,19	22,01	26,24	24,04
PX1FA14	Post	55,05	20,84	25,54	22,35
PX1FA15	Post	58,44	24,34	27,25	26,28

Table 5 Samples of first phalanges from Cova de les Pixarelles.

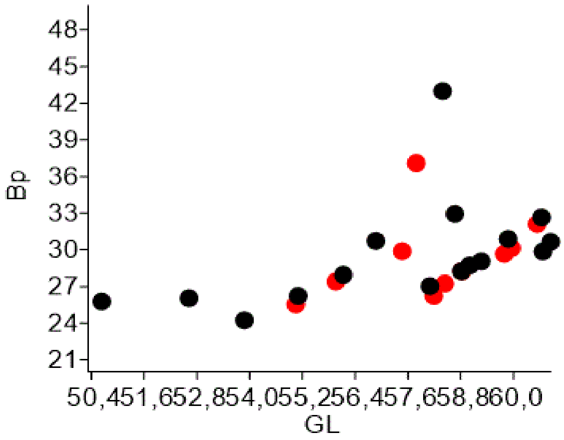

Figure 9 Dispersion plot of Gl and Bp measurements of the first phalanges of Bos taurus Pixarelles (in red the samples used for geometric morphometrics and finite element analysis).

code	Ant/Posr	GL(mm)	Bp(mm)	Bd(mm)	SD(mm)
PX2FA1	Ant	42,72	32,22	29,26	26,21
PX2FA2	Post	39,4	28,89	23,03	22,6
PX2FA3	Ant	38,55	27,27	23,28	21,8
PX2FA4	Post	38,71	28,43	24,35	23,79
PX2FA5	Post	41,27	30,99	25,76	25,54
PX2FA6	Post	37,95	30	25,08	24,28
PX2FA7	Post	38,49	26,67	22,06	21,19
PX2FA8	Post	38,35	28,42	23,79	23,1

Table 6 Samples of second phalanges from Cova de les Pixarelles.

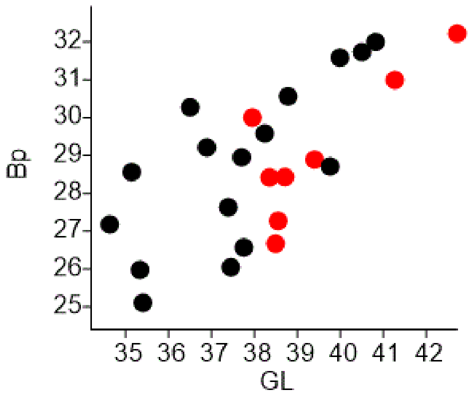

Figure 10 Dispersion plot of Gl and Bp measurements of the second phalanges of Bos taurus Pixarelles (in red the samples used for geometric morphometrics and finite element analysis).

3.4.2. Samples of pig mandibles

Sus scrofa reference sample consisted of 49 specimens, 22 females and 27 males. These specimens come from hunting activity, killed at different ages (Table 7; Figure 11).

code	SX	W	D/P	eruption stade	Location
SC10	M	18,7	D	M2 formation in crypt	Rabos Terri Cornella
SC11	M	24,3	D	M2 formation in crypt	Canet d'Adri
SC13	F	24,9	D	M2 formation in crypt	Madremanya
SC37	M	30,1	D	M2 formation in crypt	Canet d'Adri
SC46	F	14,9	D	M2 formation in crypt	Palol d'Onyar - Quart
SC50	M	45	D	M2 formation in crypt	Navata
SC51	F	31,2	D	M2 formation in crypt	Vilert
SC7	M	30,3	D	M2 formation in crypt	St Llorenç de la Muga
SC12	M	32,8	D	M2 is errupting	Llançà

SC2	M	38,2	D	M2 is errupting	La Jonquera
SC36	M	34,3	D	M2 is errupting	Vilert
SC38	M	39,4	D	M2 is errupting	Vilert
SC44	F	36,6	D	M2 is errupting	Santa Cristina d'Aro
SC49	M	29,2	D	M2 is errupting	Llançà
SC52	M	47,8	D	M2 is errupting	Aiguaviva
SC6	F	28	D	M2 is errupting	Llançà
SC1	F	47,8	P	M3 formation in cryp	Santa Cristina d'Aro
SC18	M	67,8	P	M3 formation in cryp	St Llorenç de la Muga
SC27	F	54,5	P	M3 formation in cryp	St Llorenç de la Muga
SC3	F	47,7	P	M3 formation in crypt	Santa Cristina d'Aro
SC30	F	50,7	P	M3 formation in crypt	Girona
SC39	M	31,5	P	M3 formation in crypt	Llançà
SC48	M	59,3	P	M3 formation in crypt	Llançà
SC8	M	42,6	P	M3 formation in crypt	Sant Medir - Canet d'Adri
SC9	F	47	P	M3 formation in crypt	Vilobi Brunyola
SC17	F	63,6	P	M3 is errupting - third cusp is visible	Susqueda
SC21	M	60,6	P	M3 is errupting - third cusp is visible	Canet d’Adri
SC35	F	55	P	M3 is errupting - third cusp is visible	Susqueda
SC4	M	51,5	P	M3 is errupting - third cusp is visible	La Jonquera
SC23	M	55,1	P	M3 is errupting - two cusps are out	Rabos d'Empoda
SC25	M	78,2	P	M3 is errupting - two cusps are out	Navata
SC31	M	66,1	P	M3 is errupting - two cusps are out	Selva de Mar
SC5	M	62,6	P	M3 is errupting - two cusps are out	Madremanya
SC28	M	41,1	p	M3 is errupting - two cusps are visible	Albanyà
SC34	M	52,2	p	M3 is errupting - two cusps are visible	Llançà
SC40	F	43,2	p	M3 is errupting - two cusps are visible	Canet d’Adri
SC41	F	40,2	p	M3 is errupting - two cusps are visible	Sant Martí de Llémena
SC42	M	56	p	M3 is errupting - two cusps are visible	Santa Cristina d'Aro
SC14	F	58,4	P	M3 is fully errupted	Santa Cristina d'Aro
SC19	M	63,7	P	M3 is fully errupted	Susqueda
SC20	F	56,8	P	M3 is fully errupted	Llançà
SC22	M	61,2	P	M3 is fully errupted	Palol d'Onyar - Quart
SC26	F	65,6	P	M3 is fully errupted	Rabos d'Empoda
SC29	F	51,5	P	M3 is fully errupted	Girona
SC32	F	64,4	P	M3 is fully errupted	Rabos Terri Cornella
SC43	F	72	P	M3 is fully errupted	Palol d'Onyar - Quart
SC45	M	61,5	P	M3 is fully errupted	Celrà
SC15	F	56,8	P	Permanent, M3 errupting - two cusps are visible"	Palol d'Onyar - Quart
SC24	F	40,1	P	Permanent, M3 errupting - two cusps are visible"	Navata

Table 7 Relation of Sus scrofa mandibles that compose the referential with indication of the stage of dental eruption, if it is deciduous or permanent dentition (D/P), sex (SX), weight (W) and place of origin. The animals come from the NE of the Iberian Peninsula. See Figure 11.

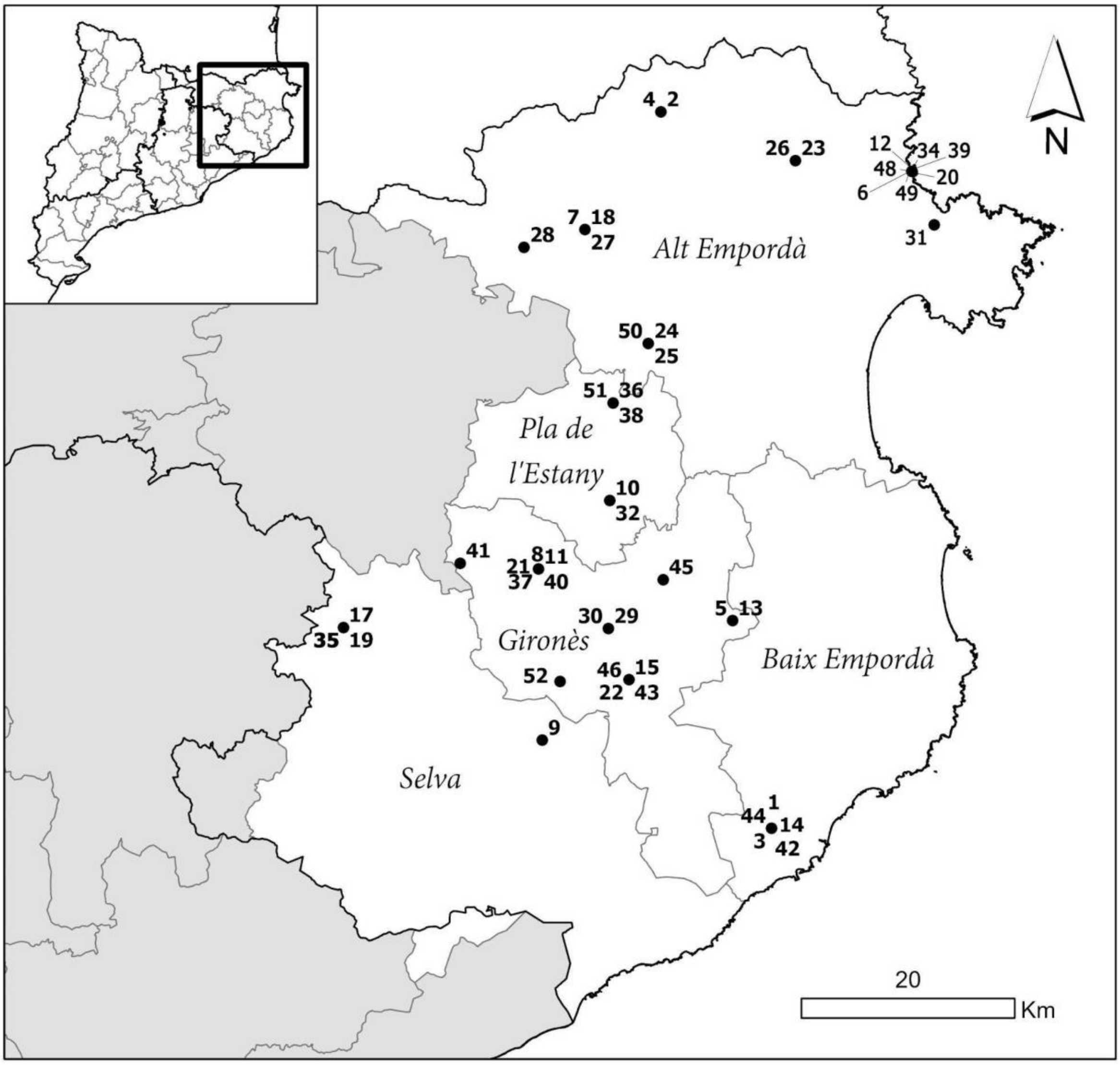

Figure 11 Locations where the sample of boars were collected.

This area is constituted by the regions of Pla de l'Estany, La Selva, Gironès, Baix Empordà and Alt Empordà, and a total of 25 different localities. Due to their ecological characteristics, this region is known as Forest Region III (Catalonia). In essence, it is a lowland region, characterized by the Empordà plain. In regard to the orography, 84% of the surface is below 400 masl and a 64% of is below 200 masl. Precisely, it is below 200 masl where we find 92% of the crops. Forests are the dominant land-cover above 200 masl. More than 60% of this whole region has a slope of less than 20%, meaning that there is a large area of soils potentially suitable for cultivation. In the flatter areas there are crops, urban areas and inland waters.

In Forest Region III, forests are the majority cover and crops represent about 31% of the region, reaching almost 40% in the regions of Pla de l'Estany and Baix Empordà. La Selva is the most forested county in this forest region and Alt Empordà is proportionally the least forested region. The proportion of scrubland is low and is especially low in Gironès, Pla de l'Estany and Selva. On the other hand, it is very high in Alt Empordà, as a consequence of the recurrence of forest fires. Both meadows and grasslands, as well as being naturally unproductive, are scarce. Artificial unproductive, which exceeds 5%, is the fourth type of cover in order of abundance, exceeding 7% in the case of Baix Empordà.

4. METHOD

4.1. Morphometrics and Linear Measurements

The study of shapes beyond the simple qualitative descriptions has a long and eventful history, dating back to the birth of illustrative craftwork when painters and sculptors started using anatomical proportions, symmetry (or lack thereof) and size as means to convey their beliefs and express ideas (Gombrich, 1995). However, it was not until the European Renaissance that architects realised that by scaling objects correctly regarding the viewpoint, 2-dimensional illustrations could have three-dimensional depth, a phenomenon later named linear perspective. In pursuit of artistic perfection, Da Vinci and Dürer proposed definitive anatomical proportions and a series of standardised isotropic and anisotropic (affine and non-affine) transformations to quantitatively describe deviation from the ideal form (MacLeod, 2017). In 1796, German polymath and naturalist Johann Wolfgang von Goethe (1749-1832) proposed a procedure juxtaposing biological forms and comparing them to understand their “morphe”, qualitative and quantitative descriptions of an organism's shape. The process was named morphology and conceived to demonstrate how the functionality of a biological structure can determine its shape and whether or not functionally homologous organs of different species possess similar morphology (Brady, 1987; Delisle, 2017). Influenced by Da Vinci, Dürer and Goethe, D’Arcy Thompson (1917: chapter 17) laid down the mathematical foundation of comparative morphology and described the ontogenetic and phylogenetical shape variations through a series of cartesian grid transformation of homologous points (Abzhanov, 2017; Bookstein, 1977). Many comparative approaches were derived from the Thompson grid transformations, which nowadays are called morphometrics. Morphometrics or shape quantitative measurement generally includes analysing patterns of shape variation and the covariance of shapes with other variables (Bookstein, 1991; Dryden & Mardia, 2016; MacLeod & Forey, 2002).

Although it may seem trivial, it is necessary at this point to put forward an accurate meaning of shape. In a literal sense, a shape is a visual representation of an object. In geometry, however (hence the term geometric morphometrics), the shape has a different definition, courtesy of David George Kendall: geometric information that remains after the removal of size, location and orientation of an object is called shape

(Kendall, 1984; Kendall *et al.*, 1999). Capturing the geometric information of an object and comparing it with another form necessitates unique sampling methods. In the case of simple geometries which follow mathematical structures (such as curves and quadrilaterals surfaces), the sampling standard is limited to parametric interpolations (polynomial, spline or Fourier), where the consequent parameters are used to quantify shape differences. For more complex objects, however, the sampling approach includes probing geometric information (*e.g.* Cartesian coordinates) at homologous locations across the sample pool. In the context of morphometrics, homologous loci are called landmarks and the whole process is known as landmark-based geometric morphometrics.

Morphometrics can be divided into two branches, traditional and geometric, depending on the nature of the measured observation. Traditional morphometrics, also known as biometry, has been traditionally used to quantify the rudimentary shape (the generic essence of form, not confused with Kendall's definition) and size of living organisms. The method incorporates subjecting continuous observations including but not limited to linear distances, area, volume, body mass, age, angles and ratios to several multivariate statistics, such as principal component analysis (PCA), factor analysis, mixture analysis, discriminant analysis, canonical variate analysis and multivariate analysis of variance (Cooke & Terhune, 2015; Marcus, 1990; Reyment, 1991; Rohlf & Marcus, 1993). On the one hand, traditional morphometrics ignores geometric shape information, and measured observations are usually highly collinear, which mandates an extra step to alleviate the issue. On the other hand, however, it is fast, cost-effective and crucial in specific scenarios such as body size and allometric studies (R. M. N. Alexander *et al.*, 1979; Bartosiewicz, 1993; Christiansen, 2002) in archaeozoology and biological distance (Pietrusewsky, 2018) in physical anthropology. The main factor behind the moderate simplicity of traditional morphometrics is its data-gathering procedure. Linear distances, angles and other biometric descriptors can be measured using a calliper (digital or conventional) or direct quantification of specimens (*e.g.* age profiling). In contrast, geometric morphometrics necessitates specimen digitisation, a complex system of converting physical shape information into digital data.

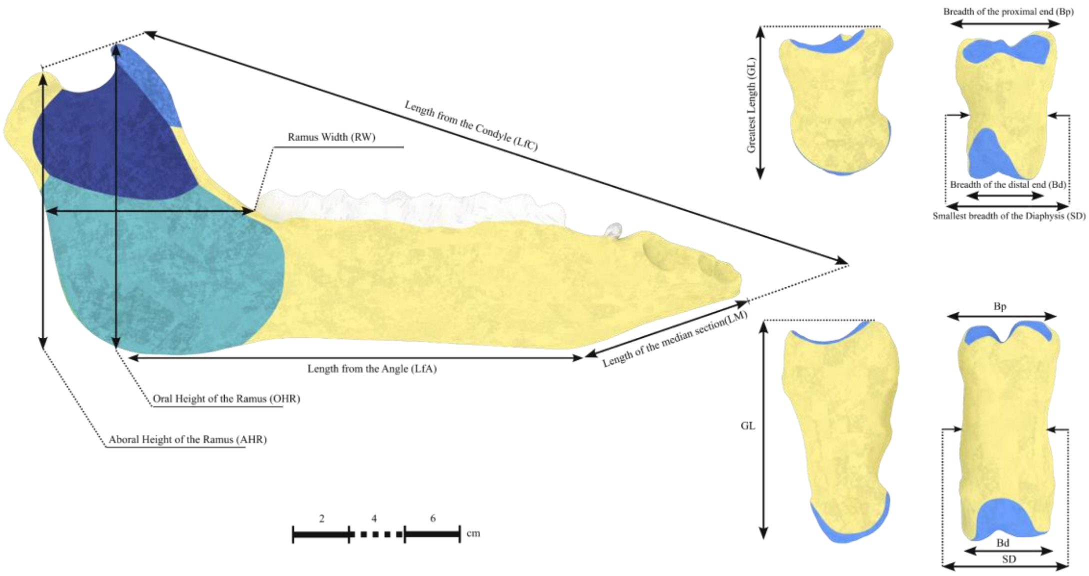

Figure 12 The linear measurements of Sus scrofa mandible and Bos first and second phalanges, following Von Den Driesch, 1976. Areas of interest, such as bone-to-bone contact surfaces and muscle insertion areas, are painted in different shades of blue.

As mentioned before, animal husbandry underlines two primary anthropogenic events: controlling animals' feeding, foraging and mating behaviours and inserting selective pressure on them to meet desirable behavioural, cultural or economic criteria. Assessment of these two events benefits greatly from traditional biometric (morphometrics) studies. For example, the factor of size (following Von Den Driesch, 1976 measurements) and tooth wear index can potentially determine the age and sex and even sometimes species of bone remains in archaeological assemblages (Greenfield, 2015; Schmölcke & Groß, 2021; Lemoine *et al.*, 2014; Magnell, 2015; Millard, 2015; O'Connor, 2015; Yu *et al.*, 2022). In the present study, six linear distances of the *Sus scrofa* mandible and four of the *Bos taurus/primigenius* first and second phalanges were recorded (Figure 12). The mandible measurements include the length of the Gonion caudale - Infradentale (length from the mandible angle, or LfA for short), the distance between the aboral side of the Condyle process and the Infradentale (length from the Condyle, or LfC for short), the length of the Mental protuberance - Infradentale (length of the mandible median section, or LM for short), the distance between Gonion caudale and the aboral side of the third molar (Ramus width, or RW for short), the aboral height of the Ramus (AHR) and the oral height of the Ramus (OHR). In the case of *Bos taurus/primigenious* phalanges (the first and second phalanges), the linear measurements consist of the phalanx's greatest length (GL), breadth of the proximal end (Bp), breadth of the distal end (Bd) and the smallest breadth of the diaphysis (SD).

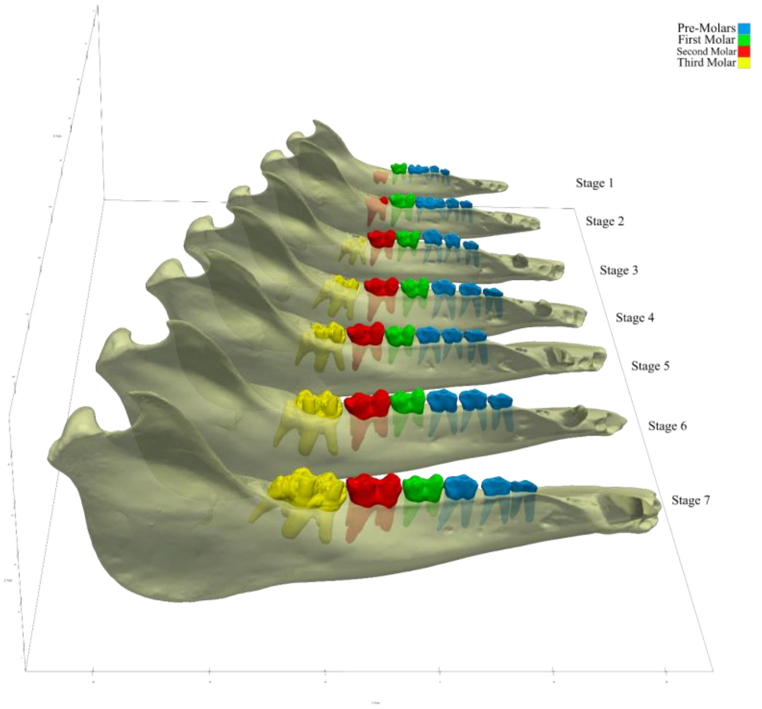

Figure 13 Postnatal growth stages of the Sus mandible reflected in the position of the second or/and third molar teeth. The first two stages represent deciduous dentitions.

The *Sus scrofa* specimens were age-profiled into seven stages based on the second and third molar growth stages, following Lemoine *et al.*, (2014) procedure with some modifications (Figure 13). The first stage corresponds to 6-8 months old ages when deciduous teeth exist and the second molar (M2) is forming in the crypt, though it has not erupted yet. Stage 2 highlights the 7-10 months interval when deciduous teeth exist and M2 has emerged. Level 3 marks 8-12 months of age when deciduous teeth shedding has been over, all teeth are permanent, and the third molar (M3) is forming in the crypt. The next phase, stage 4, points to 12-16 months of age when M3 starts to erupt, and two of the M3 cusps are visible. Stage 5 underlines 16-18 months of age when M3 is still erupting and two of the cusps are out of the crypt. Stage 6 underscores the 18-30 months interval when the third cusp of M3 is visible. Finally, phase 7 marks 30-52 months of age when M3 has fully erupted.

4.2. Geometric Morphometrics: Geometry Digitisation and Data Acquisition

Traditional morphometrics is fast to implement and can provide primary quantitative shape descriptors, such as length-width or height ratios. However, more than simple biometrical measurements are required to capture the geometric essence of a shape. Regardless of the approach to geometric morphometrics (landmark or non-landmark methods), the first step is data gathering which involves converting geometric data to digital information (*i.e.* readable by computers). In a two-dimensional scenario, digitisation includes taking pictures of specimens using a digital camera or scanning analogue film photographs of samples. In a three-dimensional experiment design, however, depending on the nature of the research, three digitisation techniques have been proposed to acquire data for geometric morphometrics: 1- laser scanning method, suitable for digitising the external structure of the intended geometry; 2- photogrammetry, which is a passive method (uses environment light source for registering a geometry) also meant to capture external shape information; 3- computerised tomography (CT) scanning, appropriate for registering external as well as internal shape information. The digitised data can be subjected to various morphometrics approaches together with different simulations, such as finite element analysis, which will be discussed in the next chapter. In the present research, the photogrammetry was not deemed accurate enough and substituted by the laser and CT scanning protocols; however, for more information on the subject, readers are referred to Georgopoulos & Stathopoulou (2017).

4.3. Laser Scanning: Fundamentals of the geometry registration

Laser scanning is an active registering method that relies on capturing an object's three-dimensional spatial information directly from a light source (*e.g.* laser beam) reflected by the said object. Following a simplified schematic, laser scanners are at least equipped with a laser emitter, which actively discharges the laser beam (in pulses or continuously) and a receiver, which captures the light source reflected by the target geometry. Laser scanners fall into two categories based on the assumed principles to resolve spatial ambiguity: pulse-based and structured light scanners.

Pulse-based scanners are based on the range measurement principle (also known as the Time-of-Flight or ToF for short), additionally equipped with an internal digital clock, and their emitter discharges beams in pulses and defines spatial coordinates of a single point on the target geometry at a time. By moving the emitter quickly, the ToF scanner can pinpoint every locale within its field of view (FoV) and measure thousands of points per second in most cases (Figure 14). Scanning open-air environments and large objects such as buildings are common use for these scanners.

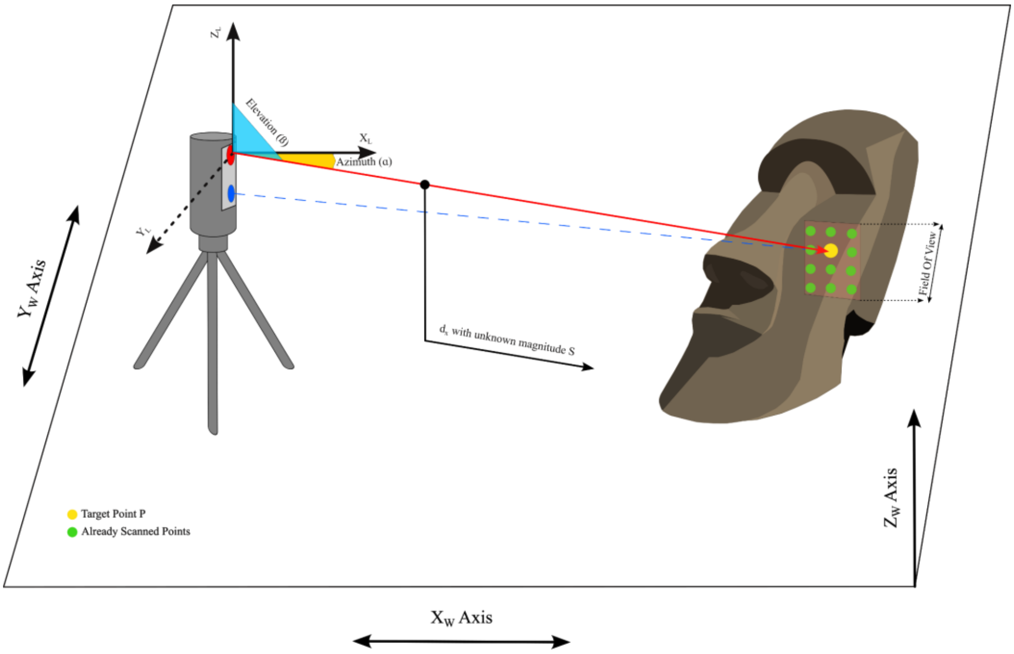

Figure 14 The schematic working principle of a Pulse-based scanner. The world coordinates are denoted as Xw, Yw and Zw, and the laser emitter coordinate axes are defined as XL, YL and ZL. The laser pulse displacement vector dx is highlighted in red, and its reflection is painted blue. Point P is a point which is being scanned. To obtain the spatial location of point P in the scanner coordinate system (eq. (3)), the magnitude of the line dx (S) has to be calculated using eq. (2). The elevation and azimuth angles of a laser pulse are known characteristics of the scanner.

ToF principle is based on Newton's second law, indicating that if the acceleration rate is constant, it is possible to contemplate average velocity as the first derivative of displacement regarding time, such that:

$$\tilde{v} = \frac{dx}{dt} \tag{1}$$

Where $\underline{v}$ stands for average velocity (of a laser beam), x and t represents displacement (in this context, displacement vector between the emitter (LE) and a point reflecting the laser beam) and time (two-way laser beam travel time) respectively. Since the average velocity of the laser (speed of light ≊ 3.108 Km/s) and the dt (measured by the internal scanner clock) both are known, one can re-write the eq. (1) to calculate the displacement vector dx:

$$dx = 3.108e^{8} \times \frac{dt}{2} \tag{2}$$

By knowing the distance (magnitude of the displacement vector dx, denoted by S), elevation (vertical angle ß) and azimuth (horizontal angle ɑ), coordinates of the point in question (Xp, Yp and Zp) can be defined using the law of sines (Wu *et al.*, 2022):

$$Xp = S.\cos\beta.\cos\alpha; \quad Yp = S.\cos\beta.\sin\alpha; \quad Zp = S.\cos\beta \tag{3}$$

On the other hand, structured light scanners are suited for scanning smaller objects with complex geometries (*e.g.* biological specimens) from closer distances, with a higher resolution. They are sometimes built as portable handheld devices equipped with an emitter propagating laser beams continuously, which can concurrently pinpoint all points in their field of view and a receiver, functioning as a camera to capture the reflected laser beams. Unlike pulse-based scanners, structured light scanners record spatial information by projecting continuous light patterns such as strips or grids toward a geometry (Figure 15). The projected laser patterns create a plane LP with a known normal vector n, such that $n = [a, b, c]^T$. Consider P'_0 as a random known point on the LP and P as a point on the target geometry. In order to calculate the Cartesian coordinates of P in the world coordinate system, following Alonso *et al.*, (2020), the first step is to describe the LP implicitly.

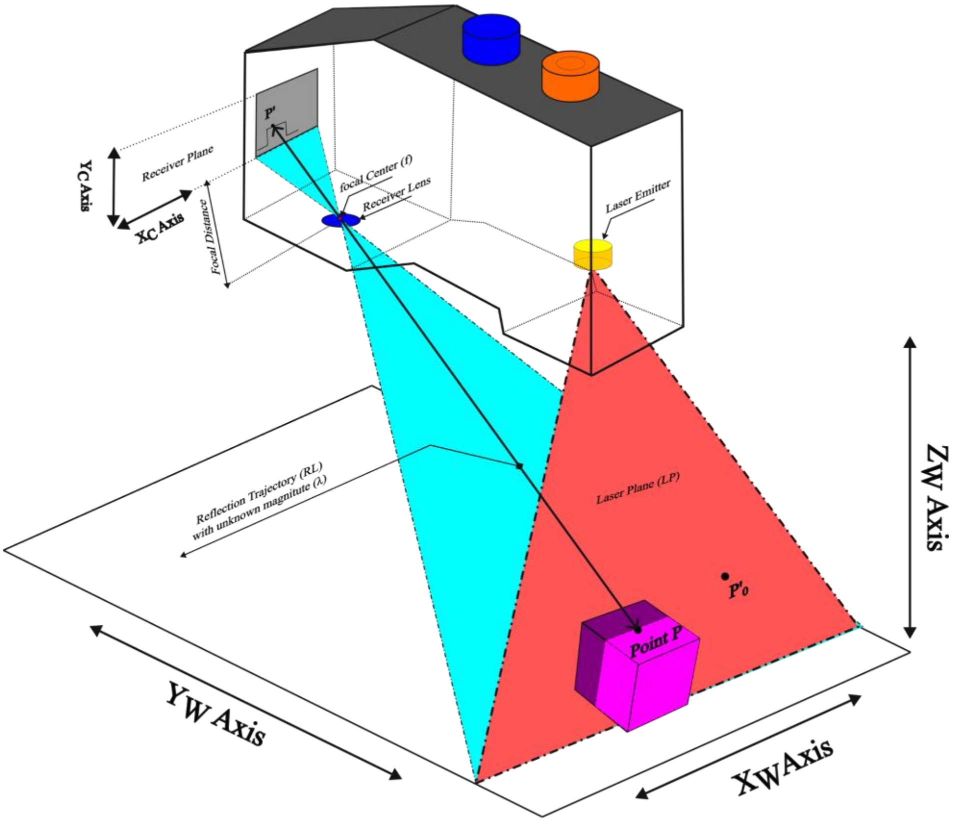

Figure 15 The schematic working principle of a structured light scanner. The world coordinates are denoted as Xw, Yw and Zw, and the receiver coordinate axes are defined as XC and YC. Point P is a point on the surface of geometry, P' is the reflection of the P in the receiver coordinate system and P'0 is a random point with known coordinates on the laser plane (LP). To obtain the location of the point P, one must first calculate the magnitude of the line connecting P to P' (RL) using eq. (6). The unit normal of the plane LP and the direction of the line RL are intrinsic characteristics of the scanner and can be recalculated via the calibration process.

$$PL = \{P : n(P - P_0')\} \tag{4}$$

Point P reflects the laser light toward the receiver (camera) via a trajectory line RL, with an unknown length (λ) and known directional unit vector v. Denoting the receiver focal centre as f, one can describe RL parametrically.

$$RL = \{f + \lambda v, \lambda \in \mathbb{R}\} \tag{5}$$

Assuming that PL and RL intersect at a single point (if and only if $n \times v \neq 0$), then the intersection of the line RL and the plane PL contains exactly one point, point P, which belongs to the PL and RL simultaneously. Therefore, by substituting eq. (5) in eq. (4), it is possible to calculate the unknown λ:

$$n(P - P_0') = n(f + \lambda v - P_0') = 0 \implies \lambda = \frac{n(f - P_0')}{nv} \tag{6}$$

With the multiplication of the magnitude λ and directional vector v, the spatial location of the point P in the world coordinate system can be calculated. In the presented research, a handheld structured light scanner, CREAFORM GO!SCAN 20, with a capture resolution of 0.1mm, was used for digitising *Sus scrofa* mandibles.

4.4. Laser Scanning: Post-Processing

Regardless of the underline procedure, the main output of a laser scanner is 3-dimensional raw coordinates of the registered points, also called a point cloud. To digitally reconstruct the surface of a scanned geometry, one needs to define how points connect to their neighbours using a point cloud triangulation or surface reconstruction procedure. Point cloud triangulation is a progressing subject in the computer vision field and incorporates several algorithms, including but not limited to Delaunay triangulation (Boissonnat, 1984; Sloan, 1987), Ball-Pivoting (Bernardini *et al.*, 1999), and Poisson (Kazhdan *et al.*, 2006) mesh reconstruction strategies. The surface reconstruction problem can be summarised as finding a 3-dimensional geometry whose boundary is a surface on which the set of unstructured cloud points (points with ambiguous connectivity) are located. The most minimalistic approach is creating structured points (points with known connectivity) by drawing three points at a time from the cloud and assigning them to form triangles, hence the name triangulation. Each triangle is called an element, and together, they form a polygonal surface mesh. The challenging part is the fact that any triplets in the cloud can form a triangle; therefore, the resulting polygon is not unique, and more often, it does not approximate the original scanned geometry well. The solution is to restrict and put conditions on some characteristics of the triangular elements (*e.g.* a minimum or maximum vertex angle or relative distance) or the polygon itself. In a general 3-dimensional scenario, the constructed polygon must be a closed surface (no loose elements condition). A polygon is a closed surface if it follows the simplicial conditions (Giblin, 2010: chapter 2), indicating that 1- elements must be disjoint, or if not, must have a single or two common vertex/vertices, 2- considering the totality of triangular elements as a collection denoted by T, all members of T must be connected, 3- for every vertex v which is shared between multiple triangles belongs to the T, the linkage of the opposite edges of v must form a simple closed polygon. In addition to the no loose elements condition, different reconstruction methods also enforce various additional prerequisites. Delaunay triangulation (named after Russian mathematician Boris Nikolayevich Delaunay), for example, constructs structured points (points with known connectivity) where no vertex lies within the circumcircle of any triangular element (the circle passing through the three vertices of a triangle is called its circumcircle). The process begins with generating a triangulation and then continues by checking if any vertices fall within the circumcircle of another triangle. If they do so, swapping the diagonal separating the two triangles will fulfil the condition (Sloan, 1987).

The Ball-Pivotting algorithm (BPA) restricts the triangulation by putting a maximum distance cap on the vertices of a triangular element. Starting from a random point in the cloud, BPA rolls a virtual ball with a predefined radius (defined by the user) and captures three points within its circumference. The three points form a triangle, and then the ball pivots against one of the triangle's three sides and rolls again. The ball continues to roll until the polygonal mesh is wholly formed (Bernardini *et al.*, 1999). Compared to the Delaunay triangulation, BPA is more robust in dealing with noisy scanned data, but it has its limitations. The algorithm is sensitive to the size (radius) of the ball, and if the geometry has a complex shape (*e.g.* creases and valleys), a large radius size does not capture the details and simplifies the geometry. In addition, the triangulation might be terminated prematurely if the ball falls off the geometry (*e.g.* when the geometry has holes or points are unevenly spaced in the cloud).

The Poisson surface reconstruction (PSR) strategy is the most robust and recent among the more popular triangulation algorithms. It is categorised as an implicit surface reconstruction method in which the polygonal surface is constructed by interpolating a 3-dimensional plane into the point cloud. PSR can be summarised in three steps (Kazhdan *et al.*, 2006): 1- calculating normals to create a vector field, 2-

defining the implicit function (indicator function) over the scalar field and 3- extracting the iso-surface. The first step necessitates extra information regarding the normal direction of points in the cloud, which are provided by laser scanners; otherwise, one can calculate them using principal component analysis. The second step includes finding the indicator function whose gradient (∇) approximates the provided vector field. When a function is not integrable, such as the indicator function, this problem can be solved using a linear least squares optimisation:

$$\min_X \|\nabla X - \overrightarrow{V}\| \tag{7}$$

Where X and V stand for the indicator function and the vector field, respectively. By applying the divergence operator to eq. (7), a Poisson equation can be formulated:

$$\Delta X \approx \nabla . \nabla X = \nabla . \overrightarrow{V} \tag{8}$$

Where ∆X stands for the Laplacian (divergence of the gradient) of the indicator function. After solving the Poisson equation (eq. (8)), the final step is extracting iso-surfaces from the indicator function, utilising a variation of the Marching cubes to octree representations (Kazhdan *et al.*, 2007). In the present research, the surface reconstruction process was performed using VXmodel, a post-processing software that accompanies CREAFORM portable laser scanners.

4.5. Computerised Tomography (CT) Scan: Fundamentals of the geometry registration

CT scanning is another active registering method that relies on capturing an object's characteristic property, (uncalibrated) density, from an X-ray source absorbed by the said object. CT scanners are equipped with an X-ray emitter (tube), which discharges pulses of high penetrating (high-energy) electromagnetic radiation and a receiver in the opposite direction of the emitter, which captures the ray source passed through the target geometry. Depending on how the emitter moves relative to the object, CT scanners are divided into two types: axial and helical. In the axial scanner, as the name suggests, the emitter moves in the axial direction and discharges discontinuous pulses of X-ray at certain intervals along the axis of movement. The Z-directional resolution of the scanned data depends on the said intervals. In helical scanners, however, the emitter rounds around the geometry in a spiral pattern while continuously emitting the X-ray beam, and the Z-directional resolution of the scanned data depends on the distance between helices (Hu, 1999). As the X-ray passes through the object, its attenuation is measured as the difference between the initial intensity and the intensity of the ray captured by the receiver. The ratio of the attenuation to the local thickness of the scanned geometry is called the Hounsfield units (μ) and can be calculated as follow (Bushberg *et al.*, 2011):

$$\mu = \frac{ln(D_0 - D_X)}{X} \tag{9}$$

Where D_0 and D_x stand for the initial intensity and the intensity of the X-ray at the depth X, respectively. At each specific interval (depending on the set Z-directional resolution), the scanner produces a grey-scale slice of an image populated with the Hounsfield units. A compilation of all slices of a scanned object, together with some other information such as the date of scan, creates a file standard system named DICOM (abbreviation of Digital Imaging and Communications in Medicine).

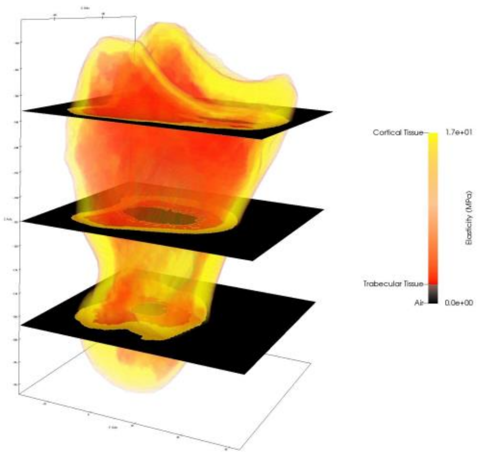

Figure 16 The voxel grid of a Bos first phalanx, constructed from a DICOM stack, and renderred volumetrically

DICOM slices can be interpolated to a three-dimensional image and rendered volumetrically (Figure 16), or can be segmented (*e.g.* selecting pixels within a specific Hounsfield range) to create a point cloud. The resultant point cloud can be triangulated, following the same procedure mentioned for the laser scanners. The polygonal mesh can be used in the geometric morphometric analysis or converted to patches of spline surfaces suitable for the finite element analysis.

4.6. Geometric Morphometrics: Why Landmarks?

The digitisation of geometry provides a domain of study appropriate for quantitative geometric analysis. Consequently, each domain must be sampled into morphometric variables, fitting for comparative univariate or, more probably, multivariate statistics. Unlike descriptive statistics, comparative studies highlight (geometric) differences across specimens using purposive sampling. Assuming each digitised sample represents a distinct population, various purposive sampling strategies, namely maximum variation and homogeneous, can be applied to answer two fundamentally different questions. When the study aims to compare common morphological characteristics across populations, such as geometric size and displacement maps (Toussaint *et al.*, 2021), the symmetric distortion energy of conformal maps (Koehl & Hass, 2015) and parametric description of (gastropod) coiling patterns (Raup & Michelson, 1965), the maximum variation sampling strategy is recommended. In these scenarios, which can be categorised as landmark-free morphometric methods, geometric information is reduced to spatially independent variables representing different morphological aspects of each population.

In contrast, homogeneous sampling is advisable when comparing more local and detailed morphological characteristics of digitised domains. For this purpose, it is necessary to probe geometric information (*e.g.* Cartesian coordinates) at homologous locations across all specimens. Following Kendall's definition of shape (Kendall, 1984; Kendall *et al.*, 1999), which was mentioned earlier, homologous probing entails establishing a standard coordinate system to make registered geometric information spatially independent. The process of determining a common coordinate system, which is also called rigid registration, or superimposition, involves overlaying all specimens on top of a template (such as the average of all samples or a specific individual) and calculating a transformation matrix that minimises the spatial distance between each specimen and the template. Based on the implementation, rigid registration can be achieved automatically or manually. The automated registration techniques, such as iterative closest point, or ICP for short (Besl & McKay, 1992), can also be utilised in landmark-free morphometrics (*e.g.* Pomidor *et al.*, 2016), calculate the transformation matrix by solving a non-linear optimisation problem which minimises the said spatial distance. Since the automated procedure is based on a non-linear optimisation, the results' quality depends on the problem's initial formulation to avoid local minima (Mohtashami *et al.*, 2022), and therefore, it does not guarantee the best transformation matrix. Manual registration, on the other hand, is considerably laborious but is more robust and reliable. It requires the manual selection of correspondent locations called homologous landmarks for each digitised domain (Bookstein, 1991: chapter 3). For this reason, manual registration is named the landmark-based superimposition (or Procrustes superimposition), and the following morphometrics procedures are anointed as landmark-based morphometrics. The details regarding the Procrustes superimposition will be discussed in the next section. In the present study, landmark-based morphometrics was chosen to capture morphological information since it is more reliable and computationally efficient than automated methods. For more information about automated registration techniques, readers are referred to Tam *et al.*, (2013).

4.7. Geometric Morphometrics: Landmarks and their types

Three distinct perspectives exist on the homology of landmarks: biological, functional and mathematical. The biologically homologous landmarks (Bookstein, 1990; 1991:chapter:3) define biologically identical locations such as the intersection point of three or more tissues, the centre of tiny inclusions and the intersection of curvy structures with the plane of symmetry (type I), protrusions and curvature maxima (type II), and the so-called external points such as endpoints of the largest diameter of a specimen, centre of gravity, intersection of curvy structures and evenly-spaced intervals along a curve or over a surface (type III). Bookstein further discussed that the underlying digitisation process and morphometric analysis of type I and type II landmarks are identical, and the result of their morphological analysis potentially reflects biomechanical factors. Type III landmarks, however, do not necessarily correspond to significant biological or biomechanical conditions; they are reportedly deficient since their location is contingent upon the location of the other landmark and (or) the orientation of the specimen (Bookstein, 1990; Bookstein *et al.*, 2002; Gunz *et al.*, 2005; MacLeod, 2013), and one needs to interpret their morphometric results discreetly. Since their proposal, categorising biological landmarks (also called Bookstein landmarks) has been a source of confusion amongst morphologists and morphometricians. Some of the issues are related to nomenclature. For instance, Sforza *et al.*, (2013) referred to types I, II and III as anatomical, geometrical and extremal landmarks, respectively. Bookstein (1990) himself, in the same publication, appointed different names (anatomical, processual and extremal) to the three types of landmarks. Stull *et al.*, (2014) suggested more explicit definitions for the three types of Bookstein landmarks. They distinguished type 1 as landmarks which pinpoint biologically distinctive patterns of form, type II as landmarks defined by geometrical criteria and type III as landmarks whose locations depend on other landmarks' locations. The other primary source of confusion arises from the uncertainty of assigning one of the three types to a landmark. The ambiguity of type assignment is pronounced specifically between types II and III landmarks, where, for example, it is not clear that the mandibular gonion (a point at the intersection of lines tangent to the posterior border of the ramus and the lower border of the mandible) belongs to the type III (Bookstein, 1990) or type II (Sforza *et al.*, 2013). This issue can be alleviated by substituting type III landmarks with mathematically homologous landmarks, which will be discussed in the following sections.

In evolutionary biology and functional morphology, homology is a concept comparable to what was discussed above, but it has a different interpretation. In functional morphology, as the name suggested, homology refers to the likeness of the function. For example, the fingertip of the distal phalanges in a human hand is homologous to the distal extremity of the *Bos* third phalanx. Some evolutionary biologists proposed different terminology, such as analogous or correspondence instead, to avoid confusion with biological homology (Klingenberg, 2008), while others (de Pinna, 1991) believe the existence of multiple terms for a similar concept is a source of confusion and insist on the use of homology in functional and evolutionary biology as well. Therefore, functionally homologous landmarks are the same as the Bookstein landmarks.

Mathematically homologous landmarks were proposed to address the deficiency of the type III landmarks, *i.e.* the dependency of their placement to the location of the other landmark and (or) the orientation of the specimen. In a morphological sense, homology is not limited to the pointwise corresponding locations; structures such as bone-to-bone contact surfaces, muscle insertion areas, the outline of specimens (in a 2-dimensional scenario) and tissue surfaces can also be homologous. Meanwhile, it is challenging to represent a structure with a single landmark (Oxnard, 1978). To overcome the problem, Bookstein (1990) initially proposed type III landmarks, suggesting that the essence of a structure can be captured by its centroid or equidistant sampling (putting equidistant landmarks along a curve if the structure is represented as an outline, otherwise in a grid pattern over the surface) of the said structure. In the same publication, he argued that equidistance landmarking is deficient since the location of such type III landmarks does not necessarily reflect the morphology of the structure and the choice of the starting point (and the endpoint in the case of an open curve) and the resolution of the sampling (number of equidistant landmarks) have more impact on the resultant landmark configuration than the geometry of the structure. The proposed solutions (or better state them as mitigations) were to integrate mathematically defined shape descriptors (outline analysis) or mathematically defined landmarks (sliding semi-landmarks) into the analysis, which lessens (do not altogether remove; hence mitigation might be a better choice of the expression instead of solution) the inter-dependency of the morphometric results.

Outline analysis is a collection of methods specifically designed to capture the geometric information of the outline of a structure. Rohlf (1990) summarised the premise of the outline approach as 1- registering geometric information (such as the tangent of a curve) at equidistant locations along the outline of a structure or 2- dividing an outline curve into numbers of equal-length segments (the segment number must be consistent through all specimens), interpolating each segment as a parametric curve and registering the parameters instead as morphometric descriptors (*e.g.* Fourier and Eigenshape analysis). These descriptors are spatially independent and can be used directly in multivariate shape analysis. The major setback of the outline approach is the dimensionality of the data; it is only applicable to 2-dimensional analysis. In a 3-dimensional scenario, structures are represented as surfaces rather than curves, necessitating different strategies, such as semi-landmarks, to capture their geometric information.

To mitigate the deficiency of type III equidistant landmarks, Bookstein (1997) proposed sliding semi-landmarks for analysing curvatures in 2-dimensional data, which was later generalised to 3-dimensional analysis (curves and surfaces) by Gunz *et al.*, (2005). The general premise of sliding (semi) landmarks is allowing equidistance landmarks to slide from their original position alongside a curve or over a surface, minimising "morphological differences" across all specimens. As a result, the new location of slid landmarks also recollects the structure's geometrical information rather than solely reflecting the spatial information of the other landmarks. The term "morphological differences" in this context refers to disparities of a single quantitative criterion representing the overall shape of each specimen. The bending energy (Bookstein, 1996a) and the Procrustes distances (Sampson *et al.*, 1996) are the most widely used minimisation criteria for sliding semi-landmarks. The implementation of sliding semi-landmarks will be discussed in the upcoming sections.

4.8. Geometric Morphometrics: Procrustes Superimposition

In morphometrics studies, as mentioned before, landmarks are used to probe (sample) morphological information over a series of specimens. The information is usually collected as each landmark's local Cartesian coordinates, posing significant spatial dependency. Using the raw spatially dependent landmark coordinates in multivariate statistics will introduce unwanted noise to the covariance matrix, making observation of the geometric differences very difficult, if not impossible. This problem can be solved by standardising registered coordinates based on Kendall's definition of shape: Shape is the geometric information remaining after an object's size, location, and orientation have been removed (Kendall, 1984; Kendall *et al.*, 1999) and one of the primary strategies for achieving this is Procrustes superimposition. In practice, Procrustes superimposition includes defining a global coordinate system, also called the template, and mapping the registered landmarks from their local coordinate system to the global coordinate system.

Selecting a global coordinate system (template or reference) depends on the design of a morphometric study. In comparative morphometrics, if the goal is to compare specimens against a specific reference sample and observe their morphometric disparities, then the said reference sample defines the global coordinate system and landmarks on the reference sample are called template configuration. Contrarily, if the objective is to compare specimens against their average (consensus), then the consensus landmark configuration represents the mentioned template. It is essential to clarify some terminologies regarding morphometric study designs: in the first case, the morphometrics analysis is called ordinary Procrustes analysis (OPA), and in the second case, where the average of landmarks is selected as the template, the approach is called generalised Procrustes analysis (GPA for short). In the present study, where the aim is to observe possible morphological disparities induced by sexual dimorphism (in the case of *Sus scrofa* mandible) and morphological dissimilarities in response to herd management strategies (in the case of *Bos* first and second phalanges), a single specimen was selected as the template for each scenario (an adult male specimen for *Sus* mandible and an intensively exploited domesticated specimen for *Bos* phalanges), making it feasible to observe morphological changes alongside the provided spectrum (male-female and intensive - relaxed herd management spectrums). Therefore, the implementation of the GPA approach will not be discussed here.

After choosing the type of study (*e.g.* OPA in the present research), the next step is to remove the effect of size, if it is necessary. Sometimes in evolutionary biology and ontogenetic studies, the morphological factors are studied in conjunction with body size (this is called Morphological allometry), and therefore, removing the effect of size is not encouraged (Bensmihen *et al.*, 2008; Bookstein, 2021; Milne & O’Higgins, 2012; Pélabon *et al.*, 2014). Nevertheless, when the size factor is not desirable, the geometric data (*i.e.* landmark coordinates) must be scaled to the size of the template configuration (the collection of landmarks sampled on a specimen is called landmark configuration). In geometric morphometrics, the centroid size is the primarily used quantity representing the size of a landmark configuration (Bookstein, 1986). However, other quantities such as normalised centroid size (in the case of missing landmarks, Dryden & Mardia, 2016:chapter 2), the baseline size (Dryden & Mardia, 1992) and the cubic root of the convex-hull volume (Dryden & Mardia, 2016: chapter 2) are viable alternatives. The centroid (centre of gravity) of a configuration is the arithmetic mean of coordinate components (x, y, and z in a 3-dimensional scenario) of the configuration, denoted as C ($\bar{x}$, $\bar{y}$, $\bar{z}$), and can be calculated as follow:

$$C(\overline{x}, \overline{y}, \overline{z}) = (\frac{\sum_{i=1}^{n} x_i}{n}, \frac{\sum_{i=1}^{n} y_i}{n}, \frac{\sum_{i=1}^{n} z_i}{n}) \tag{10}$$

Where n stands for the number of landmarks in a configuration and x_i, y_i and z_i represent spatial coordinates of the i^{th} landmark. The centroid size (CS) of a coordinate configuration can be calculated as follow (Dryden & Mardia, 2016: chapter 2):

$$CS = \sqrt{\sum_{i=1}^{n} ||X_i - C||^2} \tag{11}$$

Where X_i denotes the i^{th} landmark in a configuration, C represents the centroid of the configuration and $||.||^2$ stands for the Frobenius norm. In ordinary Procrustes analysis, by dividing the centroid size of each specimen (CS) by the centroid size of the template (CS_T), and after the multiplication of the resultant scalar (SF) by the corresponding landmark configuration, all samples will be scaled to the size of the template and the effect of size will be removed. The process can be implemented by assuming:

$$\mathrm{SF}_i = \frac{CS_i}{CS_T};$$

$$Conf_i = \begin{bmatrix} x_1 & y_1 & z_1 \\ \vdots & \ddots & \vdots \\ x_j & y_j & z_j \end{bmatrix};$$

$$i \in [1, n], j \in [3, m];$$

Where SF_i, CS_i and $Conf_i$ stand for scaling factor, centroid size and landmark configuration of the i^{th} sample, respectively, n and m denote the number of specimens and the number of landmarks per specimen, respectively (It is important to note that the minimum possible number of landmarks per sample is 3). Consequently:

$$ScaledConf_i = SF_i \cdot Conf_i \tag{12}$$

Where $ScaledConf_i$ denotes scaled configuration of the i^{th} specimen. In generalised Procrustes analysis (GPA), however, it is more practical to scale all landmark configurations to the unit size 1:

$$ScaledConf_i = \frac{1}{CS_i} \cdot Conf_i$$

The next step is to compute translation vectors and the rotation matrices to superimpose (scaled) configurations on the template configuration. The translation vector (t) connects a (scaled) configuration centroid to the template centroid. Calculation of the translation vector is straightforward:

$$\overrightarrow{t_i} = ScaledC_i - C_T \tag{13}$$

Where $ScaledC_i$ and C_T are centroids of the scaled i^{th} configuration and centroid of the template, respectively (calculated via eq. (10)). It is worth mentioning that if one decides not to remove the effect of size, the centroid of original i^{th} configuration must be plugged in the eq. (13). Adding a configuration to its translation vector will remove the effect of location from the said configuration.

The rotation matrix is a 3x3 matrix (in 3-dimensional space) which minimises the root mean squared deviation between a (scaled) configuration and the template. The problem, also called the Procrustes orthogonal problem, was solved initially by Green (1952), suggesting that the best rotation matrix can be calculated using the singular value decomposition (SVD). Assuming $A_{(nx3)}=(a_1, \dots, a_n)$ is a configuration of n landmarks after the removal of location (not necessarily scaled), and $B_{(nx3)} = (b1, \dots,$

bn) is the template configuration. The goal is to find an orthogonal rotation matrix R such that:

$$argmin\sum_{i=1}^{n}||Ra_i - b_i||^2$$

Where $||.||^2$ and n stand for the Frobenius (L_2) norm and the number of landmarks in the configuration, respectively. To find the R, one must first build a square covariance matrix H, such that:

$$H = A^T.B$$

Where A^T stands for the conjugate transpose of the matrix A. The next step is to decompose matrix H to its (three) components using the singular value decomposition (SVD):

$$SVD(H) = UDV^T \tag{14}$$

Where U is a unitary square matrix, D is a rectangular diagonal matrix with real numbers on the diagonal and zero elsewhere, and V^T is the conjugate transpose of V, a square unitary matrix. Finally, the best rotation matrix, R, can be calculated as:

$$R = U.V^T \tag{15}$$

In 3-dimensional space, R is a squared 3x3 matrix. Multiplication (dot product) of R into configuration A solves the orthogonal Procrustes problem. This procedure is also called partial Procrustes superimposition. Later, Kabsch (1976, 1978) and Umeyama (1991) proposed an extension to this methodology which not only calculates the best rotation matrix but also prevents possible reflection and estimates an extra scaling factor which improves the Procrustes fit. This methodology is named full Procrustes superimposition, or Kabch-Umeyama, and can be implemented right after eq. (14), as follow (Umeyama, 1991):

$$c = \frac{trace(D.S)}{\sigma^2 A} \tag{16}$$

Where trace of a matrix is the sum of the diagonal elements of a square matrix, c stands for Umeyama scaling factor, σ^2A is the average of column-wise variance of configuration matrix A, D is the diagonal matrix from eq. (14), and S denotes a diagonal matrix of size n (n = the number of landmarks in the configuration), such that:

$$S = \begin{cases} I \\ diag(1, 1, ..., 1_{n-1}, -1); if : det(U).det(V) = -1 \end{cases}$$

Where I stands for the Identity matrix. It is essential to mention that eq. (16) is true if and only if the rank of covariance matrix H is equal or greater than n-1 (*i.e.* when landmarks do not overlap, otherwise, the problem becomes ill-conditioned, and the solution is beyond the scope of this research). Then, to overcome the possible reflection, the partial Procrustes problem (eq. (15)) can be re-written as follow:

$$R = U.S.V^T \tag{17}$$

And if a full Procrustes analysis is desired, the configuration can be scaled further via scaling factor c (from eq. (16)), to obtain a better Procrustes fit:

$$R = c(U.S.V^T) \tag{18}$$

In conclusion, the overall Procrustes mapping of a landmark configuration A (scaled or non-scaled) to a template configuration B can be summarised as follow:

$$A \mapsto B = R.(A + \vec{t}) \tag{19}$$

Where $\vec{t}$ is the translation vector (eq. (13)) and R is the rotation matrix eq. (18) or eq. (17)). In addition to normalising landmarks and removing their spatial dependency, Procrustes mapping has another critical application. It can superimpose a polygonal mesh on another (*e.g.* template) mesh. By doing so, one can isometrically scale meshes to a specific extent, and remove the effect of size in mesh-related calculations, such as finite element analysis. The process immediately follows eq. (19), by building a homogenous 4x4 affine transformation matrix T which maps a mesh M to the template mesh K:

$$\mathrm{T}_{affine} = \begin{bmatrix} r_{1,1} & r_{1,2} & r_{1,3} & t_1 \\ r_{2,1} & r_{2,2} & r_{2,3} & t_2 \\ r_{3,1} & r_{3,2} & r_{3,3} & t_3 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

Where r and t are components of the rotation matrix (eq. (18) or eq. (17)) and translation vector (eq. (13)), respectively. The next step is to represent mesh vertice coordinates as a homogenous matrix M $_{(mx4)}$, where m stands for mesh number of vertices, such that:

$$\mathrm{M} = \begin{bmatrix} x_1 & y_1 & z_1 & 1 \\ \vdots & \ddots & \vdots & \vdots \\ x_j & y_j & z_j & 1 \end{bmatrix}$$
$$\mathrm{j} \in [3, m];$$

Then, the affine mapping of M to the template mesh K can be formulated as follow (Lynch & Park, 2017: chapter 3):

$$M \mapsto K = T_{affine}.M^T \qquad (20)$$

Where M^T stands for transpose of M.

4.9. Geometric Morphometrics: Procrustes Shape Descriptors

After a Procrustes superimposition and transformation of landmarks to a global coordinate system, the said landmarks can be used to derive three primarily used assortments of morphological descriptors: shape coordinates, Procrustes distance and Procrustes residuals (Bookstein, 1996b; Goodall, 1991; Klingenberg, 2020;

Rohlf, 1990, 2000). Utilising landmark coordinates (shape coordinates) as morphological descriptors requires a brief introduction to the concept of shape space and Procrustes distance. Procrustes distance is the Procrustes superimposition's goodness of fit and can be defined as the sum of squared euclidian distances between superimposed specimen landmarks and their counterparts on the template. The goodness of fit (Procrustes distance) is functional as a general shape descriptor or an optimisation criterion for sliding semilandmarks. Kendall (1984) proved that all possible configurations of a shape are situated on a (kp - k - 1 - k(k-1)/2)-dimensional hyper hemisphere, where k and p stand for coordinate dimensions (*e.g.,* in a 3D scenario k = 3) and the number of landmarks of a configuration respectively. After superimposition, this hyper hemisphere (a general term for a hemisphere with higher than three dimensions) is called Kendall shape space which has a unit radius, and the template configuration resides at its pole (Rohlf, 1990). As Kendall's shape space is hemispherical and curved, data which reside there cannot be analysed with linear statistics such as principle component analysis or ordinary linear regression (Claude, 2008: chapter 4; Rohlf, 2000). The solution is to project the hemispheric shape space into a Euclidian tangential plane at the template configuration (pole of the hemisphere), following a trigonometric relationship (Claude, 2008: chapter 4):

$$P_{x,y,z} = \frac{K_{x,y,z}}{cos(d)} \tag{21}$$

Where K is a point coordinate in Kendall's space, P stands for the projected coordinate of K on the tangent plane, and d represents the Procrustes distance of the configuration to which point K belongs.

Using landmarks coordinates or Procrustes distance as shape descriptors is suitable when the study's aim is limited to highlighting morphological variations across a sample pool (*e.g.* Harvati *et al.*, 2004; Gunz *et al.*, 2009), observing morphological covariations and integration (*e.g.* Bookstein *et al.*, 2003; Klingenberg *et al.*, 2003) and correlation with external factors such as size, geography, phylogenetic distances and diet (*e.g.* Frost *et al.*, 2003; Klingenberg & Gidaszewski, 2010). For more complex inquiries, such as functional morphology, it is inconvenient to correlate spatial coordinates to a biomechanical phenomenon. As Cooke & Terhune (2015) highlighted, the problem arises from the fact that biomechanical factors are expressed in vector form (they have magnitude and direction, *e.g.* displacement) while shape coordinates only convey spatial information, so examining the possibility of a causal relation between biomechanical and morphological descriptors are difficult if not impossible. In the case of Procrustes distances as shape descriptors, it is impossible to conduct functional morphology since they only contain information regarding the magnitude of morphological disparities rather than locally detailed shape differences (Rohlf, 1990). Formulating a pipeline integrating morphometrics into the biomechanical discipline necessitates using a series of vector quantities, such as Procrustes residuals (PR for short), as the morphological descriptors, instead of shape coordinates. A Procrustes residual vector maps a landmark from one specimen to another specimen (Bookstein, 1991: chapter 7). It can be calculated easily for each landmark by subtracting the shape coordinates of a landmark from its counterpart on another configuration (such as the template), as follow:

$$\overrightarrow{PR}_{AB} = B_{(x,y,z)} - A_{(x,y,z)} \tag{22}$$

Where PR_{AB} stands for Procrustes residual vector mapping configuration A to configuration B. This equation is a simple coordinate-wise subtraction of landmarks resulting in a vector (PR) whose (second) norm is the Euclidian distance of a landmark between two different configurations, reflecting the extent of their morphological differences at the location of that landmark. More importantly, the direction of PR provides information crucial for building a comparative platform integrating biomechanical variables, such as displacement, with morphometrics results. In addition, vector descriptors' visual representation is more informative than scalar descriptors such as Procrustes distance.

4.10. Geometric Morphometrics: Thin Plate Spline

As mentioned before, Procrustes superimposition is an affine mapping of a landmark configuration to a global coordinate system. The affine mapping minimises a quantity such as Procrustes distance by translating, scaling and rotating a landmark configuration following a reference configuration residing in the global coordinate system. The important keyword here is minimisation, not elimination. There exist recourses, namely non-affine spline functions, which guarantee to eliminate (not minimise) the morphological distances of landmark configurations by warping a configuration into a landmark layout residing in the global coordinate system. As Bookstein (1989) proposed, the thin plate spline (tps) belongs to the spline interpolator family, which explains spatial mapping between a kX3 landmark set (k number of landmarks in a 3-dimensional scenario) V, and a reference kX3 configuration Q, as a linear integration of affine mappings A (translation, scaling and rotation) with a non-linear warp mapping W, as follow (Bookstein, 1989; Ogihara *et al.*, 2015):

$$V = PW_{kx3} + Q_H A_{4x3} \tag{23}$$

Where K represents a k by k (kXk) spatial information matrix (or base function matrix), and Q_H stand for the homogenous coordinate matrix of reference set Q, such that:

$$\begin{aligned}
&\mathrm{Q}_H = \begin{bmatrix} 1 & x_1 & y_1 & z_1 \\ \vdots & \ddots & \vdots & \vdots \\ 1 & x_j & y_j & z_j \end{bmatrix} \\
&K = \begin{bmatrix} U_{1,1} & U_{1,2} & \dots & U_{1,j} \\ U_{2,1} & U_{2,2} & \dots & U_{2,j} \\ \vdots & \vdots & \ddots & \vdots \\ U_{j,1} & U_{j,2} & \dots & U_{j,j} \end{bmatrix} \\
&j \in [3, k];
\end{aligned}$$

Where U denotes the base function, which explains the pairwise spatial characteristics of landmarks in the template (reference) configuration Q. In three-dimensional space, it is expected to use pairwise Euclidian distance as the base function U, such that:

$$U_{i,j} = ||\vec{r}_{i,j}|| \tag{24}$$

Where $\vec{r}$ represents a vector connecting i^{th} landmark to the j^{th} landmark in the configuration Q, and ||.|| denotes the Euclidian norm of a vector. In two-dimensional cases, however, the logarithm of the said distance is used instead. In order to find unknown affine and non-affine transformation matrices A and W, one needs to solve the eq. (23). Since the number of unknowns is greater than the number of equations, the system has a solution if $Q^T.W = 0$. Therefore, it is possible to re-write the eq. (23) as follow:

$$\begin{bmatrix} V \\ 0_{4x3} \end{bmatrix} = \begin{bmatrix} K & Q \\ Q^T & 0_{4x4} \end{bmatrix} \cdot \begin{bmatrix} W \\ A \end{bmatrix} \equiv L. \begin{bmatrix} W \\ A \end{bmatrix} \implies \begin{bmatrix} W \\ A \end{bmatrix} = L^{-1}. \begin{bmatrix} V \\ 0_{4x3} \end{bmatrix} \qquad (25)$$

Where 0_{4x3} and 0_{4x4} denote zero paddings, and L^{-1} represents the inverse of matrix L. Bookstein (1989) proved that the solution to this function, which maps Q to V, is unique and it minimises a quantity representing the overall non-affine component of the map. He named the quantity bending energy which can be expressed as a partial integration of non-linear displacement (warp) components in x, y, and z directions, such that (Ogihara *et al.*, 2015):

$$\mathrm{BE} = \iiint_{R^3} \{ (\tfrac{\partial^2 f}{\partial x^2})^2 + (\tfrac{\partial^2 f}{\partial y^2})^2 + (\tfrac{\partial^2 f}{\partial z^2})^2 + 2(\tfrac{\partial^2 f}{\partial x \partial y})^2 + 2(\tfrac{\partial^2 f}{\partial x \partial z})^2 + 2(\tfrac{\partial^2 f}{\partial y \partial z})^2 \} dxdydz$$

Where BE stands for bending energy, which can be approximated as follow (Bookstein, 1991: chapter 2):

$$BE \approx \sum_{i=1}^{3} -\vec{V}_i^T . L_k^{-1} . \vec{V}_i \qquad (26)$$

Where $\vec{V_i}$stands for i^{th} column of the configuration matrix V (i = 3, representing x, y, and z directions) and $L_k{}^{-1}$, which is also called the bending energy matrix, denotes the upper-left kxk sub-matrix of the inversed matrix L. The Eigen analysis of the bending energy matrix provides a set of principal warps (eigenvectors) and their eigenvalues, which are crucial to derive TPS shape descriptors. It is worth restating that, unlike Procrustes superimposition, tps (like any other spline interpolator) warps a configuration and eliminates any morphological differences. Therefore, Bookstein (1989) proposed using two alternatives as shape descriptors: 1- the bending energy as a general morphological descriptor of a configuration (an analogue to Procrustes distance), and 2- warp scores, or projection of Procrustes residuals (eq. (22)) onto the Principal warp vectors, such that (MacLeod, 2010):

$$Ws = E_{kxk}.P_{kx3} \tag{27}$$

Where Ws stands for warp scores, k represents the number of landmarks, and E and P denote the principal warp matrix (with the shape of kxk) and Procrustes residuals (with the shape of kx3) respectively. In the present study, as mentioned before, Procrustes residuals were used as the shape descriptors. Therefore, TPS was exclusively utilised to 1- calculate the bending energy to slide semi-landmarks along curves and over surfaces and 2- warp polygonal meshes around the reference specimen mesh to create heatmaps highlighting morphological differences.

Warping two or three-dimensional domains is the most prominent use of TPS outside of the morphometrics and morphology territory. After providing landmark configurations of a target and the reference specimen and solving eq. (25), it is feasible to deform (morph) the target mesh into the reference using thin plate spline interpolation (Bookstein, 1989):

$$f(x,y,z) = a_1 + a_2x + a_3y + a_4z + \sum_{i=1}^{k} w_i||P_i - (x,y,z)|| \tag{28}$$

Where $a_{1:4}$ and $w_{1:k}$ represent affine and warp components obtained after solving eq. (25), k stands for the number of landmarks and $||P_i - (x, y, z)||$ denotes the Euclidian distance between i^{th} landmark in a configuration and its counterpart (P_i) in the reference configuration. Assuming a sufficient number of landmarks (and semi-landmarks) are provided to cover a mesh, eq. (28) smoothly deforms the said mesh to the shape of the reference mesh. Beyond the boundary of data (landmarks), however, tps extrapolates the deformation, which results in imprecise deformation, not matching the reference mesh perfectly.

4.11. ArchaeoToolbox: A geometric morphometric software

ArchaeoToolbox is an opensource software, developed by the authors in C++ to digitise Bookstein landmarks and sliding semilandmarks in three-dimensional space, with capabilities to perform ordinary Procrustes superimposition (full and partial), principle component analysis and visualising the results. The software consists of two modules: geometry and linear algebra. The geometry module consists of various classes of VTK (Schroeder *et al.*, 2006) and Open CASCADE (www.opencascade.com) libraries, which are responsible for importing polygonal meshes of the Wavefront (.obj) and PLY formats, exporting polygonal meshes as legacy vtk format (suitable for further analysis in Paraview, Ayachit, 2015), interacting with the meshes to digitise Bookstein and pre-slider landmarks, and visualising the results of superimposition as well as principal component analysis. The linear algebra module consists of multiple classes of Eigen library (www.eigen.tuxfamily.org), which is responsible for sliding the pre-sliders, superimposing landmarks and performing principal component analysis. The graphical user interface was developed in Qt 5 (https://doc.qt.io/qt-5.15/).

The data storage follows the hierarchical database structure, a model in which data is stored in the form of records and organised into a tree-like or parent-child structure, where one parent node can have many child nodes connected through links. The top (parent) branch of the hierarchy is reserved for the name of a specimen, and the children are polygonal mesh information (vertices coordinates and the connectivity matrix), fixed (Bookstein) landmarks coordinates, curve semi-landmarks coordinates, parametric curves (the sliding domain of curve semi-landmarks), surface semi-landmarks coordinates, parametric surface patches (the sliding domain of surface semi-landmarks), and the Procrustes residual matrix. After importing a polygonal mesh file, the file's name will be assigned as the parent of the specimen data hierarchy (it is possible to rename it later), and the mesh information obtained from the file will be stored in the polygonal mesh information child. Upon any operation, *e.g.* digitisation of fixed landmarks, the operator (*e.g.* fixed landmarks digitiser function) requests necessary information from the database (*e.g.* polygonal mesh information of specimen “4”). When the said operation is done, it assigns the results to the relevant branch of the database (*e.g.* fixed landmarks coordinates).

4.12. ArchaeoToolbox: Digitising Semi-landmarks

The digitisation process depends on the type of the desired landmarks. In the case of fixed (Bookstein) landmarks, following a mouse's left click while pressing the CTRL key, a ray (an algebraic vector) will be shot from the user's camera point of view toward the renderer window, crossing the point that the mouse located. If the ray hits an object (*e.g.* a polygonal mesh), the first contact location will be recorded (in an x, y, z triplet) as the location of a fixed landmark in the relevant database. In the case of sliding semi-landmarks, however, the process is more complex. The first step in digitising curve and surface patch semi-landmarks is registering pre-sliders. Pre-sliders are (more or less) equidistant type III Bookstein landmarks. To make pre-slider registration fast and efficient, ArchaeoToolbox uses parametric curves and surface splines to define sliding domains. The process starts with digitising spline control points, identical to the digitisation of fixed landmarks. Then, after interpolating control points (using Open CASCADE interpolators), the parametric splines will be evaluated at equal intervals depending on the desired number of semilandmarks to register pre-sliders, and the control points will be assigned to the database to re-define parametric domains instantaneously when it is necessary. It is essential to mention that the structure of splines (their starting point and direction) must be kept identical throughout all specimens.

The next step is to slide the registered pre-sliders following Gunz *et al.*, (2005) procedure, which minimises the bending energy (eq. (26)). As mentioned in the previous chapters, sliding semi-landmarks allow equidistance TypeIII landmarks (pre-sliders) to slide from their original position alongside a curve or over a surface, minimising morphological quantities such as bending energy across all specimens. The direction of the pre-sliders movement can be confined to the tangent of the sliding domain at the location of each pre-sliders. To follow the procedure, ArchaeoToolbox first assembles a 3k x 2m sparse tangential direction matrix U, where k and m are the total number of landmarks and the number of pre-sliders, respectively. The row-wise extent of U represents the global spatial dimensions (x, y, and z). At the same time, the column-wise scope of U describes the local tangential dimensions (v and w, representing a two-dimensional plane), such that:

$$\text{if } \{\mathrm{i} \in SS \cup CS\}: \\ U_{i,j} = v_j^x; \\ U_{k+i,j} = v_j^y; \\ U_{2k+i,j} = v_j^z;$$

$$if\{i \in SS\}: \\ U_{i,j+m} = w_j^x; \\ U_{k+i,j+m} = w_j^y; \\ U_{2k+i,j+m} = w_j^z;$$

$$i \in [1,k]; j \in [1,m]$$

Where SS and CS denote surface slider and curve slider sets respectively, $v^{x,\ y \text{ or } z}$ and $w^{x,\ y \text{ or } z}$ represent x, y or z components of unit tangent vectors and k and m are the total number of landmarks and the number of pre-sliders, respectively. In practice, populating matrix U can be described in the following pseudo-code:

```
TC_kx3 = [Matrix  of fixed + pre-slider coordinates];
SliderList_m = [List  of TC row  indices corresponding to the pre-sliders];
for(i = 1; i =< k; i++){
        if(i^th landmark is a Curve slider){
                1) Ask database for the curve control points;
                2) Interpolate curve spline;
                3) Query the tangent unit vector ($\vec{v}$) of the curve spline at i^th landmark;
                4) j = index of i in the SliderList ;
                5-1) U[i, j] = x component of $\vec{v}$;
                5-2) U[2i, j] = y component of $\vec{v}$;
                5-3) U[3i, j] = z component of $\vec{v}$;
        }
        else if(i^th landmark is a Surface slider){
                1) Ask database for the surface control points;
                2) Interpolate surface spline;
                3) Query the tangent unit vectors($\vec{v}$ and $\vec{w}$) of the spline at i^th landmark;
                4) j = index of i in the SliderList ;
                5-1) U[i, j] = x component of $\vec{v}$;
                5-2) U[2i, j] = y component of $\vec{v}$;
                5-3) U[3i, j] = z component of $\vec{v}$;
                5-4) U[i,2j] = x component of $\vec{w}$;
                5-5) U[2i,2j] = y component of $\vec{w}$;
                5-6) U[3i, 2j] = z component of $\vec{w}$;
        }
}
```

The eq. (26) of bending energy can be re-written in a non-integrational manner by concatenating x, y and z dimensions of configuration matrix V into a new vertical vector $\overrightarrow{\gamma_{3xk}}$, such that:

$$\gamma^T = \begin{bmatrix} x_1 & \dots & x_k & y_1 & \dots y_k & z_1 & \dots & z_k \end{bmatrix}$$

Similarly, the bending energy matrix (${L_k}^{-1}$) can be re-written as a large (3k x 3k) symmetric sparse matrix to match the dimension of $\vec{\gamma}$, such that:

$$S = \begin{bmatrix} L_K^{-1} & 0 & 0 \\ 0 & L_K^{-1} & 0 \\ 0 & 0 & L_K^{-1} \end{bmatrix}$$

Accordingly, bending energy (eq. (26)) can be re-formulate as:

$$BE = -\gamma^T.S.\gamma \tag{29}$$

Where BE stands for bending energy. In order to slide pre-sliders while minimising the BE, Archaeotoolbox finds a vector of scalars $\overrightarrow{T_{3k}}$, which scales x, y and z components of unit tangent vectors (matrix U) appropriately. Eventually, the scaled U translates $\vec{\gamma}$ to a new position, such that:

$$\gamma = \gamma^0 + UT \tag{30}$$

Where γ^0 stands for the initial (vectorised) position of pre-sliders. The newly defined pre-sliders (they have already slid, yet are still pre-sliders) must be projected back to their sliding domain (this step is called relaxation). The process of slide-relaxation is iterative, and every time a newly translated $\vec{\gamma}$ replaces the older one, which will be projected back to the domain until no significant decrease in the BE can be observed (less than 0.1%). After the completion of the iterative process, the pre-sliding landmarks will be turned into sliding semi-landmarks.

The eq. (30) is a weighted least-squared problem, which can be solved for T, as follow (Gunz *et al.*, (2005)):

$$T = -(U^T.S.U)^{-1}.U^T.S.\gamma^0 \tag{31}$$

To solve the eq. (31), ArchaeoToolbox uses complete orthogonal decomposition, implemented in the Eigen library:

https://eigen.tuxfamily.org/dox/classEigen_1_1CompleteOrthogonalDecomposition.html.

4.13. Statistical Analysis: Principal component analysis (PCA)

Principal component analysis is a multivariate method initially designed to analyse a set of inter-correlated dependent observations (variables) by reducing the set dimensionality without losing any information (Hotelling, 1933), but eventually became a vital multipurpose tool, which has been utilised in various scientific fields to detect outliers, remove the effect of size, and highlighting the most crucial data descriptor, or feature selection (Abdi & Williams, 2010; Guo *et al.*, 2002; Rousseeuw & Hubert, 2011; Somers, 1986). In geometric morphometrics, the main application of PCA is dimension reduction. In the recent decade, sliding semi-landmarks were improved and adapted to the 3-dimensional domains, making it possible for morphometricians to densely sample morphological information (via landmarks) without concerning biological or functional homology. Simultaneously, geometry-capturing technologies, such as laser scanners, have been improved and become more affordable for scientists, diverting their endeavour from solving two-dimensional problems into three-dimensional subjects. A combination of these two factors brought the issue of data redundancy and strong variable collinearity to the attention of the morphometricians community. Moreover, the visualisation of Procrustes shape descriptors became exponentially more challenging since the dimensionality of the shape space was not limited to a couple of 2-dimensional landmarks anymore. Consequently, principal component analysis has been almost coupled with the Procrustes shape descriptors, notably Procrustes residuals.

The principal components (PCs) of a set of n-dimensional data points (*e.g.* Procrustes residuals of k landmarks in a 3-D space, where n = kx3) are a set of unit vectors $\vec{v}$, where $\overrightarrow{v_\imath}$ is orthogonal to $\overrightarrow{v_{\imath-1}}$ ($i \in [1, n]$) and is aligned with the axes of $\mathrm{i^{th}}$ largest variance in the data (the $\mathrm{i^{th}}$ best linear fit). By projecting the (original) data on the components, PCA creates new sets of data (called PC scores), where every set explains a certain amount of observed variation in the data. Therefore, each set of scores which is a linear combination of the original (n) dimensions, can be used as a standalone (1-D) representation of the actual n dimensions, and by doing so, one can reduce the data dimension from n to one. The dimensionality reduction (from n to 1, 2 or 3 by selecting one, two or three PCs) makes the visualisation of the high-dimensional data possible. Moreover, since the (principal) components are orthogonal, they are linearly uncorrelated, and accordingly, scores are also uncorrelated. The orthogonality of PC scores makes them a robust contender to replace highly collinear descriptors.

Assume a kx3 dimensional matrix A, populated with centred Procrustes residuals of k superimposed landmarks in a configuration. The process of PCA starts with assembling a kxk square covariance matrix of H, such that:

$$H = A^T.A$$

Where A^T stands for the conjugate transpose of matrix A. Singular value decomposition of matrix H (eq. (14)) results in the matrices of eigenvalues (D) and eigenvectors (U) of H. The next step is sorting (in descending order) columns of U based on their corresponding eigenvalues in D. Columns of eigenvector matrix U represent principal components of the original data A, and its rows represent descriptors. Some procedures, such as feature selection, rely on the values of U columns, called loadings. After re-ordering U, the first column is PC1, expressing the highest variance in data. The next comes PC2, PC3, et cetera. To obtain PC scores, one must project A onto U, as follow:

$$S = U_{sorted}.A \tag{32}$$

Where S stands for the matrix of PC scores, which its dimensions are identical to the original matrix A. Each column in matrix S corresponds to the principal component axes (*e.g.* first column is the score of the PC 1).

In addition to dimension reduction and resolving redundancy and collinearity issues, PCA can be used to find a descriptor with the most significant effect on the data variance. Finding the most effective descriptor, also called feature selection, has recently become a significant part of different fields of science. In morphometrics, if one chooses to use PCA on Procrustes residuals, it is possible to find a descriptor with the most significant effect on a principal component. Since Procrustes residuals are spatial information, finding the most influential descriptor reveals the most morphologically distinct location with the highest disparity from the reference configuration. The location can be further analysed biomechanically to examine if the cause of the morphological discrepancies is related to the biomechanical factors. Finding the most influential features is a simple procedure. As mentioned before, column-wise values of the sorted matrix U are called loadings. In each column, which corresponds to a principal component, the highest value of the loading is the most impacting descriptor, which can also be visualised as a biplot of the corresponding principal component.

4.14. Biomechanical Simulation: Finite Element Analysis

Most natural phenomena, such as heat diffusion, the flow of liquid or gas, and the deformation of solid structures, are governed by more than one variable. The behaviour of such systems over a temporal or spatial interval can be predicted by solving the relevant partial differential equation (Oñate, 2009). A partial differential equation (PDE) is a mathematical equation consisting of two or more independent variables, an unknown function (dependent on those variables, *e.g.* displacement), and partial derivatives of the unknown function regarding the independent variables. A particular solution to a partial differential equation is a function that must be defined over a d-dimensional domain (Ω). Most of the time, the domain has a complex shape, making it difficult, if not impossible, to find the exact solution to the PDE. The alternative is to approximate the (numerical) solution by subdividing the domain Ω into a finite set of simpler elements and solving the equation element by element. Such an approximation approach is called finite element analysis, and a collection of such elements approximating a domain is called structural mesh.

In the case of the deformation of a solid object (also called elasticity problems or solid mechanics), finite element analysis (FEM) aims to predict how the object behaves under certain mechanical conditions (traction force, pressure, et cetera).

The process can be summarised as providing a system of actions (known data, *i.e.* governing equations) to assemble a mathematical model (PDE) to predict the response (Unknown data, *i.e.* displacement in the presented research). It is worthwhile to clarify the difference between displacement and deformation to avoid confusion. Displacement happens at the local level and is the distance from which one point moved from its original location, which can be measured in terms of distance and rotation. Deformation, on the other hand, is the actual distortion of a whole object. In nature, systems of action and responses are spatial and temporal, *i.e.* they are functions of time and space. Therefore, a realistic (mathematical) model is considered a dynamic model. In addition, most biological materials follow a non-linear elastic behaviour, which adds an extra level of complexity to the model. Complex models are (computationally) expensive to solve. However, it is possible to simplify the model by assuming the magnitude of applied force (or displacement) is small enough to create a linear stress-strain relationship; therefore, the material (*i.e.* bone tissue in the present research) follows the linear elastic behaviour (Keaveny *et al.*, 1994). This assumption streamlines the PDE, makes it possible to remove the temporality of the actions (knowns) and response (unknowns) and simplifies a complex dynamic-viscoelastic model to a steady-state linear elasticity problem.

4.15. Finite Element Analysis: Equilibrium of forces in the linear elasticity

The first step in the finite element method is to define a set of equations (also called governing equations) describing correlations between the field of interest (*e.g.* displacement) with the known quantities. For a linear(-ised) elasticity problem, the governing equations include the equilibrium equation (Newton's second law of motion), stress-displacement correlation (geometry-driven equation), and stress-strain relationship (material law, or Hook’s law). The equilibrium implies that the magnitude of forces (F) acting on an object is a product of mass (m) and acceleration (a), or simply, $\Sigma F = ma$. There are two kinds of forces acting on a deformable body: contact force and body force. As the name suggests, contact force (also called external forces, *e.g.* traction) is applied on the surface of a solid and occurs when the body is in contact with its surroundings. On the other hand, body force is applied to the volume of a solid and results from forces acting inside a solid body, such as gravitational forces. Since the field of interest is displacement and not rigid body motion, by equating the acceleration to zero, the equilibrium equation can be written as a static equation:

$$\vec{T} + \vec{b} = 0 \tag{33}$$

Where $\vec{T}$ and $\vec{b}$ stand for vectors of contact force and body force, respectively. Based on the definitions of contact and body force, eq. (33) can be written as a summation of the integration of contact forces over the surface (S) and the integration of body force over the volume (V), such that:

$$\int_V \vec{b}.dV + \int_S \vec{T}.dS = 0 \tag{34}$$

Which summarises all forces (contact and body forces) in all directions (x, y and z, notice that forces are provided in the vector form). It bears repeating that displacement is the field of interest (or prime field) in linear elasticity problems. Therefore, first, it is necessary to substitute force vectors of eq. (34) with another quantity which takes the equilibrium equation closer to displacement, *i.e.* stress (σ). Stress, by definition, is the force per unit area ($\sigma = F/A$). Accordingly, one can decompose a contact force ($\vec{T_i}$; $i \in [x, y, z]$) to its resultant 3x3 stress tensor matrix (σ_{ij}; $i, j \in [x, y, z]$) and a local surface normal vector ($\vec{n_j}$; $j \in [x, y, z]$), such that:

$$T_i = \sigma_{ij}.n_j \tag{35}$$

Where:

$$\mathrm{T}_i = \begin{bmatrix} T_x \\ T_y \\ T_z \end{bmatrix} ;$$

$$\sigma_{ij} = \begin{bmatrix} \sigma_{xx} & \sigma_{xy} & \sigma_{xz} \\ & \sigma_{yy} & \sigma_{yz} \\ Symmetry & & \sigma_{zz} \end{bmatrix} ;$$

$$n_j = \begin{bmatrix} n_x \\ n_y \\ n_z \end{bmatrix}$$

The matrix σ_{ij}in eq. (35) is also called the Cauchy stress tensor. By substituting eq. (35) with the second term of eq. (34), the equilibrium equation can be rewritten as follow:

$$\int_V \vec{b}.dV + \int_S \sigma_{ij} n_j.dS = 0 \tag{36}$$

By looking at the second term of eq. (34) and eq. (36), it is noticeable that contact force and its resultant stress tensor are integrated over a surface. Nonetheless, the stress tensor must be integrated over a volume to study the effect of contact force inside a solid. This step can be accomplished using the Gauss divergence theorem, stating that the vector's outward flux via a closed surface is equivalent to the volume integral of the divergence over the area within the surface (Stolze, 1978). Therefore, it is possible to write the second term of eq. (36) as an integral of the divergence of the stress tensor σ_{ij} over the volume, as follow:

$$\int_S \sigma_{ij} n_j.dS = \int_V \nabla \sigma_{ij}.dV \tag{37}$$

Where $\nabla \sigma_{ij}$ represents the divergence function such that:

$$\nabla \sigma_{ij} = \begin{bmatrix} \frac{\partial \sigma_{x,x}}{\partial x} + \frac{\partial \sigma_{x,y}}{\partial y} + \frac{\partial \sigma_{x,z}}{\partial z} \\ \frac{\partial \sigma_{y,x}}{\partial x} + \frac{\partial \sigma_{y,y}}{\partial y} + \frac{\partial \sigma_{y,z}}{\partial z} \\ \frac{\partial \sigma_{z,x}}{\partial x} + \frac{\partial \sigma_{3,2}}{\partial y} + \frac{\partial \sigma_{3,3}}{\partial z} \end{bmatrix}$$

By replacing the second term of eq. (36) with eq. (37), the equilibrium equation can be written as follow:

$$\int_V \vec{b}.dV + \int_V \nabla\sigma_{ij}.dV = 0 \tag{38}$$

It is essential to mention that the body force $\vec{b}$, such as gravity force, is a function of the density of the domain, which is a known constant. In this research, cattle trabecular and cortical bone densities were selected as 1.93 and 1.99 g/cm3(Gong *et al.*, 1964), respectively, and Sus mandibular bone density was chosen as 1.62 g/cm3 (Zhang *et al.*, 2001).

At this stage, the equilibrium equation is one step closer to being written regarding displacement. Following Hook's law, the next step is replacing stress tensors with strain. By definition, strain is the rate of material elongation or compression parallel to the stress direction. In a compact form, the strain of an isotropic material can be expressed as $\varepsilon = \sigma/E,$ where E stands for Young's (elasticity) modulus, which is a known constant. In the present research, it was assumed that bone is an isotropic material. This assumption further simplifies the finite element problem by removing the material's directionality. For cattle cortical and trabecular bone, the elastic moduli were selected as 10G Pa (Reilly & Burstein, 1975) and 0.76 GPa (Ryan & Williams, 1989), respectively, and for Sus mandible, the value was selected as 0.24 Gpa (Misch *et al.*, 1999). In a three-dimensional domain, however, the stress-strain relationship is additionally influenced by another quantity, Poisson's ratio (ν), or the ratio of material expansion-contraction to the material elongation-compression perpendicular to the stress direction. Similar to the elasticity modulus, Poisson's ratio is also constant, and it was reported to be 0.4 for skeletal tissues (Moreno *et al.*, 2007). For an isotropic material in three-dimension, the stress-strain relation can be expressed as follow (Koutromanos, 2018: chapter 7):

$$[\sigma] = C[\varepsilon] \tag{39}$$

Where:

$$[\sigma] = \begin{bmatrix} \sigma_{xx} \\ \sigma_{yy} \\ \sigma_{zz} \\ \sigma_{yz} \\ \sigma_{xz} \\ \sigma_{x7} \end{bmatrix} ; [\varepsilon] = \begin{bmatrix} \varepsilon_{xx} \\ \varepsilon_{yy} \\ \varepsilon_{zz} \\ 2\varepsilon_{yz} \\ 2\varepsilon_{xz} \\ 2\varepsilon_{x7} \end{bmatrix} ;$$

$$C = \frac{E}{(1+\nu)(1-2\nu)} \begin{bmatrix} 1-\nu & \nu & \nu & 0 & 0 & 0 \\ & 1-\nu & \nu & 0 & 0 & 0 \\ & & 1-\nu & 0 & 0 & 0 \\ & & & \frac{1-2\nu}{2} & 0 & 0 \\ & & & & \frac{1-2\nu}{2} & 0 \\ Symmetry & & & & & \frac{1-2\nu}{2} \end{bmatrix}$$

It is noteworthy that the quantity C is called the stiffness matrix. Based on the infinitesimal theory of elasticity, the relation between strain tensor and displacement vector $\vec{U}$ in the Cartesian coordinate system can be represented as follow (Asemi *et al.*, 2014):

$$[\varepsilon] = L\vec{U} \tag{40}$$

Where:

$$[\varepsilon] = \begin{bmatrix} \varepsilon_{xx} \\ \varepsilon_{yy} \\ \varepsilon_{zz} \\ 2\varepsilon_{yz} \\ 2\varepsilon_{xz} \\ 2\varepsilon_{xy} \end{bmatrix} ; \vec{U} = \begin{bmatrix} u \\ v \\ w \end{bmatrix} ;$$

$$L = \begin{bmatrix} \frac{\partial}{\partial x} & 0 & 0 \\ 0 & \frac{\partial}{\partial y} & 0 \\ 0 & 0 & \frac{\partial}{\partial z} \\ 0 & \frac{\partial}{\partial z} & \frac{\partial}{\partial y} \\ \frac{\partial}{\partial z} & 0 & \frac{\partial}{\partial x} \\ \frac{\partial}{\partial y} & \frac{\partial}{\partial x} & 0 \end{bmatrix}$$

The equilibrium equation (eq. (38)) can also be written (by abuse of notation) in the derivative matrix form as follow:

$$L^T[\sigma] + \vec{b} = 0 \tag{41}$$

Where L^T stands for transpose of the derivatives matrix L (eq. (40)), $\vec{b} = [b_x, b_y, b_z]^T$ is the vector of body force, and $[\sigma] = [\sigma_{xx}, \sigma_{xy}, \sigma_{zz}, \sigma_{yz}, \sigma_{xz}, \sigma_{xy}]^T$. According to eq. (39) and eq. (40), strass $[\sigma]$ can be depicted as a function of the displacement vector $\vec{U}$, such that $[\sigma] = CL\vec{U}$, and therefore, it is finally feasible to write the linear elasticity equilibrium in terms of displacement as follow:

$$L^T CL\vec{U} + \vec{b} = 0 \tag{42}$$

After defining loading boundary conditions (providing values of displacement for some locations on the surface of domain - Dirichlet boundary condition, or similarly, providing values of stress for some places on the surface of domain- Neumann boundary condition), and selecting fixed boundaries (zero displacements, since the presented problem is a static analysis, not a rigid motion analysis), theoretically, it is possible to solve the equilibrium to find the resultant displacement. However, in reality, it may not be possible. The eq. (42) is called the strong form of the linear elasticity equilibrium since it mandates a strong assumption regarding the field of interest (displacement). Displacement is a second-degree derivative of location; therefore, at every point in the domain (solid deformable object), it must be possible to take two derivatives of displacement. In simpler terms, displacement must be a smooth function all over the domain, and in three-dimensional scenarios, this is not achievable except for a few cases (a more technical definition of a smooth function in this context refers to a function belonging to the first-order Sobolev space, which is a function which itself and its first derivative are square-integrable over a domain, according to Kinnunen, 2017). One solution to the problem is discretising the domain into a finite number of smaller, mathematically well-defined disjoined sub-domains (*e.g.* cube or tetrahedron) whose displacement function (or any other field of interest such as heat transfer) satisfies the smoothness condition. Then, by serialising (unifying) each element's reaction (displacement) to the local loading conditions, one can approximate the resultant displacement at the level of the whole domain. This solution is a numerical approximation. Before describing the procedure of numerical approximation, however, it is vital to provide more information about the elements and their types.

4.16. Finite Element Analysis: Elements and shape functions

In finite element analysis, elements are the discretisation units of a domain Ω, forming a structural mesh over the domain of interest. Each element is usually denoted as $\Omega^e;\ e\ \in [1, Nel]$, where Nel stands for the number of elements to which the domain was discretised (*e.g.* Ω^7 denotes the seventh element of a structural mesh). Element shapes are mathematically simple, such as a hexahedron or tetrahedron (or square or triangle in a two-dimensional domain), making the field of interest (*e.g.* displacement) a smooth function belonging to the first-order Sobolev space. Each element consists of a constant number of nodes and faces. For example, in three-dimensional space, a first-order tetrahedral element consists of four nodes and four faces, a second-order tetrahedral element has an extra node at the middle of each edge (nine nodes in total), and a first-order hexahedral element has six faces and eight nodes. For an element, the nodal values of a field of interest are used to interpolate that field anywhere inside that element. Therefore, high-order elements approximate the field of interest more accurately, although their computational cost is exponentially higher. Following the same logic, hexahedral elements are more accurate than tetrahedral ones; however, their higher cost aside, they are not suitable for discretising complex biological domains. The first-order tetrahedral elements (SOLID45 in Ansys or C3D4 in Abaqus) were used in the present study to construct structural meshes.

4.17. Methodology Pipeline: Bovine phalanges

Samples were cleaned and anatomically (posterior-anterior) labelled following Dottrens (1946) approach and prepared for the computerised tomography scan. The scanning procedure was accomplished using a 16-slice General Electric CT scanner with a spatial resolution of 0.3, 0.3, 1.25 (mm) in the X, Y and Z axes, respectively. The resultant DICOM stacks were imported to 3D-Slicer (www.slicer.org) to proceed with the segmentation. Image tacks were isotropically resampled to new 0.3, 0.3, 0.3 (mm) dimensions. This voxel size provides a minimum of 4-5 voxel thickness across the thinnest section of phalanges, which is necessary for the accuracy of the finite element analysis (Gröning *et al.*, 2013; Camacho *et al.*, 1997). The polygonal meshes were subjected to two distinct procedures: 1- They were imported to the ArchaeoToolbox for the geometric morphometrics procedure, and 2- They were solidified to become ready for finite element analysis.

Regarding the geometric morphometrics preparation, two templates, each containing ten fixed (Type II) landmarks, two curves of 20 semilandmarks (defining the periphery of the proximal and distal joints) and two (surface) patches of 100 semilandmarks (covering the proximal and distal joints) was created for the first and second phalanges, separately (Figure 17).

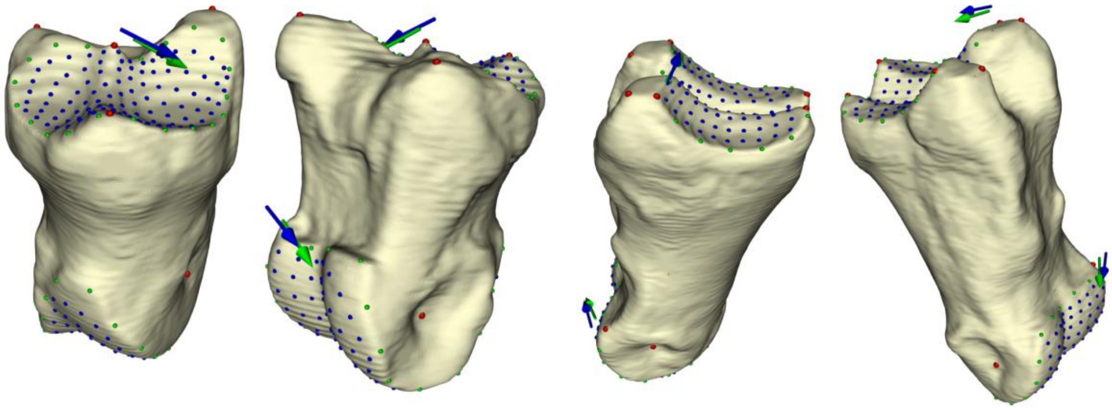

Figure 17 Landmark configurations of the first (right) and second (left) phalanges. Fixed landmarks are painted red, curve sliders green, and surface sliders blue. The (blue and green) arrows indicate the direction of the curve and surface patches. To keep the landmark numbering consistent through all specimens, one needs to construct curves and surface patches in the same direction as the template.

Accordingly, phalanx landmarks were digitised, and after a full Procrustes superimposition (also performed via ArchaeoToolbox), Procrustes residuals of each specimen were exported for further statistical analysis. As mentioned before, due to the significantly high colinearity of the landmark-based data, the statistical procedure began by conducting a principal component analysis on the Procrustes residuals. Then the resulting scores were tested against available data, such as anatomical information and locality (settlement location), to observe the impact of said known factors on the variance of the morphological components. The significance of the impact was tested by Kruskal–Wallis analysis of variance (Kruskal & Wallis, 1952), which is robust against heteroscedasticity of variance. The significantly affected components were selected, and their corresponding eigenvalues were examined to discover the landmark with the most influence (highest eigenvalue) on the said component. Then different specimens at various spectrums of the target component were examined at the location of the most influential landmark (MIL). At this stage, a series of finite element analyses were performed to determine if morphological disparities at the MIL had any biomechanical explanation, for instance, by observing the strain rate probed at MIL across some specimens (*e.g.* the ones residing at two extremes of a principal axis).

Finite element results are firmly size dependent, and the variance of biological data (partially) reflects the allometric effect of size. Consequently, in a comparative scenario such as this research, the FEM results of biological data must be subjected to an (allometric) size removal procedure. The alternative is to normalise (scale them to size) the FEM inputs, *i.e.* specimen geometries, before performing the analysis. Using the same transformation matrix, which was used to superimpose digitised landmarks, the corresponding polygonal mesh of each specimen was transformed to a unit-size scale. Next, The Topology Toolkit (Tierny *et al.*, 2018) was used to divide each polygonal mesh into a series of quadrilateral patches by extracting the Morse-Smale complex of a selected eigenvector of the mesh Laplacian (Laplace-Beltrami) matrix (the process described by Dong *et al.*, 2005). Using Open CASCADE (www.opencascade.com), each quadrilateral patch was converted to a Non-Uniform Rational Basis Spline (NURBS). After joining NURBS to a single manifold solid model, each specimen was exported as a STEP (Standard for the Exchange of Product Data) file format. The process of solidifying polygonal meshes was done in the C++ environment. Solid meshes were directly subjected to finite element analysis.

As mentioned in the last chapter, the structural static finite element was chosen to examine the potential reasons behind morphological disparities across specimens. For this, it was mandatory to at least define two types of boundary conditions to make the force-displacement partial differential equation solvable: fixed Dirichlet boundary (imposed on the field of interest, *i.e.* displacement) and Neumann force (loading) boundary (imposed on the derivative of the field of interest, *i.e.* force) conditions. For both the first and second phalanges, the distal joint of the phalanges was chosen as the fixed constraint, while the proximal joint was selected as the force insertion area (Figure 18). In addition, a unique frictionless boundary was selected to imitate the restraining effect of ligaments. The frictionless boundaries, which allow tangential movement but restrict normal (orthogonal) motion, were imposed on axial and abaxial palmar eminences of both the first and second phalanges.

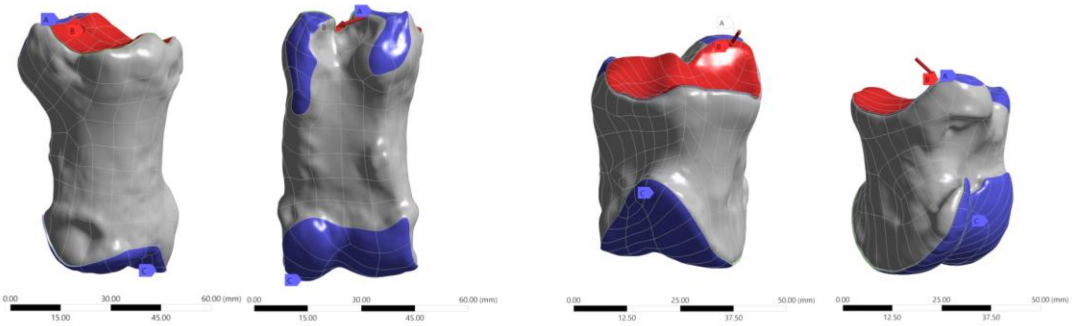

Figure 18 Finite element analysis boundary conditions imposed on first and second Bos phalanges. Boundary A denotes frictionless constraints, B locates force insertion, and C highlights the no displacement (fixed) region.

After defining the boundaries on a domain (solid mesh of a specimen), the domain was divided into a finite number of elements through the structural meshing procedure. The results of a finite element analysis significantly depend on the size of structural elements. Smaller element size increases the accuracy of the results, although it also increases the size of the partial differential problem exponentially, eventually making it impossible to solve it using a home computer or laptop. Marcé-Nogué *et al.*, (2016) proposed a balance between accuracy and computational burden, or as they called QUIM (Quasi Ideal Mesh), for the size of the structural mesh, by calculating its error of the arithmetic mean (or median). In the present research, an error of 10% or lesser was chosen for the structural mesh. After solving the force-displacement problem for 1 Pascal pressure, the strain value at the location of the most important landmark (MIL) was probed. Comparing the probed strain provides a reliable tool to interpret a morphological principal axis.

4.18. Methodology Pipeline: *Sus scrofa* hemi-mandibles

Sus mandibles were processed and analysed similarly to *Bos* phalanges, with the only difference being the way *Sus*'s mandible geometry was captured. Mandible geometries were digitised by a handheld structured light scanner, CREAFORM GO!SCAN 20, with a resolution of 0.1mm. Similar to *Bos* phalanges, mandible meshes were imported to ArchaeoToolbox for geometric morphometric analysis. An adult male specimen (sc19) was chosen to build the template. The template consisted of seven fixed landmarks, 100 curve semilandmarks and 500 surface semilandmarks (Figure 19).

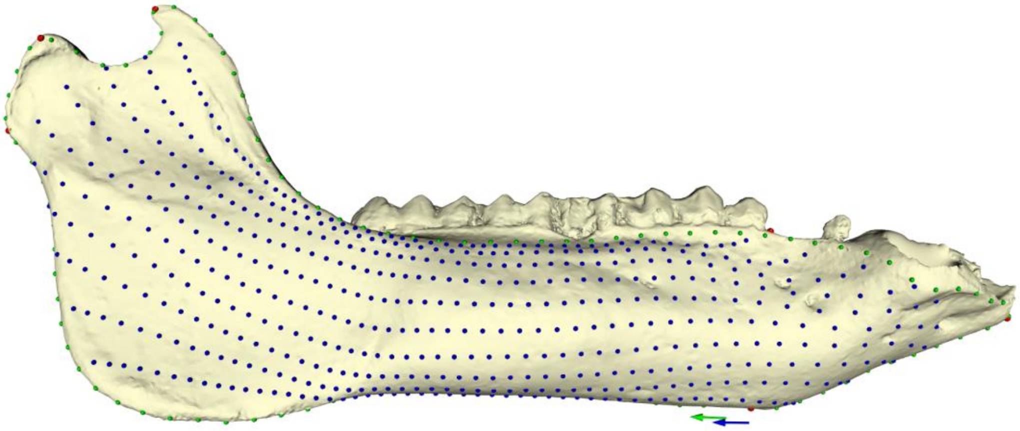

Figure 19 Landmark configurations of Sus scrofa hemi-mandible. Fixed landmarks are painted red, curve sliders green, and surface sliders blue.

5. RESULTS

5.1. Bovines of Tell Halula

5.1.1. Bovines of Tell Halula: Biometry of first phalanges

The greatest length (GL) of Tell Halula's first phalanges ranged between 67 to 77.31 (mm), with an arithmetic mean of 73.35 (±2.71 millimetres estimated error for the 95% confidence interval, or CI for short) and a standard deviation (Std for short) of 4.04 millimetres. The GL values of Tell Halula's first phalanges did not significantly differ (Kruskal-Wallis rank sum test) from the *Bos primigenius* greatest length (Figure 20, left). The smallest breadth of the diaphysis (SD, not to be confused with the standard deviation abbreviation, Std) of Tell Halula's first phalanges varied from 25.92 to 36.03 millimetres while exhibiting an arithmetic mean of 31.65 (±2.05 mm, 95% CI) and a standard deviation of 2.81 millimetres (Figure 20, right).

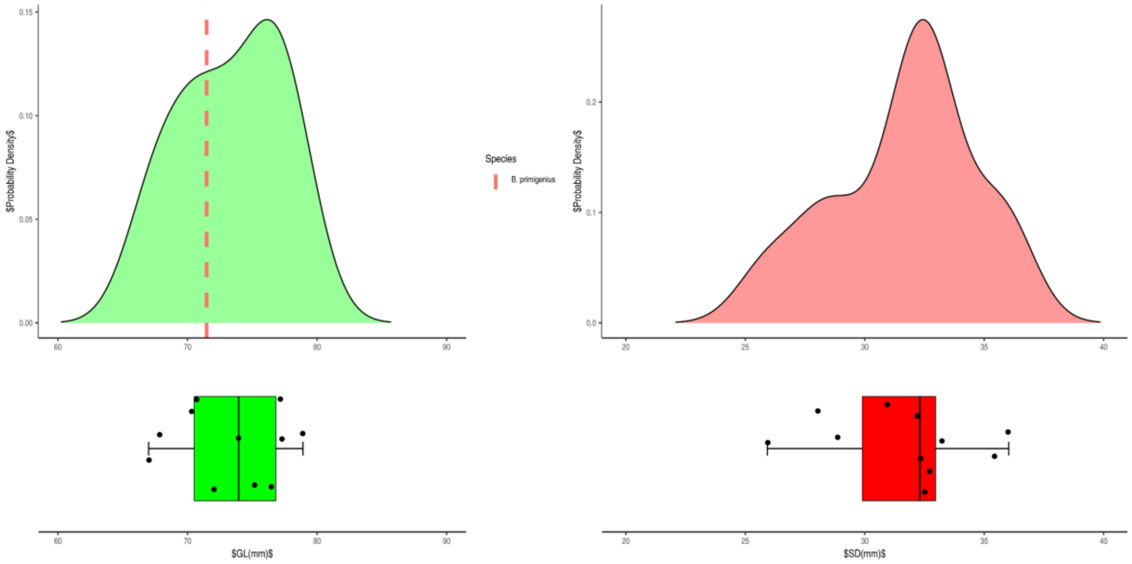

Figure 20 Graphs showing the greatest length (left, in green) and the smallest width of the diaphysis (right, in red) of cattle's first phalanges excavated from Tell Halula. The referential measurements are presented as a vertical red line (if they were available for the analysis) indicating an average aurochs dimensions.

The breadth of the proximal epiphysis (Bp for short) was expanded between 31.02 and 43.1 millimetres, with an arithmetic mean of 36.46 (±2.5 millimetres, 95% CI) and a standard deviation of 3.71 millimetres. On the other hand, the breadth of the distal epiphysis (Bd for short) observed range was from 27.74 to 35.58 millimetres with a lower arithmetic mean of 33.17 (±3.04 millimetres, 95% CI) and standard deviation of 4.52 millimetres, compared to Bp. Following the same trend as GL, both Bp and Bd did not significantly differ from aurochs dimensions (Figure 21).

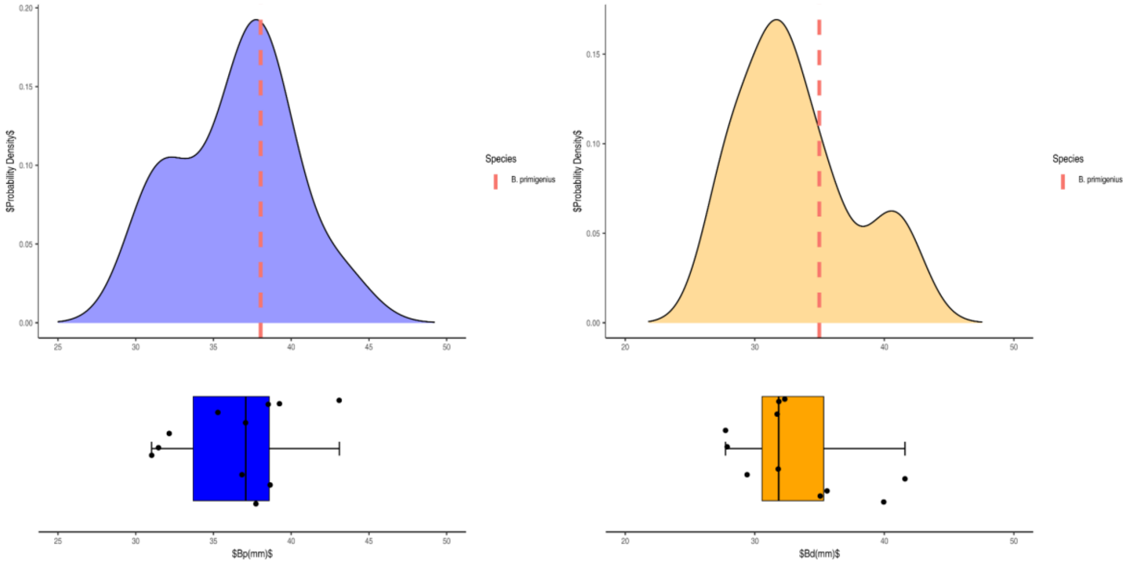

Figure 21 Probability density plots of the Greatest breadth of the proximal (Left, in blue) and the distal epiphysis (right, in orange) of cattle first phalanges, excavated from Tell Halula. The referencial measurements are presented as a vertical red line (if they were available for the analysis) indicating an average aurochs dimensions.

Using the greatest length (GL) as the explanatory variable of size, a linear regression was carried out separately for each SD, Bp, and Bd measurement to determine how much variance can be explained by the allometric effect of size. In addition, the homoscedasticity (equal scatter of residuals) assumption of linear regressions was tested using Koenker's test (Koenker & Bassett, 1982), which is robust enough for contaminated data with a long tail or multi-modality (Lyon & Tsai, 1996). The results of the three regression models are available in Table 8. The adjusted R-squared values indicated that 36-44% of the observed variance in the linear (biometric) measurements was resolvable by the size of individual specimens.

Model	**Intercept**	**Slope**	**F-Statistic**	**P-value**	**Adjusted R-squared**
SD ~ GL	-4.4752	0.4925	F(1, 9) = 6.7	0.03	0.36
Bp ~ GL	-10.9894	0.6469	F(1, 9) = 8.85	0.01	0.439
Bd ~ GL	-24.6072	0.7878	F(1,9) = 8.81	0.015	0.438

Table 8 Results of ordinary linear regressions of Tell Halula's cattle first phalanges measurements.

To further analyse the variation of data, a paired correlation test was conducted to investigate the possibility of collinearity, *i.e.* the mutual effect of measurements on each other. The paired test results are provided in Figure 22, showing the existence of highly significant collinearities between observations.

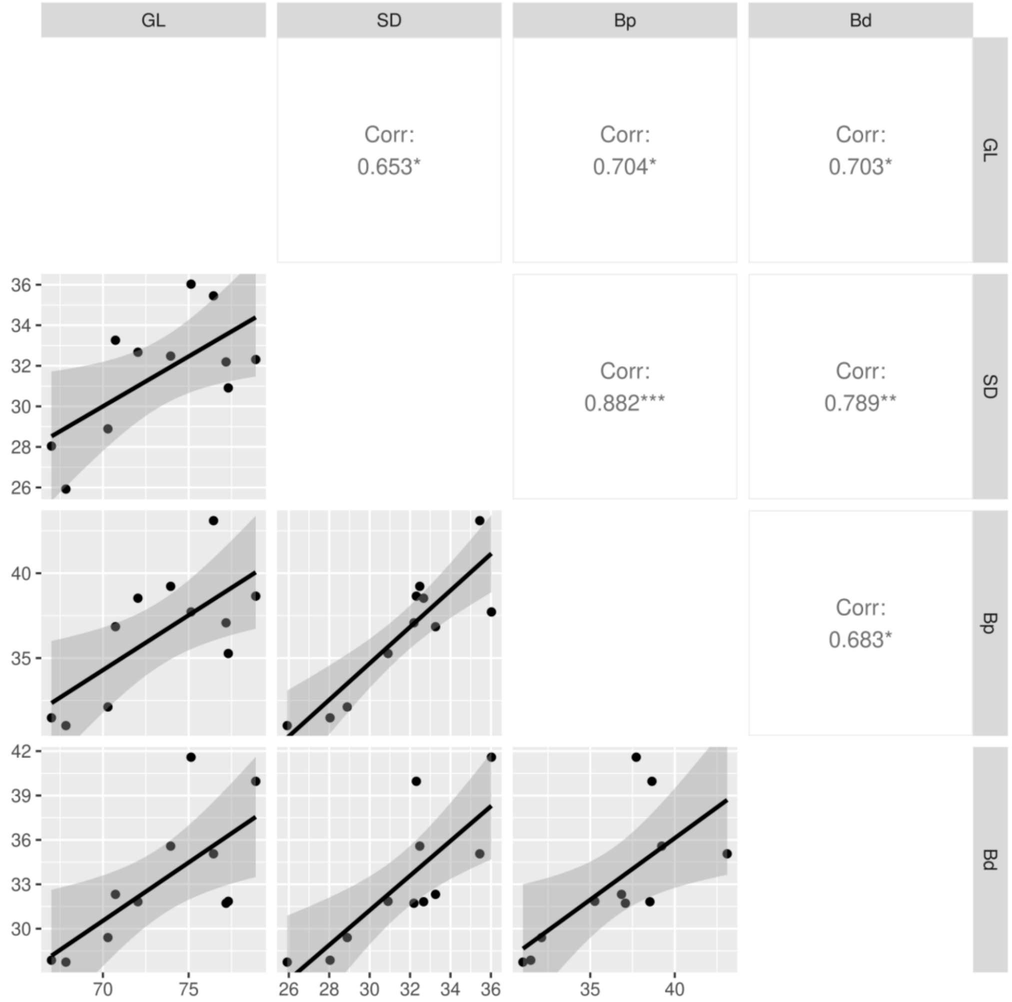

Figure 22 All permutations of correlations between biometric measurements taken from Bos first phalanges (Tell Halula specimens). All biometric descriptors are significantly collinear.

The allometric effect of size and collinearity introduces noise in data variance, making it impossible to study the potential impact of external factors, such as sexual dimorphism, anatomy, speciation and/or herd management, on the biometric measurements. The mentioned problems were circumvented by principal component analysis and observing the variance of principal component scores instead of the original variables. Since the principal component analysis depends on the singular value decomposition of the covariance matrix, data were centred first. The reference principal component analysis was conducted (trained) using external reference biometric measurements (Gl, Bp and Bd) of *Bos* phalanges from the Near East. The result of the first phalanges referential PCA is depicted in Figure 23.

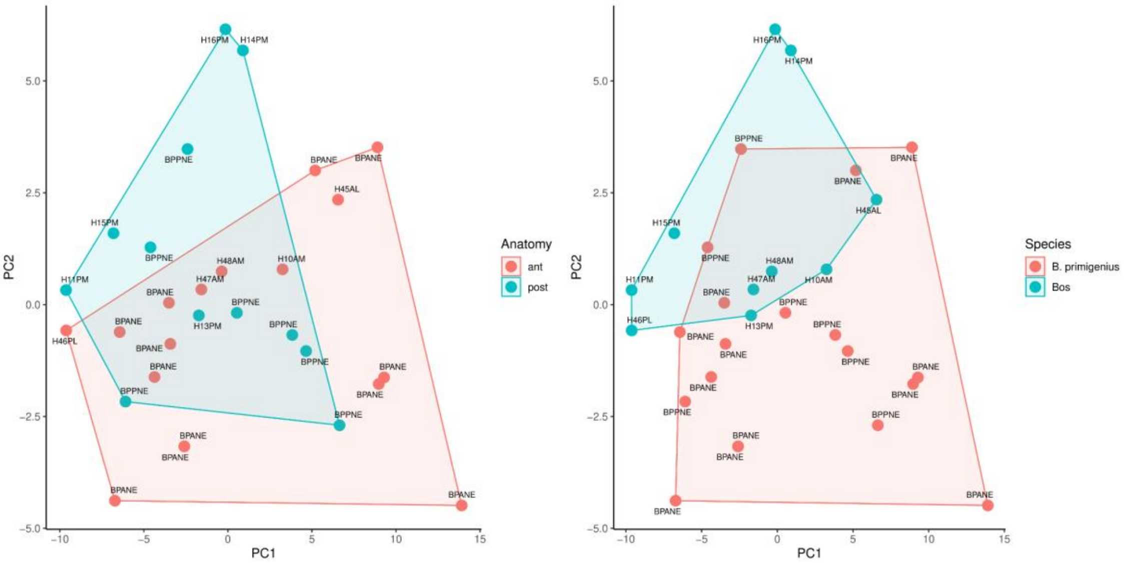

Figure 23 Results of the referential principal component analysis of biometric measurements of Bos first phalanges.

The first PC (PC1) explained 81% of the reference data variance. After sorting the relevant eigenvector, it was revealed that PC1 was almost equally contributed by GL (25.8%), Bp (38%) and Bd (36.1%). Available referential information indicated that PC1 did not correspond to anatomical or species information (Figure 23, left). The second PC (PC2) explained 15% of the variance, while it was contributed mainly by GL (58.7%) and Bd (26.2%). PC2 significantly (c^2 (1, 29) = 7.8, p = 0.01, where c^2 denotes Kruskal-Wallis chi-squared) corresponded to species information (Figure 23, right), although with noticeable overlap. The third PC explained 4% of the data variance and, similar to PC1, did not correspond to the available information. The lack of correspondence to the anatomical factor was possibly rooted in the anteriorisation of posterior phalanges due to the heavy exploitations (Helmer *et al.*, 2018).

By having information about the nature of the principal referential axes (*i.e.* PC2 corresponds to species), the biometric measurements of Tell Halula's first phalanges were projected on the referential PC1 and PC2 axes. The result of the projection is depicted in Figure 24.

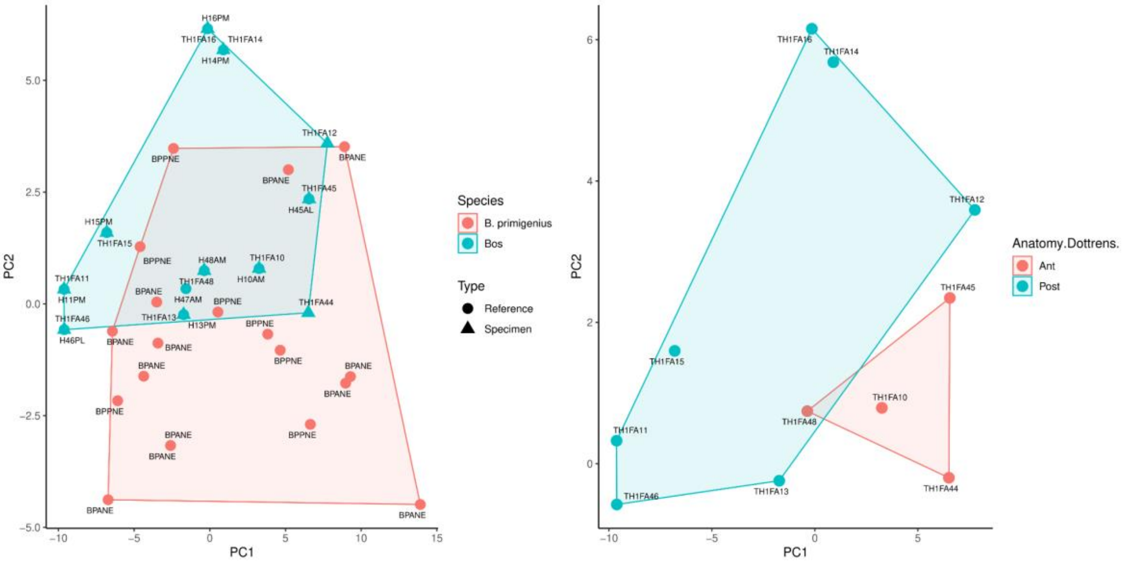

Figure 24 The biometric measurements of the Tell Halula's specimens (first phalanges of Bos) after being projected on the two referential principal axes, PC1 and PC2. The anatomical information of phalanges was assumed following Dottrens (1946) procedure.

5.1.2. Bovines of Tell Halula: Morphometrics of first phalanges.

In the context of the Tell Halula zooarchaeology, morphological variability of *Bos* phalanges echoes anatomical information, as well as adaptive locomotory responses to external factors such as limiting foraging and decreasing gait cycles imposed by farmers and herders, and heavy-duty exploitations (*e.g.* draughting, tilling and transportation). In addition, since Tell Halula hosted farming communities from the Middle pre-pottery Neolithic to the pre-Halaf era, different herd management strategies are also among the potential causes of data variance. Separating the mentioned sources of morphological variability, however, necessitates 1- removing data redundancy (out of hundreds of landmark-driven variables, finding a few ones which significantly influence the specimen morphological characteristics) and 2- explanative procedure, such as finite element analysis, connecting morphological information (*i.e.* Procrustes residuals) to the biomechanical regulations, examining if the mentioned influential variable is the possible source of morphological divergence. Starting with the information redundancy, after digitising landmarks and performing Procrustes superimposition, the resultant Procrustean residuals were subjected to principal component analysis to investigate the significant reason behind the morphological variation of *Bos* first phalanges from Tell Halula. The Scree plot of morphometric PCA is available in Figure 25. The first component (PC1) explained 31.7% of data variation, which was mainly influenced by the morphological differences of abaxial palmar eminence (landmark 29, Figure 26, top-left). The second principal axis, PC2, described 18.1% of data variation reflecting morphological disparity at the axial ventral base of the first phalanges (Figure 26, top-right).

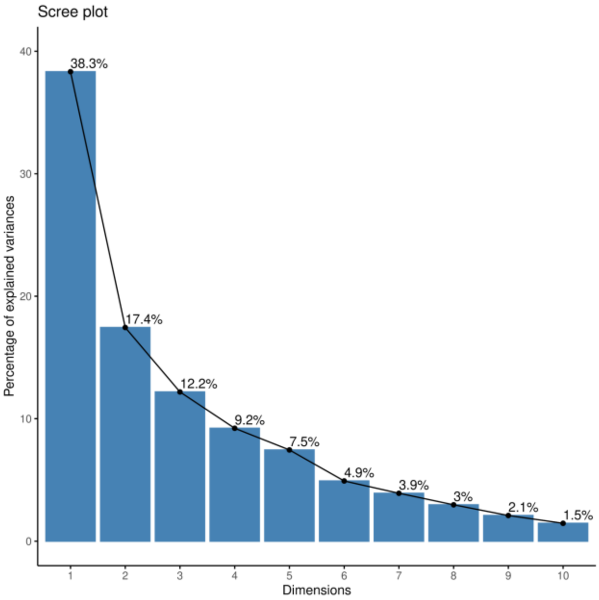

Figure 25 Scree plot of Principal component analysis conducted on Procrustes residuals of Bos first phalanges from Tell Halula

PC3 represented 15.2% of the variance, corresponding to dissimilarities at the abaxial ventral base of specimens (Figure 26, down-left). Moreover, the fourth axis, PC4, described 11.7% of the variance and was influenced by the axial palmar-distal process (Figure 26, down-right).

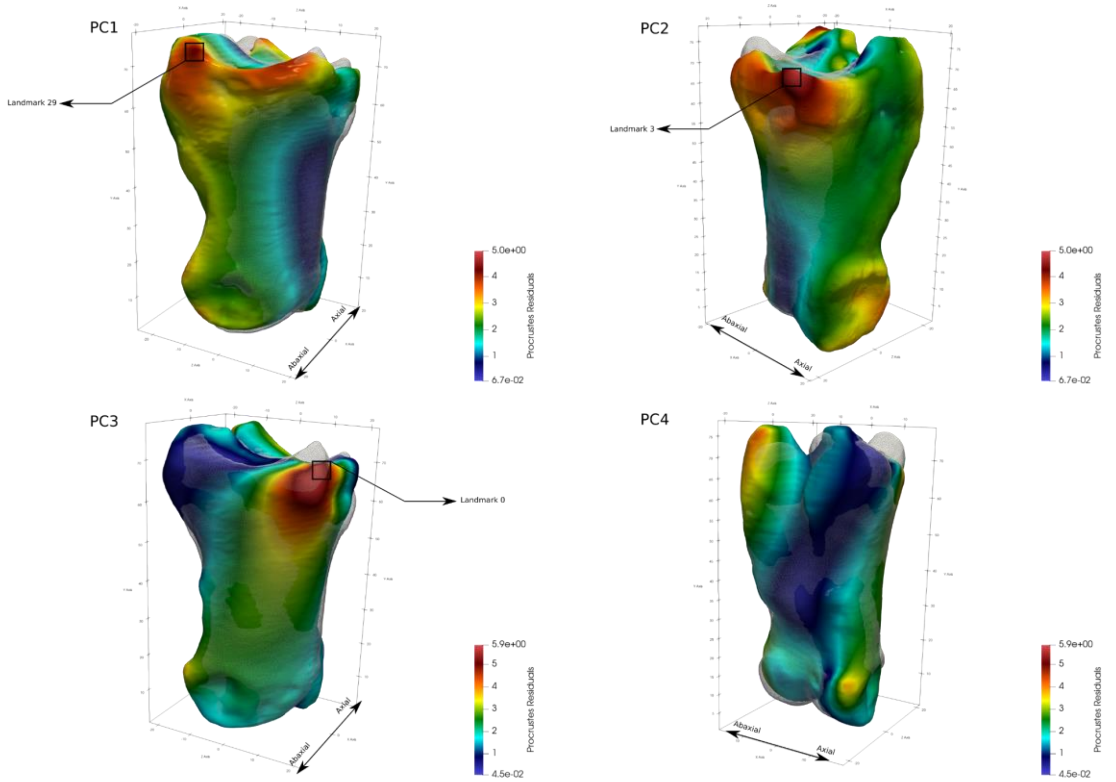

Figure 26 The local morphological discrepancies from the template specimen (Procrustes residuals) contributed the most to the four major morphometric PCA (PC1 to PC4). The template is depicted in an opaque white mesh imposed on each sample.

In order to decipher principal component dimensions, a series of finite element analyses were perpetrated, and the consequent strain values were sampled at the locations of landmarks which had the most impact on each morphometric principal component axis. Starting with the PC1, the resultant strain value at “landmark 29” (the most influential landmark on PC1, located at the abaxial-palmar plane) was ascending along the first principal axis (Figure 27). Lower strain is an indicator of robustness, suggesting that the specimen is adapted (through the remodelling process) to a higher mechanical environment, due to the anatomical characteristics (anterior or medial phalanges endure more pressure compared to the posterior and lateral ones, due to the weight of chest and head and standing posture of cattle, respectively) or the effect of herd management and exploitation. Differentiating the morphological effects of anatomical and human-induced factors requires incorporating more morphological principal spaces.

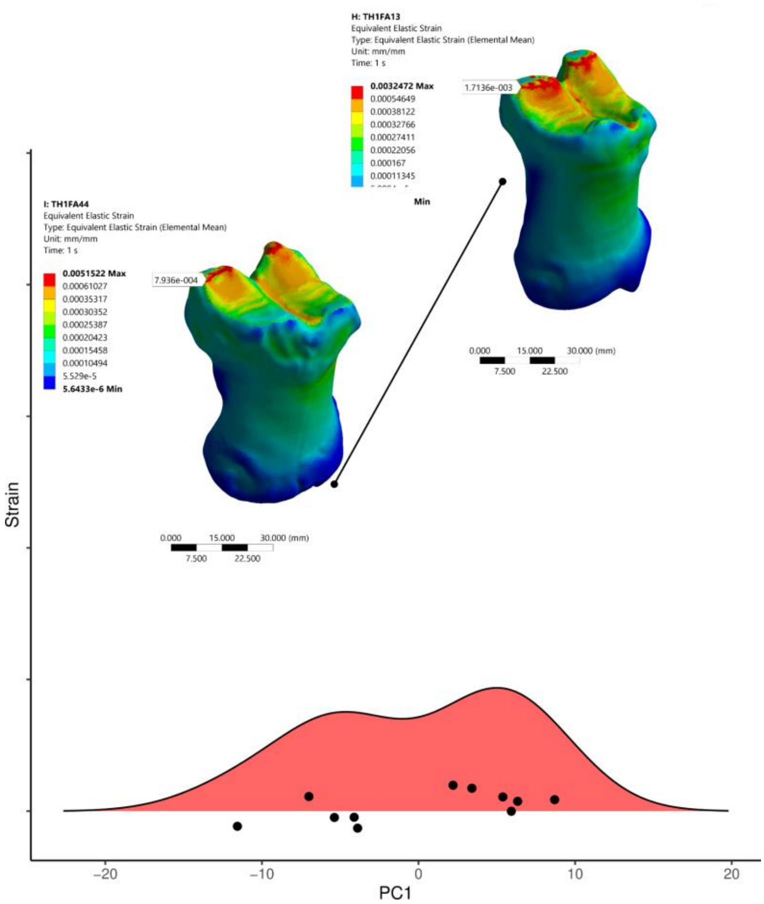

Figure 27 The first principal component of Procrustes residuals of first phalanges (Tell Halula specimens) plotted against the resultant strain values of 1MPa pressure. The strain was measured at landmark 29 (the most influential landmark on PC1, located at the axial-palmar plane).

The second morphometric principal axis of Tell Halula's specimens (first phalanges), representing morphological disparities at the axial ventral base (landmark 3), was also examined by finite element analysis. *Bos*'s first phalanx ventral axes (axial and abaxial) do not endure body weight except at the initial contact phase of gait. Consequently, the ventral protrusions are stress-sensitive, reflected in the finite element strain values sampled at "landmark 3". Sampled strain values were slightly ascending along the PC2 axis (Figure 28), suggesting that the second principle axis reflects primarily undifferentiable (potentially anatomical-related) mechanical environment variations along the axial ventral direction, except for the noticeably low strain values at "landmark 3" coupled with the depression of the ventral-axial process, such as the specimen at the end range of the second principle component (specimen TH1FA12), denote a pattern of extreme and long-lasting exploitation.

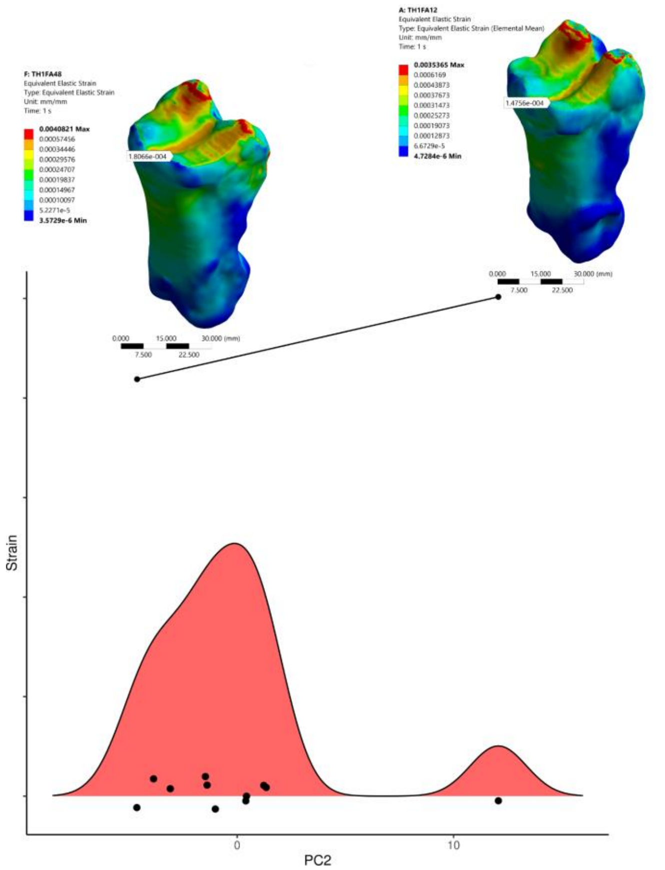

Figure 28 The second principal component of Procrustes residuals of first phalanges (Tell Halula specimens) plotted against the resultant strain values of 1MPa pressure. The strain was measured at landmark 3 (the most influential landmark on PC2, located at the ventral-abaxial plane).

The third morphometric principal component mirrored the PC2 and depicted the morphological variation at “landmark 0”, the axial ventral process (base) of the first phalanges. Finite element results depicted an ascending pattern of strain along PC3, where specimens at the lower range of principle scores had less strain at “landmark 0” due to the adaptation to higher mechanical stress (Figure 29-A). A Kendall’s rank correlation test (Khamis, 2008) was conducted between PC3 scores and Tell Halula’s occupation phases to investigate if any significant correlation exists between herding management and morphological feature of the first phalanges (Figure 29-B). The result showed that the correlation is positive and highly significant ($\tau = 0.56$, p = 0.02), suggesting that from the occupation phase 4 to 16 (MPPNB to LPPNB), the intensity of the *Bos* exploitation was reduced significantly, or the nature of exploitation was shifted from traction (which put extra pressure on the ventral axis of phalanges) to another type.

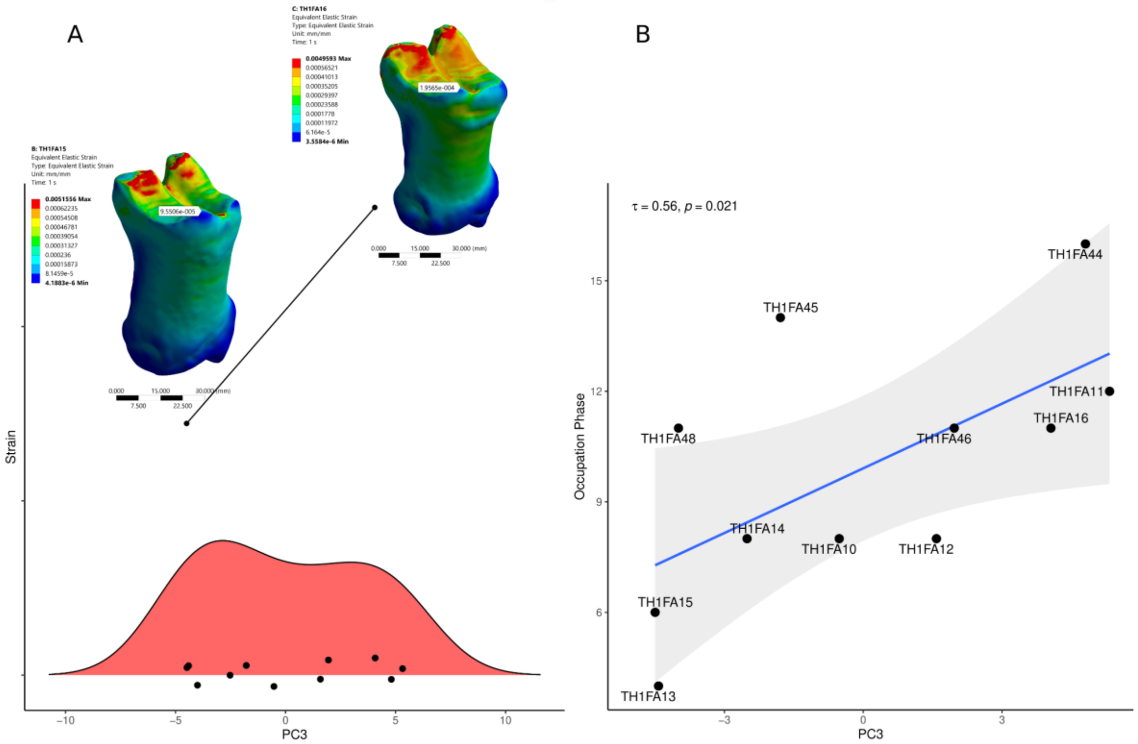

Figure 29 A: The third principal component of Procrustes residuals of first phalanges (Tell Halula specimens) plotted against the resultant strain values of 1MPa pressure. The strain was measured at landmark 0 (the most influential landmark on PC3, located at the ventral-axial plane). B: Kendall's rank correlation between PC3 scores and Tell Halula's Occupation phases.

Integrating the morphological disparities of the palmar (PC1) and ventral (PC3) axes of the first phalanges suggested that the anatomical factors primarily influence Tell Halula’s morphological variation, that is, anterior-posteriority (PC1, explained variance = 38.3%) and exploitation patterns (PC3, explained variance = 12.2%), where no significant correlation can be observed between the intensity of exploitation and anatomically-induced morphological disparities (Figure 30). Lack of correlation between anatomical factors and PC3 indicate that the resultant mechanical load of exploitation was equally distributed along anterior-posterior axes.

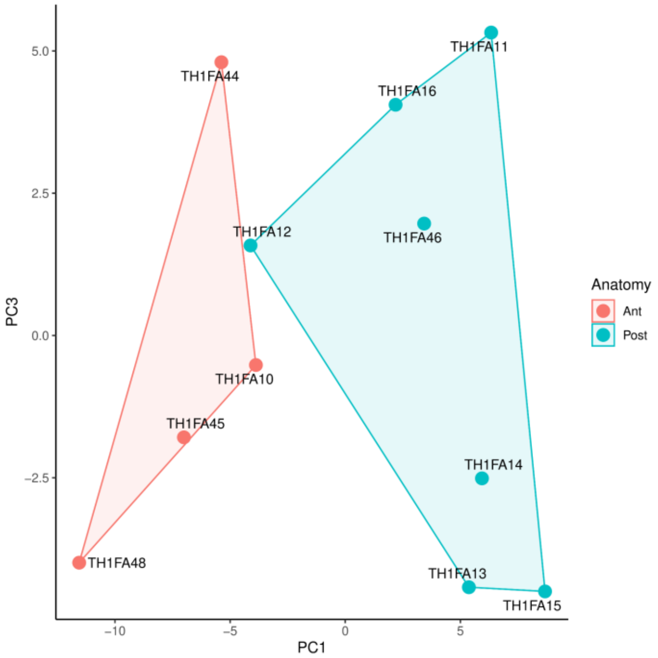

Figure 30 The first and third principal components of Procrustes residuals of first phalanges (Tell Halula specimens). Specimens were grouped based on the anatomical characteristics adopted following Dottrens (1946).

5.1.3. Bovines of Tell Halula: Biometry of second phalanges

The greatest length (GL) of Tell Halula's second phalanges ranged from 41.43 to 56.39 (mm) with an arithmetic mean of 49.34 (with an estimated error of 1.04 millimetres at 95% confidence interval) and a standard deviation of 3.66 millimetres. The Gl values of the second phalanges were significantly larger than the *Bos primigenius* referencial greatest length (Figure 31, left, $c^2(1, 69) = 8.37$, $p < 0.01$). The smallest breadth of the diaphysis (SD) of Tell Halula's second phalanges varied from 22.46 to 35.07 millimetres while displaying an arithmetic mean of 28.57 (±0.83 mm, 95% CI) and a standard deviation of 2.93 millimetres. SD values of Tell Halula’s second phalanges did not significantly differ from the referential *Bos* *primigenius* measurements (

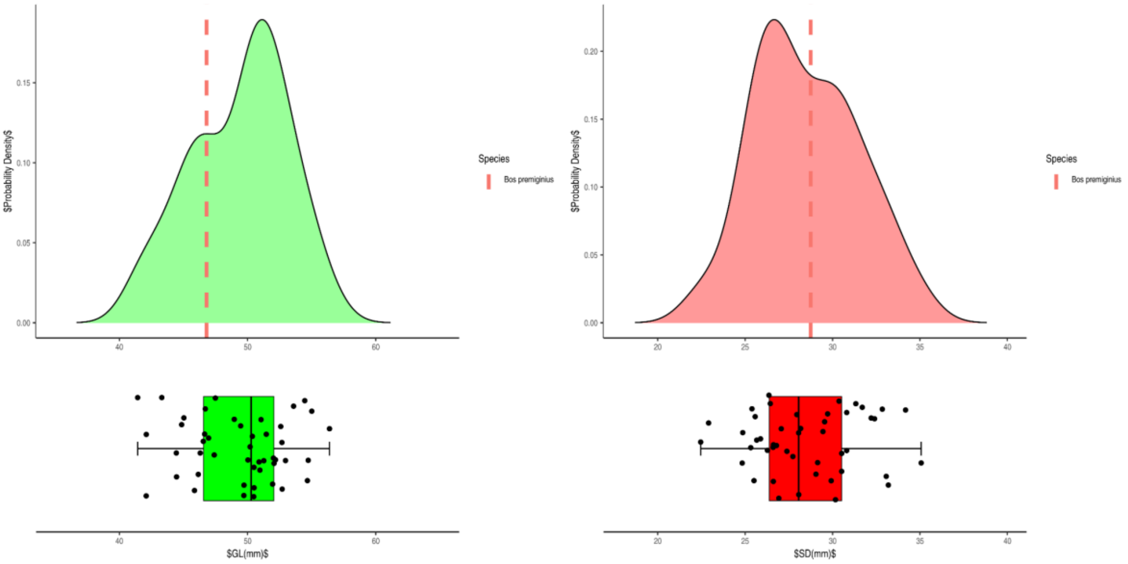

Figure 31, right).

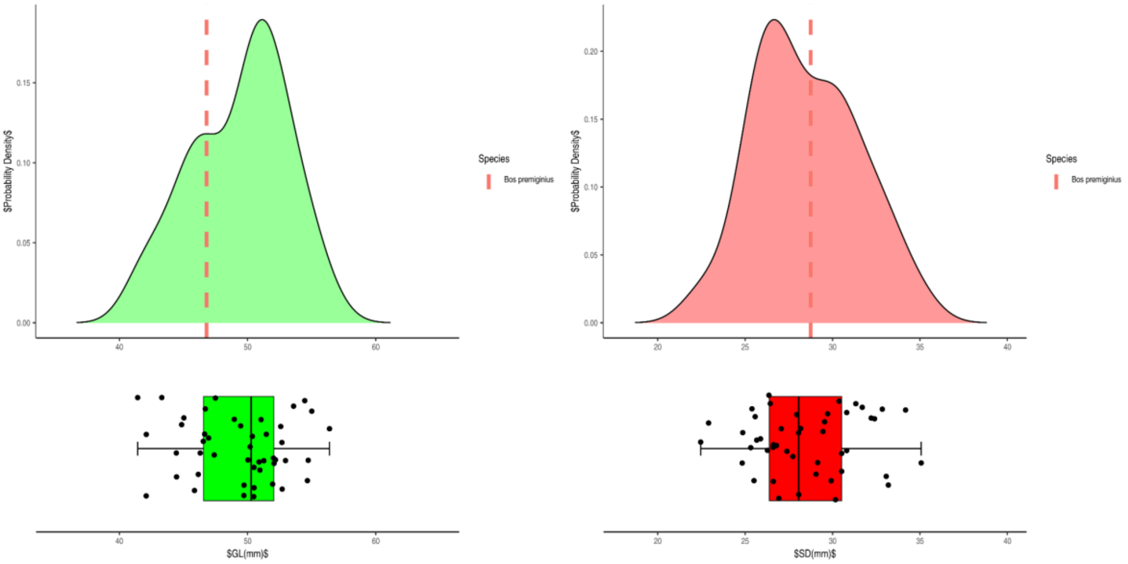

Figure 31 Probability density graph of greatest length (left, in green) and the smallest width of the diaphysis (right, in red) of cattle's second phalanges excavated from Tell Halula. The distributions of both measurements are bimodal. The referencial measurements are presented as a vertical red line (if they were available for the analysis) indicating an average aurochs dimensions.

The breadth of the proximal epiphysis (Bp) was expanded between 27.91 and 40.73 millimetres, with an arithmetic mean of 34.78 (±0.96 millimetres, 95% CI) and a standard deviation of 3.39 millimetres (Figure 32, left). The observed range of breadth of the distal epiphysis (Bd) was from 24.75 to 36.81 millimetres with an arithmetic mean of 30.30 (±0.98 millimetres, 95% CI) and a standard deviation of 3.44 millimetres (Figure 32, right).

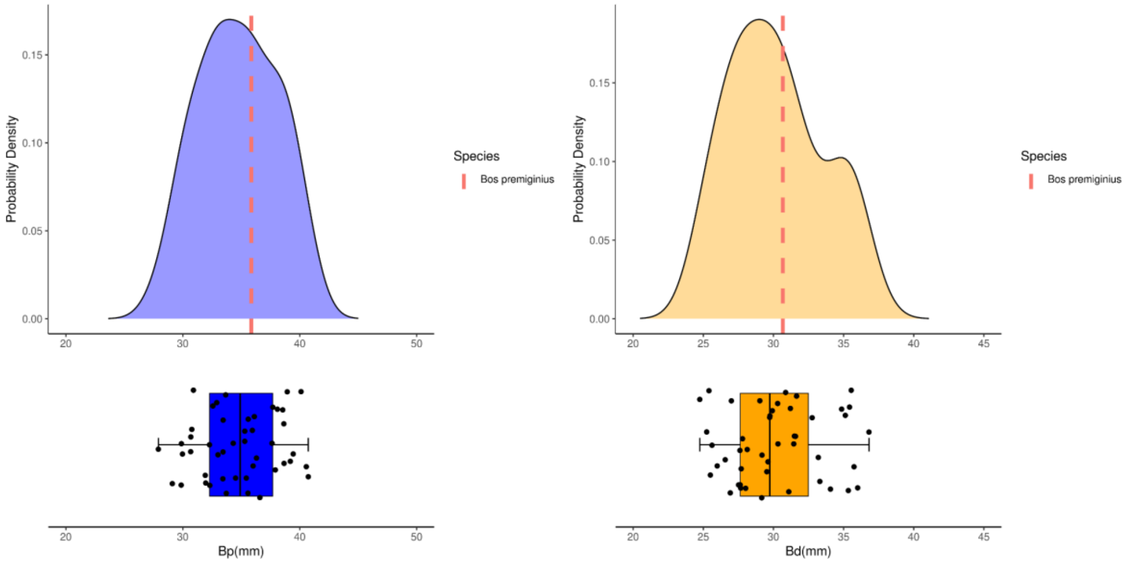

Figure 32 Probability density plots of the breadth of the proximal (Left, in blue) and the distal epiphysis (right, in orange) of cattle second phalanges, excavated from Tell Halula. The referential measurements are presented as a vertical red line (if they were available for the analysis) indicating an average aurochs dimensions.

In the same way, as with the first phalanges, a linear regression was conducted separately for SD, Bp, and Bd measurements to determine how much variance could be explained by the allometric effect of size. In addition, the homoscedasticity (equal scatter of residuals) assumption of linear regressions was tested using Koenker's test (Koenker & Bassett, 1982), which is robust enough for contaminated data with a long tail or multi-modality (Lyon & Tsai, 1996). Resultantly, out of three measurements, residuals of the GL-Bd model of Tell Halula's second phalanges showed a significant heteroskedasticity (SBP(1, 48) = 4.44, p = 0.03, where SBP stands for the studentised Bruesch-Pagan statistic); therefore, a robust regression model with a heteroskedasticity consistent variance-covariance matrix (HC1) was implemented instead (MacKinnon & White, 1985). The results of the three regression models are available in Table 9.

Model	**Intercept**	**Slope**	**F-Statistic**	**P-value**	**Adjusted R-squared**
SD ~ GL	-0.1228	0.5799	F(1, 44) = 51.89	<0.01	0.5307

Bp ~ GL	1.25	0.67	F(1, 44) = 58.83	<0.01	0.5624
*Bd ~ GL	1.25	0.678	F(1, 44) = 58.83	<0.01	0.5624
* Robust Regression model with a heteroskedasticity consistent variance-covariance matrix (HC1).					

Table 9 Results of ordinary linear regressions of Tell Halula's cattle second phalanges measurements.

The adjusted R-squared values indicate that 53-53% of the observed variance in the linear (biometric) measurements is explicable by the size of individual specimens. To further analyse the variation of data, a paired correlation test was conducted to investigate the possibility of collinearity. The paired test results are provided in Figure 33 All permutations of correlations between biometric measurements taken from Bos second phalanges (Tell Halula specimens). All biometric descriptors are significantly collinear., showing the existence of highly significant collinearities between observations.

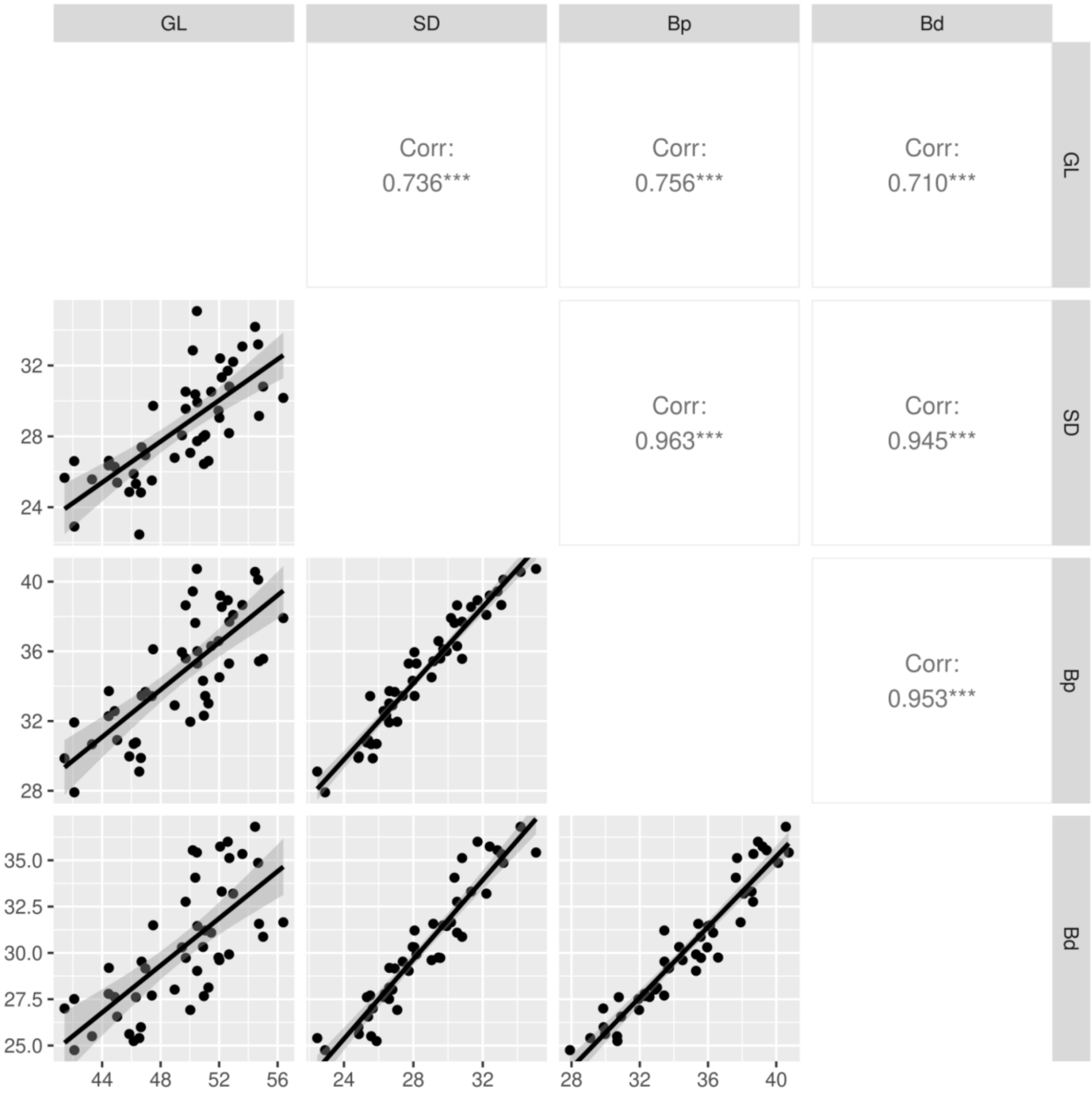

Figure 33 All permutations of correlations between biometric measurements taken from Bos second phalanges (Tell Halula specimens). All biometric descriptors are significantly collinear.

A principal component analysis was performed on linear measurements to observe their influence on the variance without unwanted consequences of colinearity and allometric size effect (Figure 34). First, the reference principal component analysis was compiled using *Bos primigenius* linear measurements. The result of Reference PCA showed that the first PC explained 74% of the variance and reflected the (almost) equal contribution of GL (16.7%), SD(26%), Bp(26.7%), and Bd(30.4%). The second PC (which explained 17% of the variance) was contributed by GL(64%) and Bd(33%), the third PC by Bp (49.2%) and SD(35.3%), and the fourth PC by

GL(16.5%), Bp(15.7%), SD(33.9%), and Bd(33.7%). None of the referencial principal scores inhibited significant impact of the known factor (*i.e.* anatomical information).

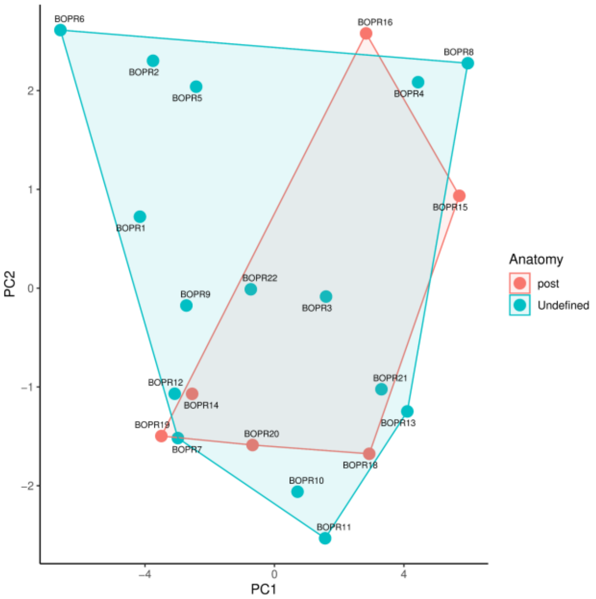

Figure 34 Results of the referential principal component analysis of biometric measurements of Bos second phalanges.

Consequently, the biometric measurements of Tell Halula’s second phalanges were projected on the referential PC1 and PC2 axes. The result of the projection is presented in Figure 35.

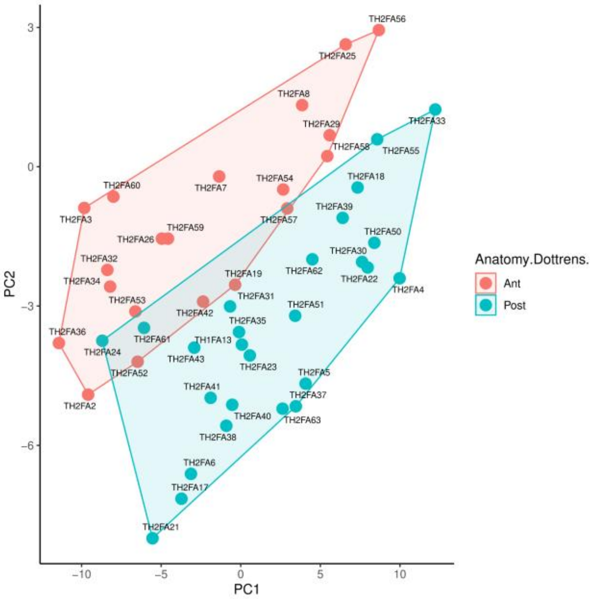

Figure 35 The biometric measurements of the Tell Halula's specimens (second phalanges of Bos) after being projected on the two referential principal axes, PC1

and PC2. The anatomical information of phalanges was assumed following Dottrens (1946) procedure.

5.1.4. Bovines of Tell Halula: Morphometrics of second phalanges

After digitising landmarks and performing Procrustes superimposition, the resultant Procrustean residuals were subjected to principal component analysis to investigate the significant reason behind the morphological variation of *Bos* second phalanges from Tell Halula. The Scree plot of morphometric PCA is available in Figure 36. The first component (PC1) explained 63.7% of the variance, mainly influenced by the morphological differences at the distal epiphysis (landmark 6, Figure 37, left). Unlike the first phalanx, *Bos*'s second phalanx is short and robust, and it is morphologically affected by persistence elements such as anatomical-ecological factors and the impact axes (*e.g.* axial or abaxial) of the other elements, such as herd management, can be unpredictable. Accordingly, the first morphological principal component of the second phalanges reflected the specimens' anatomical (anterior-posterior) positioning. Moving alongside PC1, the second phalanges became distally even more robust and broader, more adapted to endure the mechanical environment, confirmed by finite element analysis (Figure 38).

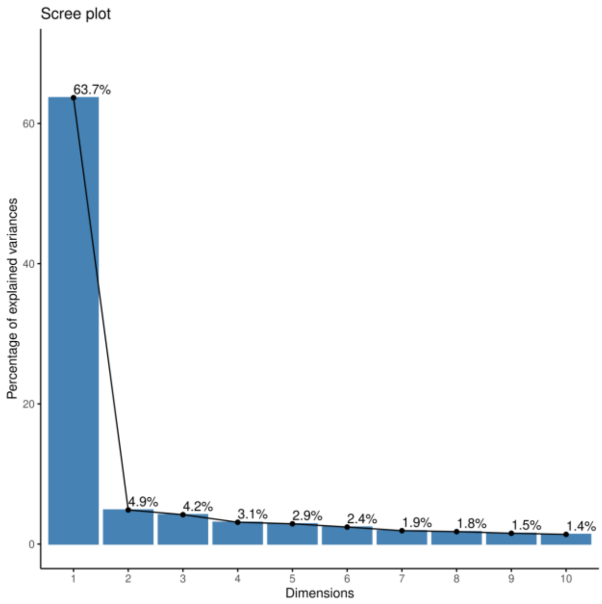

Figure 36 Scree plot of Principal component analysis conducted on Procrustes residuals of Bos second phalanges from Tell Halula.

Examining the potential effect of animal husbandry and exploitation was proceeded by a series of Analyses of variance, seeking for significant variation of morphometric (Procrustes residuals) PCs in different archaeological contexts: Middle Pre-Pottery Neolithic-B (MPPNB), Late Pre-Pottery Neolithic-B (LPPNB), and pre-Halaf. The first ten principal components were examined, and the ninth PC responded non-significantly to the Neolithic periods (visible trend, Figure 39-right).

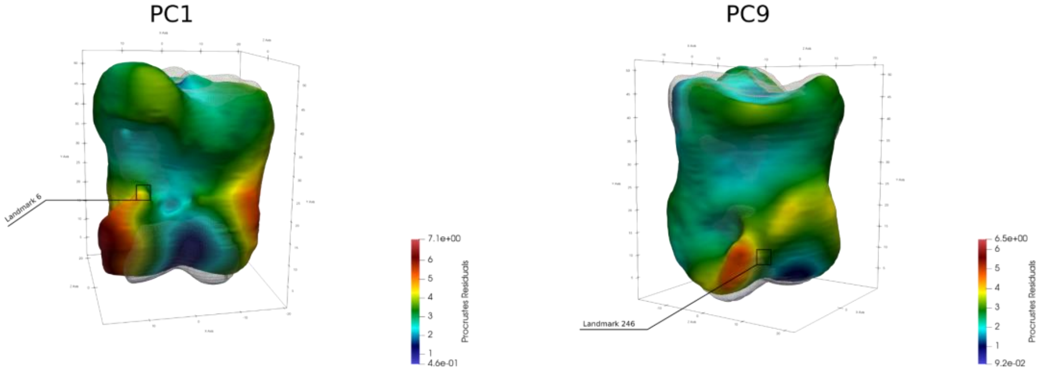

Figure 37 The local morphological dissimilarities from the template specimen (Procrustes residuals) contributed the most to the two relevant morphometric PCA (PC1 and PC9). The template is depicted in an opaque white mesh imposed on each sample.

The PC9 was mostly influenced by landmark 246, located at the distal groove of the second phalanges (Figure 37, right).

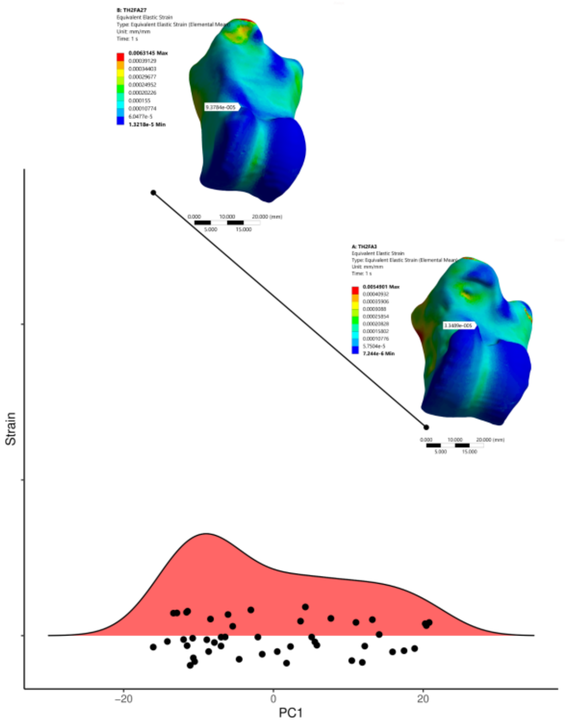

Figure 38 The first principal component of Procrustes residuals of second phalanges (Tell Halula specimens) plotted against the resultant strain values of 1MPa pressure. The strain was measured at landmark 6 (the most influential landmark on PC1, located at the ventral-abaxial plane).

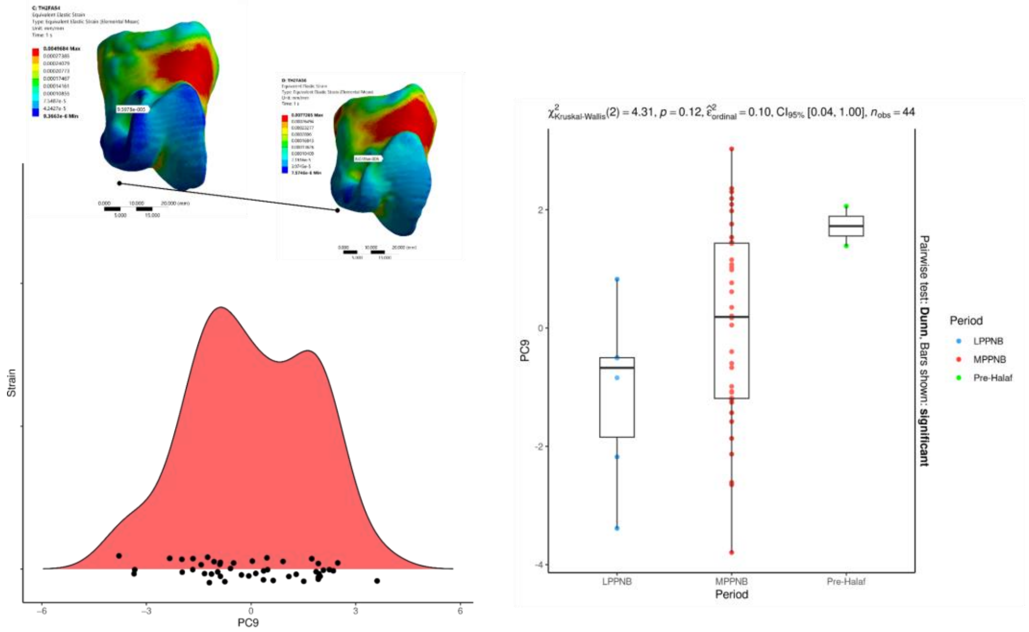

Figure 39 The ninth principal component of Procrustes residuals of second phalanges (Tell Halula specimens) plotted against the resultant strain values of 1MPa pressure. The strain was measured at landmark 246 (the most influential landmark on PC9, located at the distal groove). B: Influence of different periods (MPPNB to Pre-Halaf) on PC9, tested via Kruskal-Wallis rank sum test.

Two finite element analyses were conducted, helping to understand the biomechanical importance of morphological changes at landmark 246 (Figure 39, left). The results of FEA revealed that by moving along PC9, sampled strains were descending, and specimens became locally more robust at the landmark (246).

Integrating the morphological information of PC1 and PC9 of the second phalanges (Figure 40) indicated that the morphology of the second phalanx is intensely regulated by anatomy, as expected. Moreover, similar to the first phalanges, there is a descending trend between MPPNB and LPPNB strain patterns, although more LPPNB data are needed to make a clear statement.

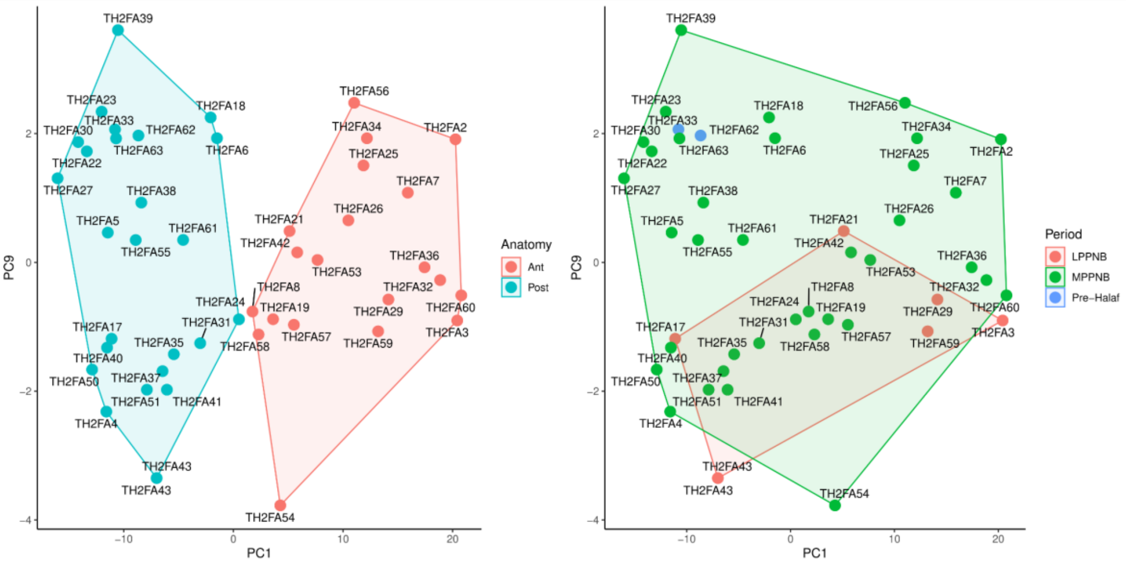

Figure 40 The first and ninth principal components of Procrustes residuals of second phalanges (Tell Halula specimens). Specimens were grouped based on the anatomical characteristics (left) adopted following Dottrens (1946) and the archaeological period (right).

5.2. Bovines of La Draga

5.2.1. Bovines of La Draga: Biometry of first phalanges

According to the linear measurements, La Draga's first phalanx greatest length (GL) ranged from 57.6 to 74.2 (mm), with a mean of 64.26 (±1.69 millimetres estimated error for the 95% confidence interval) and a standard deviation of 4.08 millimetres. Compared with the reference measurements of European *Bos primigenius*, most of

La Draga's first phalanges (except five individuals) were prominently shorter than the referential average greatest length, except one specimen, LD1FA29 (Figure 41, left).

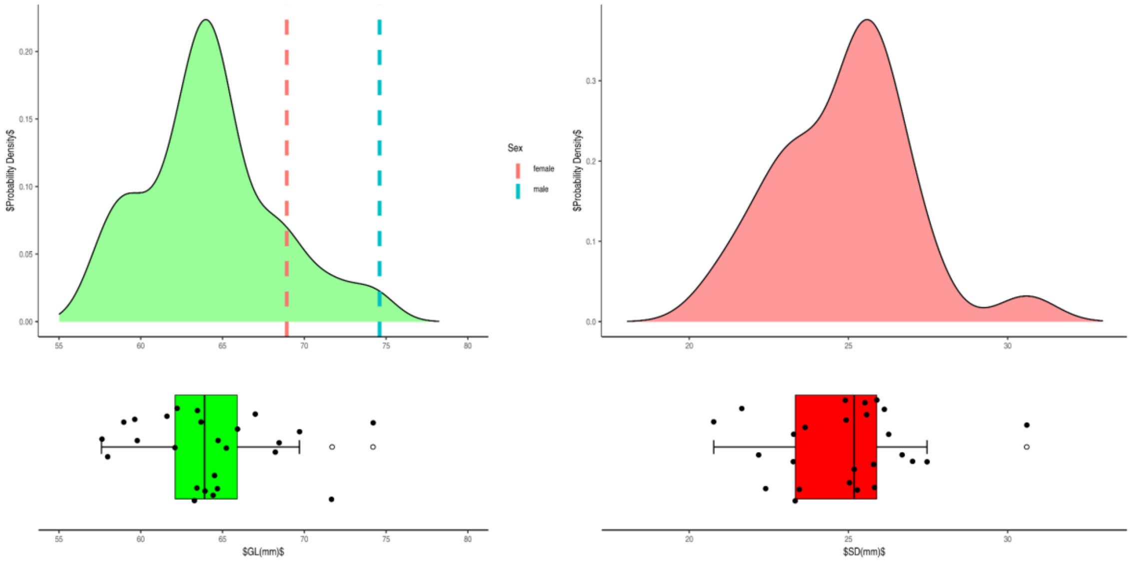

Figure 41 Probability density graph of greatest length (left, in green) and the smallest width of the diaphysis (right, in red) of cattle's first phalanges excavated from La Draga. The referencial measurements are presented as two vertical red (female) and blue (male) lines (if they were available for the analysis), indicating average aurochs dimensions.

On the other hand, the smallest breadth of the diaphysis (SD) of La Draga's first phalanges varied from 20.77 to 30.6 millimetres, exhibiting an arithmetic mean of 24.88 (±0.87 mm, 95% CI) and a standard deviation of 2.11 millimetres (Figure 41, right). The breadth of the proximal epiphysis (Bp) was expanded between 25.25 and 35.36 millimetres, with an arithmetic mean of 29.86 (±0.97 millimetres, 95% CI) and a standard deviation of 2.35 millimetres. The breadth of the distal epiphysis (Bd) observed range was from 22.62 to 32.71 millimetres with a lower arithmetic mean of 26.15 (±0.93 millimetres, 95% CI) and standard deviation of 2.25 millimetres, compared to Bp. Both epiphysial width measurements were significantly slimmer than the average of the corresponding reference (aurochs) measurements (Figure 42)

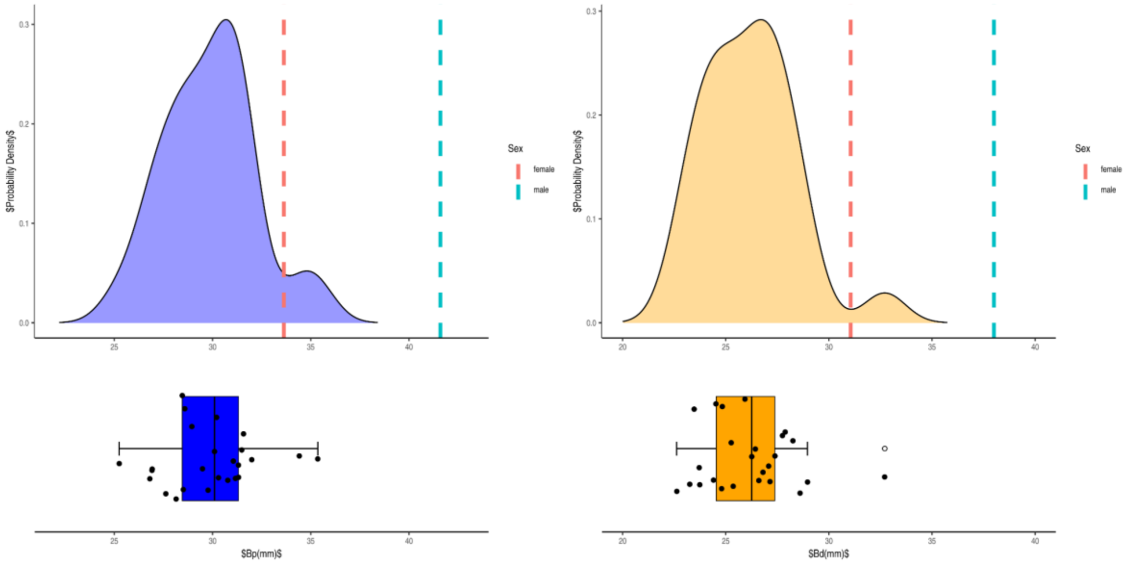

Figure 42 Probability density plots of the breadth of the proximal (Left, in blue) and the distal epiphysis (right, in orange) of cattle first phalanges excavated from LaDraga. The referencial measurements are presented as two vertical red (female) and blue (male) lines (if they were available for the analysis), indicating average aurochs dimensions.

A series of comparative linear correlation tests showed that La Draga's first posterior phalanges diametric measures (SD, Bp, and Bd) did not significantly correlate with the greatest length, while the anterior measurements, except Bp, were highly significantly colinear with GL (Figure 43).

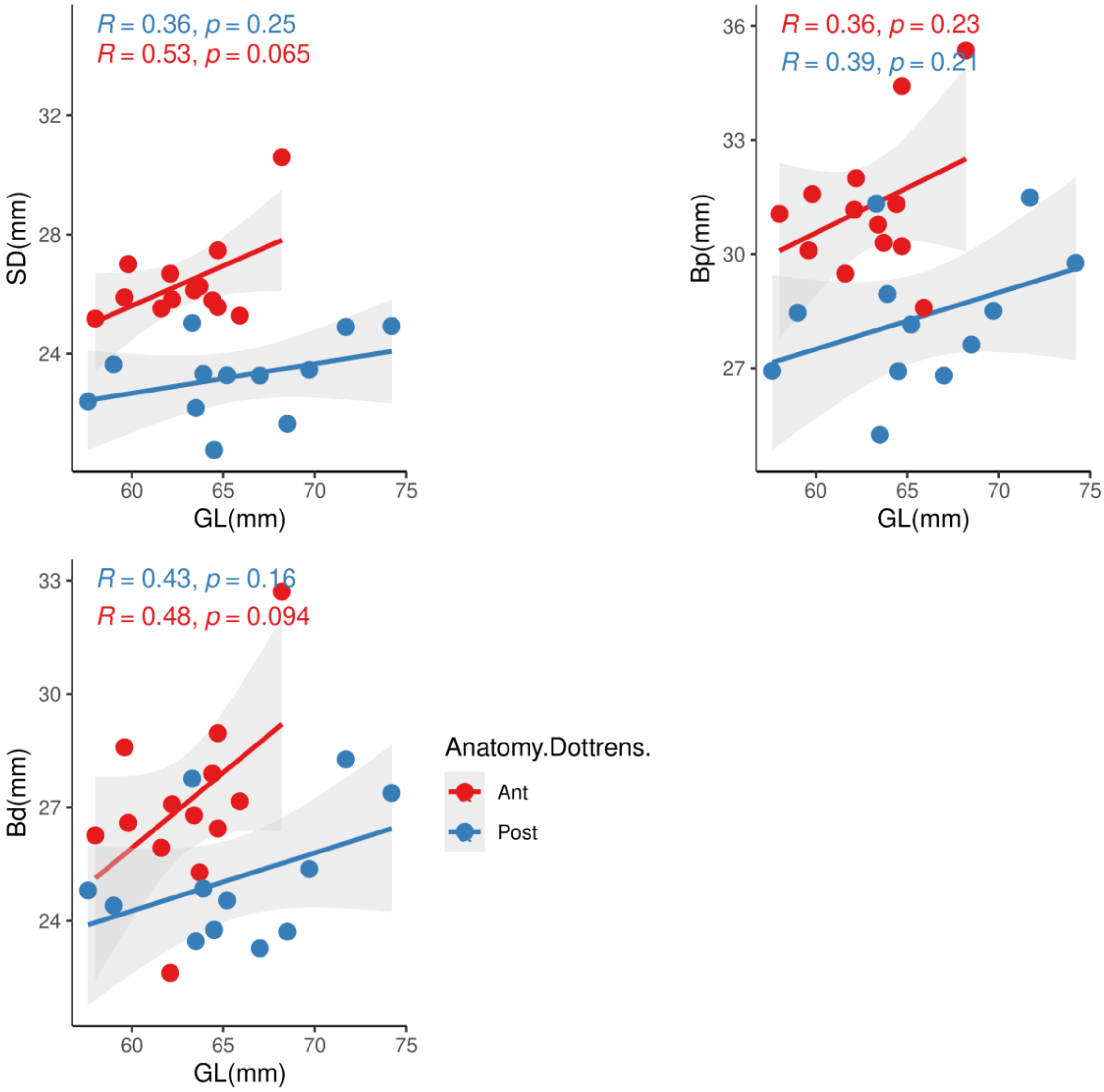

Figure 43 Correlations between diametric measurements and GL in anterior and posterior first phalanges (La Draga Samples).

Two referential principal components were trained using 1- GL, Bp and Bd for reference specimens (European *Bos primigenius*) with known gender and 2- GL, SD, Bp, and Bd for reference samples with known anatomical location (anterior-posterior). The results of the referential principal components are provided in Figure 44.

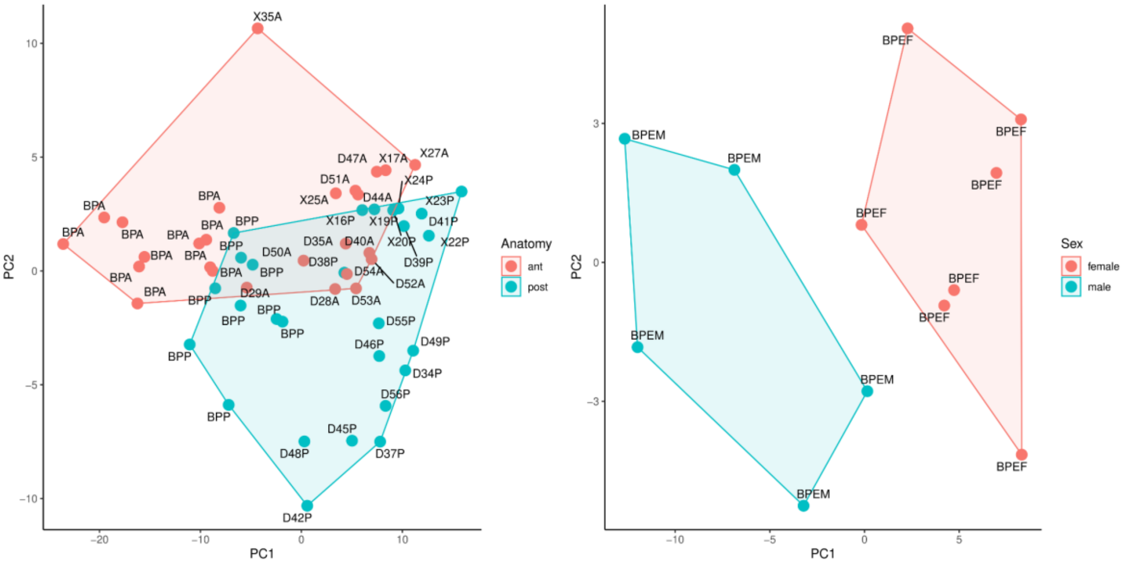

Figure 44 The referential principal component spaces regarding anatomical (left) and gender (right) factors. They were defined by the reference material's linear measurements.

In the case of anatomical reference principal space, the first component was influenced by more or less equal combinations of the greatest length (21%), SD (24%), Bp(25.7%), and Bd(28%). The second component, however, was influenced the most by GL (54%), reflecting the allometric effect of size on the data variance. The third component was represented mainly by Bd (46%), and the fourth component by SD (48%) and, to a lesser degree, Bp (41.6%). Regarding the gender reference principal space, the first component was influenced by equal combinations of the greatest length (34.5%), Bp(33.6%), and Bd (31.8%). The second component reflected the allometric size effect, and the third represented the most by Bp (51%) and Bd (47%). Consequently, the biometric measurements of La Draga’s first phalanges were projected on the referential PC1 and PC2 axes. The projection result is presented in Figure 45.

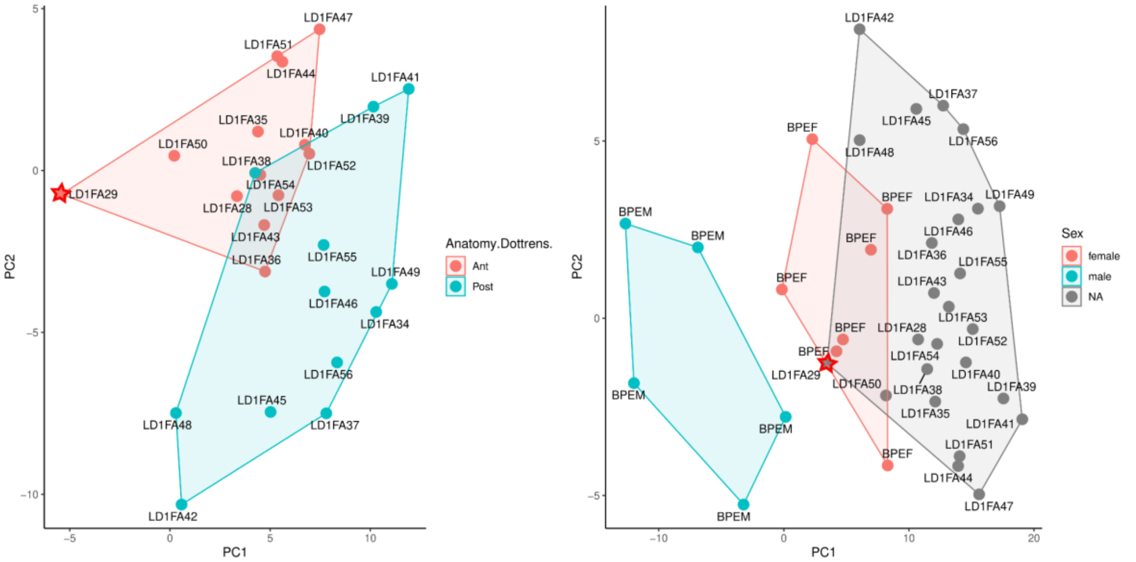

Figure 45 Principal component scores of La Draga's first phalanges after being projected on anatomical (left) and gender (right) principal axes. A red star marks specimen LD1FA29 (potentially a female auroch). Specimens with no prior information about their gender are marked as NA.

5.2.2. Bovines of La Draga: Morphometrics of first phalanges

After digitising landmarks and executing Procrustes superimposition, the resultant Procrustean residuals were subjected to principal component analysis to investigate the significant reason behind the morphological variation of *Bos* first phalanges from La Draga. The Scree plot of morphometric PCA is available in Figure 46. The first component (PC1) explained 35.2% of data variation, which was mainly influenced by the morphological differences of axial ventral eminence (landmark 3, Figure 47, top-left) and highly significantly described anatomical disparities (anterior-posterior) in the first phalanges of La Draga (C2 (1, 25) = 5.99, p = 0.01).

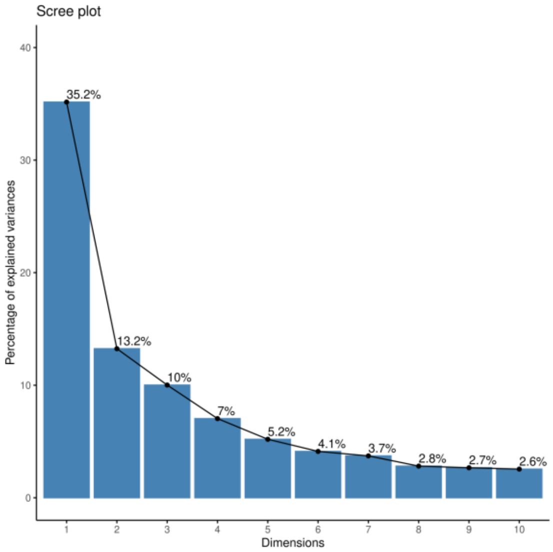

Figure 46 The percentage of morphological variation of La Draga's first phalanges, described by ten significant principal axes of Procrustes residuals after performing the principal component analysis (Scree plot).

The second principal axis, PC2, described 13.2% of the variance, reflecting morphological discrepancy at the abaxial ventral base of the first phalanges (landmark 0, Figure 47, top-right). Although PC2 had nothing significant to do with the anterior-posteriority of the phalanges, its corresponding most influential landmark ("landmark 0") was located at a stress-sensitive location. As mentioned before, the abaxial plane of the first phalanges is naturally off-axis and, consequently, is more sensitive to mechanical loads. The reflection of more than 10% of morphological variation without any significant correlation with the anterior-posteriority suggests the existence of an unknown morphologically important factor, such as the medial-laterality of phalanges or herd management and exploitation.

The third principal component described 10% of the data variation, reflecting morphological deviation at the ventral extreme of the distal diaphysis (Landmark 42, Figure 47, down-left) and also highly significantly reflected anatomical (anterior-posterior) disparities in the first phalanges of La Draga (C2 (1, 25) = 5.73, p = 0.02).

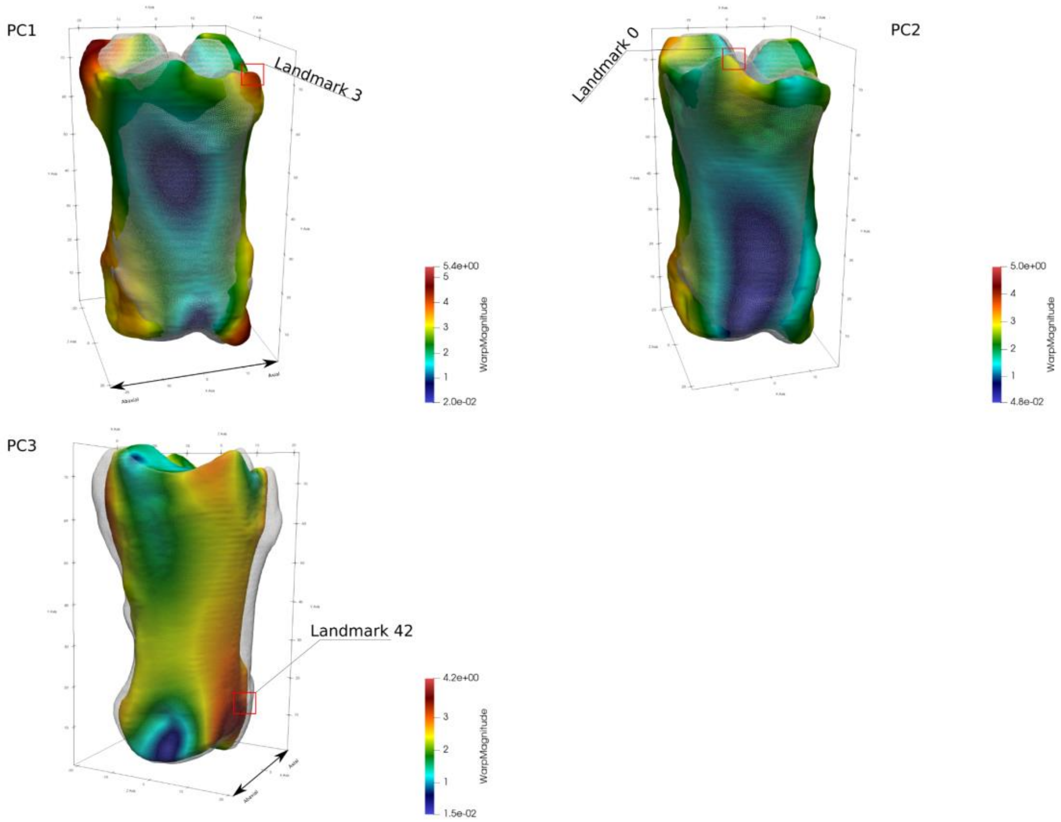

Figure 47 The local morphological discrepancies from the template specimen (Procrustes residuals) contributed the most to the three major morphometric PCA (PC1 to PC3). The template is depicted in an opaque white mesh imposed on each sample.

Integrating PC1 and PC3 information highlights that the anatomical factor (anterior-posteriority) was responsible for a total of 45.2% of morphospace variance. Scores of the first principal component had an inverse correlation with the broadening of the axial side of the proximal epiphysis, and scores of PC3 had a direct correlation with the distal width (not breadth) of the first phalanges. The accuracy of anterior-posterior segregation using the said PCs was 72% (seven overlapping samples out of 25, Figure 48).

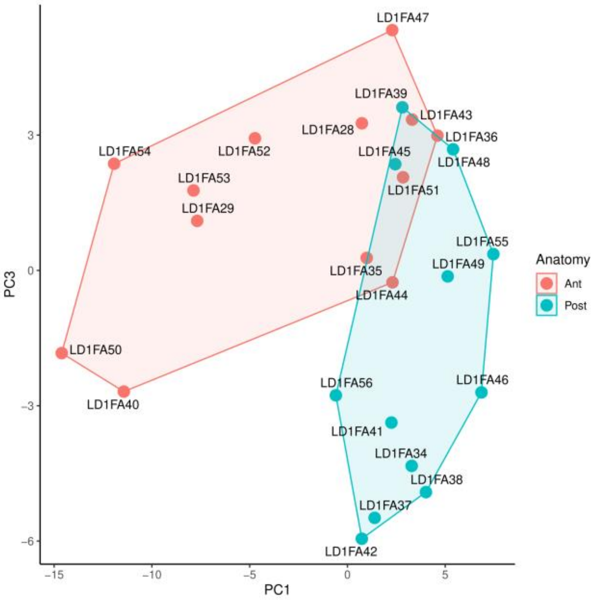

Figure 48 The first and third principal components of Procrustes residuals of first phalanges (excavated from La Draga). Specimens were grouped based on the anatomical characteristics adopted following Dottrens (1946).

5.2.3. Bovines of La Draga: Biometry of second phalanges

La Draga's second phalanx's greatest length (GL) ranged from 38.37 to 47.03 mm, with a mean of 42.97 mm (with an estimated error of ±0.74 millimetres for 95% CI) and a standard deviation of 2.01 millimetres. GL measurements of La Draga's second phalanges fell into two clusters, one significantly shorter than the referential GL (European *Bos primigenius*) and the other as long as the aurochs (Figure 49, left). Regarding the diametric measurements, the smallest breadth of the diaphysis (SD) of La Draga's second phalanges varied from 19.98 to 28.30 millimetres, exhibiting an arithmetic mean of 23.58 (±0.82 mm, 95% CI) and a standard deviation of 2.25 millimetres. The SD values of La Draga’s second phalanges also fell into two distinct clusters, one significantly slimmer than reference SD and the other as thick as auroch phalanges (Figure 49, right).

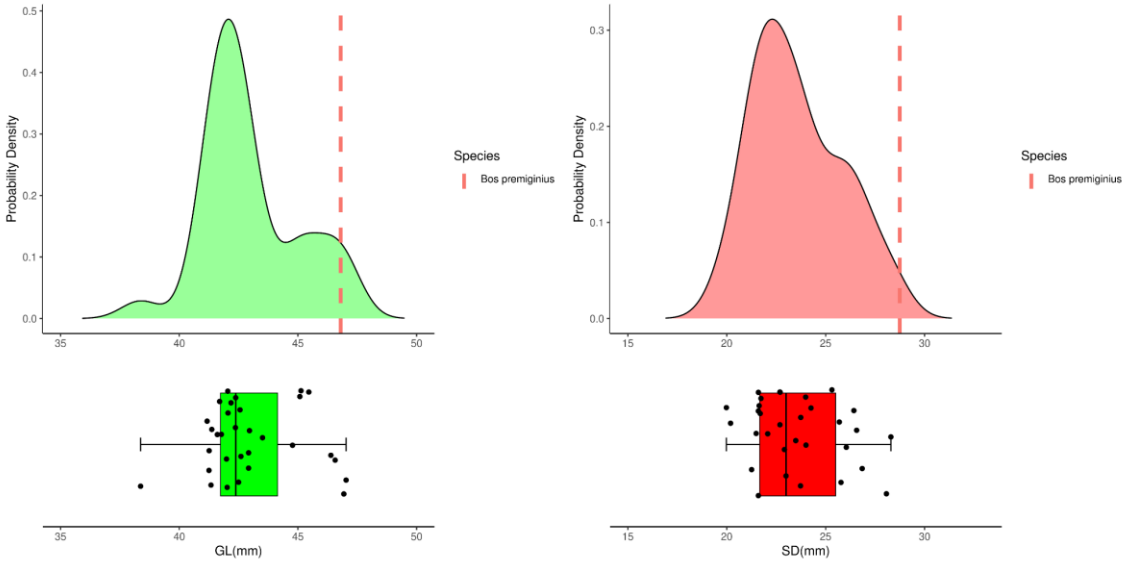

Figure 49 Probability density graph of greatest length (left, in green) and the smallest width of the diaphysis (right, in red) of cattle's second phalanges excavated from La Draga. The referencial measurements are presented as a vertical red line (if they were available for the analysis) indicating an average aurochs dimensions.

The breadth of the proximal epiphysis (Bp) in La Draga's second phalanges was expanded between 26.47 and 35.43 millimetres, with an arithmetic mean of 29.60 (±2.6 millimetres, 95% CI) and a standard deviation of 2.21 millimetres. On the other hand, the breadth of the distal epiphysis (Bd) observed range was from 22.08 to 31.34 millimetres with a lower arithmetic mean of 25.13 (±0.83 millimetres, 95% CI) and higher standard deviation of 2.26 millimetres, compared to Bp. Unlike the reference measurements (aurochs), most specimens had slimmer Bp and Bd values; however, individuals with significantly thicker epiphyses were also present amongst the specimens (Figure 50).

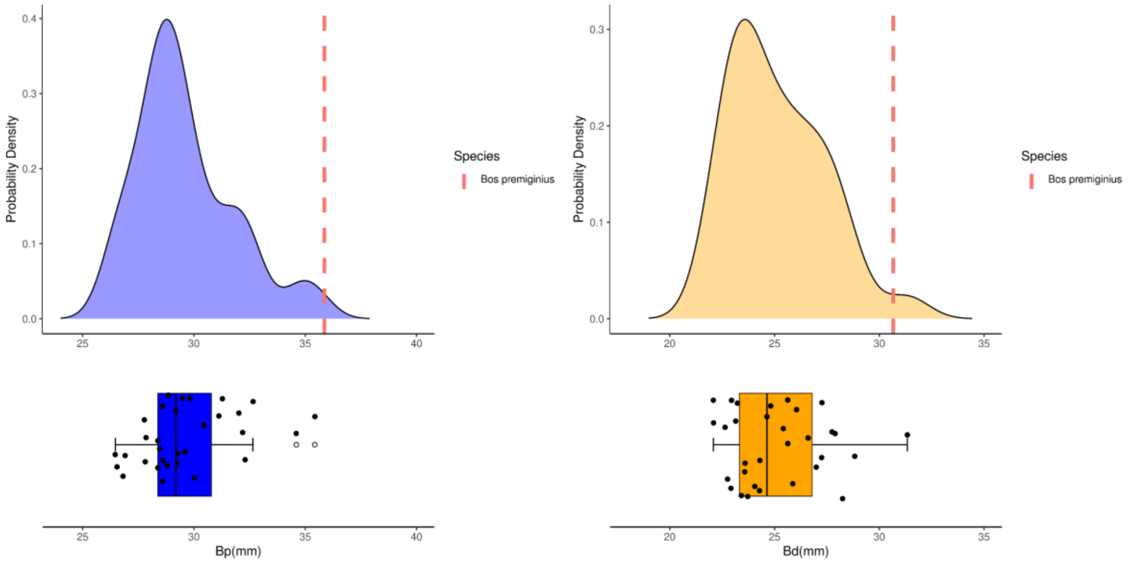

Figure 50 Probability density plots of the breadth of the proximal (Left, in blue) and the distal epiphysis (right, in orange) of cattle second phalanges, excavated from LaDraga. The referencial measurements are presented as a vertical red line (if they were available for the analysis) indicating an average aurochs dimensions.

The allometric effect of size was estimated by linear regression separately for SD, Bp, and Bd measurements. Beforehand, Koenker's test (Koenker & Bassett, 1982) was utilised to test the homoscedasticity assumption of linear regressions, which is robust for handling contaminated data (Lyon & Tsai, 1996). The results of the three regression models are available in Table 10.

Model	**Intercept**	**Slope**	**F-Statistic**	**P-value**	**Adjusted R-squared**
SD ~ GL	-7.9852	0.7346	F(1, 29) = 22.12	<0.01	0.41
Bp ~ GL	-3.7809	0.7767	F(1, 29) = 28.87	<0.01	0.48
Bd ~ GL	-5.9073	0.722	F(1, 29)	<0.01	0.39

Table 10 Results of ordinary linear regressions of La Draga's cattle second phalanges measurements.

The resultant adjusted R-squared values of linear regressions suggested that 39-41% of the variance in the linear measurements existed due to the allometric size. As before, a referencial principal component analysis was trained employing European *Bos primigenius* specimens to remove colinearity and unwanted allometric size. The result of the referencial PCA is provided in Figure 51.

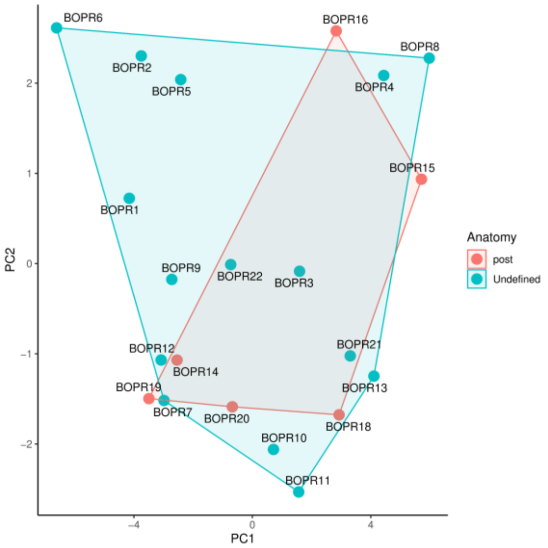

Figure 51 The referential principal spaces of anatomical factors. They were constructed based on the linear measurements of European Bos primigenius second phalanges.

The first referential principal component was an equal contribution of GL(16%), SD(26%), Bp(26.7%), and Bd(30%). The second referential component was mainly contributed by GL (64.2%), the third by Bp (49.2%) and SD (35.3%), and the fourth component by SD (33.9%) and Bd (33.7%). Accordingly, the biometric measurements of La Draga's second phalanges were projected on the referential PC1 and PC2 axes. The projection result is presented in Figure 52.

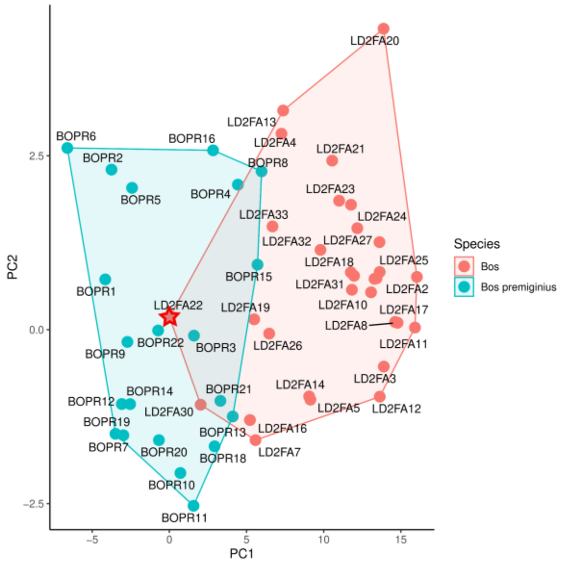

Figure 52 Principal component scores of La Draga's second phalanges after being projected on the referential principal axes. A red star marks specimen LD2FA22 (potentially an auroch).

5.2.4. Bovines of La Draga: Morphometrics of second phalanges

In an attempt to Determine the significant cause of the morphological variation in *Bos*'s second phalanges from La Draga, the resultant Procrustean residuals of Procrustes superimposition were subjected to principal component analysis. The Scree plot of morphometric PCA is available in Figure 53. The first PC described 54.9% of the variance and was influenced the most by “landmark 6”, located at the distal abaxial side, similar to Tell Halula’s second phalanges (Figure 37, left).

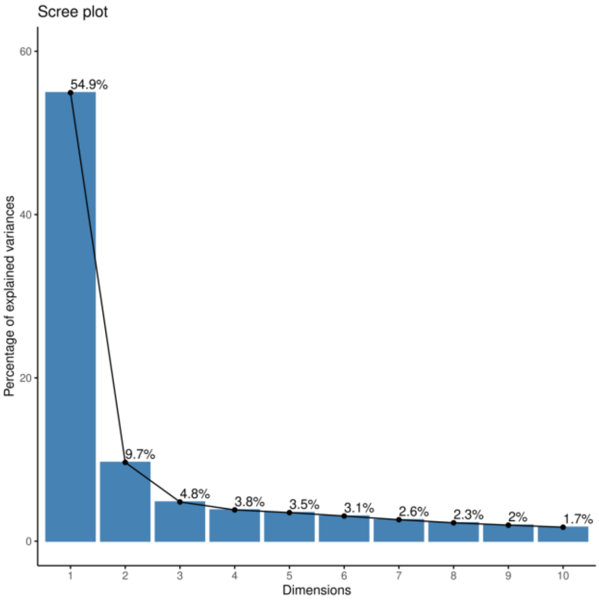

Figure 53 Scree plot of Principal component analysis conducted on Procrustes residuals of Bos second phalanges from La Draga.

The first morphometric principal component reflected anatomical (anterior-posterior) feature significantly (c^2(1, 31) = 17.2266, $p < 0.001$). The second morphological principal component described 9.7% of the variance and was mostly influenced by landmark 246, located at the distal groove of the second phalanges, identical to Tell Halula’s PC9 (Figure 37, right). The accuracy of anterior-posterior segregation using the first PC was 96.77 % (one overlapping sample out of 31, Figure 54).

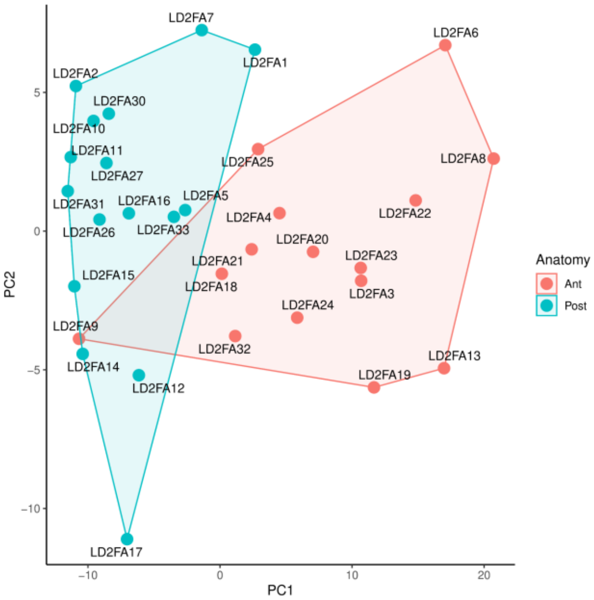

Figure 54 The first and second principal components of Procrustes residuals of second phalanges (excavated from La Draga). Specimens were grouped based on the anatomical characteristics adopted following Dottrens (1946).

5.3. Bovines of Cova de les Pixarelles

5.3.1. Bovines of Pixarelles: Biometry of First phalanges

The greatest lengths of Pixarelles' first phalanx ranged from 55.05 to 60.54 mm, with a mean of 58.20 mm (estimated error of 1.24 millimetres for the 95% confidence interval) and a standard deviation of 1.74 mm. The first phalanges of Pixarelles were shorter than those of referential European *Bos primigenius* greatest length measurement (Figure 55, left).

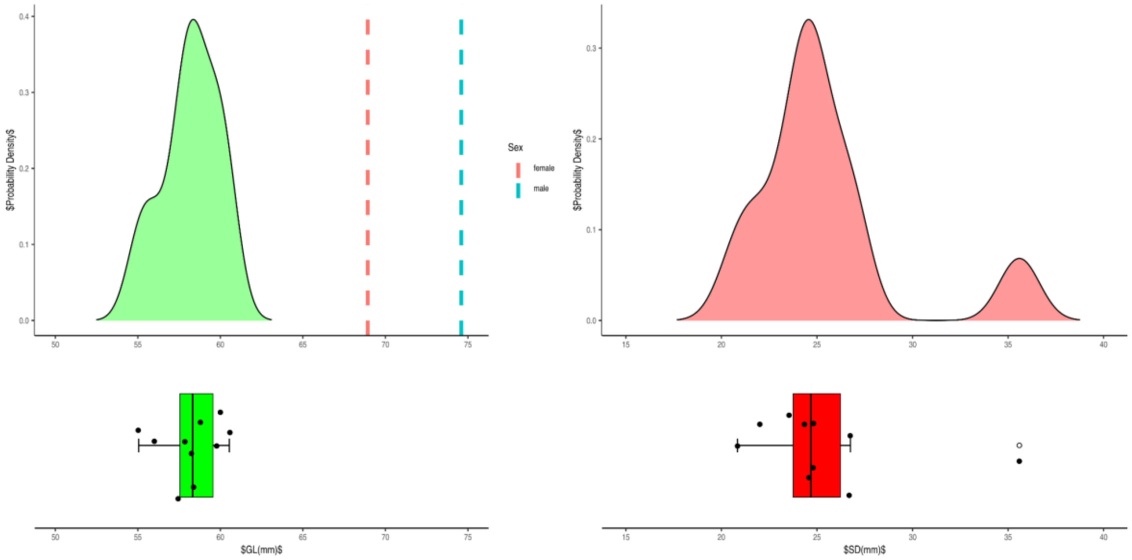

Figure 55 Probability density graph of greatest length (left, in green) and the smallest width of the diaphysis (right, in red) of cattle's first phalanges excavated from Pixarelles. The referencial measurements are presented as two vertical red (female) and blue (male) lines (if they were available for the analysis), indicating average aurochs dimensions.

The smallest breadth of the diaphysis (SD) of Pixarelle's first phalanges ranged between 20.84 and 35.59 mm and possessed an average of 25.40 mm (95% CI = 2.88) and a standard deviation of 4.02 mm (Figure 55, right). Regarding the epiphyseal scope, the breadth of the proximal epiphysis (Bp) ranged between 25.54 and 37.10 (mm) and it possessed an arithmetic mean of 29.36 millimetres (estimated error of 2.41 millimetres for the 95% confidence interval) and a standard deviation of 3.37 (mm). The breadth of the distal epiphysis (Bd) spanned between 22.35 and 32.99 (mm), with a mean value of 26.67 millimetres (95% CI = 2.12) and a standard deviation of 2.96 mm. Both of the diaphysis diametric measures were significantly thinner than the corresponding referential values, although one exception was observed, too (Figure 56).

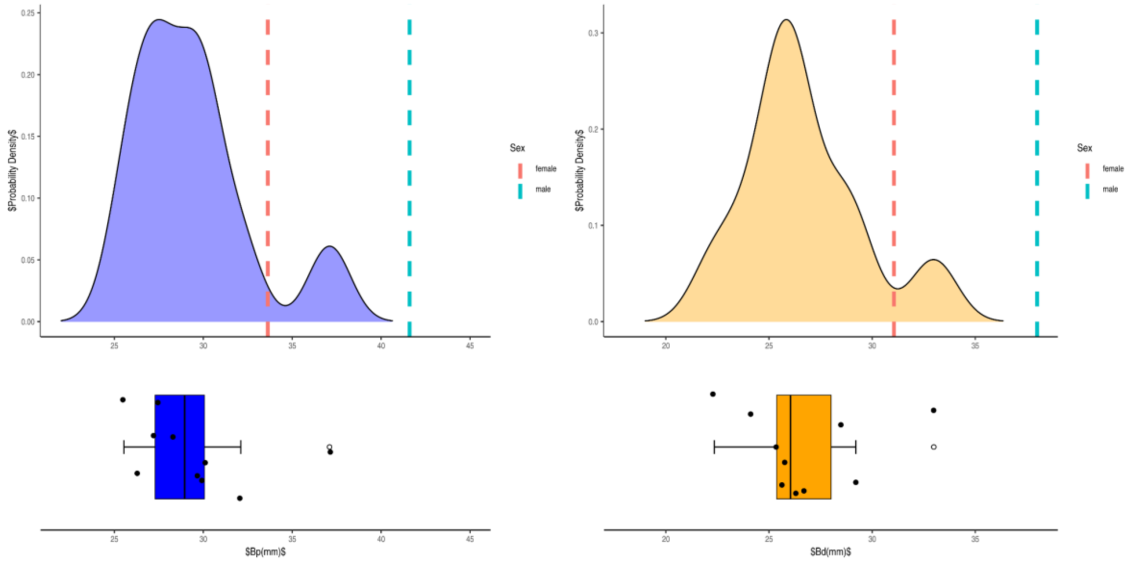

Figure 56 Probability density plots of the breadth of the proximal (Left, in blue) and the distal epiphysis (right, in orange) of cattle first phalanges excavated from Pixarelles.The referencial measurements are presented as two vertical red (female) and blue (male) lines (if they were available for the analysis), indicating average aurochs dimensions.

The allometric effect of size was estimated for SD, Bp, and Bd by a series of linear regressions; however, the homoscedasticity assumption of linear regressions was tested beforehand (Koenker & Bassett, 1982). The results of the three regression models indicated that, similar to La Draga’s first phalanges, Pixarelles’s GL values of anterior phalanges covaries differently with Bp, Bd and SD, compared to the posterior digit (Figure 57). The insignificancy of the anterior correlations is the side effect of the low number of anterior samples.

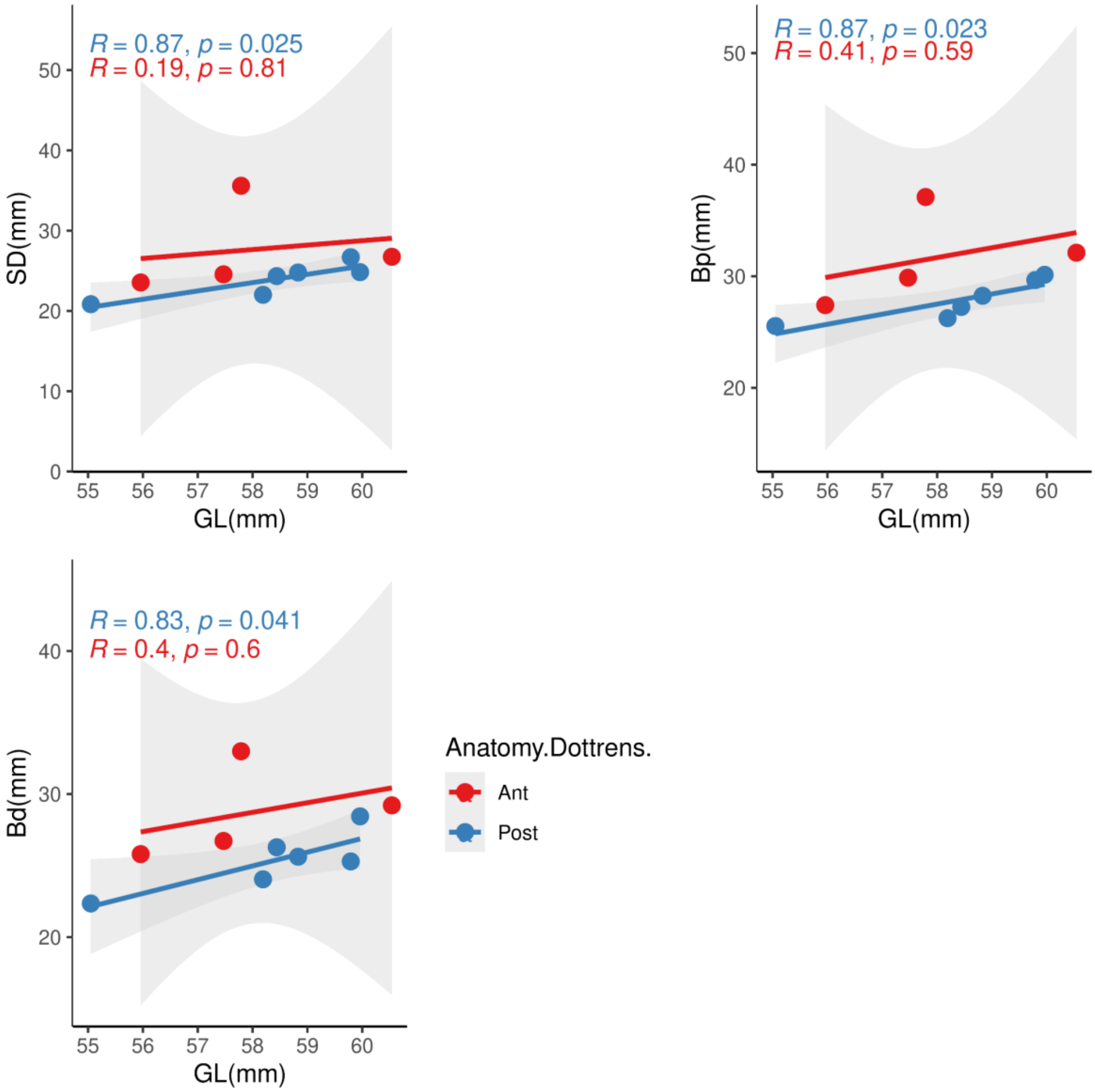

Figure 57 Correlations between diametric measurements and GL in anterior and posterior first phalanges (Pixarelles Samples).

Pixarelles's linear measurements were projected on the same two referential principal components, which were compiled for La Draga's first phalanges. The result of the projection is available in Figure 58.

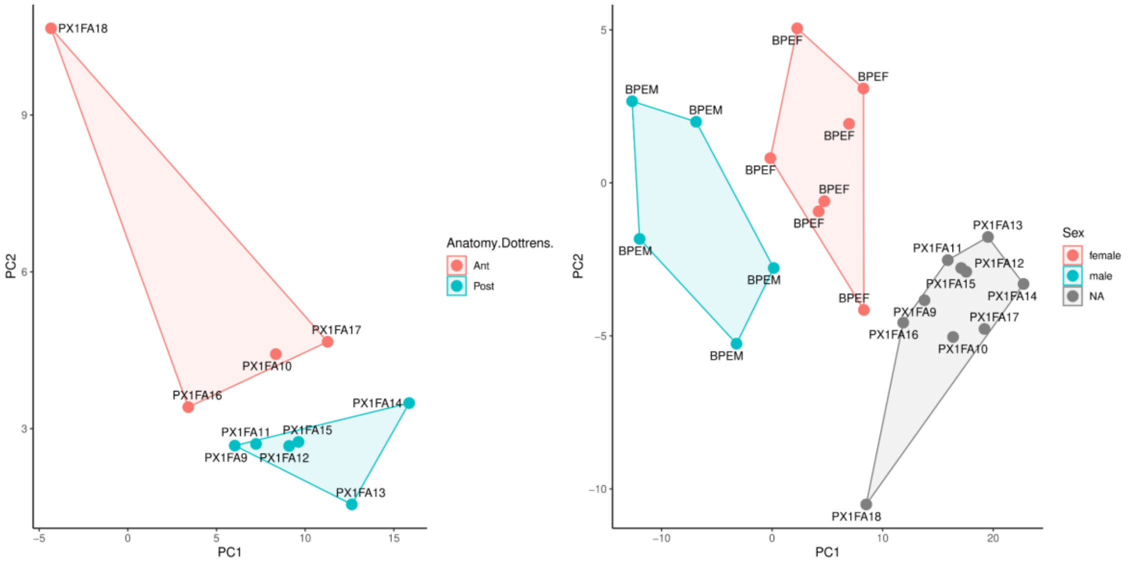

Figure 58 Principal component scores of Pixarelles's first phalanges after being projected on anatomical (left) and gender (right) principal axes.

5.3.2. Bovines of Pixarelles: Morphometrics of first phalanges

Using the resultant residuals of Procrustes superimposition, principal component analysis was conducted to determine the significance of the morphological variation in *Bos*'s first phalanges from Pixarelles. The Scree plot of morphometric PCA is available in Figure 59.

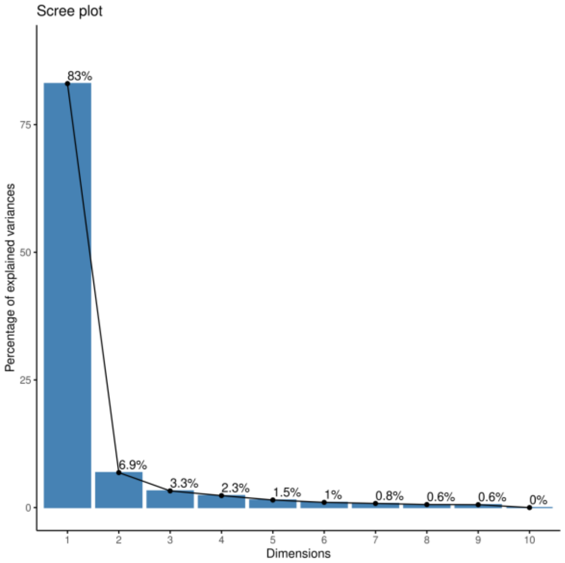

Figure 59 Scree plot of Principal component analysis conducted on Procrustes residuals of Bos first phalanges from Pixarelles.

The first principal component described 83% of the variance and was mostly influenced by “landmark 27”, located at the abaxial ridge of the proximal diaphysis (Figure 60, right), suggesting that PC1 was mainly affected by a single individual (statistical outlier) which was exhibiting a significant proximal broadening. The first PC also significantly described anatomical (anterior-posterior) variation (c^2 (1, 10) =4.54, p= 0.03, Figure 60, left).

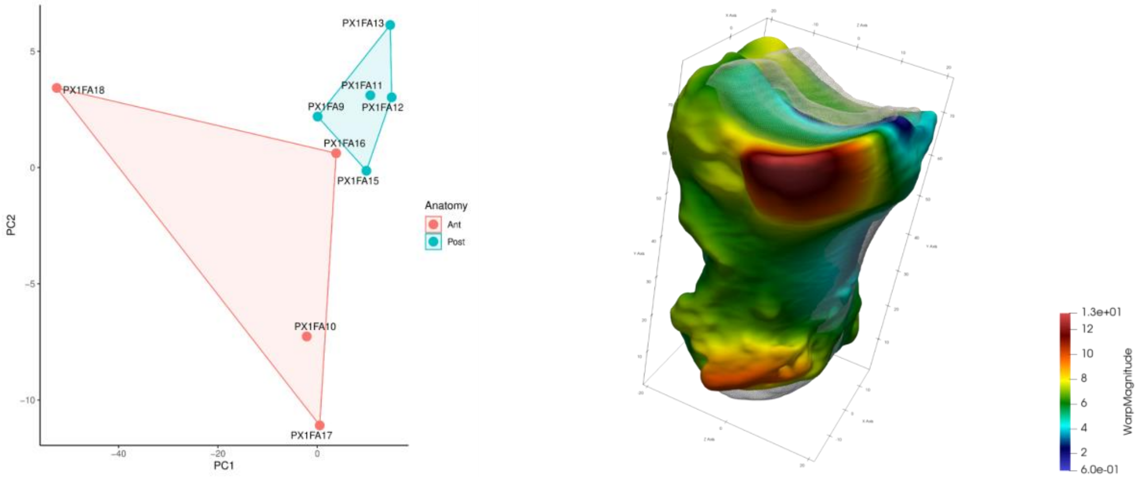

Figure 60 Left: The first and second principal components of Procrustes residuals of first phalanges (excavated from Pixarelles). Specimens were grouped based on the anatomical characteristics adopted following Dottrens (1946). Right: The outlier individual in PC1, imposed on the template specimen (white transparent mesh).

5.3.3. Bovines of Pixarelles: Biometry of Second phalanges

Pixarelles's second phalanx's greatest length (GL) ranged from 37.95 to 42.72 mm, with a mean of 39.43 mm (with an estimated error of ±1.40 millimetres for 95% CI) and a standard deviation of 1.68 mm. Pixarelles had significantly shorter second phalanges (than the average referential values (Figure 61, left).

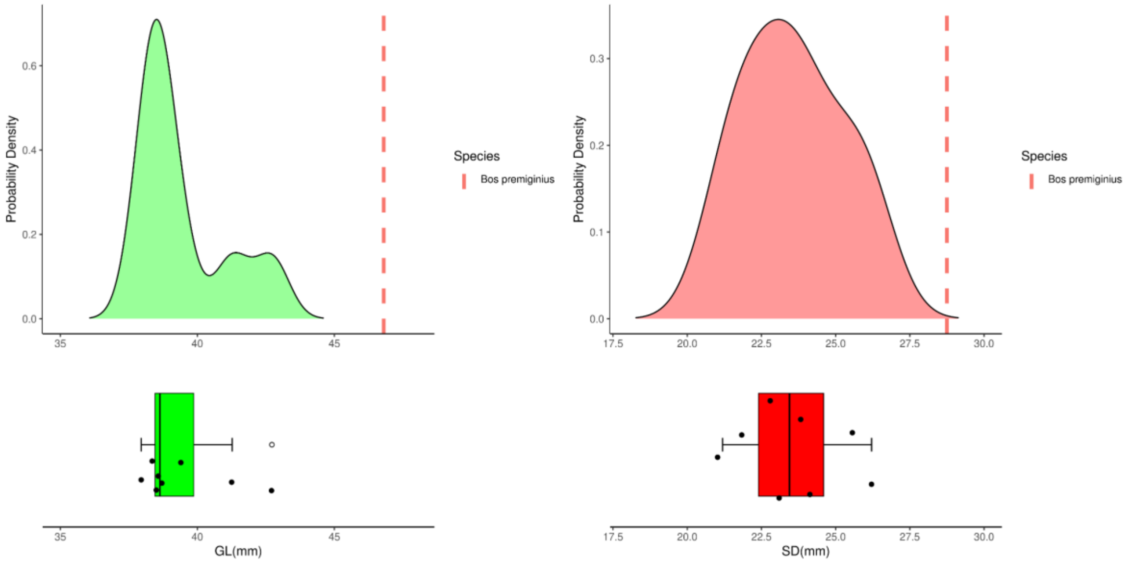

Figure 61 Probability density graph of greatest length (left, in green) and the smallest width of the diaphysis (right, in red) of cattle's second phalanges excavated from Pixarelles. The referencial measurements are presented as a vertical red line (if they were available for the analysis) indicating an average aurochs dimensions.

The smallest diaphysis-to-diaphysis (SD) measures of Pixarelle's second phalanges varied between 21.19 and 26.21 mm, with an arithmetic mean of 23.56 mm (95% CI = 1.46) and a standard deviation of 1.75 mm. Similar to GL, SD measures were also significantly thinner than referential SD (Figure 61, right). As far as epiphyseal measurements are concerned, the proximal epiphysis (Bp) measured between 26.67 and 32.22 millimetres, had an arithmetic mean of 29.11 millimetres (estimated error of 1.56 millimetres for the 95% confidence interval) and a standard deviation of 1.86 (mm). Distal epiphysis breadth ranged between 22.06 and 29.26 millimetres, with a mean value of 24.58 millimetres (95% CI = 1.86) and a standard deviation of 2.23 millimetres. Both of the epiphyseal diametric measures were lesser than the corresponding referential values, although a few exceptions were observed, too (Figure 62).

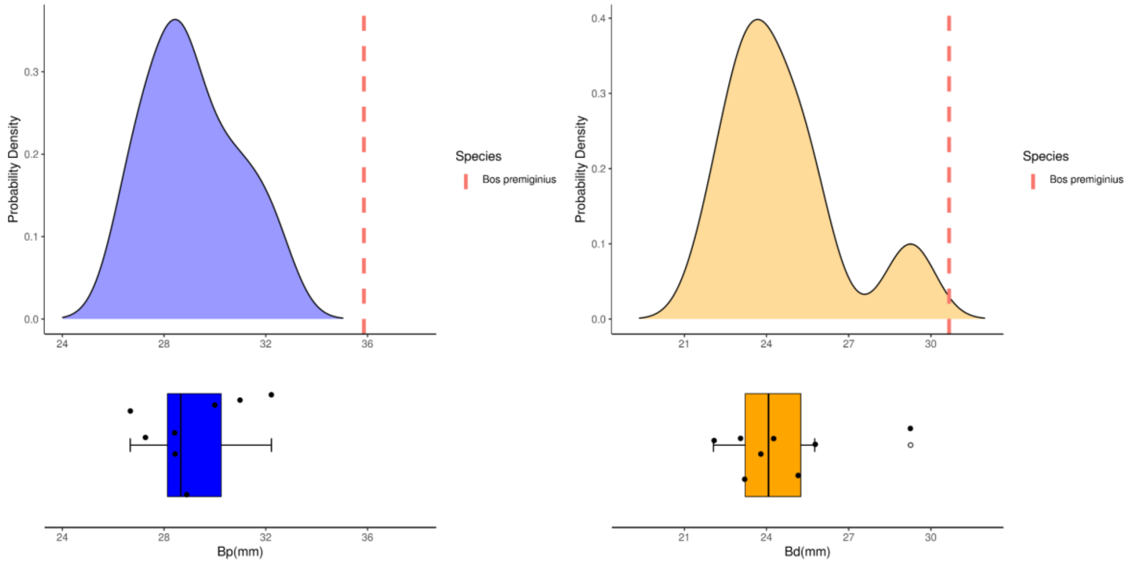

Figure 62 Probability density plots of the breadth of the proximal (Left, in blue) and the distal epiphysis (right, in orange) of cattle second phalanges, excavated from Pixarelles. The referencial measurements are presented as a vertical red line (if they were available for the analysis) indicating an average aurochs dimensions.

The allometric effect of size was estimated by linear regression separately for SD, Bp, and Bd measurements, after testing the homoscedasticity assumption (Koenker & Bassett, 1982). The results of the three regression models are available in Table 11.

Model	**Intercept**	**Slope**	**F-Statistic**	**P-value**	**Adjusted R-squared**
SD ~ GL	-7.2566	0.7816	F(1, 6) = 7.78	0.03	0.49
Bp ~ GL	-5.8938	0.88	F(1, 6) = 10.65	0.01	0.58
Bd ~ GL	-18.174	1.08	F(1,6) = 12.16	0.013	0.61

Table 11 Results of ordinary linear regressions of Pixarelles's cattle second phalanges measurements.

Linear measurements were projected on the referential principal axes which were compiled before for La Draga specimens (Figure 63). The result of the projection is presented in

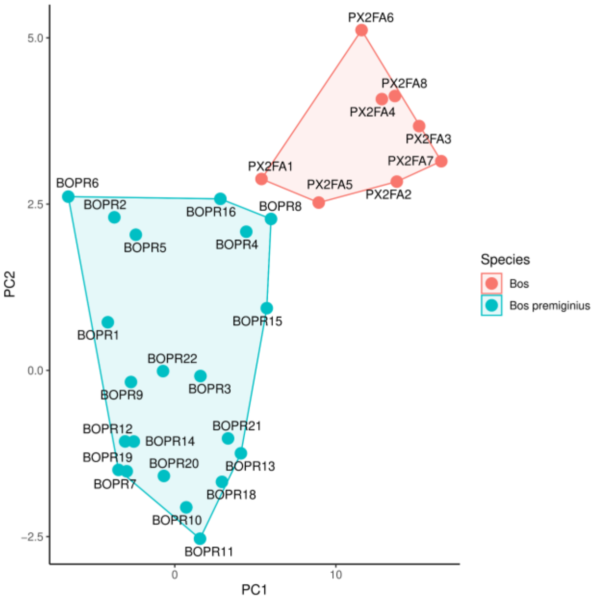

Figure 63 Principal component scores of Pixarelles's second phalanges after being projected on anatomical principal axes.

5.3.4. Bovines of Pixarelles: Morphometrics of second phalanges

In an attempt to Determine the significant cause of the morphological variation in *Bos*'s second phalanges from Pixarelles, the resultant residuals of Procrustes superimposition were subjected to principal component analysis. The Scree plot of the morphometric PCA is available in Figure 64, right. The first PC (covering 51.4% of the variance), identical to the PC1 of Tell Halula and La Draga’s second phalanges, was influenced by “Landmark 6” at the distal abaxial axis of the diaphysis (Figure 37, left). Anatomical differences (anterior-posterior) was significantly reflected by PC1 ($c2(1, 8) = 4$, $p = 0.05$, Figure 64, left).

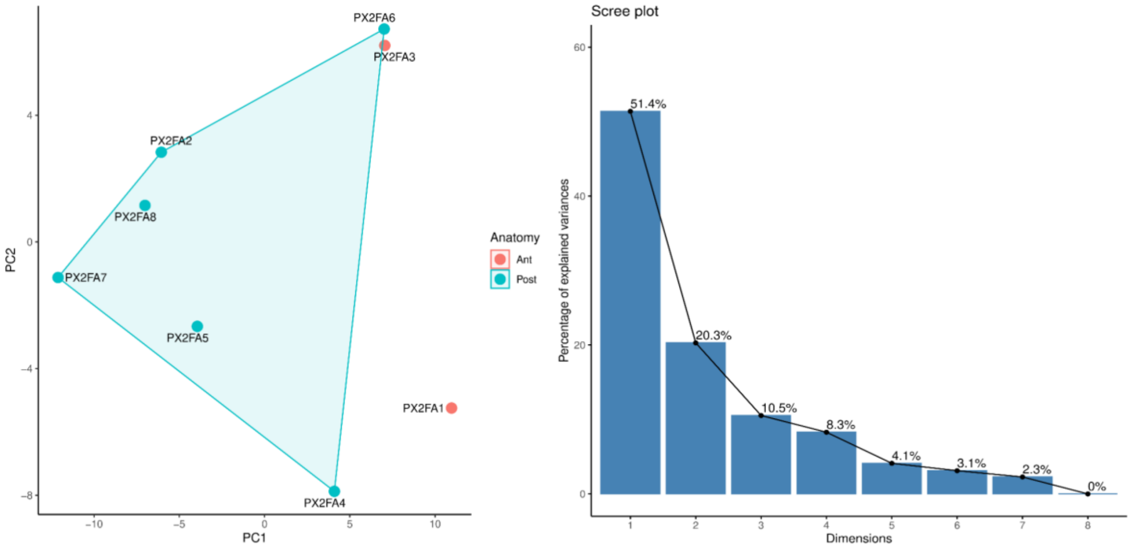

Figure 64 Left: The first and second principal components of Procrustes residuals of first phalanges (excavated from Pixarelles). Specimens were grouped based on the anatomical characteristics adopted following Dottrens (1946). Right: Scree plot of Principal component analysis conducted on Procrustes residuals of Bos second phalanges from Pixarelles.

5.4. Comparative Morphometric study: Bovines of La Draga and Pixarelles

A comparative analysis of previously studied settlements, such as La Draga and Pixarelles, will enable us to comprehend herd management and the effects of external mechanical environments (imposed by humans in the context of this research) on the morphology of *Bos* phalanges native to the Iberian peninsula. In the case of the first phalanges, La Draga's Procrustes residuals were pooled with Pixarelles data and then subjected to a principal component analysis. The Scree plot of the resultant morphometric PCA revealed that the first two morphological components described 72.3% of the morphological variance, PC1 and PC2, which significantly reflected the anatomical (anterior-posterior) factor ($c^{2}{}_{PC1}(1, 35) = 9.02$, $p < 0.01$; $c^{2}{}_{PC2}(1, 35) = 4.05$, $p = 0.04$) (Figure 65).

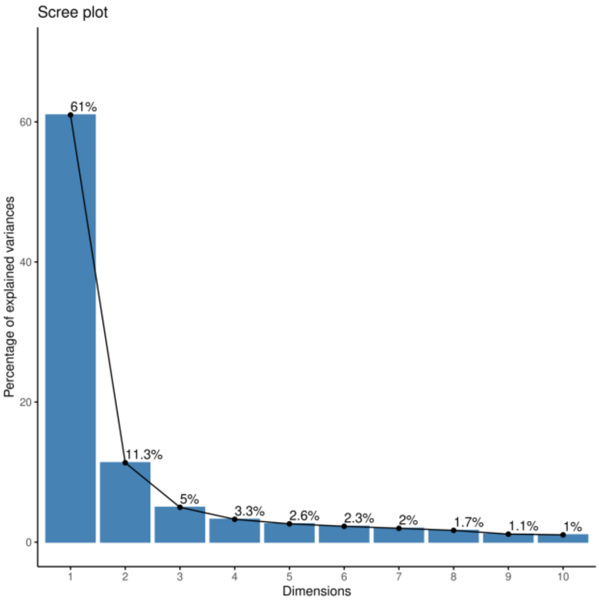

Figure 65 Scree plot of Principal component analysis conducted on Procrustes residuals of Bos first phalanges from Pixarelles and La Draga (pooled samples).

The morphological difference between specimens of Pixarelles and La Draga explained 4.5% of the variance and was significantly reflected by the fifth principal component, PC5 (c2(1, 35) = 8.53, p < 0.01). The most significant landmark of PC5 was "landmark 8", located at the distal axial ligament attachment point (Figure 66, left), where the corresponding principal component scores correlate positively with an increase in the distal breadth of the diaphysis (Figure 66, right).

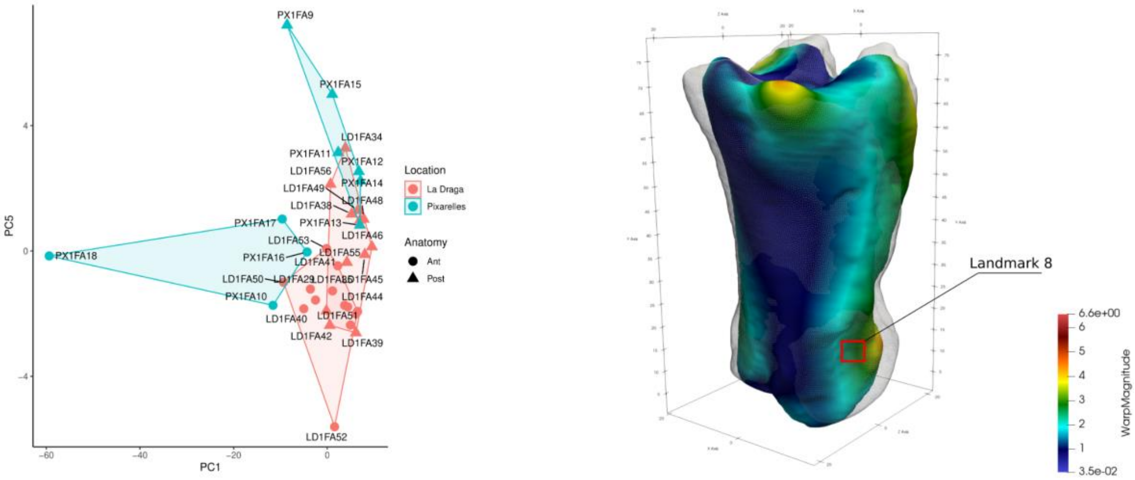

Figure 66 Left: The first and fifth principal components of Procrustes residuals of first phalanges (from pooled samples of La Draga and Pixarelles). Specimens were grouped based on the settlement location and the anatomical characteristics adopted following Dottrens (1946). Right: The local morphological discrepancies between La

Draga (mesh with Procrustes residual heat-map) and Pixarelles specimens (white transparent mesh) contributed the most to the fifth morphometric component.

Following a similar procedure, a principal component analysis was performed on the Procrustes residuals of the pooled Pixarelles-LA Draga's second phalanx specimens. Due to the unbalanced number of anterior phalanges in Pixarelles and La Draga, the comparative morphometrics study was pursued exclusively on posterior samples. The amount of morphological variation (Figure 67) described by the first component was 52.5%, significantly ($c^2(1, 22) = 5.91$, $p = 0.01$) describing local morphological disparities (locality of the settlements, *i.e.,* Pixarelles and La Draga), and was mostly influenced by "landmark 44" located at the abaxial distal ridge of the second phalanges (Figure 68, right)

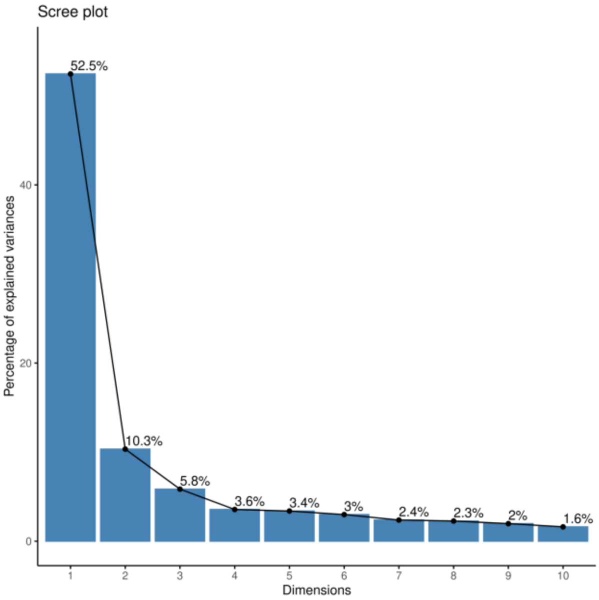

Figure 67 Scree plot of Principal component analysis conducted on Procrustes residuals of Bos second phalanges from Pixarelles and La Draga (pooled samples).

By understanding the direction of PC1, it was observed that the second phalanges of Pixarelles, like the first phalanges, were distally more robust than La Draga specimens (Figure 68, left).

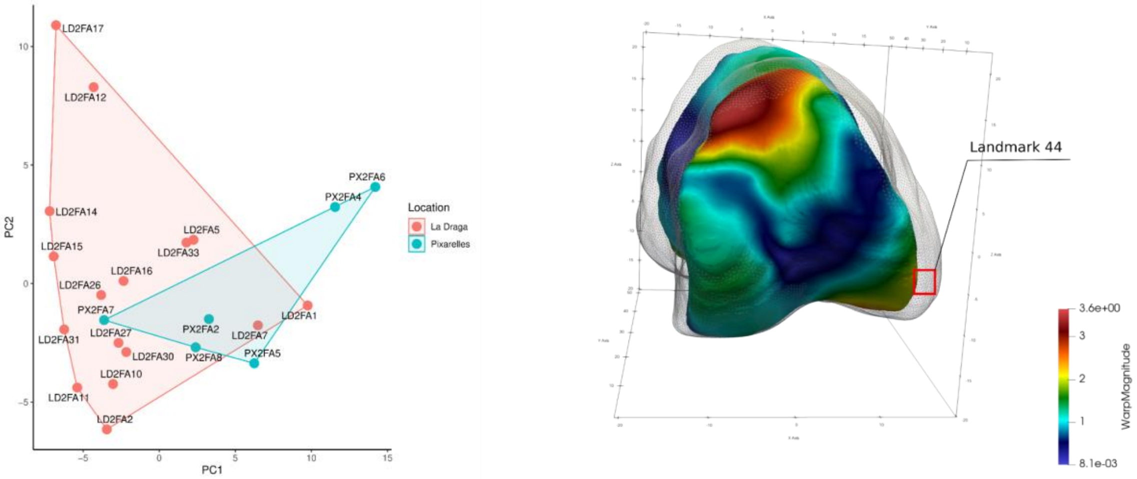

Figure 68 Left: The first and second principal components of Procrustes residuals of posterior second phalanges (from pooled samples of La Draga and Pixarelles). Specimens were grouped based on the settlement location. Right: The local morphological discrepancies between Pixarelles (white transparent mesh) and La Draga specimens (mesh with Procrustes residual heat map) contributed the most to the first morphometric component.

5.5. Comparative Biometric study: Bovines of La Draga and Pixarelles

Pixarelles first phalanges are slightly shorter than La Draga specimens while exhibiting similar diametric dimensions. Their greatest length had a significantly higher standard deviation compared with La Draga's first phalanges (Figure 69).

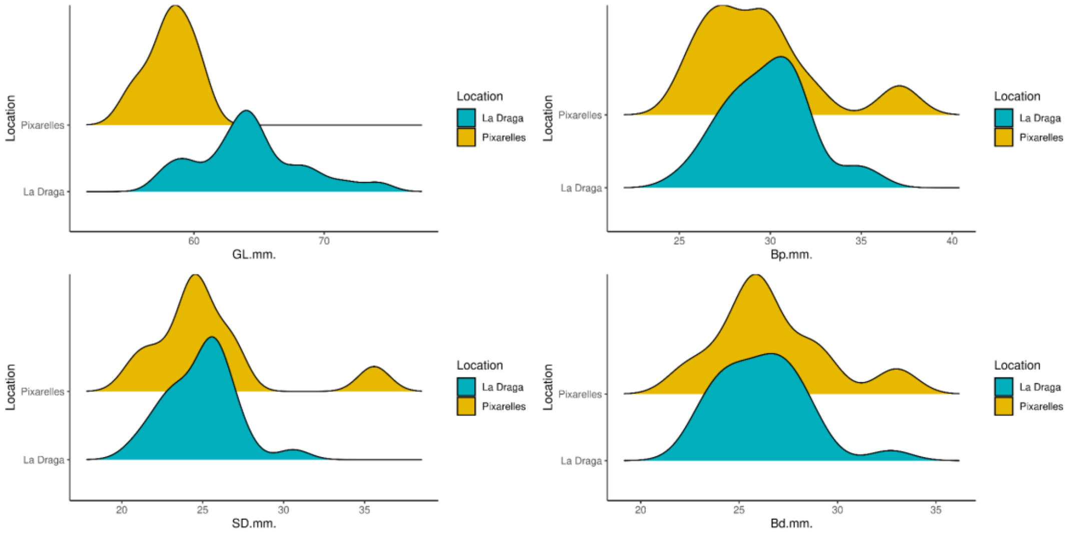

Figure 69 Comparing probability distributions of linear measurements taken from the first phalanges of La Draga (blue) and Pixarelles (yellow).

In the case of the second phalanges, similar to the first phalanges, Pixarelles specimens are shorter while exhibiting more or less similar diametric dimensions. Their breadth of the distal diaphysis had a slightly higher standard deviation, compared with La Draga's samples (Figure 70).

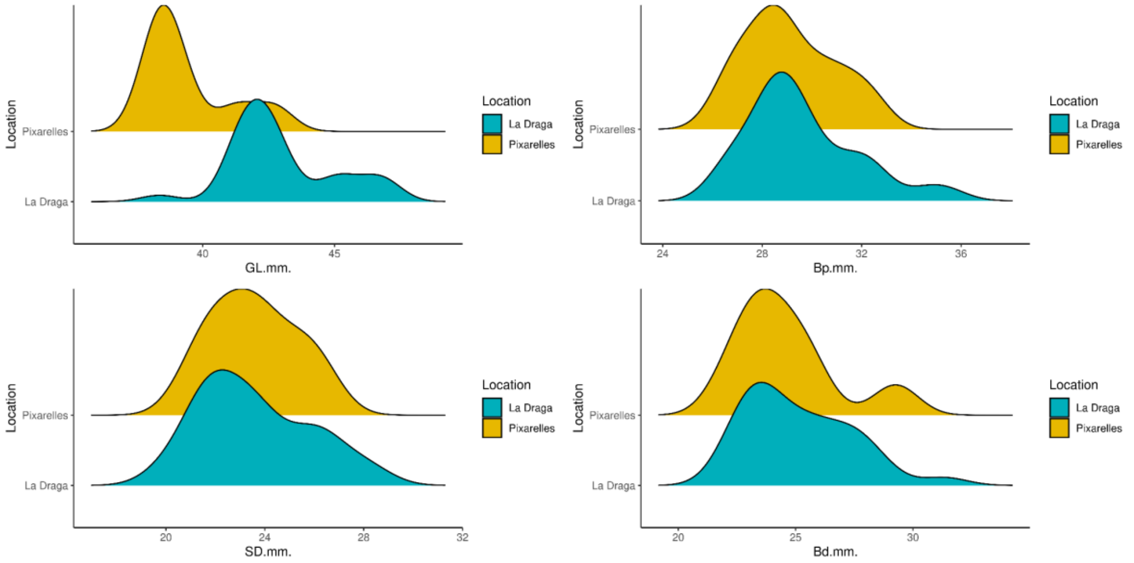

Figure 70 Comparing probability distributions of linear measurements taken from the second phalanges of La Draga (blue) and Pixarelles (yellow).

As mentioned before, linear measurements were subjected to principal component analysis to remove collinearity and select the proportion of the variance in the measures related to the allometric size (and potentially discard it). Since the components are a disproportionate combination of observations (variables, *e.g.* GL and SD), establishing a standard was necessary to understand the nature of each principal axis. Accordingly, two separate principal component analyses were conducted using reference data with known gender and anatomical information. The results of the referential principal component analyses are provided in Figure 44.

The principal component analysis of specimens was accomplished by projecting the linear measurements of the first phalanges (of La Draga and Pixarelles) on the reference principal axes, which were defined earlier. The result of the projection is provided in Figure 71.

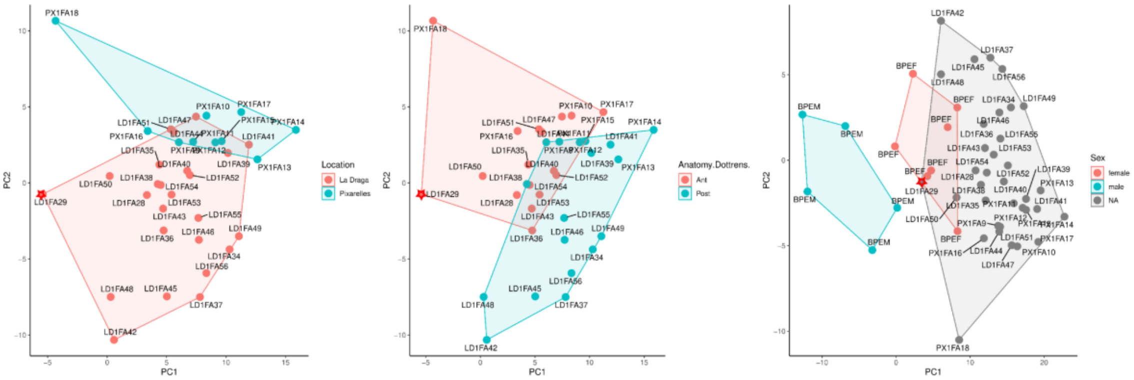

Figure 71 Principal component scores of La Draga and Pixarelles's first phalanges (pooled data) after being projected on local (left), anatomical (middle) and gender (right) principal axes. A red star marks specimen LD1FA29 (potentially a female auroch).

The local information (location of the settlements, *i.e.* La Draga or Pixarelles) was tested against the anatomical principal component scores to confirm if it had any significant impact on the data variance.

Consequently, it was revealed that the second component of anatomical space (Figure 71, left) was (highly) significantly impacted by the location of settlements (c2(1, 35) = 14.42, p < 0.01). Based on the information established by the referential principal spaces (Figure 44, left), the significance was rooted in the size difference between La Draga (on average, shorter) and Pixarelles (on average, longer). The first and second components of the anatomical space significantly corresponded to the anatomical disparities ($c^{2}_{PC1}(1, 35) = 7.69$, p=0.01; $c^{2}_{PC2}(1, 35) = 4.46$, p = 0.03), which highlighted the increase of all dimensions (GL, Bp, Bd, and SD) in anterior first phalanges (Figure 71, centre). The projection of the linear measurements on the referential gender principal spaces revealed that at least one of La Draga’s specimens (LD1FA29) is potentially a female auroch (Figure 71, right).

A similar procedure was undertaken to investigate the dimensional variance in the second phalanges of La Draga and Pixarelles. Based on available *Bos primigenius* reference data, anatomical reference principal axes were constructed (Figure 51). The principal component analysis of specimens was accomplished by projecting the linear measurements of the first phalanges (of La Draga and Pixarelles) on the reference principal axes, which were defined earlier. The result of the projection is provided in Figure 72.

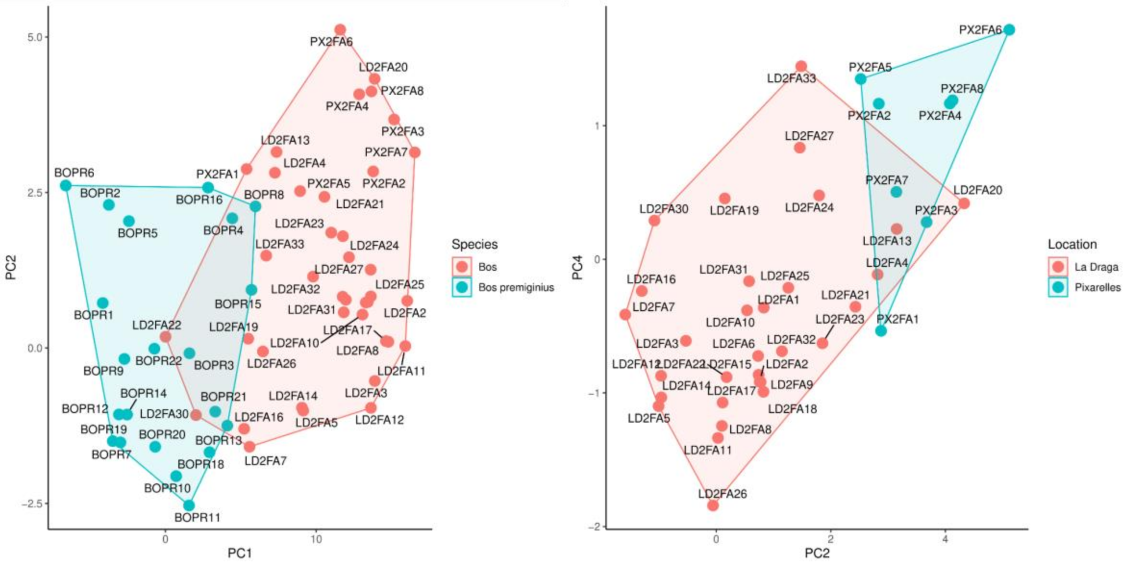

Figure 72 Left: Principal component scores of La Draga and Pixarelles's first phalanges (pooled data) after being projected on the locational first and second principal axes. Right: The linear measurements after being projected on locational second and fourth principal axes.

The first and second components significantly reflected size differences between *Bos primigenius* (from the reference) and the rest of the samples. PC2 indicated that Pixarelles' specimens had longer second phalanges, similar to the first phalanges, whereas PC4 highlighted that Pixarelles' second phalanges are medial-distally thicker and more robust, suggesting the effect of mechanical environment or environmental factors (*e.g.,* slope of the ground). This information agrees with the morphometric-based analysis on the first phalanges, which also suggested Pixarelles' first phalanges were more robust distally than La Draga's.

5.6. Building proxies for archaeozoology: metrical, morphological, and biomechanical analysis of how age, sex and feeding habits are represented in bones and teeth. The case of *Sus scrofa* mandibles.

5.6.1. *Sus scrofa*: Full Procrustes Morphometrics of mandibles

Morphology of *Sus* mandible, like other mammalians, is a complex outcome of external factors such as weight, climate, geography (Owen *et al.,* 2014), elevation (Endo *et al.*, 2002), diet (Navarrete Belda & Saña Seguí, 2017; Montuelle *et al.*, 2020;

Neaux, Louail, *et al.*, 2022) and internal elements like age, sex and behaviour (Von Den Driesch, 1976; Košinová *et al.*, 2022). The available (hemi) mandible specimens possessed two distinct phenotypical features: high condyle and low condyle phenotypes. Utilising the bite force evolution model proposed by Hylander (2017) and Montuelle *et al.*, (2020), individuals with higher condyle positions were assigned to the hard diet category, while those with lower condyle locations were assigned to the soft diet category. A series of full Procrustess superimpositions were performed to observe if geometric morphometrics can capture and separate variables (*i.e.* sex, age, diet and location) responsible for mandibles' geometry. Accordingly, the resultant Procrustes residuals were subjected to a principal component analysis after the full Procrustes superimpositions stage. The first and second components described 61.7% and 11.6% of the morphological variance (Figure 73).

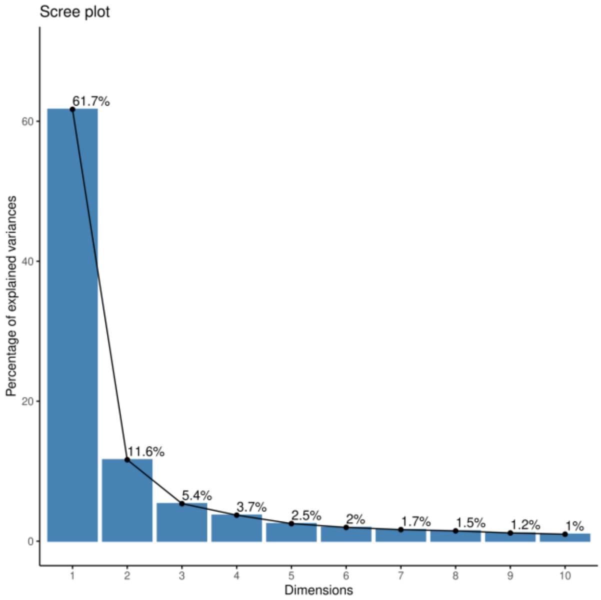

Figure 73 Scree plot of Principal component analysis conducted on Procrustes residuals of Sus scrofa hemi-mandibles.

The most influential landmark of PC1 was "Landmark 167", located at the ventral side of the mandibular body (Figure 74, top), suggesting that the height of the mandibular body had the most impact on the morphological variance. In addition, a robust analysis of variance (Kruskal–Wallis H test, Kruskal & Wallis, 1952) and the consequent Bonferroni post hoc test (Dunn, 1961), revealed that age-related morphological disparities of *Sus scrofa*, specifically between 6-12 and 30-52 Moo (month old) individuals is highly significant (c^2 (7, n=50) = 15.56, p=0.03; Bonferroni p-value = 0.013).

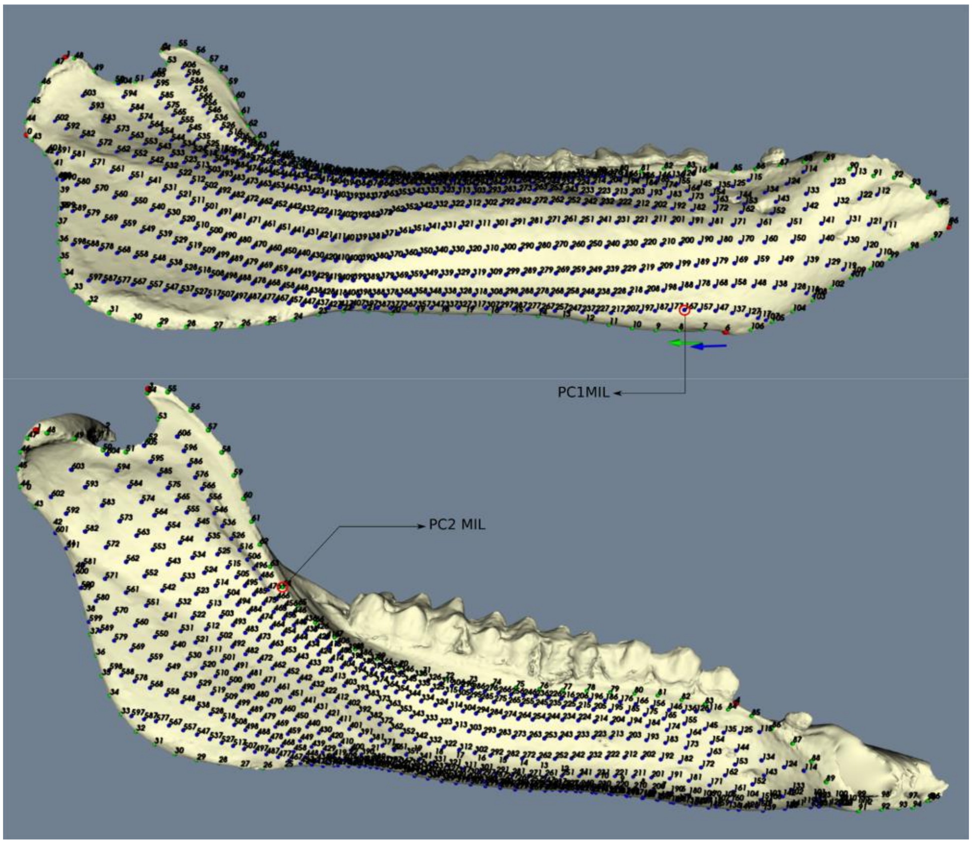

Figure 74 The Most Influential Landmark (MIL) of the first and second morphological component of Sus scrofa hemi-mandible

The second morphological component (PC2), on the other hand, was impacted mainly by “Landmark 64”, representing the thickness of the ramus at the ramus-body conjunction (Figure 74, bottom), where hard diet consumers had a more robustified Ramus base comparing with soft food eaters. In addition, the Kruskal-Wallis test showed that soft and hard diets have significantly different morphological impacts on the *Sus scrofa* mandible (c^2(1, 50) = 4.6507, P = 0.03). Finally, in a search for the principal component, which reflected sexual dimorphism, it was revealed that the 6th component (2% of morphological variation) and 7th component (1.7% of morphological variation) significantly corresponded with gender (c^2(1, 50) = 6.62, p=0.01 and c^2(1, 50) = 4.8, p = 0.03, respectively). PC6 was influenced by “landmark 96” (indicating the shortening of the mandible body in females compared to males) and PC7 by “landmark 6”, located at the tip of the Coronoid process (Figure 75).

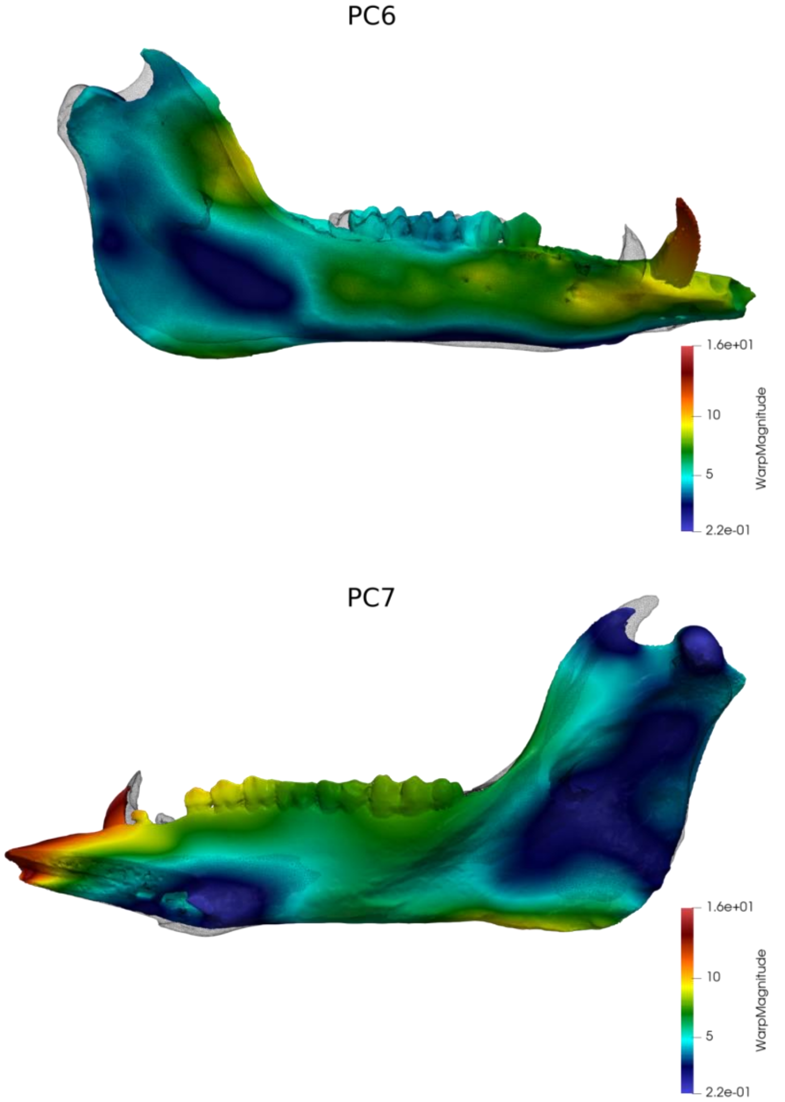

Figure 75 Two main Sus scrofa mandible phenotypes are reflected in PC6 and PC 7 of Procrustes residuals. In the PC 6 case (Up), a female specimen (grey transparent mesh) was superimposed on a male sample. While both are scaled to the unit size, female is shorter than male. In PC7, however, the female specimen has a shorter Coronoid process and longer and more straight Ramus.

Since most of the morphological variance was explained by age classes (PC1), it was decided to observe sexual dimorphism separately for each class. It was more convenient to combine classes which did not have a significant shape difference (based on the results of the Bonferroni test). Accordingly, 3-6 and 6-12 months old samples were pooled into a class named AB, 12-16 and 18-30 months old to class CD, 30-52 and 52-72 months old to EF, and finally, 72-96 and older than 96 months were assigned to class GH. A principal component analysis was performed on

Procrustes residuals of each class's specimens, and their first two components were plotted to observe male-female segregation (Figure 76). The only significant morphological dimorphism was recorded for combined class CD (c^2 (1, 17) =5.787, p = 0.02).

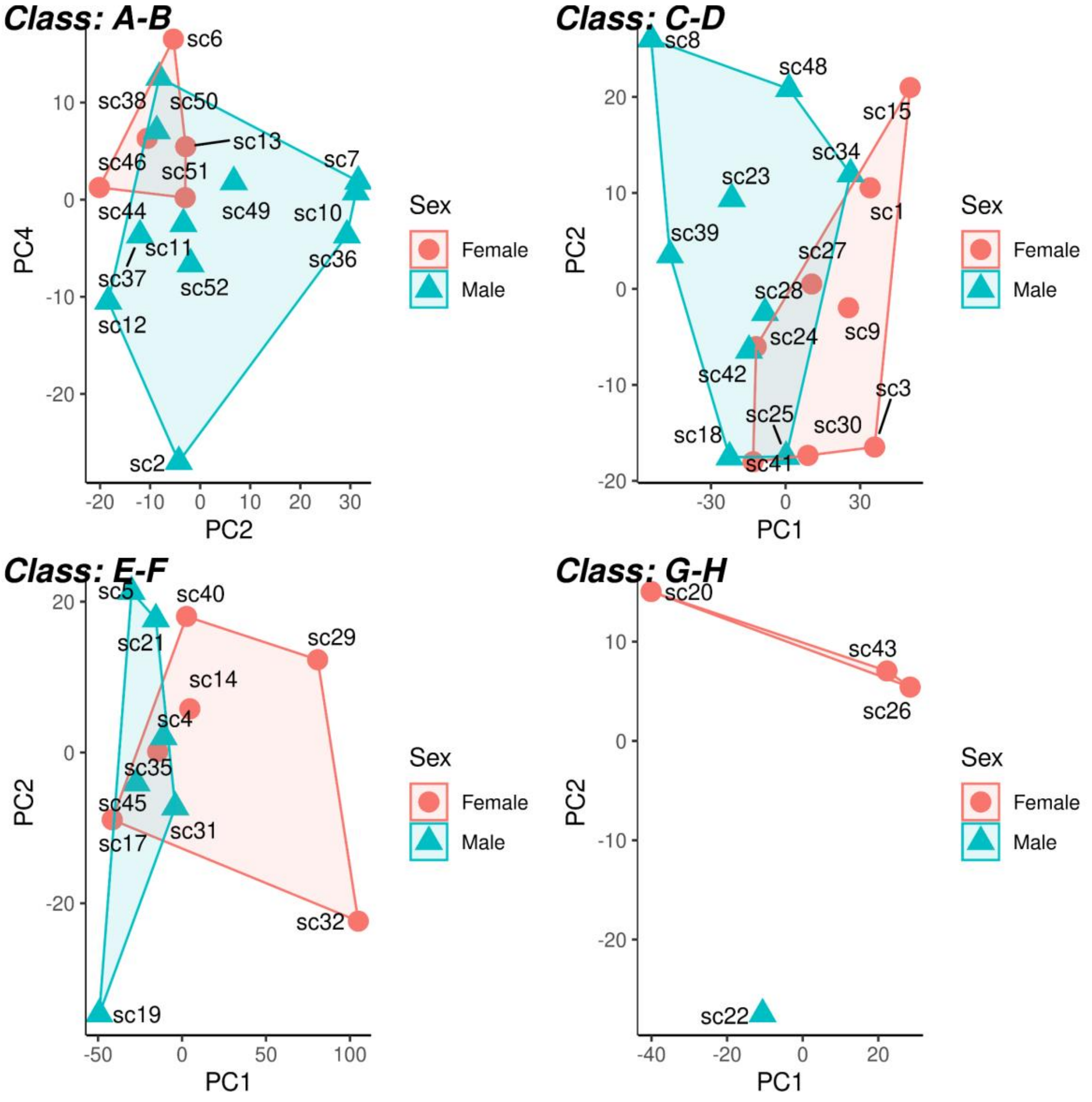

Figure 76 Principal component scores of Procrustes residuals of specimens (Sus scrofa hemi-mandibles) after being pooled into four age categories. For more information about combined age classes, refer to the text. Out of four, only CD members exhibited significant sexual dimorphism.

6. DISCUSSION

6.1. Directional asymmetry as a tool to study animal husbandry

There exists a prominent mediolateral asymmetry in the *Bos* phalanges. Not only the medial digits are shorter and thicker than the lateral ones (Muggli *et al.*, 2011; Parés-Casanova *et al.*, 2020), but also, within the scope of a single phalanx, the axial side of the proximal joint is depressed, and the axial side of the distal joint is overextended. *Bos* phalanges are slightly spread off-axis (like an upside-down V) to distribute the animal's weight better and stabilise its gait. This off-axis spread causes mediolateral asymmetry by rendering an uneven weight distribution, in favour of the medial axis, during locomotion. At the rest state (standing still, not lying down), however, the balance of the force will be in favour of the lateral axis of the posterior and medial axis of anterior limbs, although the load during the rest state is only limited to the animal's weight, which is less than half of the locomotory load (Fischer *et al.*, 2022; van der Tol *et al.*, 2003; van der Tol *et al.*, 2003). Phalanges exhibit another directional asymmetry: dorsopalmar asymmetry, which predictably reflects the dorsopalmar imbalance of weight distribution due to the flexion angle. At the stationary stage, depending on the anterior-posteriority of the digits, the flexion angle varies between 10-20 degrees (Bartosiewicz, 2008), which shifts the weight distribution dorsally. The angle is steeper during animal locomotion, reaching even 50 degrees in some individuals (Pluk *et al.*, 2012). Therefore, the palmar side of the phalanges experiences mechanical load mainly during a short push-off period (van der Tol *et al.*, 2003).

Two directional asymmetries (mediolateral and dorsopalmar) create four zones (quarters) with different stress sensitivities, *i.e.* morphological adaptations to endure strain. The zones with less sensitivity, such as the dorsal-axial quarter, are naturally supposed to endure more physical pressure. Therefore, if they experience morphological changes (*e.g.* locally become more robust), it is difficult to separate the mechanical factors (anatomy, gender or human intervention) affecting the morphological variance. On the other hand, more stress-sensitive quarters, such as palmar-abaxial, are not supposed to endure an excessive load, so they morphologically react to such change quicker (or they break and cause lameness or other skeletal problems). Moreover, it is easier to highlight the cause of load imbalance at sensitive quartes since they endure harsh loading conditions less frequently. These two specifications make directional asymmetry an ideal indicator for detecting human-induced disturbances in the mechanical environments of phalanges.

The anteriorisation of posterior phalanges (Helmer *et al.*, 2018) and disproportionate changes in phalanges linear measurements (Bartosiewicz *et al.*, 1993) can also be categorised as directional asymmetric indicators of domestication. This chapter will discuss the use of biometric measurements and geometric morphometrics in conjunction with finite element analysis to separate the natural causes of morphological variance from human-induced factors.

6.2. Evolution of *Bos* herd management and exploitation in Tell Halula (MPPNB - Pre Halaf):

From a one-dimensional perspective, the greatest length of Tell Halula's first and second phalanges did not significantly differ from the referential *Bos primigenius* specimens. In addition, the available samples (n_{1FA}=11, n_{2FA}=46) belonged to moderately large animals taken from different occupation phases. There was a non-significant increase in the greatest length of the first and second phalanges from MPPNB to LPPNB. As expected for mixed samples of aurochs and cattle, the standard deviation of the greatest length of Tell Halula's specimens was higher than *Bos primigenius*.

Upon performing principal component analysis to remove the multicollinearity of linear measurements, as well as the allometric size effect, it was revealed that the anatomical factor (anterior-posteriority) and species (*B. taurus* versus *B. primigenius*) had a visible impact on the variance of the linear measurements (Results: Figure 5 and 16). In the case of the first phalanges, the available labels (known information) of the referential data helped us to establish the *Bos primigenius* domain in the measurement space of the first and second principal components. The referencial principal component showed that (Results: figure 4-right) *B. primigenius* first phalanges are bulkier than the rest (having a larger diametric to length ratio, note that PC2 of the linear measurements of the first phalanges primarily represented the greatest length, while PC1 represented diametric measures of Bp and Bd). Applying the referential principal component to Tell Halula measurements revealed that 66% of specimens had *Bos primigenius* likeness.

The homogeneity of the size in Tell Halula's phalanges and their resemblance (in the context of linear measurements) to the Near Eastern *Bos primigenius* suggests that the domestication of cattle in Tell Halula was autochthonous, *i.e.* the progenitors were part of the Near Eastern natural fauna. As a counter-argument, wild (hunted) skeletal remains in the archaeological assemblage could contribute to noise in the variance of data. The remains of hunted animals dominated Tell Halula's archaeological assemblage, and it was not until late MPPNB and early LPPNB that domesticated Bos remains became more dominant (Peters *et al.*, 1999). Moreover, Zeder (2001) pointed out that a co-dependent relationship exists between size factor, gender, age, location and time, which need to be addressed before drawing any conclusion. Our approach to separate noise from variance was first to incorporate the anatomical factor into the equation. Anterior metapodials are expected to be structurally (regarding mineral density and morphology) more robust than posterior ones (Bartosiewicz, 1993; Bartosiewicz *et al.*, 1993; Gündemir *et al.*, 2020; Ocal *et al.*, 2004)), due to the asymmetric live weight distribution in quadrupeds. A change in the pattern of anterior-posterior dimensions of the Bos skeleton, *i.e.* the emergence of thicker and more robust posterior metapodials, can be a sign of a disruption in the mechanical environment of animal limbs, potentially mediated by exploitation and physical work (Bartosiewicz *et al.*, 1993), and can be considered as a marker for animal husbandry.

In the present research, anterior bones have larger diametric dimensions (Bp and Bd for the first and Bd for the second phalanges) based on the first two principal components of the linear measurements. The said difference was more pronounced and statically significant for second phalanges ($c^2(2, 46) = 27.16$, $p < 0.01$; Results: Figure 16), possibly due to the higher number of samples ($n_{1FA}=11$ versus $n_{2FA}=46$). Regardless, observing the first PC scores indicated that some posterior individuals, namely TH1FA12, TH2FA24 and TH2FA61, resembled higher combined Bp-Bd values than the others (worth reiterating that PC1 in both anterior and posterior phalanges is mostly a combination of Bp and Bd). These three specimens belonged to small-medium individuals (compared to the average of the presented sample) who might experience heavy exploitation; however, other factors could affect the thickness (or robusticity) of their phalanges. Sexual dimorphism and genetic variation, for example, are among the more prevalent ones. The lack of resolution and the codependency of the "more robusticity" as a marker of *Bos* exploitation imposes another significant obstacle: it is impossible to observe the dynamic of robusticity alteration during a given time interval, specifically as large as MPPNB-LPPNB.

On the other hand, geometric morphometrics benefits from the fact that a user can decide the location and resolution of recorded morphological disparities. Following the same logic, which regarded the increase of diametric dimensions of anterior metapodials as one of the exploitation markers, observing strain-related morphological shifts at locations which are not meant to endure harsh mechanical conditions is an unnatural phenomenon, potentially caused by the intervention of humans in the lifestyle of the animal in question. In *Bos* phalanges, as mentioned before, the stress-sensitive zones are abaxial and dorsal planes, which manifest directional asymmetry of load distribution during the locomotion or stationary stage.

In the case of the first phalanges (n_{1FA}=11), the first morpho-space (first principle component of the Procrustes residuals), and consequently the highest morphological variance, reflected the anatomical (anterior-posterior) factor. Locally, the first morpho-space was more influenced by the abaxial-ventral morphological dissimilarities (landmark 29, Results: Figure 26, up-left). The different rates of the asymmetric thickening of the first phalanges along the abaxial axis in anterior and posterior digits agree with the cattle pressure plate data (van der Tol *et al.*, 2003). Although the abaxial axis tolerates lesser pressure during gait cycles than the axial axis, this pressure is noticeably higher in anterior metapodials. Since the dorsal axis is less stress sensitive, it is impossible to identify if another source of pressure, gender-related or anthropogenic, acted as a cofactor of anatomical specifications. A series of finite element analyses also showed that the said morphological asymmetry, or thickening, at "landmark 29" correlates with the resistance of phalanges to the local deformation (strain values were measured at LM29 across different samples, Results: Figure 27).

The second morpho-space showed the localisation of morphological disparities at the palmar-axial (landmark 3, Results: Figure 26, up-left), one of the two stress-sensitive quarters. The variance of the second morpho-space did not change between any of the available known groups of specimens (anterior-posterior, occupation phases and Neolithic periods). Two possible factors, however, could affect the second-largest morphological variation: mediolaterally anatomical positioning and cattle management and housing. Finite element results showed that the principal scores of the second morphospace correlate negatively with the resultant strain, suggesting that higher scores represented individuals who adapt (deformed) to endure more loading conditions. The rate of adaptation, nonetheless, was different for anterior-posterior bones.

On the one hand, the overall shape of the phalanges (visual assessment) resembled slender lateral digits at the lower principal scores, compared with the bulkier individuals at the higher end of the second morpho-space spectrum, hinting the anatomical characteristic as one of the potential variance influencers. On the other hand, the higher the amount of time a cattle stands at a place, *e.g.* due to a rigorous housing strategy, the unbalanced weight distribution in favour of medial digits (of anterior) and lateral digits (of posterior) (Van Der Tol *et al.*, 2002) exaggerates the mediolateral morphological disparities. However, without anatomical knowledge (mediolaterally labelled specimens), it is unfeasible to separate relevant morphological variances and expand the discussion further.

The third morpho-space of the first phalanges depicted the significance of morphological dissimilarities at the palmar-abaxial (at landmark 0, Results: Figure 26, down-left), the most stress-sensitive quarter. The most crucial aspect of this morpho-space was its significant positive correlation with Tell Halula’s occupation phases (Results: Figure 29, right). Finite element analysis showed that higher principal scores of the third morphospace had higher strain values probed at “landmark 0”, implying that from MPPNB to LPPNB (phases 6 to 16), the first phalanges became palmar-abaxially less (morphologically) adapted to high mechanical environments. The possible implications of this morphological adaptation in the context of Tell Halula's archaeozoology will be discussed shortly after discussing the morphometrics of the second phalanges.

Regarding the second phalanges of Tell Halula's specimens (n_{2FA}=46), the highest morphological variance, similar to the first phalanges, was described by anterior-posteriority of the digits, reflected the most at the location of "landmark 6", the edge of the distal abaxial-ventral quarter (Results: Figure 37). Although the anatomical-related morphological adaptation pattern is different in the second phalanges, similar to the first phalanges, their asymmetric thickening along the abaxial axis in anterior and posterior digits agrees with the cattle pressure plate data (van der Tol *et al.,* 2003). Individuals with higher scores of the first morpho-space exhibited significantly higher distal-abaxial width (not to be confused with distal breadth).

After the first morpho-space, until the ninth, no significant morphological difference was observed amongst the known labelled groups (anatomical, occupation phase and the Neolithic period), implying that 21.2% of the morphological variation cannot be explained based on the available information. The ninth morpho-space, regardless, slightly corresponded (a non-significant trend, Results: Figure 39, right) to the Neolithic periods (MPPNB, LPPNB, and Pre-Halaf), where the width of the distal groove decreased from MPPNB to LPPNB and increased again in Pre-Halaf (Figure 39-left). Although the observed trend agreed with the third morpho-space of the first phalanges, the small sample size with high component scores in the Pre-Halaf ($n_{\text{Pre-Halaf}}$ = 2) most probably exaggerated the differences between MPPNB and LPPNB. The second phalanges are short, robust, and resist mechanical load without significant deformation. They are only responsible for 0.5% of lameness cases in cattle, which is lower than the 2% share of the first phalanges (Newcomer & Chamorro, 2016). Therefore, low variability in the morphology of the second phalanges was expected.

Combining the observed morphological variances of the first and second phalanges of Tell Halula with the finite element analysis results, three possible scenarios are disputable regarding cattle herd management from MPPNB to LPPNB. The first case is the possibility of a significant decrease in *Bos* exploitation, from more intensive routines in MPPNB to less intensive strategies during the LPPNB. The lack of morphological adaptability to harsher mechanical environments in the first and the second phalanges (albeit manifested as a non-significant trend, but a trend nonetheless). This scenario has been examined via the percentage of species in the archaeological assemblies. Considering the percentages of representation, an increase in *Bos taurus* exploitation is observed from occupation one to occupation seven, an occupation for which a maximum peak is recorded. There is a progressive decline (with occasional increases) from occupation phase seven onwards until occupation phase twenty-five. From this point onwards, the percentages stabilise and gradually decrease from occupation phase thirty-one to thirty-six.

The second scenario is the possibility of diversifying *Bos* exploitation into unknown but more physically demanding activities, which was discontinued after several generations. Furthermore, the third possible scenario is a shift in cattle housing from a free-to-graze-around during MPPNB to a more strict or lack of free-ranging. Large grazers, such as *Bos*, move slowly and irregularly while grazing. The grazing gait necessitates slower gaiting cycles to stabilise the animal while it stretches the neck down to graze (Usherwood & Smith, 2018). The slower gait cycle could prolong the duration of the push-off stage, therefore extending the loading time on the palmar axis of phalanges, which can trigger the consequence of morphological adaptation. Postulating this theory can explain the significant correlation between occupation phases and the observed decrease in the robusticity of the abaxial-palmar quarter.

It is essential to briefly return to anatomical effects on data variance before concluding Tell Halula's discussion. Comparing the anatomic separation results of the morpho-spaces (Results: Figures 30 and 40, left) with the biometric first and second principal components (Results: Figures 5-right and 16) revealed that while biometric measurements suggesting that the three specimens TH1FA12, TH2FA24 and TH2FA61 asymmetry potentially caused by anthropogenic activities (*e.g.* exploitation) morphometrics data confirmed only one of them, TH1FA12 as the individual with anteriorisation features (Results: Figure 30). This inconsistency between the biometric and morphometrics results is rooted in the low resolution of the biometric measurements, where the "more diametrically robust" as a general description of the specimen can be an output of several factors, such as sexual dimorphism of weight. Geometric morphometrics, however, can be coupled with finite element analysis to assess a high-resolution domain on a specimen for the existence of asymmetry-related morphological adaptations.

6.3. Evolution of *Bos* herd management and exploitation in the Iberian Peninsula, La Draga:

La Draga specimens belonged to medium size cattle (n_{1FA} = 25, n_{2FA}=31), mostly smaller than the referential European *Bos primigenius* females except for a few individuals, including LD1FA29 and LD2FA22, belonging to the first and second phalanges respectively (Results: Figures 22 and 30). The existence of auroch individuals was in accordance with the previously published data on meat production in La Draga, where the contribution of domestic species to meat production would have accounted for 85.11%, while wild species would have contributed, in relative terms, an amount proportional to 14.58 (Saña, 2011). La Draga's first phalanges GL and SD correlation trend (Results: Figure 43, Up-left) significantly differs from the local *Bos primigenius* population. In La Draga's specimens, anterior phalanges are much more slender than the Iberian aurochs, while in the posterior digits, the difference is the opposite, although non-significantly, La Draga's phalanges are more robust regarding their SD measurements. The robusticity of the posterior phalanges is an indicator of traction exploitation when the centre of mass is shifted back toward the subject of traction, causing extra pressure on posterior limbs (Bartosiewicz *et al.,* 1993). A closer look at the Results: Figure 43, Up-left suggests that particularly two specimens, LD1FA 42 and 48, influenced the GL-SD trend the most, and more probably, they belonged to the individuals intensively used for traction. The list of La Draga's cattle exhibiting osteochondritis and lipping deformation revealed that both traction cattle experienced osteochondritis, while LD1FA48 also had visible signs of articular lipping. Exploiting cattle for traction is well documented in La Draga, and the biometric results are in accordance with the previously published research (Tarrús *et al.,* 2016; Lladó *et al.,* 2008; Bosch *et al.,* 2008; Saña, 2011; Antolín *et al.,* 2014). On the matter of diaphysis of anterior phalanges, on the other hand, genetic isolation and inbreeding could be viable factors explaining the slenderness characteristics of La Draga's first phalanges. It is worth mentioning that biometric differences between La Draga's second phalanges and the local *Bos primigenius* population were neglectable, implying that choosing the right sample, with the higher potential of adaptation (morphological adaptation in the context of this research) to the external factors, is crucial to study aspects of animal biometry and biomechanics. Moreover, in sharp contrast with the sample LD1FA42 and 48, individual LD1FA34 had significantly low SD for its GL value, indicating the possibility of being an ox (Results: Figure 43, Up-left).

Regarding the effect of anatomical factors on the variance of biometric data, a sizable overlap was observed in the results of principal component analyses conducted on the referential data (Results: Figure 44, left and Figure 51) and La Draga specimens (Results: Figure 44, left, and Figure 52). As mentioned earlier, for Tell Halula’s specimens, The resolution of biometric data is not high enough to separate cofactors affecting the variance. The morphometrics principal component analysis (performed on Procrustes residuals) revealed that, unexpectedly, the first morpho-space of the first phalanges (n_{1FA}=25), which reflected anatomical (anterior-posterior) disparities, was affected the most by landmarks residing in assortments of the stress sensitivity quarters: Landmarks 3 and 21 at the more stress-sensitive axial-palmar quarter, and with slightly lower contribution, landmarks 1 and 29 at the less stress-sensitive abaxial-dorsal quarter, and landmark 9 at distal abaxial-dorsal quarter. Observing the highest anatomical-related morphological adaptation at unexpected locations strongly suggests the significant effect of the second anatomical dimension: medial-laterality of the first phalanges. Accordingly, similar to the biometric principal components, an evident overlap was observed in the first morpho-space of anterior and posterior phalanges (Results: Figure 48). Hence, the observed overlapping of anatomical characteristics measured by biometry and morphometrics can be regarded as noise introduced by the unknown anatomical information (medial-lateral variation) rather than a shift in the directional asymmetry caused by over-use and exploitation.

In the case of the second phalanges of La Draga (n_{2FA} = 31), principal component scores of biometric measurements did not significantly reflect the anatomy of the specimens because the available referential measurements (consisting of European aurochs biometrics), which were used to compile the principal component, were well-suited for *Bos primigenius-Bos taurus* separation, rather than anatomical segregation (Results: Figure 51). In addition, the first morpho-space of principal component analysis on the morphometrics data (Procrustes residuals) significantly reflected the anatomical factor (Results: Figure 54), where no sign of over-use or heavy exploitation was observed. The absence of work-related morphological adaptation (or deformation) is in accord with a very low pathological index (close to zero) reported previously for La Draga cattle (Tarrús *et al.,* 2006; Bosch *et al.,* 2008; Lladó *et al.,* 2008; Saña, 2011).

6.4. Evolution of *Bos* herd management and exploitation in the Iberian Peninsula, Pixarelles:

Pixarelles specimens (n_{1FA} = 10, n_{2FA} = 8) comprised short (compared to La Draga individuals) and moderately thick phalanges, except for an individual with exostosis, PX1FA18, which manifested extremely high diametrical dimensions, and discarded for morphometrics and finite element analysis. In the case of the first phalanges, biometric data initially suggested that, similar to La Draga, anterior phalanges were slimmer than the local *Bos primigenius* population (Results: Figure 57, up-left). However, the low number of samples (n_{1FA} = 10), in conjunction with the existence of a very slim, ox-looking individual in the sample pool (PX1FA16), implied that in the case of Pixarelles, after removing the ox outlier, the correlation trend of GL-SD was indeed not different from the aurochs population. It is worth iterating that the limited number of samples rendered the “significance” of the statistical tests irrelevant, although the existence of such a trend is important to be taken into account. Moreover, the sexual size dimorphism was more or less visible (along the first principal axes of biometric measurements), and the anatomical (anterior-posterior) disparities could explain the biometric variance of the second biometric principle axis with only one overlap (PX1FA9).

Based on the first morpho-space of the Procrustes residuals, which highlighted the anatomical-related morphological variance, the most influential landmark (38) was located at the distal edge of the diaphysis, suggesting, like La Draga, the second anatomical dimension (medial-lateral) has a significant effect on the morphological variance. Following the biometric data, the second morpho-space indicated that individual PX1FA9 (posterior sample) overlapped with anterior specimens or, to put it differently, experienced anteriorisation (known to happen due to extreme exploitation). Interestingly, the second morphos-space (influenced mostly by landmark 3 at the dorsal-abaxial quarter, Results: Figure 60) almost reflected the anatomical factors (anterior-posteriority), suggesting the existence of a synergic relation with anatomical and external mechano-environments.

In the case of the second phalanges of Pixarelles, biometric measurements (n_{2FA} = 8) showed that two individuals: PX2FA6, and 4 had an exceptionally high SD/GL ratio (I'll add figure), higher than referential data, Tell Halula and La Draga. Although the number of specimens was limited (six posterior samples), the exceptionally thick diaphysis of the two mentioned phalanges in Pixarelles, and the fact that second phalanges usually respond to mechano-environment slowly (because they are already short and robust) suggest that those individuals possibly were local to Pixarelles, and the mountainous environment of Pixarelles had a significant effect on their posterior phalanges. The number of the anterior second phalanges was very low for any analysis (n = 2), so they were neglected.

6.5. General discussion regarding the use of morphometrics, biometry and biomechanics in the archaeozoological context

During this research, it was observed that biometrical information coupled with the relevant referential measurements could successfully separate *Bos primigenius* from the rest of the sample pool. In geometric morphometrics, since the full Procrustess superimposition was the method of choice, all size-related data were removed, which made species separation impossible. On the other hand, although biometrical principal component axes could separate anatomical factors from the variance, due to their low resolution, overlapping was imminent. Even though some research articles discussed the existence of biometric overlap as a sign of extreme cattle exploitation, the possibility of other cofactors, such as sexual size dimorphism, adds a level of uncertainty to the use of biometric measurements for observing anomalies of directional asymmetry. Moreover, biometric ratios such as GL/SD were deemed informative for comparing cattle herds with their local *Bos primigenius* to observe similarities or possibly isolation or hybridisation and even investigate the effect of environment on the general morphology of phalanges. However, we did not have the luxury of referential information for geometric morphometrics, a factor limiting the questions we could answer.

Geometric morphometrics coupled with finite element analysis was particularly useful in separating the impact of anatomical-related factors from the variance of the data, and verifying whether the biometrical data highlighted anthropological factors. Although morphometric approaches could benefit from referential data, the effect of the basic mechano-environment of phalanges, *e.g.* locomotion, on the morphological adaptation, or any deviation from the said adaptation, was successfully recorded and even the existence of unknown cofactors (such as the second anatomical factor, medial-lateral) could be attested. It is necessary to iterate that biometry and morphometrics potentially complement each other to ask new questions and verify the possible answers.

6.6. Effects of Sexual dimorphism and diet on the *Sus scrofa* mandible

Mandibles are known to evolve to provide more biting-chewing force or to have a longer gape. The mechanical characteristics of chewing, across all mammalians, depend on two factors: the height of the mandibular condyle, and the length of the jaw. Following conventional wisdom, higher positioned condyle, such as the mandibular structure in ruminants, provides a larger moment of arm for the medial pterygoid and masseter muscles, which in turn, produce a stronger bite and chewing force, but limits the angle of gape. The principal component analysis of *Sus scrofa* specimens showed that most morphological variance (97%) could not be explained by sexual dimorphism. Regarding the morpho-spaces describing 1-25% of morphological variation (spaces 6 and 7), not surprisingly, landmarks defining the height of the mandibular condyle and length of the jaw were the most important landmarks.

On the other hand, Age classes did not significantly correlate with any of the morpho-space scores. Nonetheless, after grouping individuals into pooled age classes, the effect of sexual dimorphism started to become more relevant. This suggests that in the presented sample, age has the most influence on the morphological variance. The older the *Sus* becomes, the bolder and more differentiable the sexual dimorphism becomes (Results: Figure 76). In addition, male specimens show less craniofacial variation than females, suggesting females in the provided sample pool had a wider variety of diets. Although it has been attested that the craniofacial adaptation in pigs is more or less fast, no sign of plastic morphological adaptation was observed: even very young individuals had diverse mandible morphologies. Based on the visual inspection of the mandible, it is feasible to suggest that the provided *Sus* samples were drawn from different sub-species populations, each of which evolved to exploit different types of diet.

7. CONCLUSIONS

The extent of geometric morphometrics, coupled with finite element analysis to investigate the unknown proportion of variance in zooarchaeological data, was tested through the presented research. The flexibility of geometric morphometrics to detect changes in morphological patterns, such as diminishing or exaggerating a structural asymmetry, was successfully used in the archaeozoological context to highlight human-induced changes in the *Bos* mechano-environment and separate it from the effects of anatomical factors. Furthermore, compared with the traditional biometric approaches, since the morphometric procedure collected more dense spatial details, it produced more self-explanatory data that relied less on hard-to-find referential information. Observing morphological changes, for example, at places irrelevant to the natural mechanical environment of the domain of interest, suggest the involvement of an external cofactor, such as human-mediated exploitation.

The contribution of finite element analysis to the study of cattle domestication in the Near East and Mediterranean was impeccable. Verifying observed disparities in Procrustes residuals and examining if the source of those disparities was rooted in husbandry-related activities was successfully achieved by finite element analysis. Although the general information provided by biometric measurements was informative, sometimes they failed to describe observed variation. For example, in the case of La Draga cattle management, specimens were uniquely different from the provided referential data. As a result, the principal components of biometric measurements failed to reflect the anatomical disparities (anterior-posteriority), which resulted in an overestimated number of individuals who experienced extensive exploitation. On the other hand, contrasting the observed morphological differences of the same sample pool with a series of finite element analyses revealed that the relevant morphological adaptation was caused by another dimension of anatomical factors, medial-laterality, rather than anterior-posteriority.

And last but not least, Archaeotoolbox software was successfully used for digitising all three types of morphometric landmarks and sliding semi-landmarks, performing full and partial Procrustes superimposition, performing principal component analysis and highlighting the most important landmark of each morpho-space, and displaying the resultant Procrustes residuals as an exportable heatmap. ArchaeoToolbox was used throughout the collection of morphometric information for the presented research without any performance issues or memory leaks. The novice approach of geometric morphometrics coupled with finite element analysis was utilised to study cattle management and exploitation patterns in the Near East and Western Mediterranean, which will be concluded in the following paragraphs.

7.1. Cattle Management in Tell Halula

Based on the information available for *Bos*'s first and second phalanges (n_{1FA}=11, n_{2FA}=46), it was deduced that Tell Halula's phalanges resembled the Near Eastern *Bos primigenius* biometric characteristics (*i.e.* linear measurements and their ratios were similar). In addition, phalanges possessed homogenous size, which in combination with their (biometric) likeness to the local auroch population (The Near Eastern aurochs), makes it feasible to conclude that the domestication of cattle was an autochthonous process. In addition, based on the available morphometric information in conjunction with finite element analysis, it was observed that from MPPNB to LPPNB, the morphological adaptability of phalanges to higher mechanical load significantly decreased. Accordingly, it was discussed that three scenarios could trigger the diminishing of morphological stress endurance adaptability: 1- a significant decrease in cattle exploitation, 2- a shift in the pattern of exploitation and 3- a change in the housing (penning) strategy from more free-range to more strict.

7.2. Cattle Management in Western Mediterranean

According to the biometrical analysis of the first and second phalanges of La Draga (n1FA = 25, n2FA=31) and Pixarelles (n_{1FA} = 10, n_{2FA} = 8), it was concluded that the La Draga's cattle herd did not possess significant biometrical similarity to the Iberian *Bos primigenius* population, and potentially were allochthonous and already evolved somewhere else before arriving to La Draga. Furthermore, the analysis did not point to any work-related deformation except for two individuals LD1FA 42 and 48, postulating that some adult cattle were not involved in heavy exploitation or, plausibly, the ground was soft enough to protect phalanges from injury and deformation. Finally, although sexual dimorphism was not confirmed in the morphometrics data, the previous research on the subject and the significant effect of the second anatomical dimension (medial-laterality) on the variance of data suggested the possibility of the synergic (exaggerating) impact of sexual dimorphism, or selective pressure in favour of meat production, on the anatomical data.

Pixarelles specimens, on the other hand, exhibited two cases of proximal diaphysis broadening, one coupled with high pathological deformation. The small available sample size limited any broad conclusion; nonetheless, the high variability of the greatest length in the Pixarelles's first phalanges suggested that they belonged to a highly diverse population or they came from multiple different cattle herds. Some individuals exhibited a shift in the proportion of their biometric measurements, suggesting the effect of the mountainous environment on the morphology of the phalanges. Like La Draga, a significant proportion of morpho-space variance was explained by the medial-laterality of the phalanges, hinting at the plausibility of sexual dimorphism or selective pressure in favour of heavier individuals.

7.3. *Sus scrofa* mandible morphology and sexual dimorphism

The geometric morphometric data concluded that sexual dimorphism in juvenile-adult male wild pigs is more prominent than in females. Younger individuals' mandible morphology adapts to the diet very fast, making the morphological characteristics unreliable for separating gender. Therefore, we conclude that using morphological studies to detect sexual dimorphism needs to be coupled with information about the animals' age. Besides the plastic morphological responses, evolutionary adaptation to a harder or softer diet and adaptation to a wider gape (probably beneficial to dig holes more proficiently) can have a significant role in mandible morphology.

7.4. Concerns about biometric and morphometrics studies

We conclude that biometric approaches are efficient for separating *Bos taurus* from *Bos primigenius*, albeit if suitable and well-behaved (no outliers, more or less normally distributed data) referencial data is provided. Moreover, they are fast to perform, easier to interpret and by no means outdated by geometric morphometrics. Although biometric variables have significantly lower resolution, under certain circumstances, they complement morphometric information.

Geometric morphometrics also has its own deficiencies. Morphometric data collection is time-consuming, hence why ArchaeoToolbox was developed to speed up and simplify the digitisation process. Moreover, it is more prone to human error than biometric measurements. More importantly, the Procrustes superimposition process underperforms when the domain of interest is non-linear (deviated from the oval or circular shape in a 2-D or spherical in a 3-D scenario). We conclude that in such cases (*e.g.* L shape domain of *Sus* mandible), choosing a sub-set of digitised landmarks to perform superimposition will produce a more biomechanically sensible rotation matrix.

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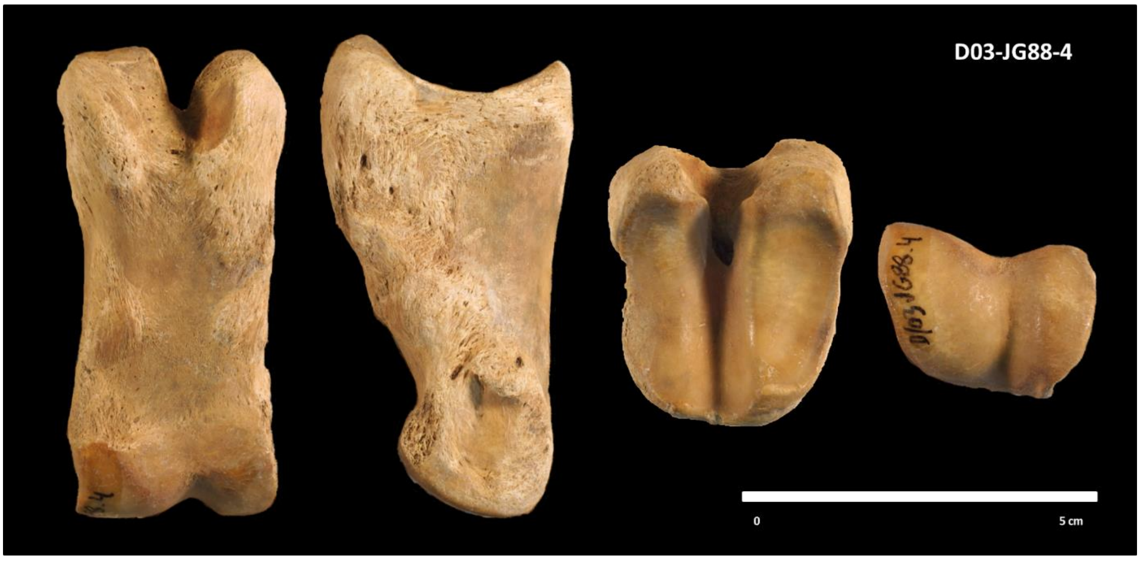
Annex I: First and second phalanges analysed

First phalanges of *Bos taurus* from La Draga




D03-JH88-2
0
5 cm


D03-JH89-2
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0
5 cm


D93-B20-34
0
5 cm


D95-CZ0.98
0
5 cm


D95-OX22-33
0
5 cm


D97-5A82-2
0
5 cm


D97-5G84-6
0
5 cm


D97-3682-13
D97/3682/13
0
5 cm


D97-JD84-19
0
5 cm


D97-JE83-6
0
5 cm


D03-JF88-40
D03 JF88-40
0
5 cm


D-209
0
5 cm


D15-JI50-11657
0
5 cm


D15-JB52-A-12031
D15-261-1.12031
0
5 cm


D-E17-28
0
5 cm


D-EST3-14
0
5 cm


D-H23-NO-3
0
5 cm

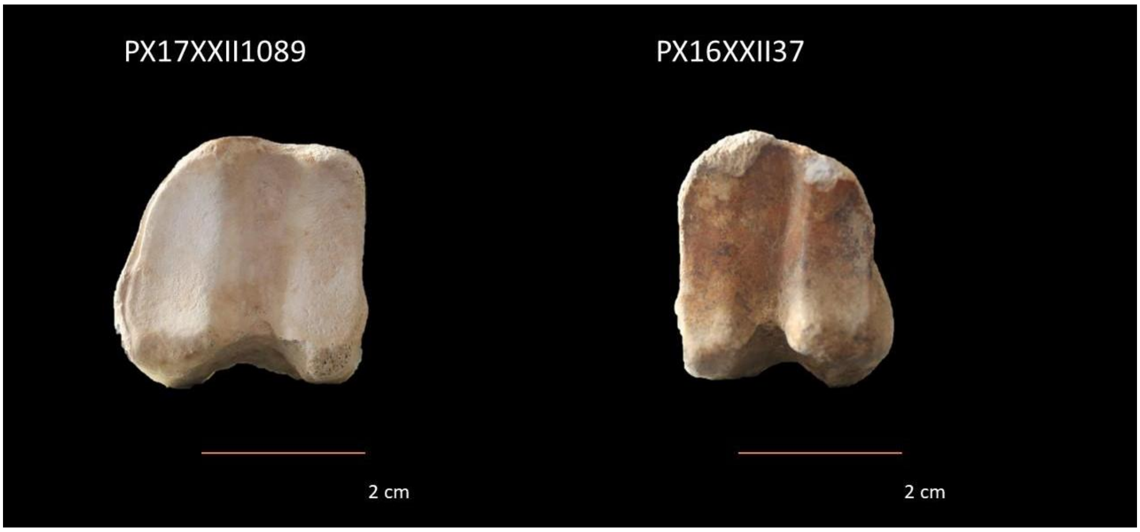

D-L18-NE4
0
5 cm


D-LL25-SE3
0
5 cm


D-ST23
0
5 cm

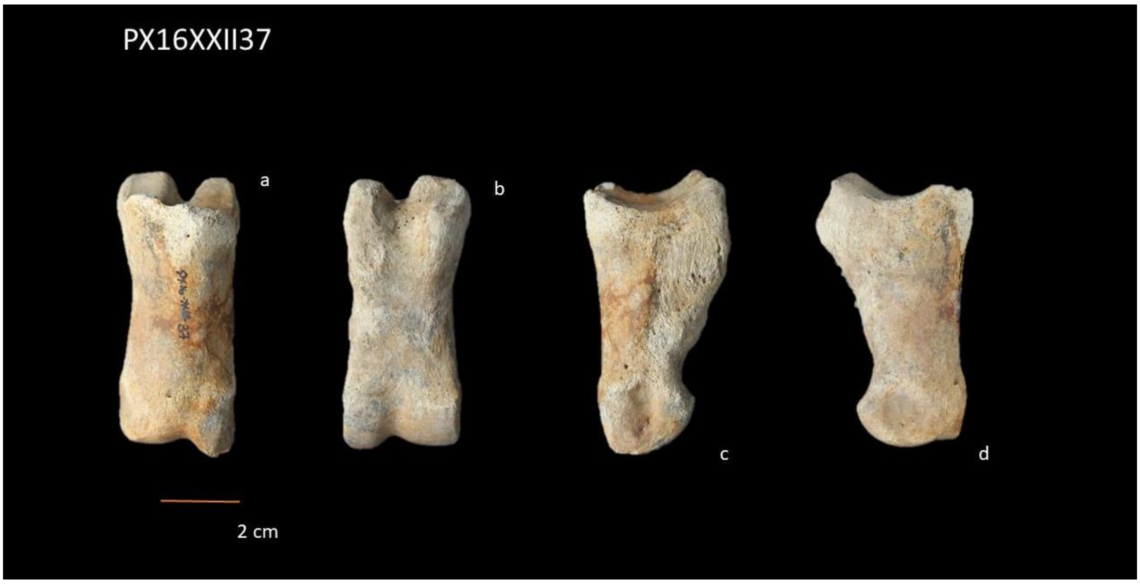

LD91-ES61-1
LD91 ES 61 1
0
5 cm

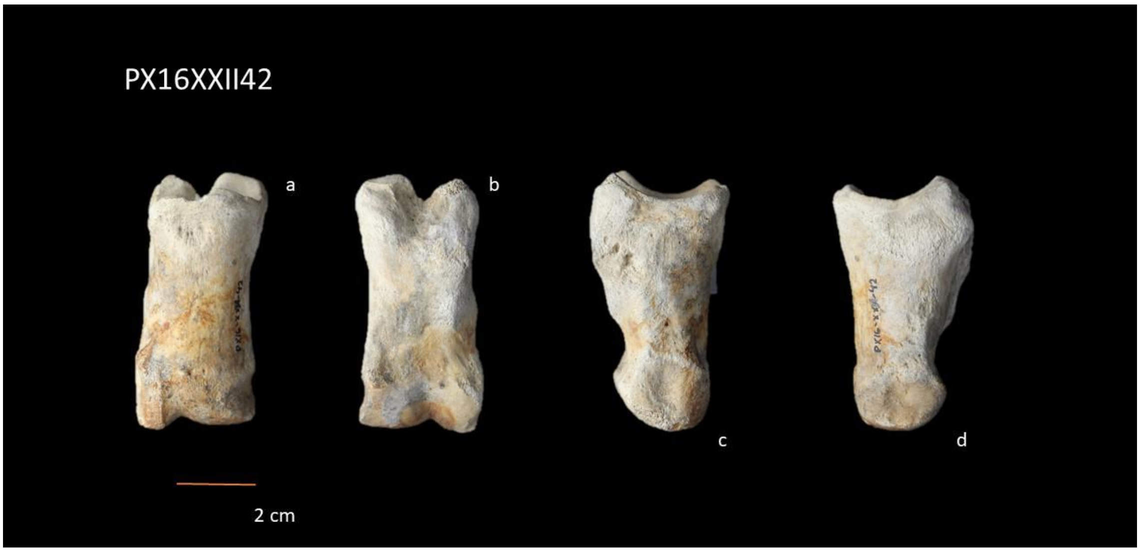
First phalanges of *Bos taurus* from Cova de les Pixarelles



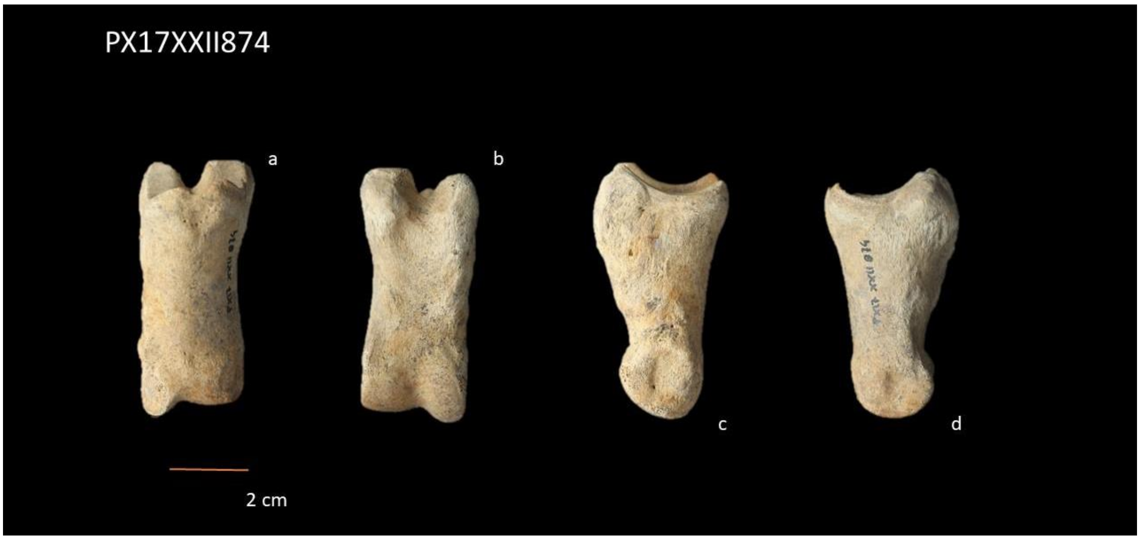

PX16XXII42
PX16XXII528
2 cm
2 cm

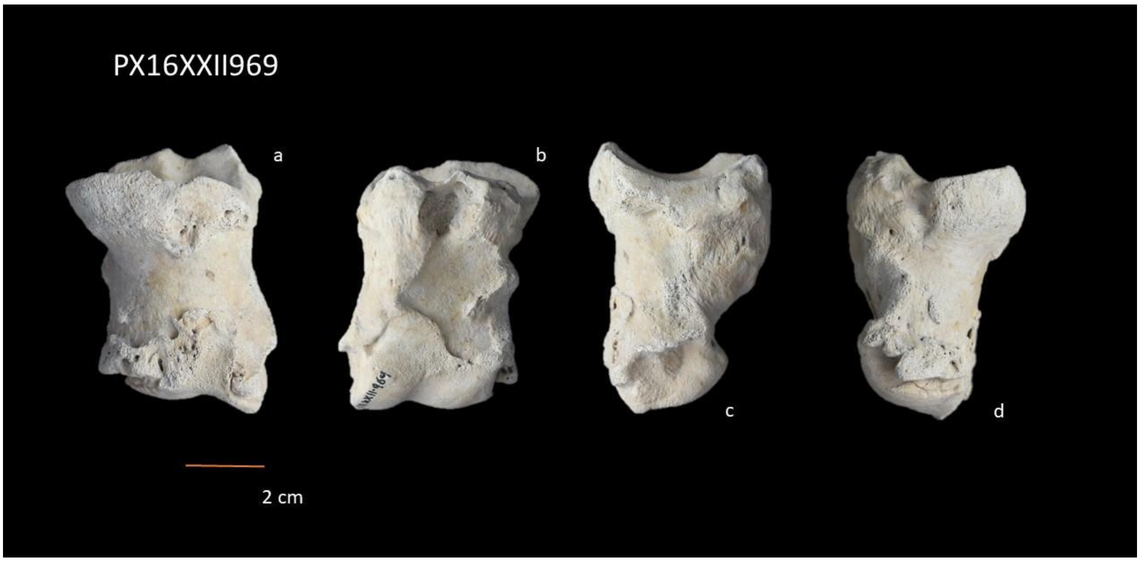

PX17XXII874
PX17XXII1055
2 cm
2 cm


PX16XXII37
a
b
c
d
2 cm

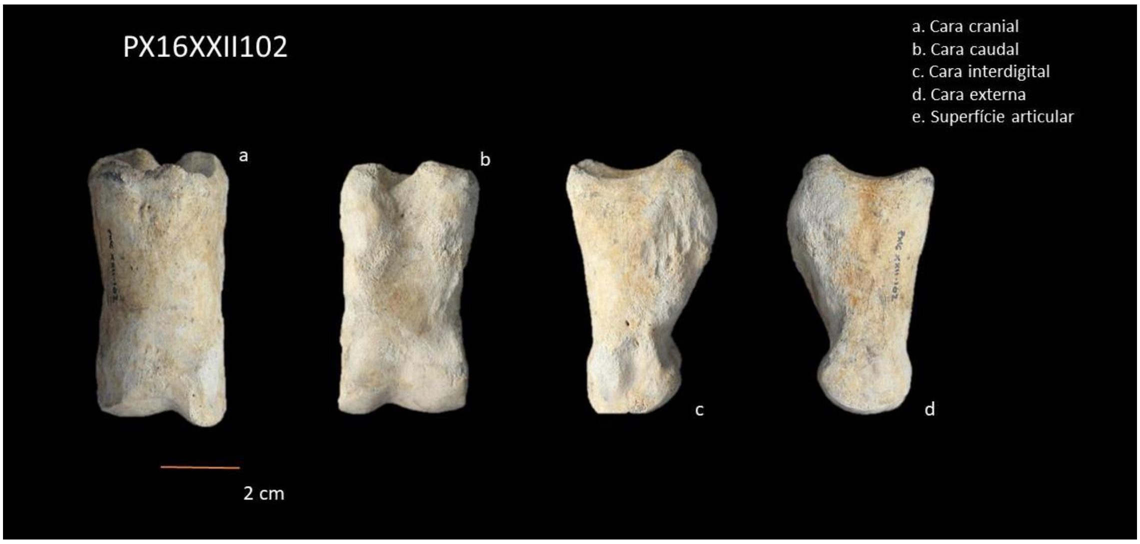

PX16XXII42
a
b
c
d
2 cm

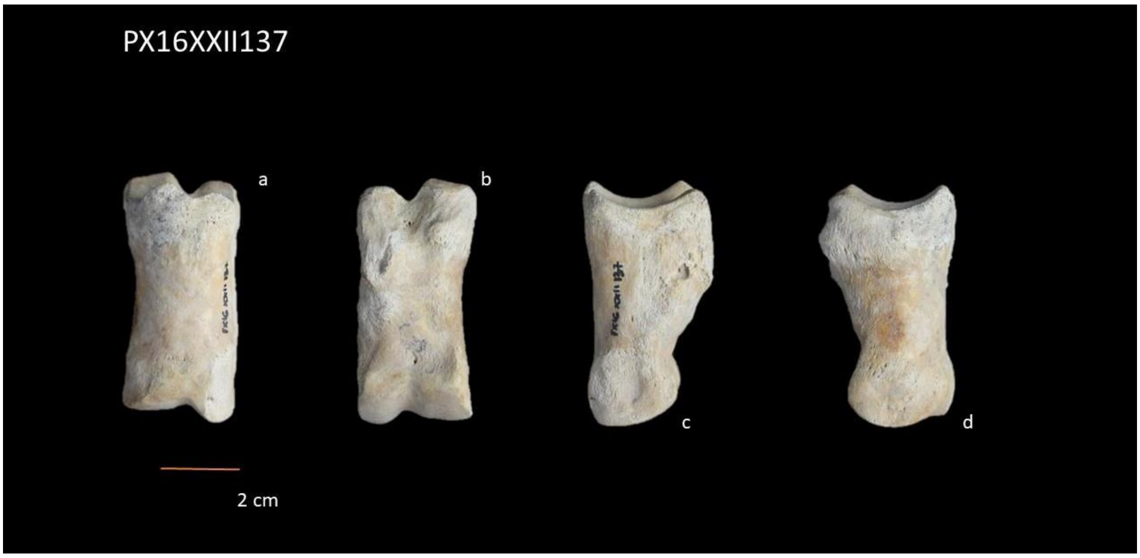

PX16XXII394
a
b
c
d
2 cm


PX17XXII874
a
b
c
d
2 cm


PX16XXII969
a
b
c
d
2 cm

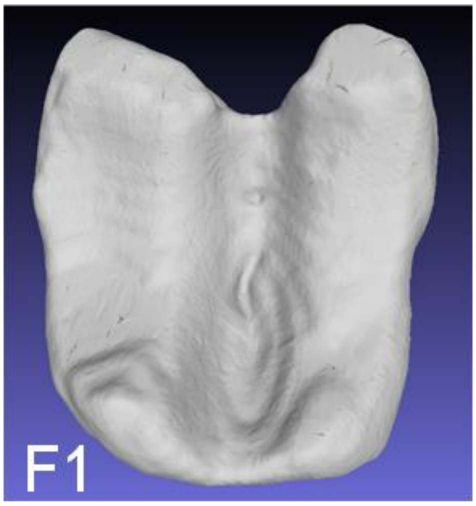

PX17XXII1055
a
b
c
d
2 cm

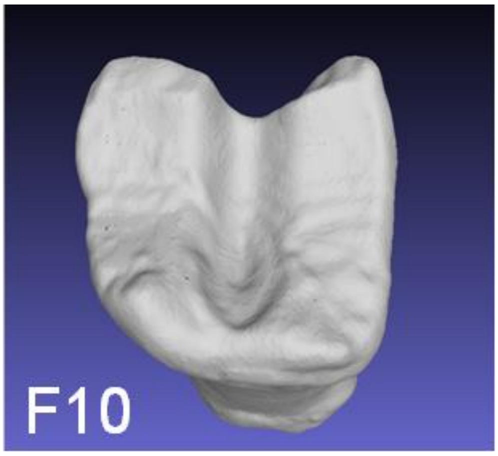

PX16XXII102
a. Cara cranial
b. Cara caudal
c. Cara interdigital
d. Cara externa
e. Superfície articular
a
b
c
d
2 cm

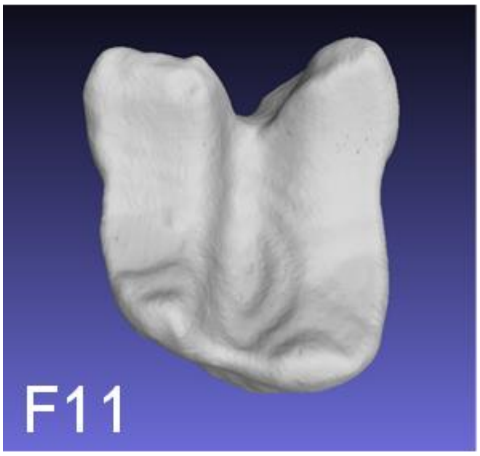

PX16XXII137
a
b
c
d
2 cm

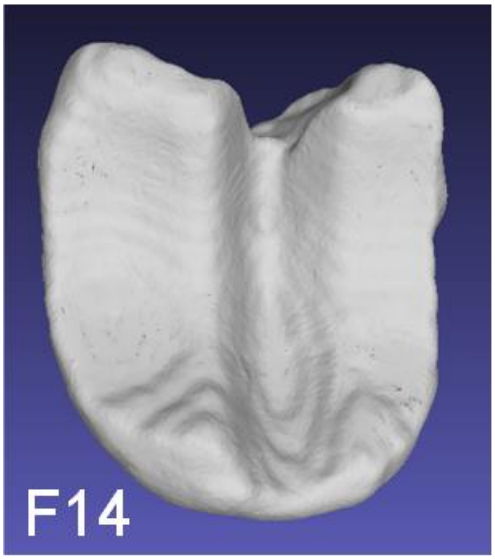

PX16XXII528
a
b
c
d
2 cm

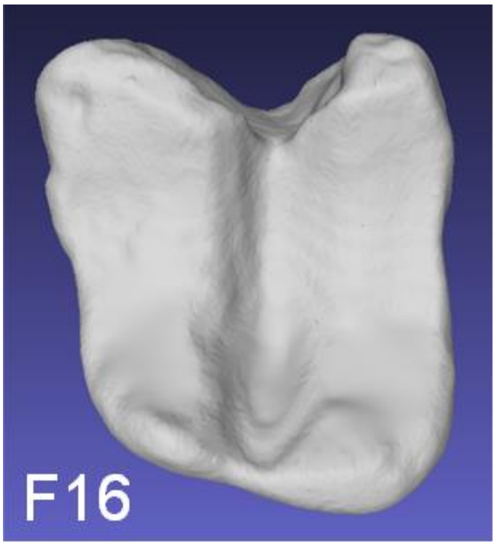
First phalanges of *Bos taurus/Bos primigenius* from Tell Halula

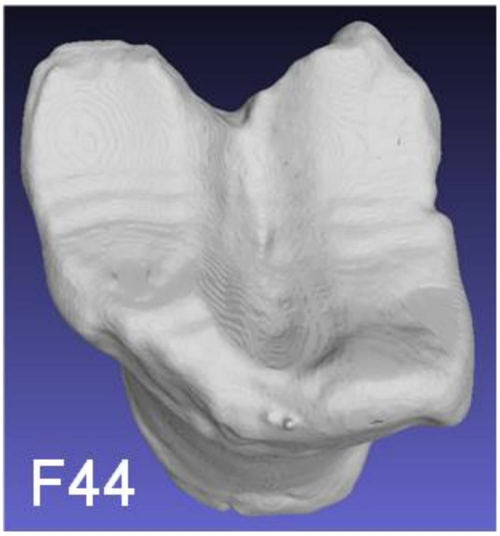


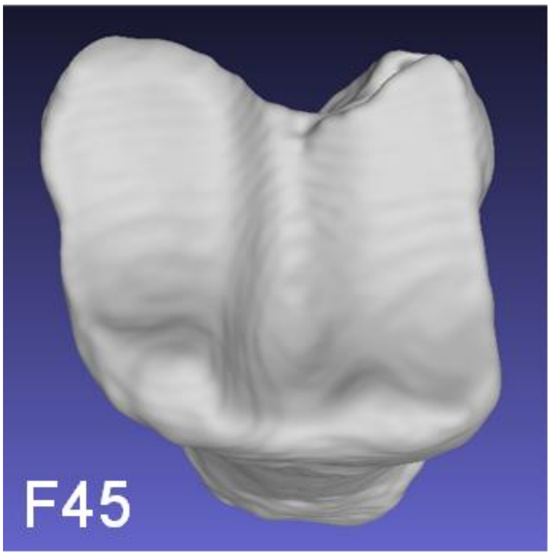


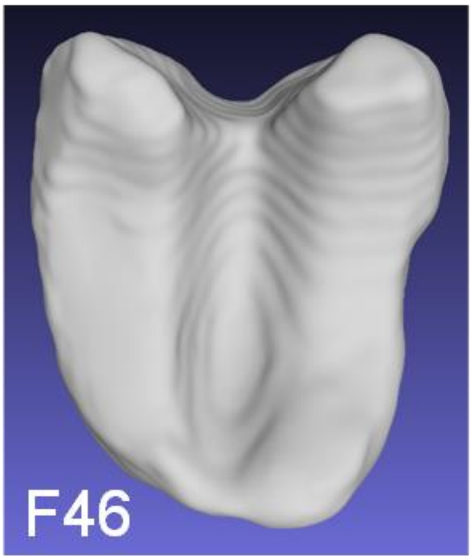


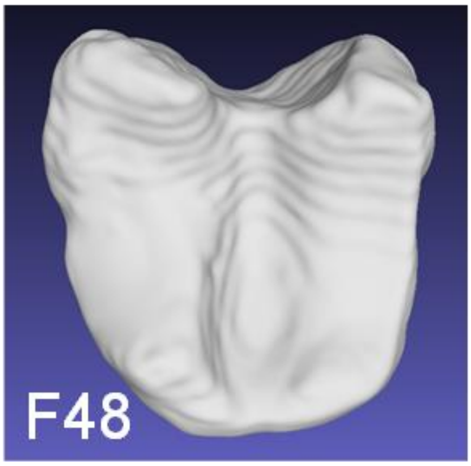



F16


F44


F45


F46


F48

Second phalanges of *Bos taurus* from La Draga


D91-H31-100
0
5 cm


D13-JB40-6276
D13.JB40.6276
0
5 cm


97-JG84-4
D97JG84-4
0
5 cm


D15-2-2002-11838
0
5 cm


D15-2-2002-11881
0
5 cm


D97-JE-8317
0
5 cm


D15-2-Z61-2-12196
D15-2-Z61-2-12196
0
5 cm


D15-2-2002-11962
D15-2-2002-11962
0
5 cm


D95-OZ21-18
D95-OZ21-18
0
5 cm


D95-C21-89
D-95
C21 89
0
5 cm


D-JH88-1
0
5 cm


D97-JD82-27
0
5 cm


D97-JD82-27
0
5 cm


D-H77-8
0
5 cm


D5-1004-650
0
5 cm


D14-JA42-9343
0
5 cm


D10-403
0
5 cm


D14-1146-8481
0
5 cm


D97-JE83-21
0
5 cm

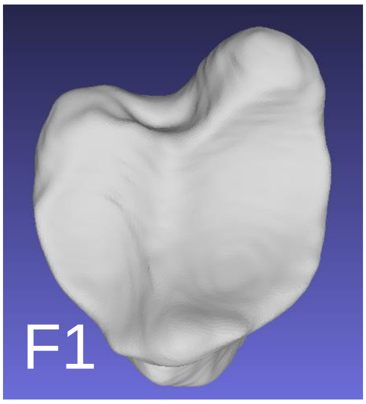

D04-JG92-8
0
5 cm

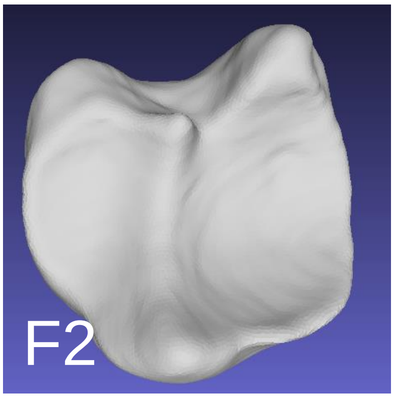

D01-JI88-1
0
5 cm

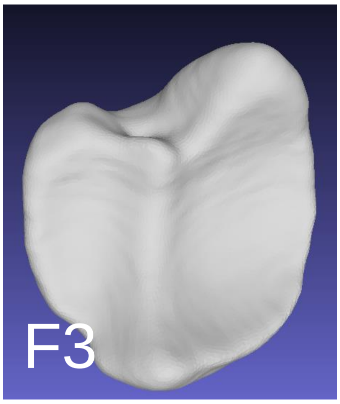

D-I30-NO-NE-134
0
5 cm

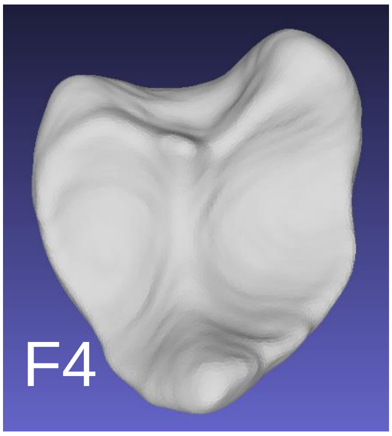

D-K16-NO-58
0
5 cm

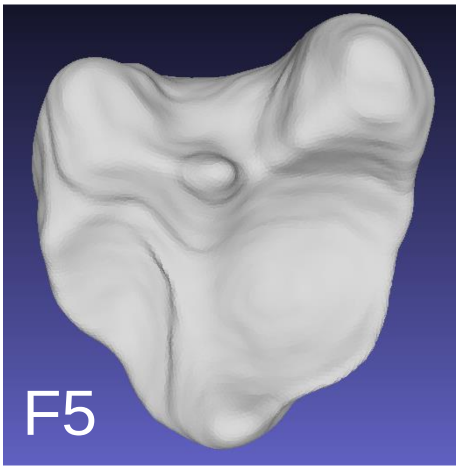
Second phalanges of *Bos taurus* from Cave Pixarelles

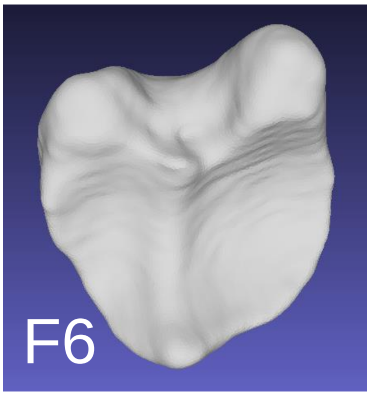


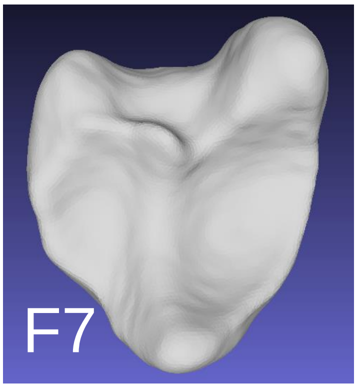


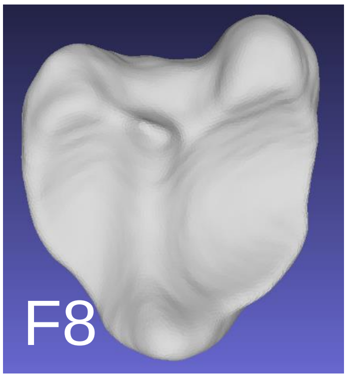




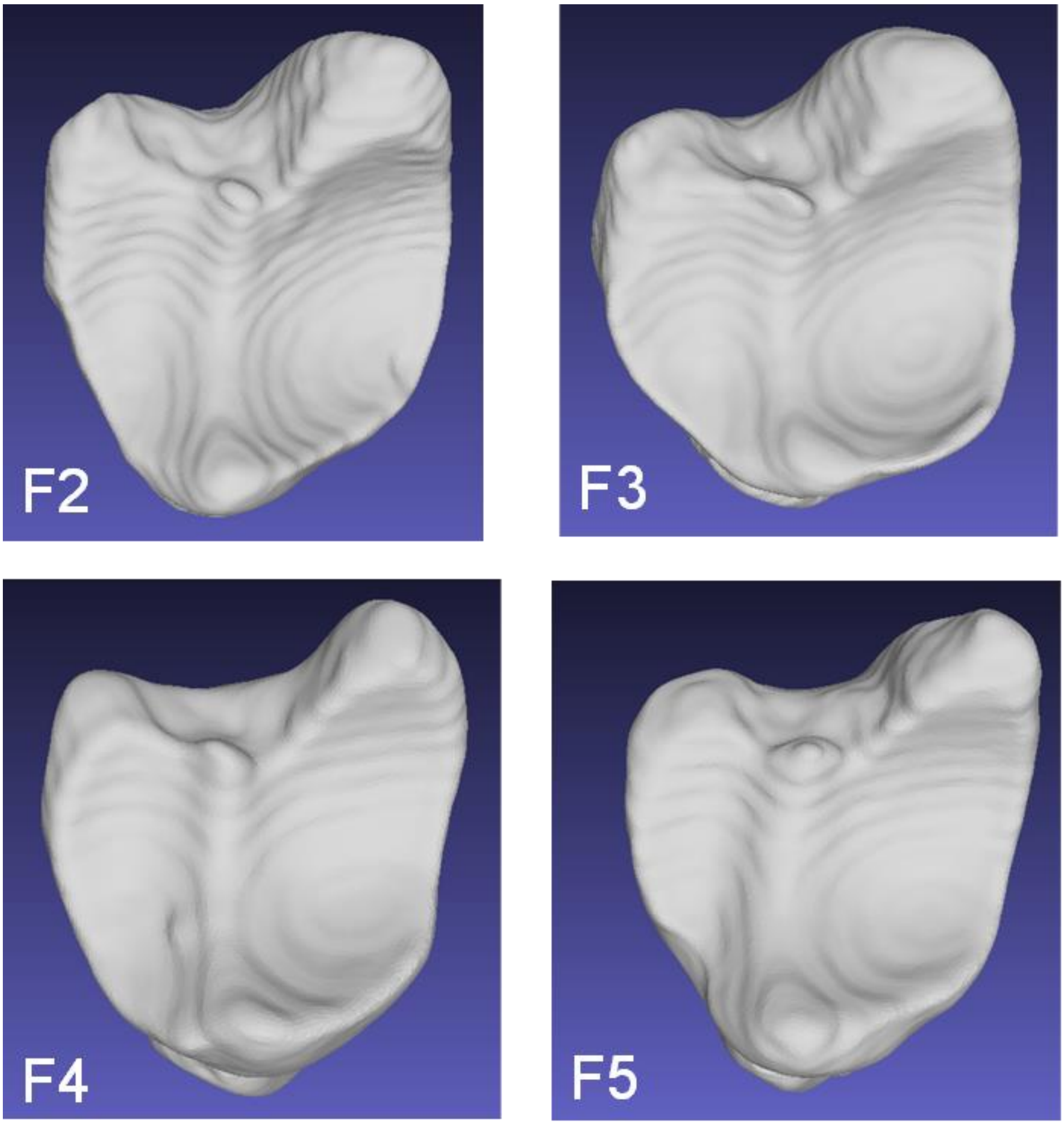


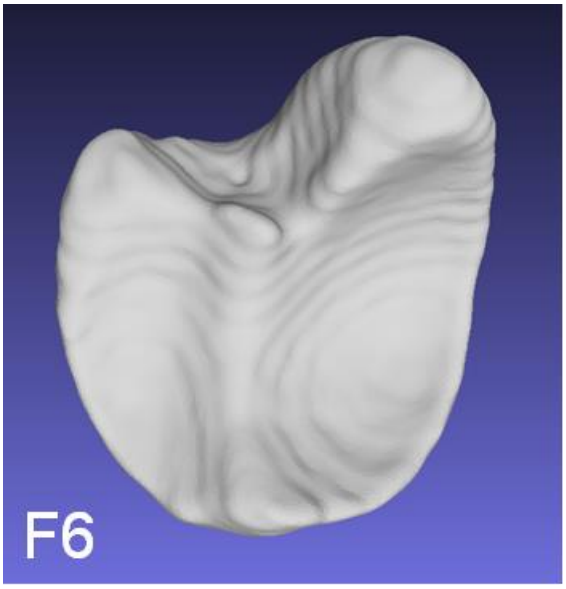






Second phalanges of *Bos taurus/Bos primigenius* from Tell Halula

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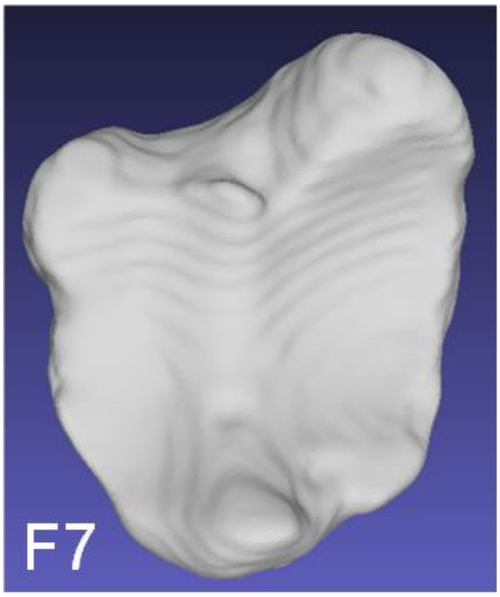
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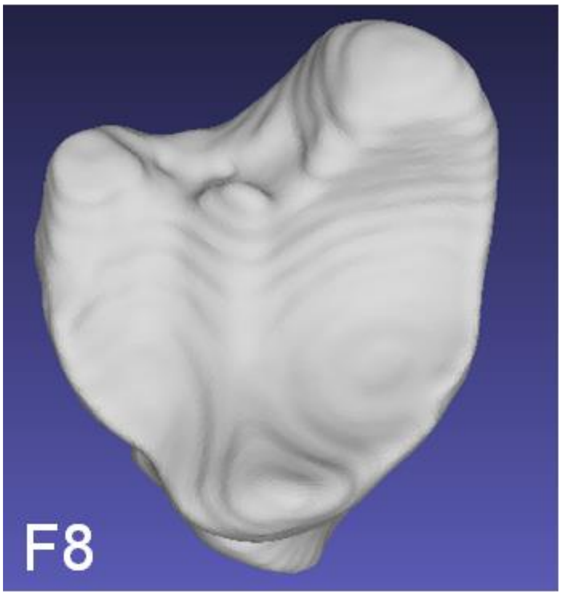
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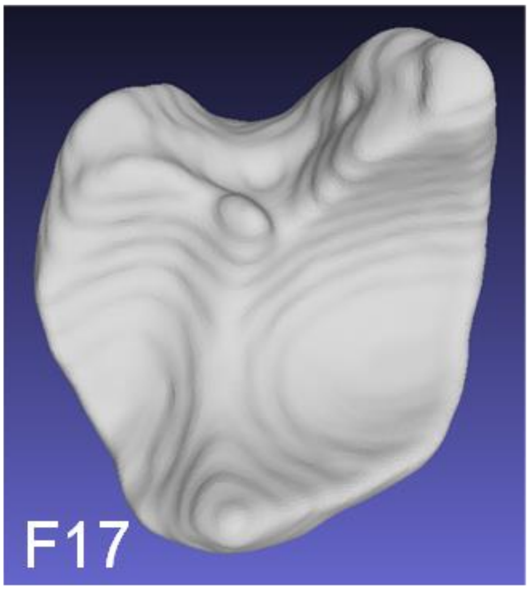
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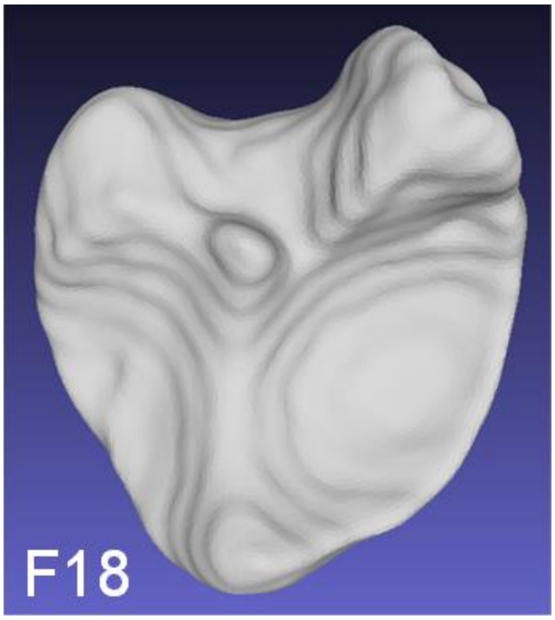
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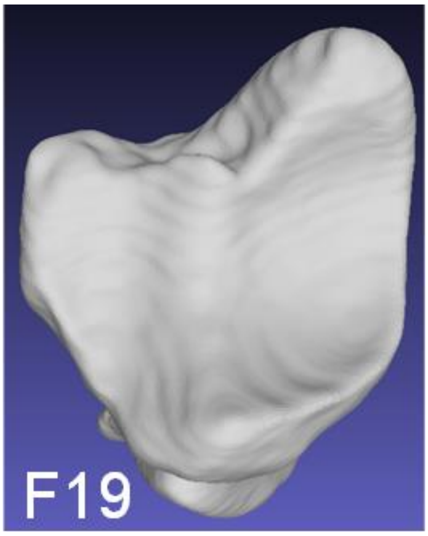
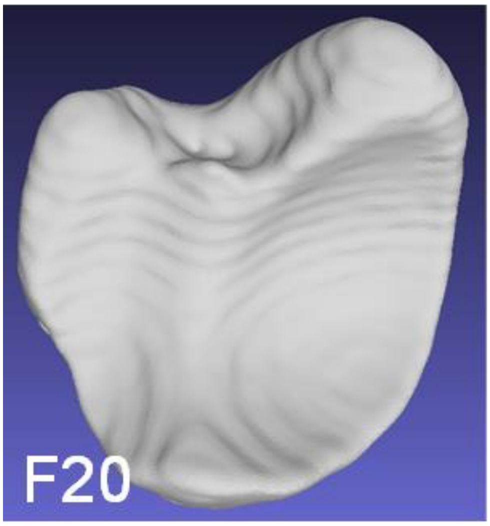

F19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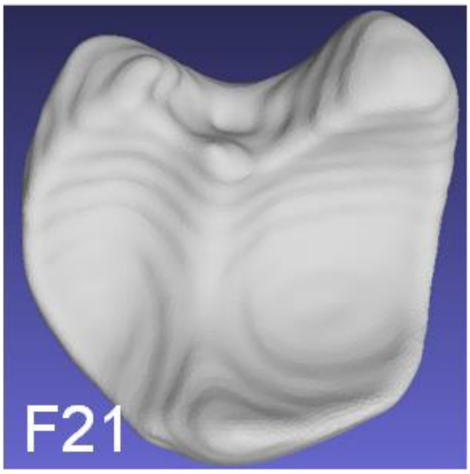
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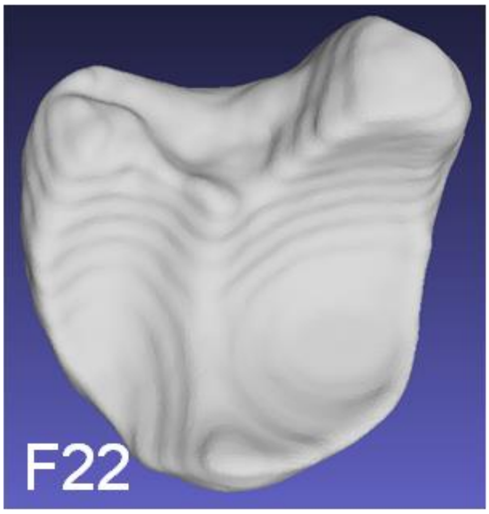
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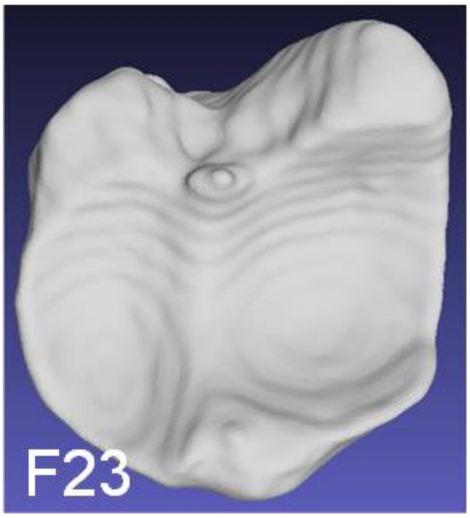
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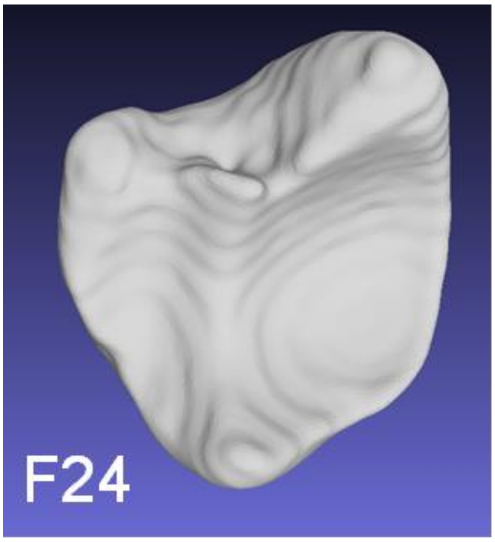
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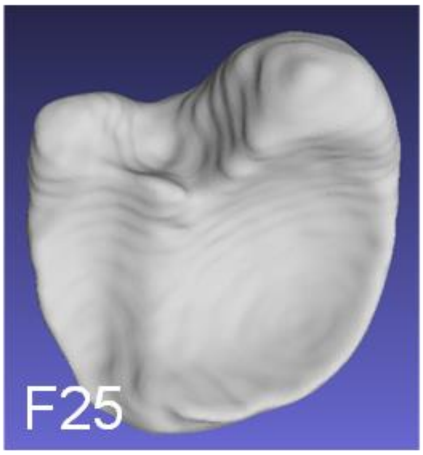
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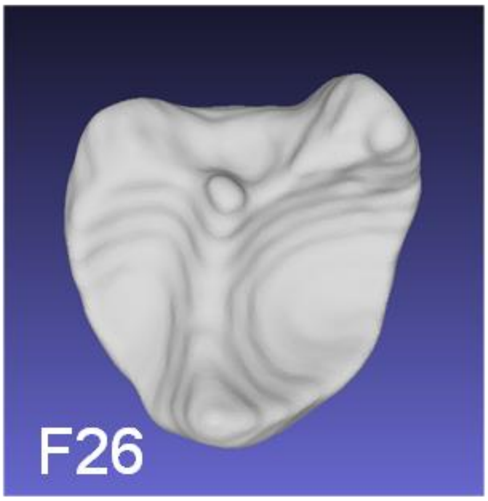
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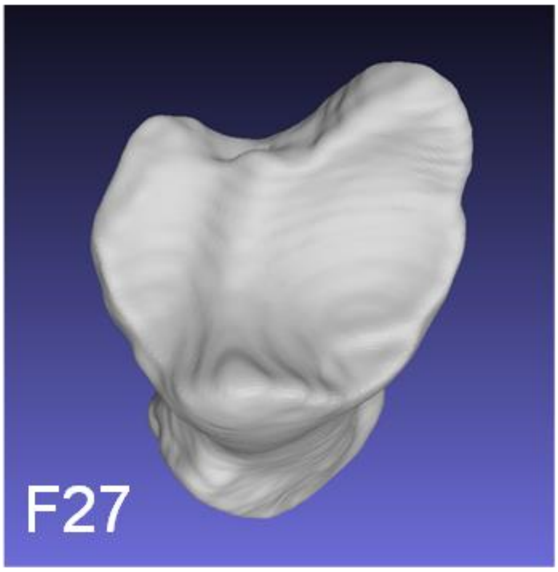
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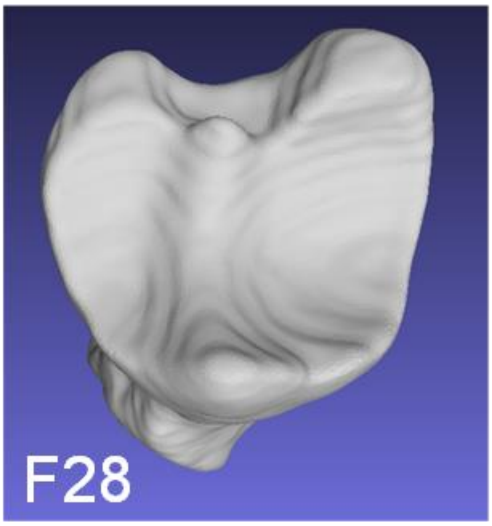
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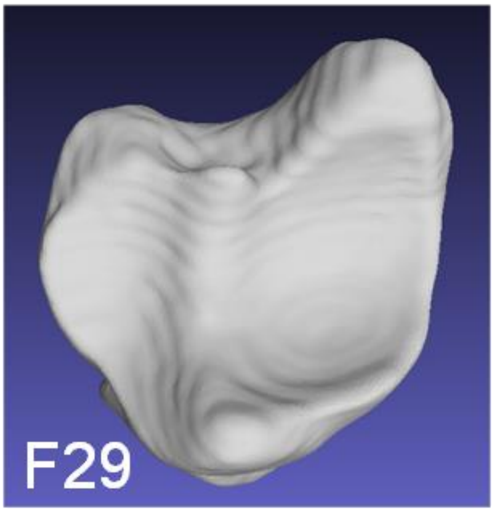
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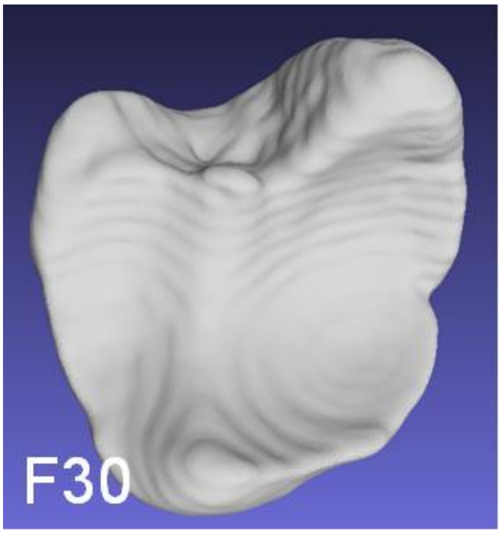
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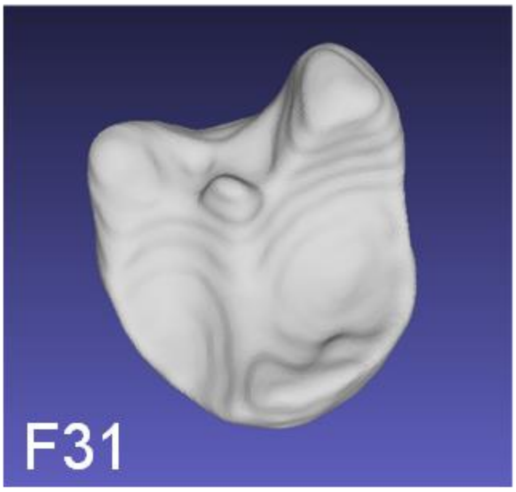
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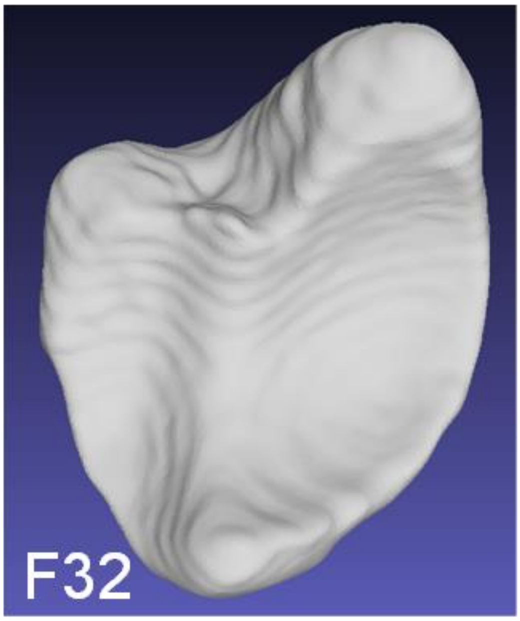
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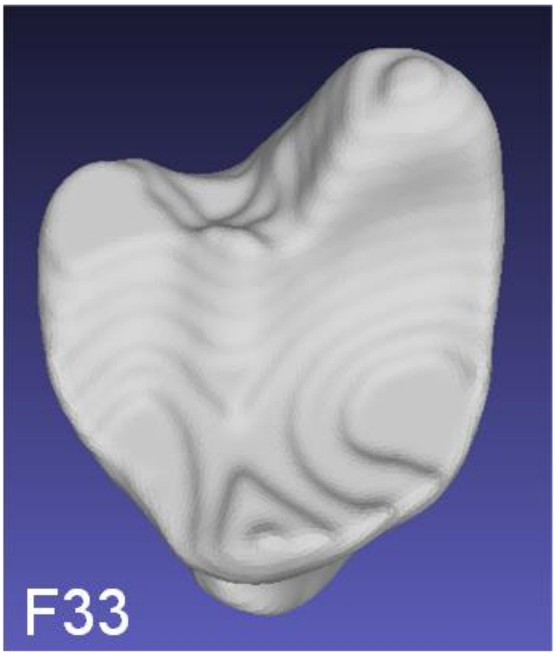
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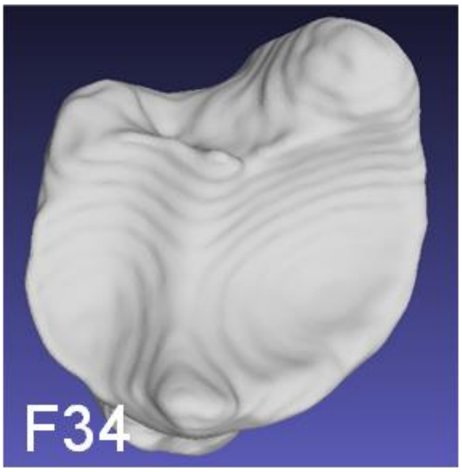
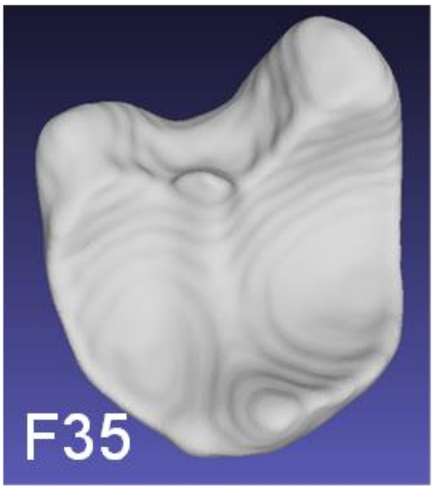

F34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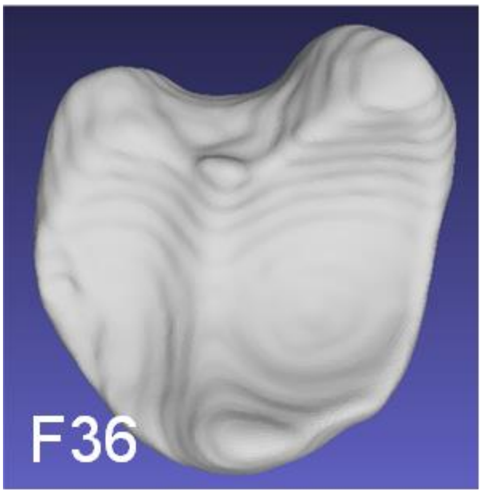
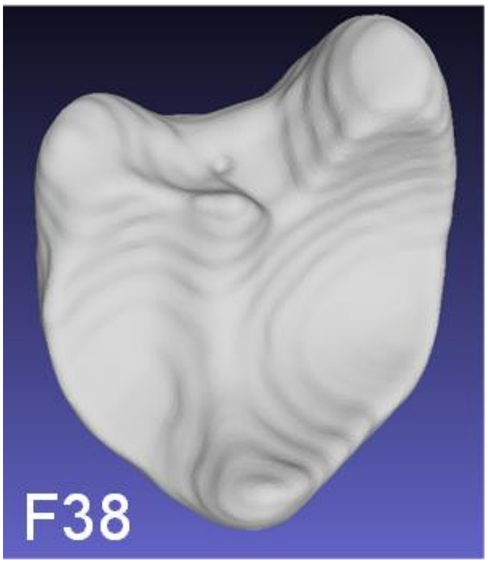
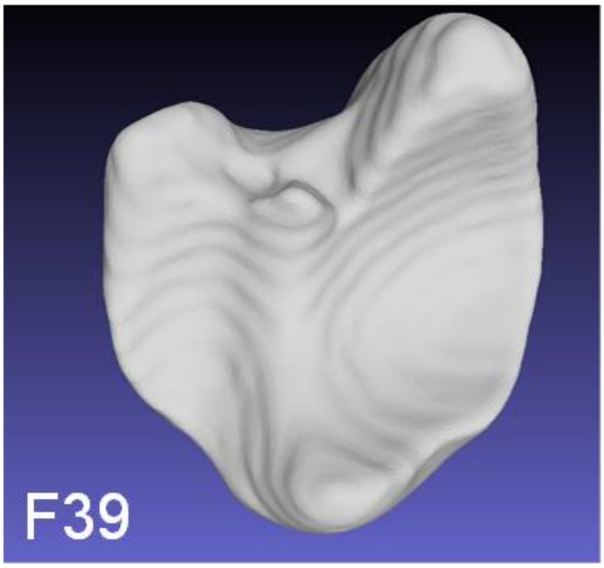


F36

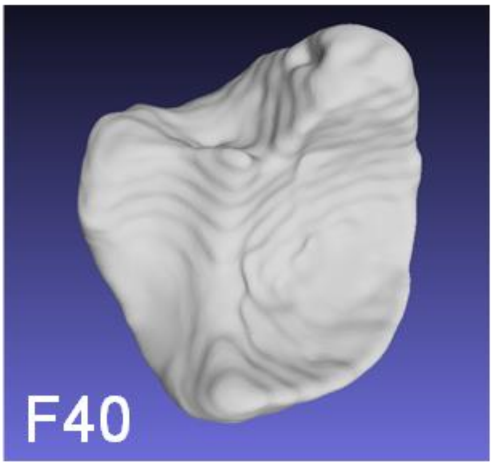
F37



F38



F39



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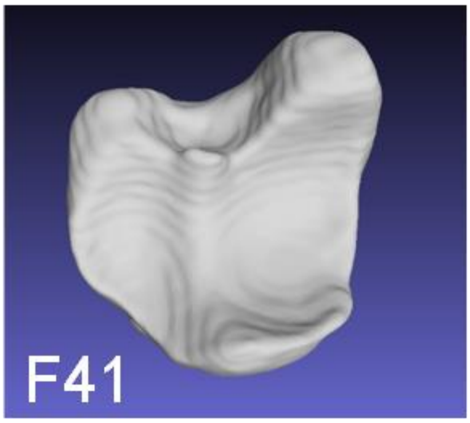
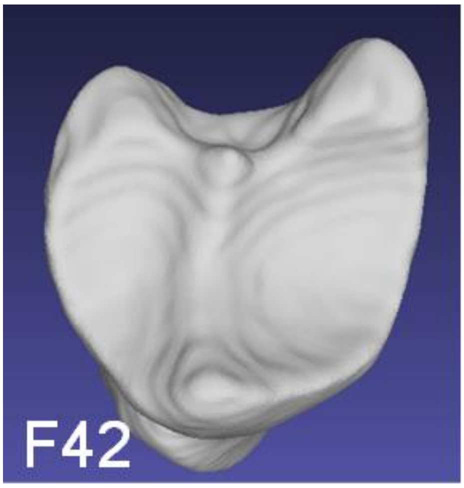
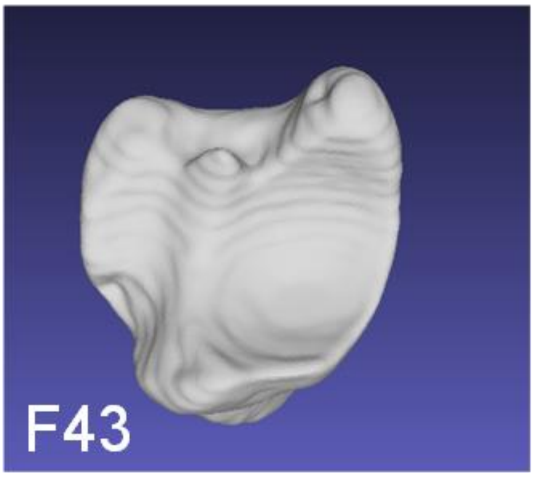


F41


F42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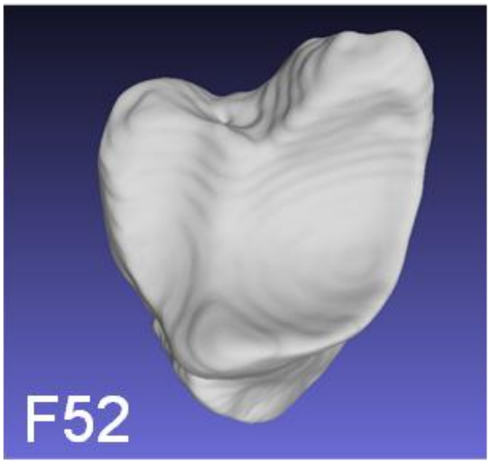
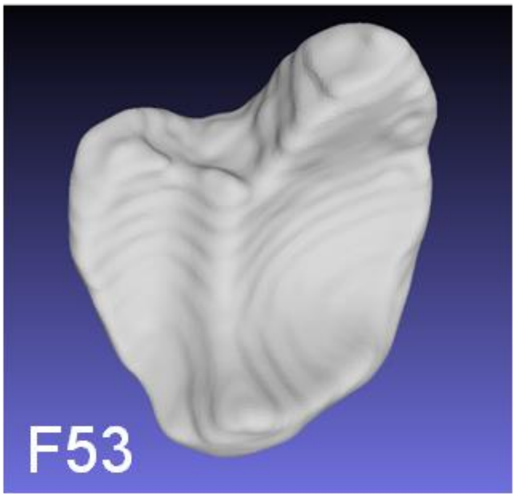
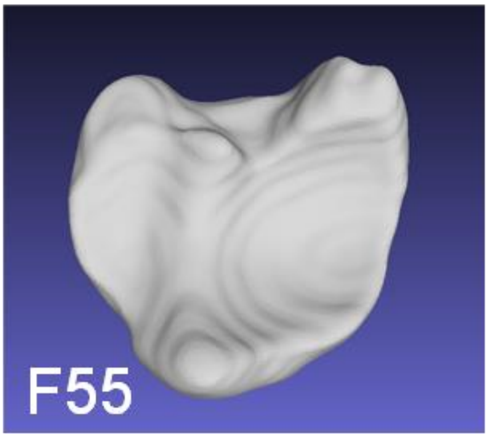
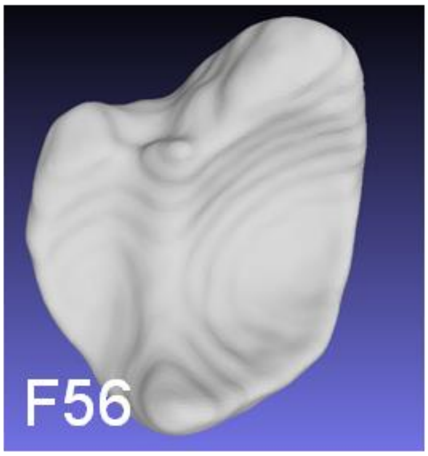
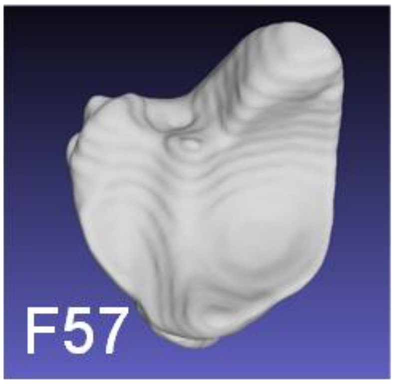
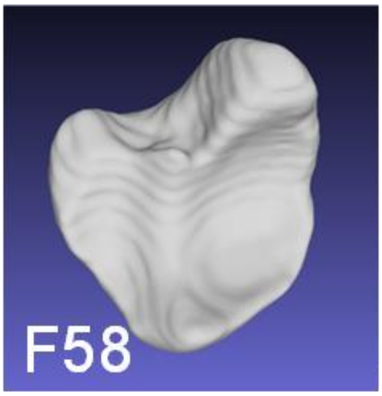

F52

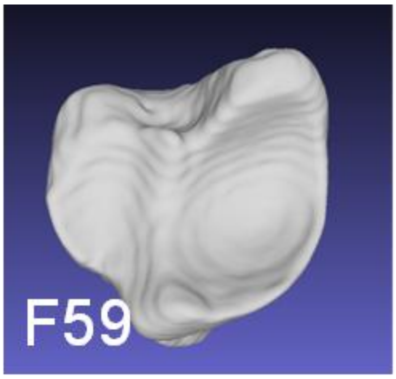

F53

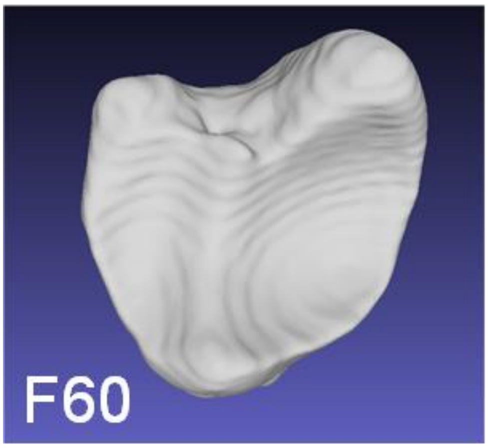

F55

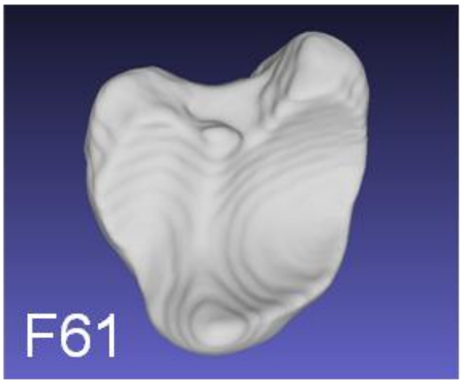

F56

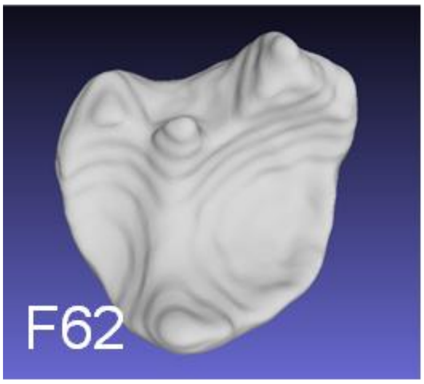

F57

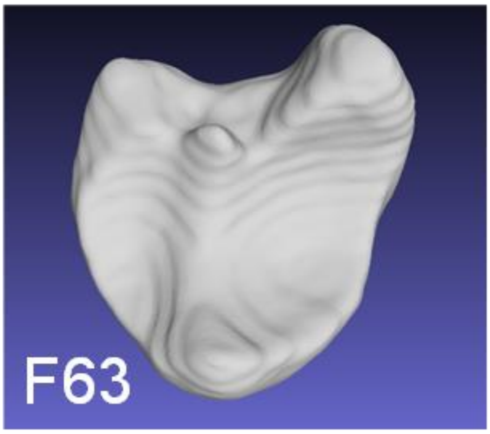

F58


F59

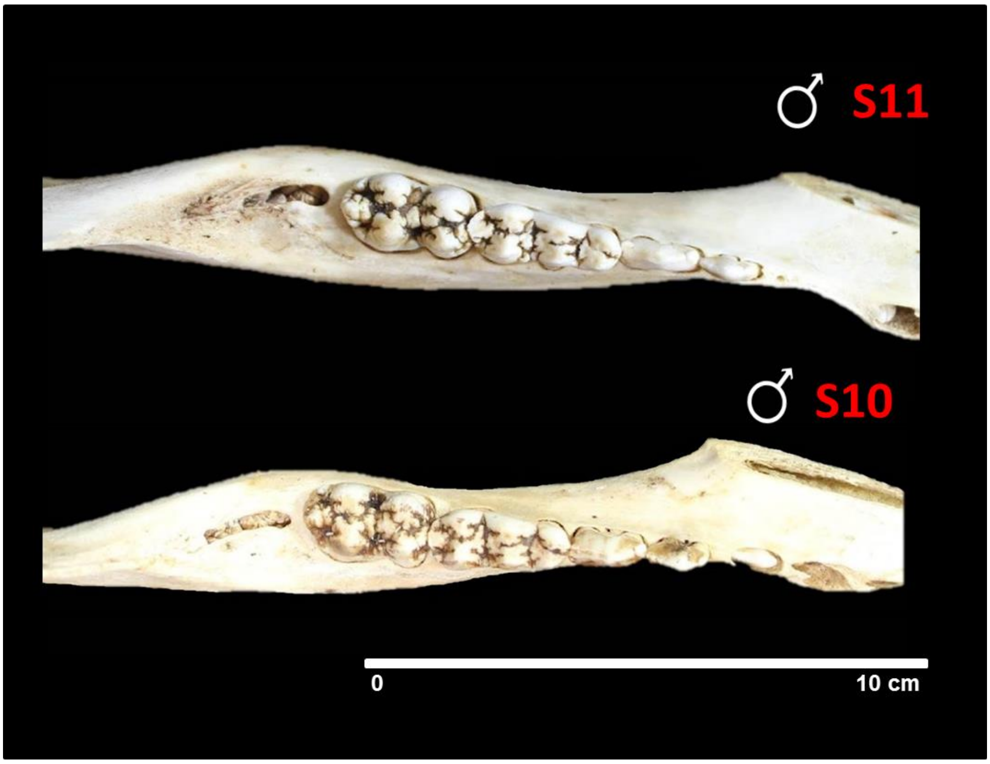

F60

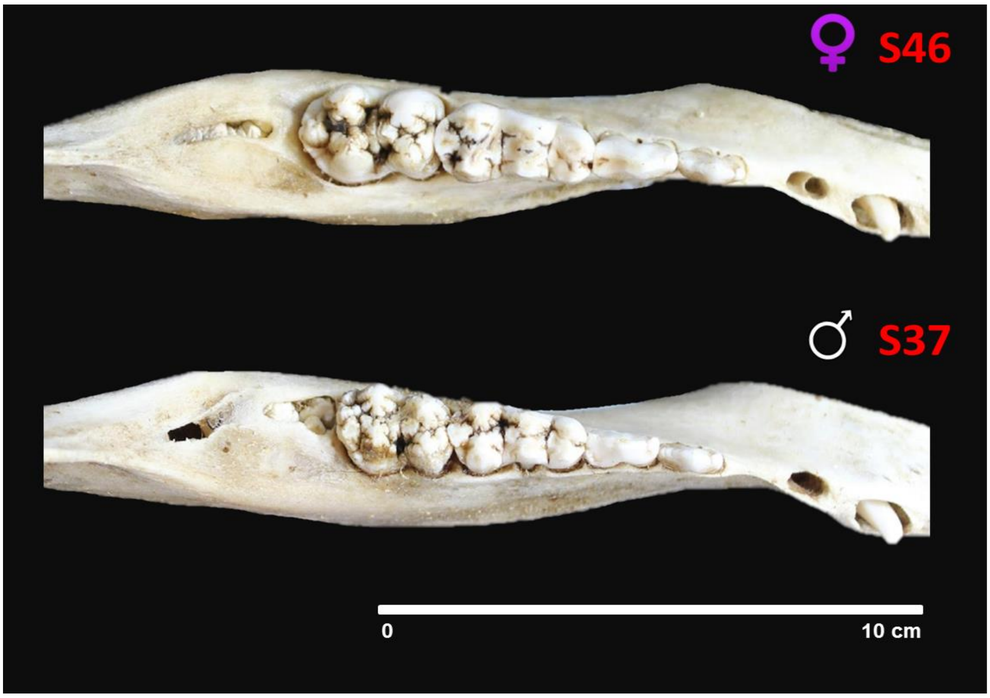

F61


F62


F63

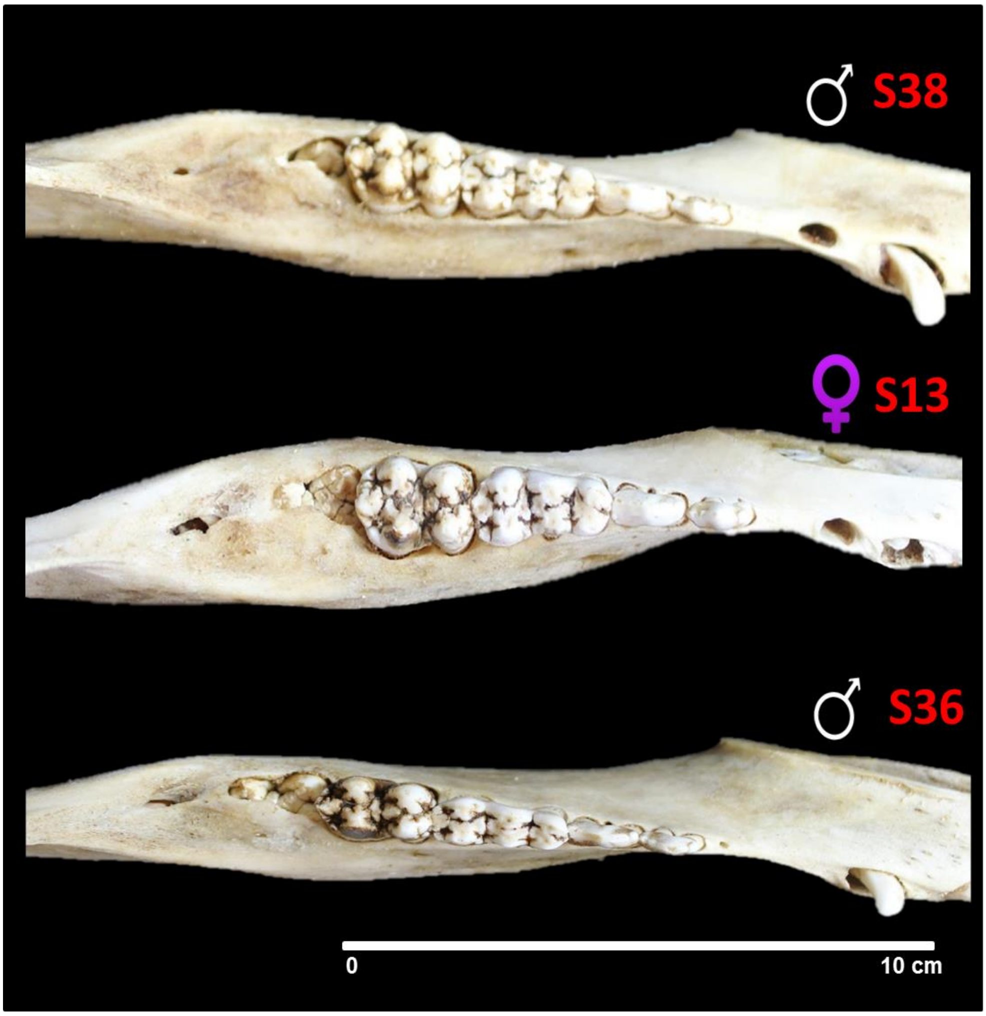
Annex II: *Sus scrofa* mandibles used in the referential ordered by age of the animals

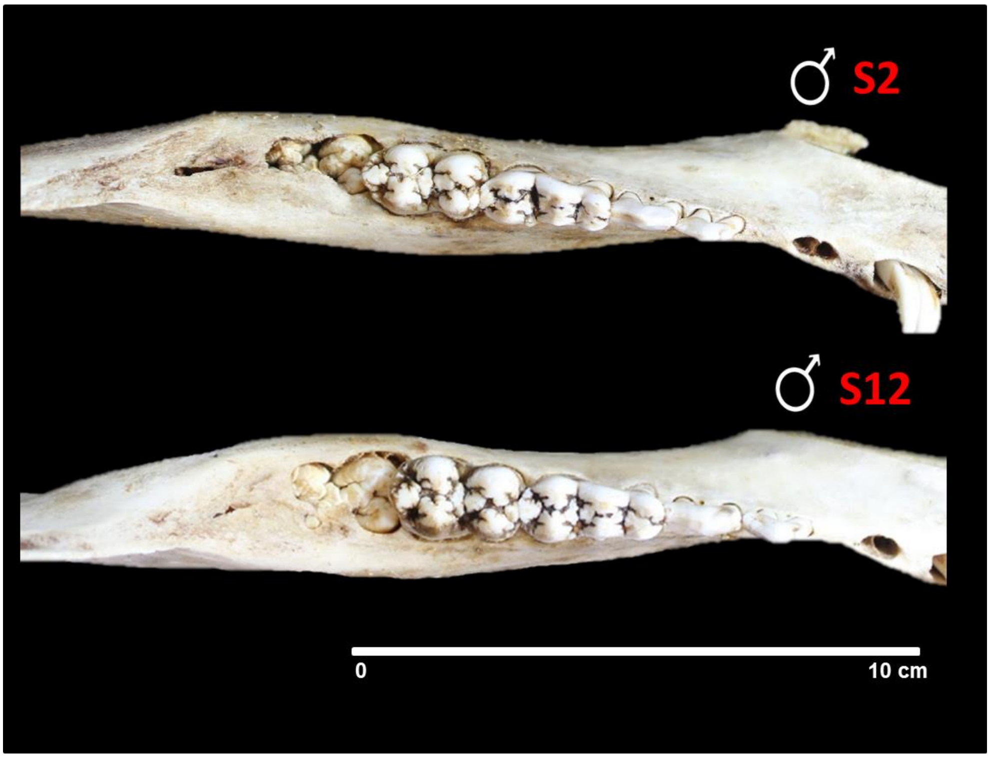

♂ S11
♂ S10
0
10 cm


♀ S46
♂ S37
0
10 cm

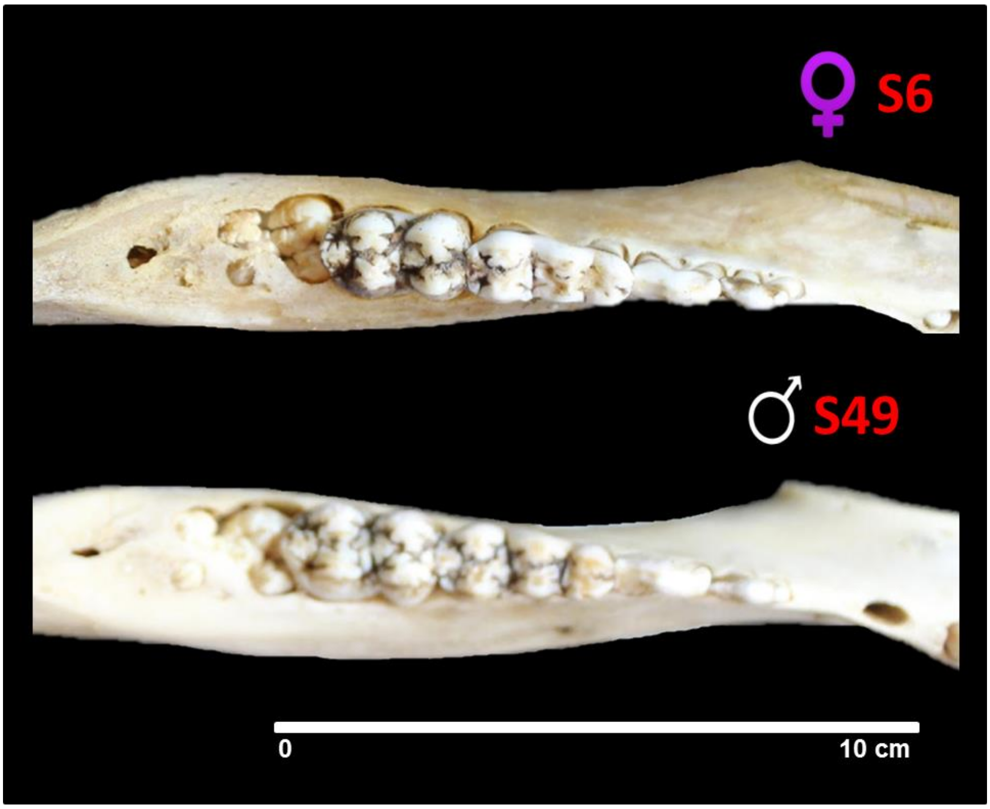

♂ S7
0
10 cm

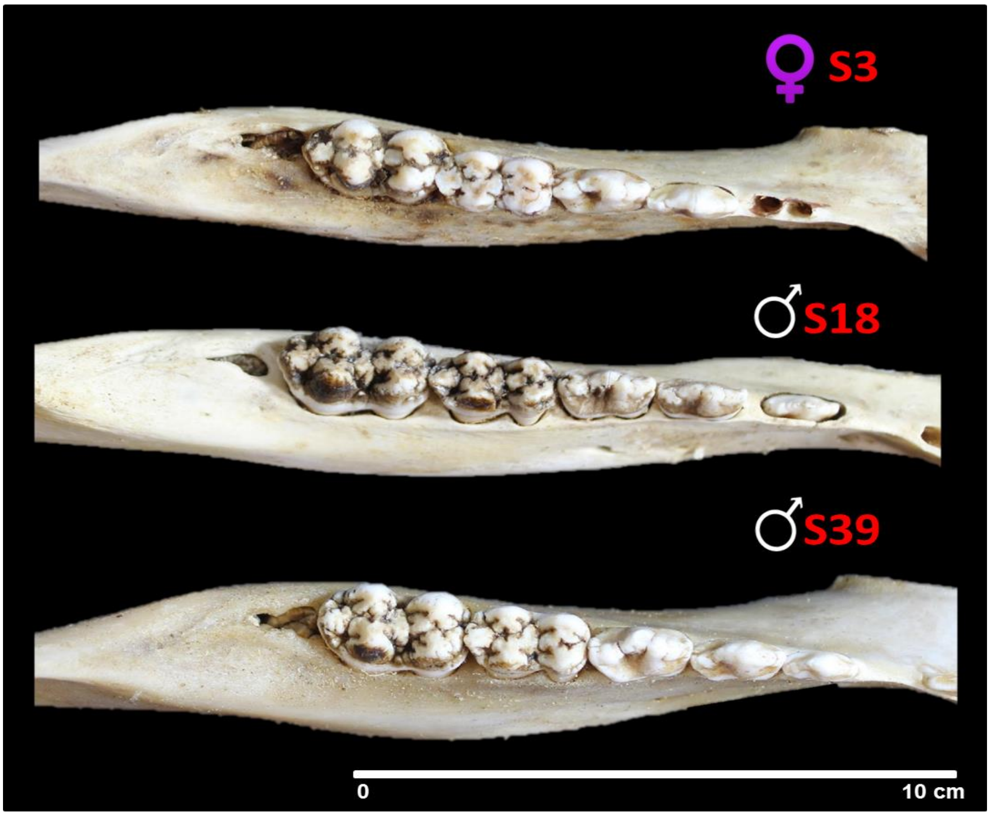

♂ S52
♀ S51
0
10 cm

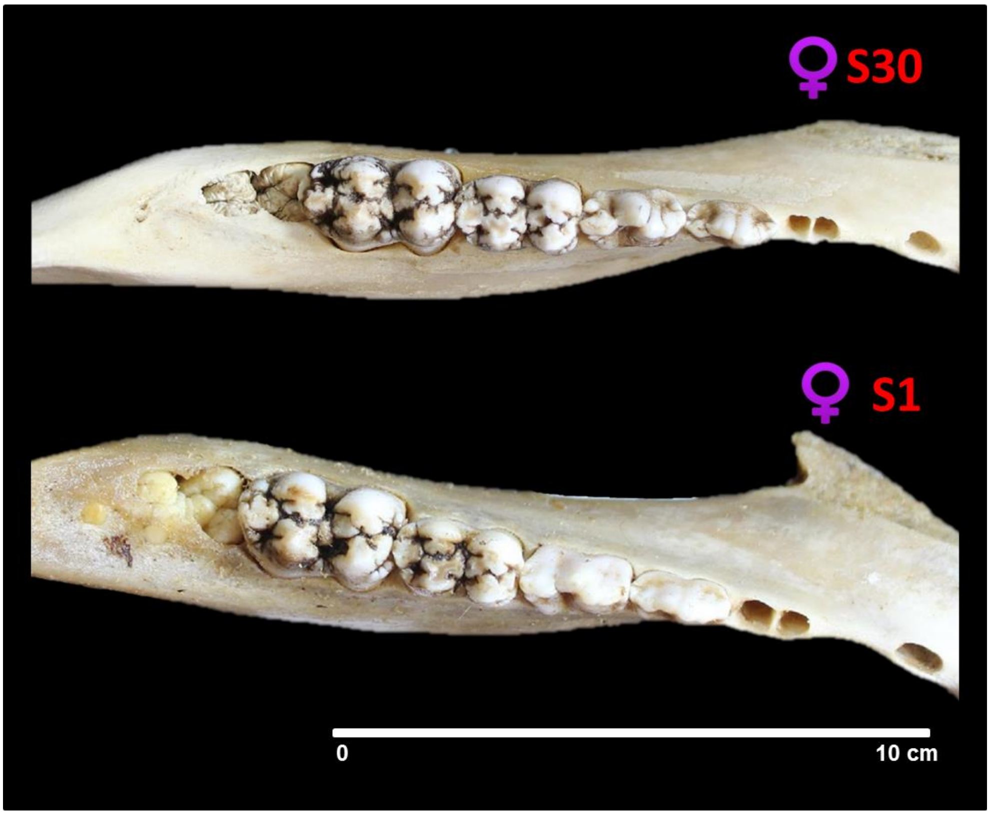

♂ S38
♀ S13
♂ S36
0
10 cm


♂ S2
♂ S12
0
10 cm


♀ S44
♂ S50
0
10 cm

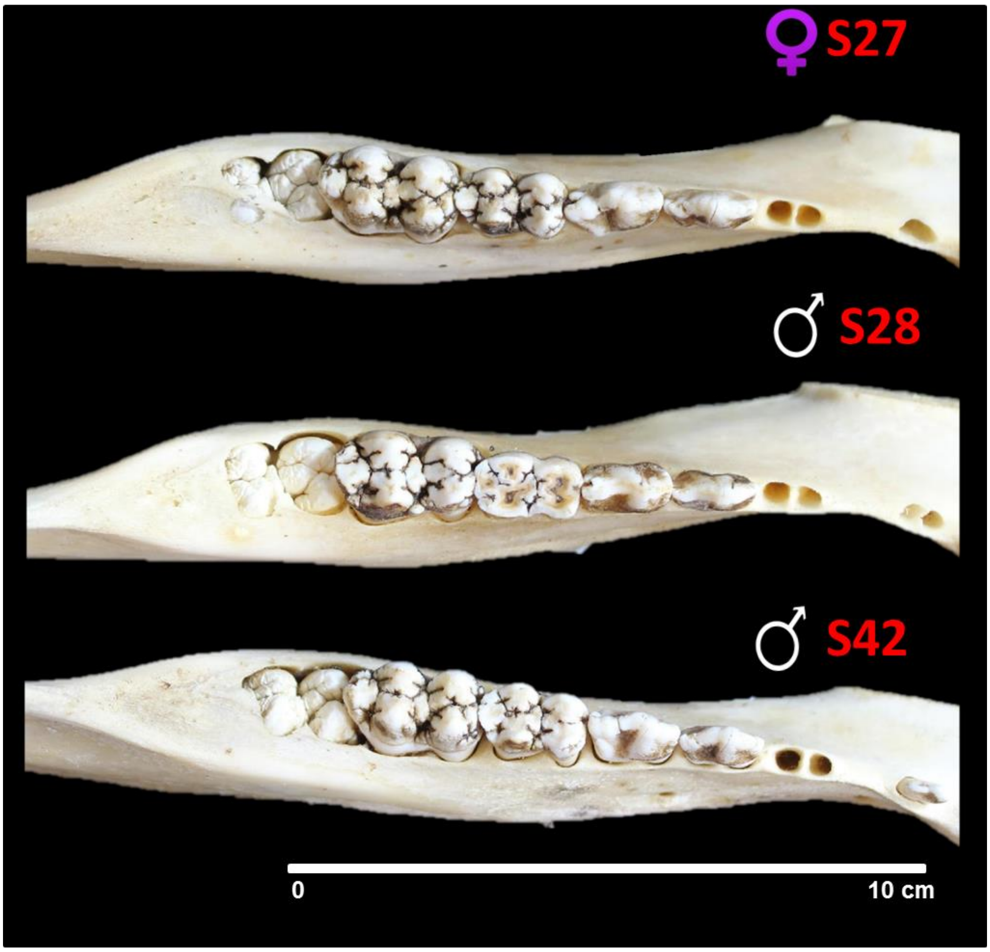

♀ S6
♂ S49
0
10 cm

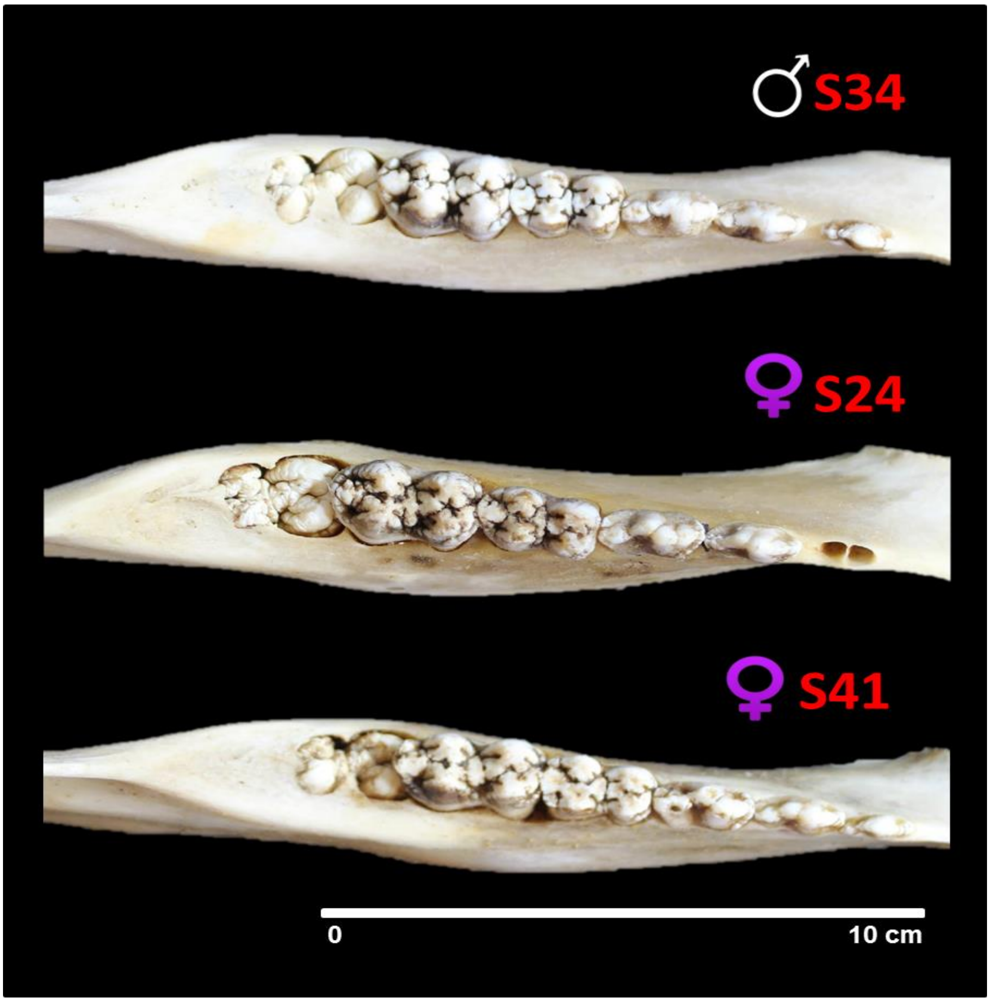

♀ S3
♂ S18
♂ S39
0
10 cm


♀ S30
♀ S1
0
10 cm


♂ S8
0
10 cm

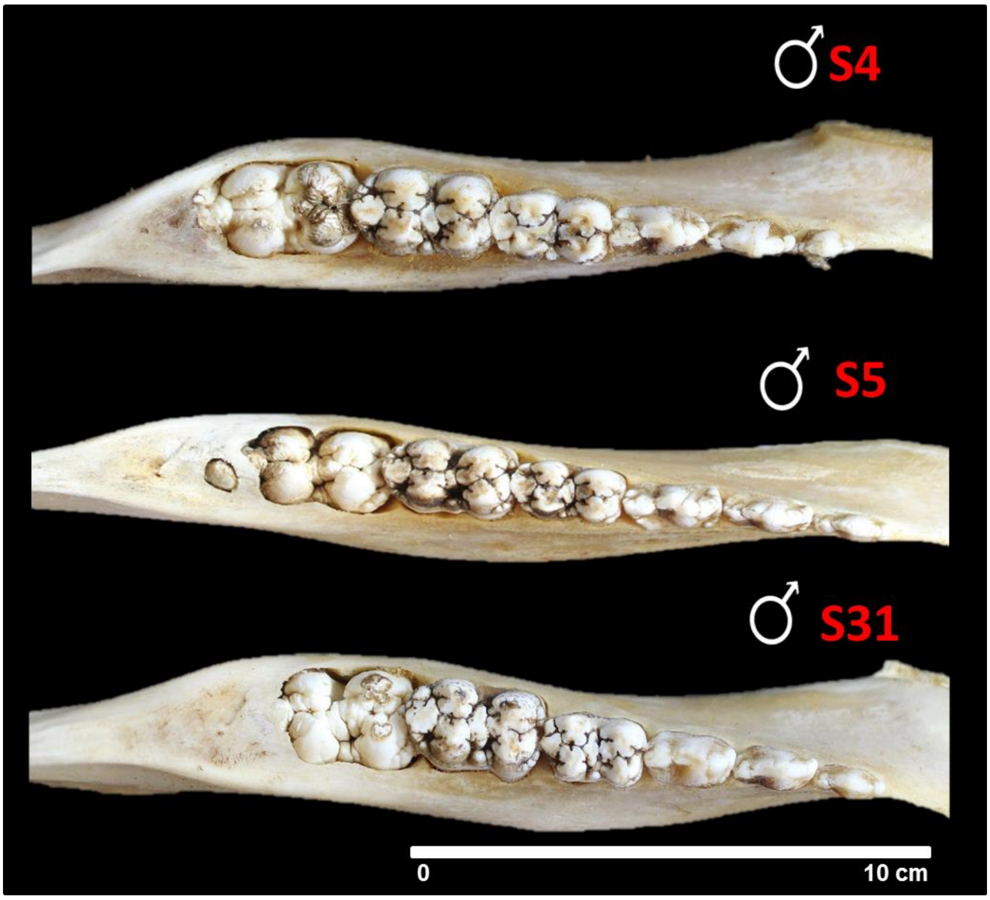

♂ S48
♀ S9
0
10 cm

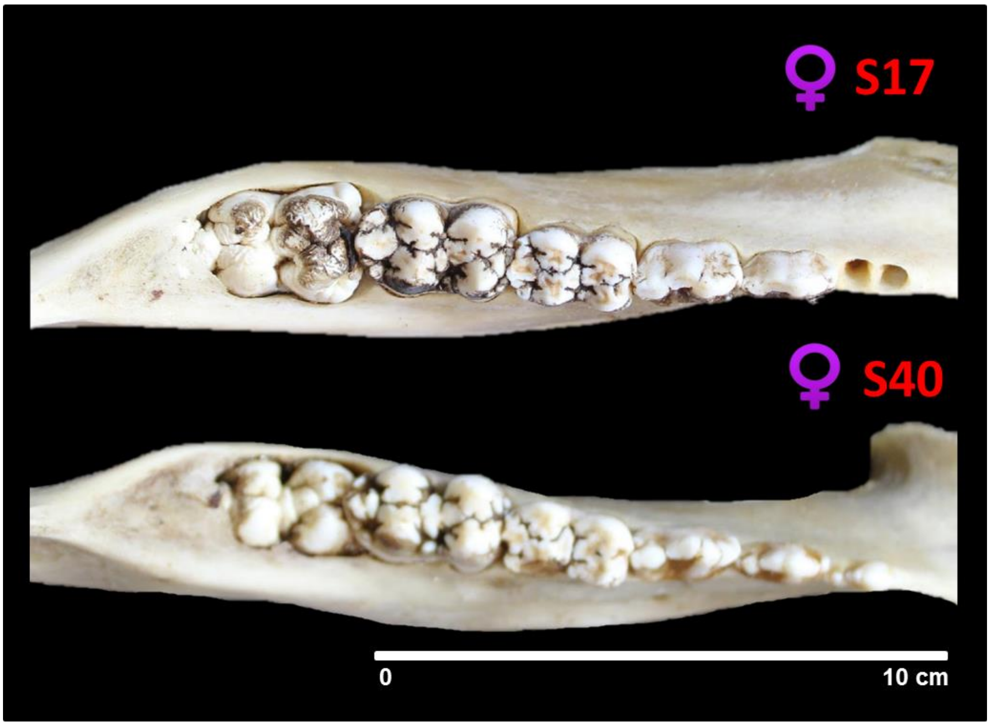

♀ S27
♂ S28
♂ S42
0
10 cm

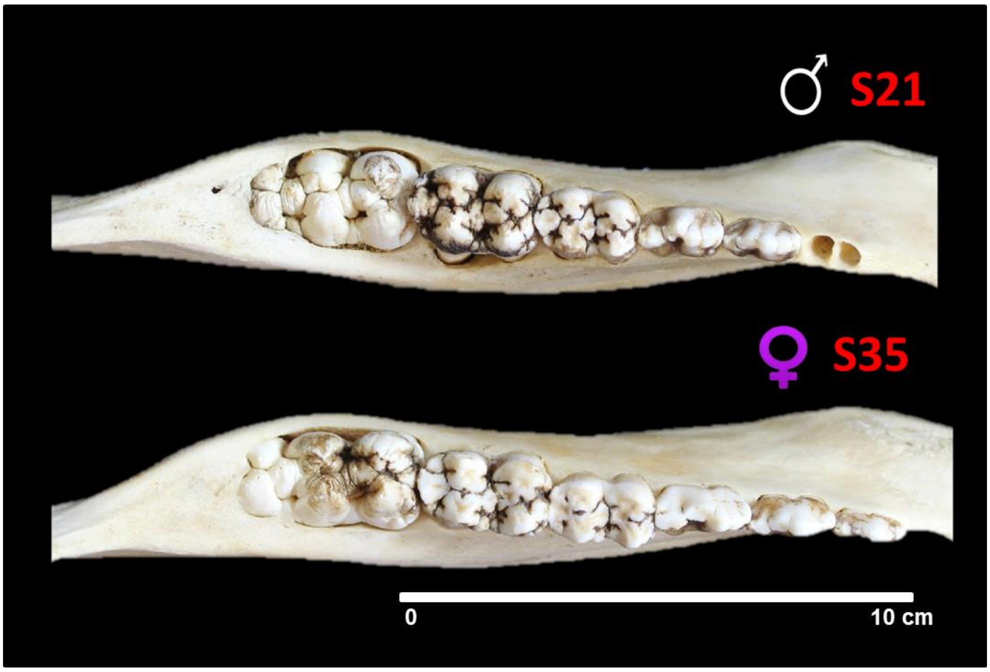

♂ S34
♀ S24
♀ S41
0
10 cm

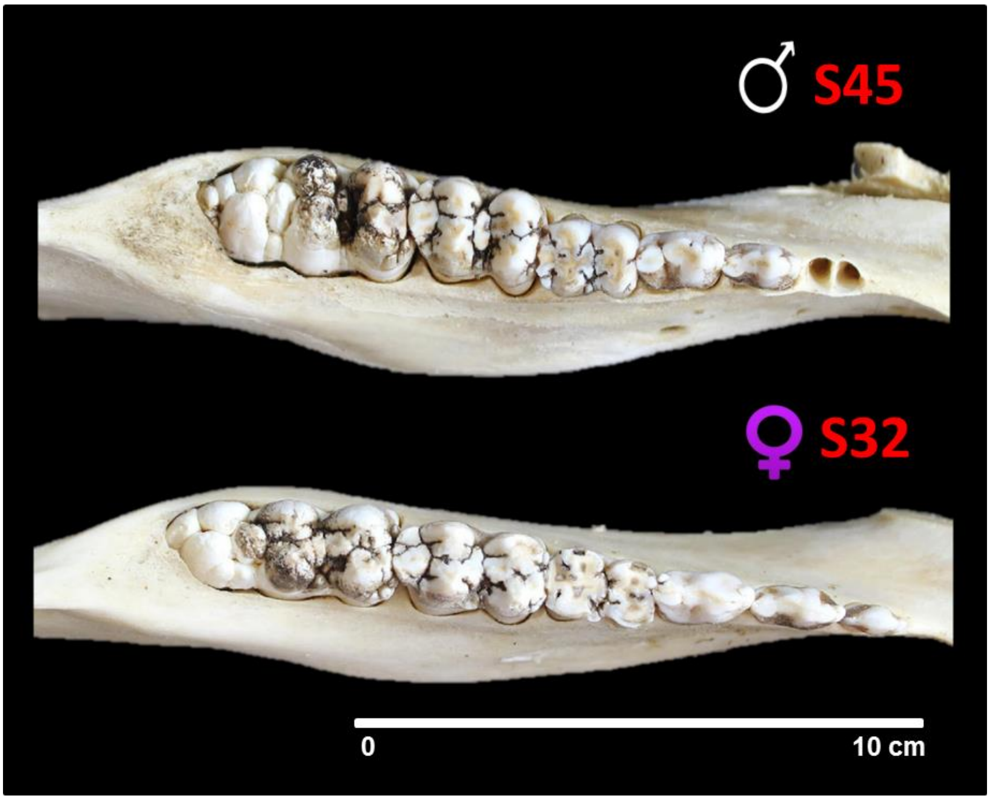

♂ S23
♂ S25
0
10 cm


♀ S15
0
10 cm

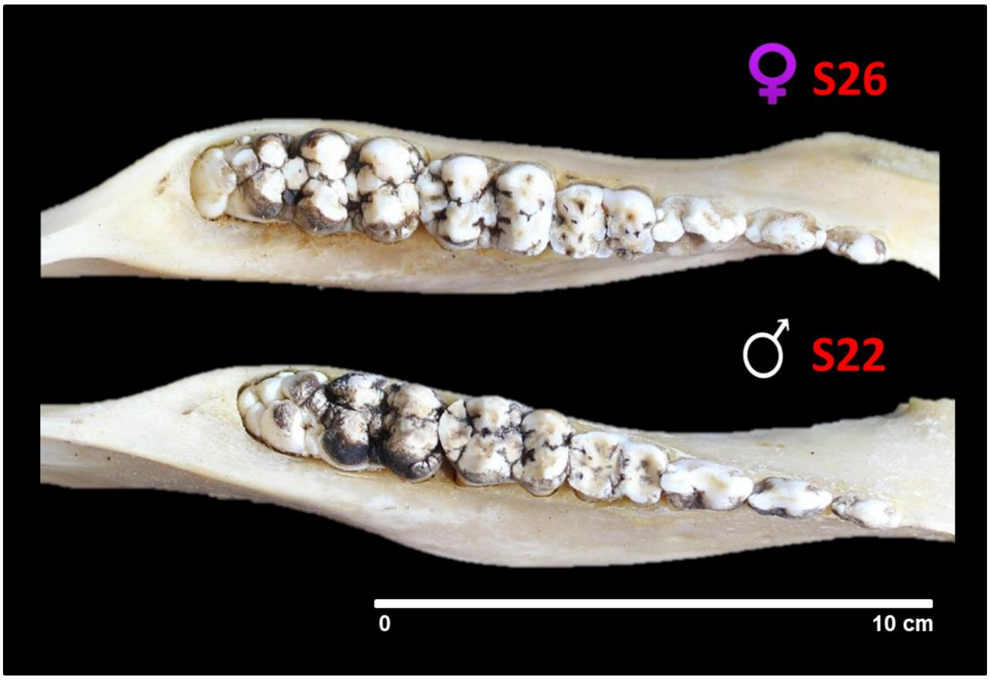

♂ S4
♂ S5
♂ S31
0
10 cm

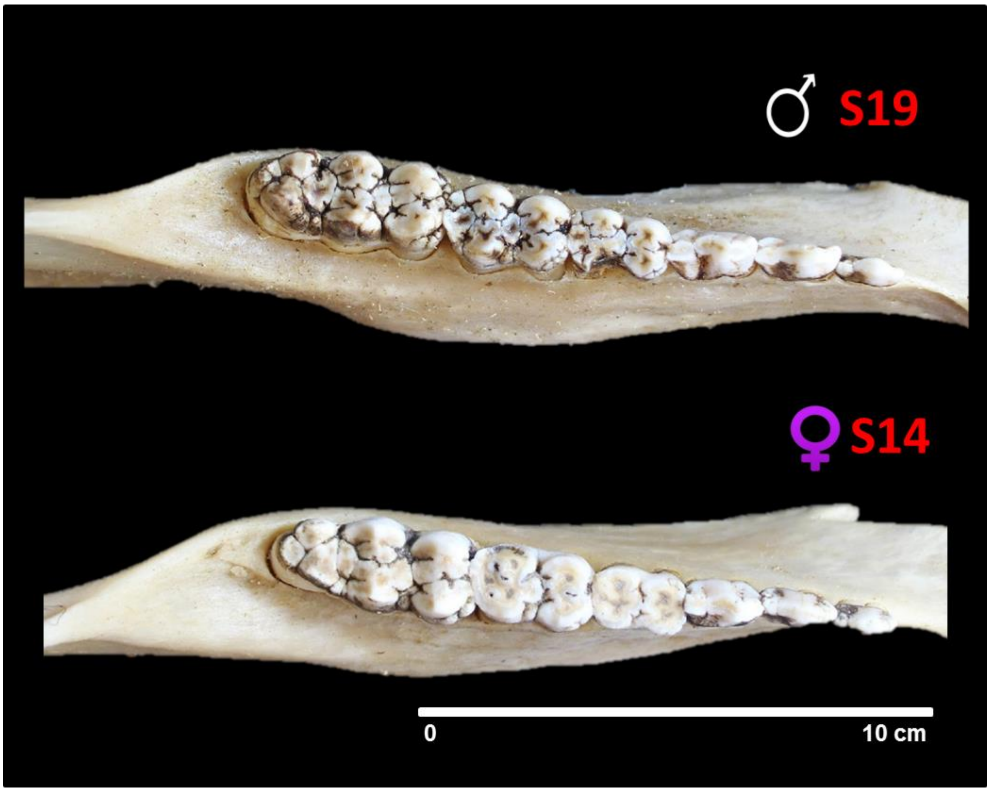

♀ S17
♀ S40
0
10 cm

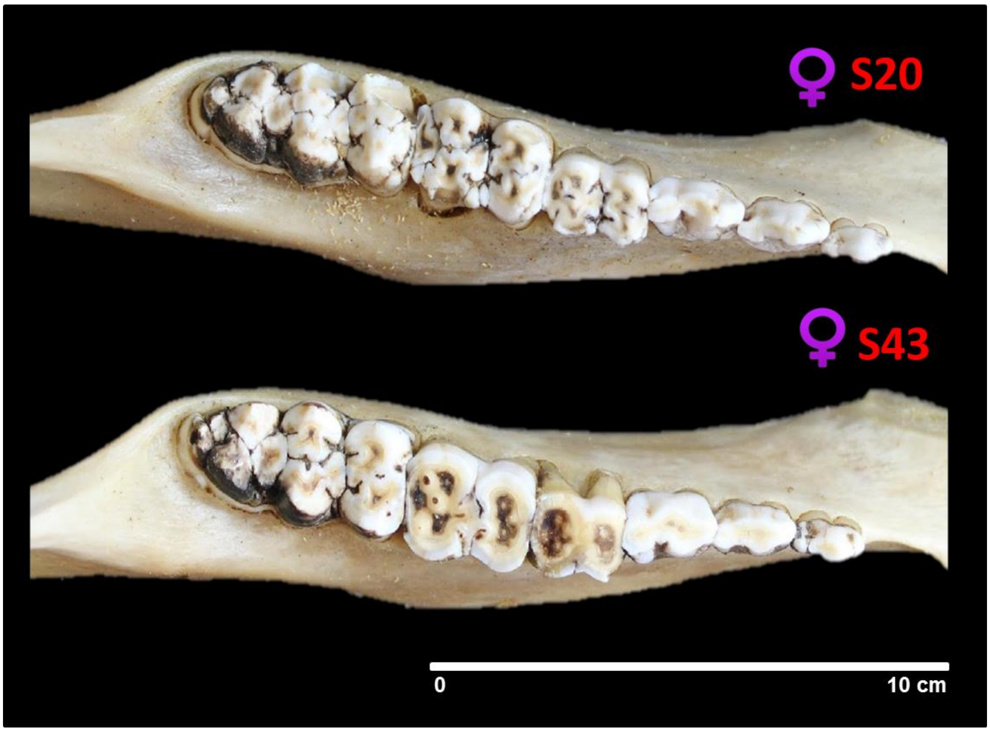

♂ S21
♀ S35
0
10 cm


♂ S45
♀ S32
0
10 cm


♀ S29
0
10 cm


♀ S26
♂ S22
0
10 cm


♂ S19
♀ S14
0
10 cm


♀ S20
♀ S43
0
10 cm

Annex III: Von den Driesch (1976) measurements of First and Second phalanges of *Bos taurus*

CODE	NAME	SITE	A/P	SPECIES	GL	SD	Bp	Bd	OP	PERIOD
HL2002_4JA11_13	TH1FA45	Tel Halula	Ant	Bos	76.45	35.45	43.1	35.06	14	LPPNB
HL2003_4IE209_b	TH1FA48	Tel Halula	Ant	Bos	72.04	32.67	38.53	31.82	11	MPPNB
TH2000_4DA6	TH1FA10	Tel Halula	Ant	Bos	73.95	32.48	39.23	35.58	8	MPPNB
HL_10	TH1FA13	Tel Halula	Post	Bos	70.73	33.26	36.85	32.32	4	MPPNB
HL2003_4H_A25_1	TH1FA11	Tel Halula	Post	Bos	67.84	25.92	31.02	27.74	12	MPPNB
HL2003_4IE209	TH1FA16	Tel Halula	Post	Bos	77.31	30.91	35.27	31.85	11	MPPNB
HL2007_4D_E198_21	TH1FA46	Tel Halula	Post	Bos	67	28.04	31.48	27.87	11	LPPNB
HL93_CALAA4CC3e22	TH1FA15	Tel Halula	Post	Bos	70.29	28.89	32.12	29.4	6	MPPNB
HL99_4DH1_16	TH1FA14	Tel Halula	Post	Bos	77.18	32.19	37.08	31.72	8	MPPNB
HL2CD3a16	TH1FA44	Tel Halula	Ant	Bos	75.14	36.0278	37.72	41.59	16	LPPNB
HL93_4BC1F	TH1FA12	Tel Halula	Post	Bos	78.91	32.3104	38.65	39.96	8	MPPNB

CODE	NAME	SITE	A/P	SPECIES	GL	SD	Bp	Bd	OP	PERIOD
D_EST3_14	LD1FA53	La Draga	Ant	Bos	63.7	26.26	30.3	25.28	-	Early Neolithic
D_L18_NE4	LD1FA50	La Draga	Ant	Bos	64.7	27.47	34.42	28.96	-	Early Neolithic
D_LL25_SE3	LD1FA52	La Draga	Ant	Bos	62.1	26.69	31.17	22.62	-	Early Neolithic
D03-JH59-2	LD1FA28	La Draga	Ant	Bos	64.4	25.79	31.32	27.89	-	Early Neolithic
D103_JF88_40	LD1FA44	La Draga	Ant	Bos	59.6	25.89	30.1	28.59	-	Early Neolithic
D95_ox22_38	LD1FA51	La Draga	Ant	Bos	59.8	27.01	31.58	26.59	-	Early Neolithic
D95-B20-34	LD1FA29	La Draga	Ant	Bos	68.2	30.6	35.36	32.71	-	Early Neolithic
D97_3682_13	LD1FA54	La Draga	Ant	Bos	63.4	26.13	30.78	26.79	-	Early Neolithic
D97_5G84_6	LD1FA35	La Draga	Ant	Bos	62.2	25.82	32	27.08	-	Early Neolithic
D97_JD84_19	LD1FA47	La Draga	Ant	Bos	58	25.18	31.06	26.26	-	Early Neolithic
D98_JF84_14	LD1FA40	La Draga	Ant	Bos	61.6	25.52	29.49	25.93	-	Early Neolithic
LD_ST23	LD1FA36	La Draga	Ant	Bos	65.9	25.28	28.59	27.16	-	Early Neolithic
LD91_ES61_1	LD1FA43	La Draga	Ant	Bos	64.7	25.57	30.21	26.44	-	Early Neolithic
D_2097	LD1FA37	La Draga	Post	Bos	68.5	21.65	27.62	23.71	-	Early Neolithic
D02_KA_90_4	LD1FA41	La Draga	Post	Bos	57.6	22.4	26.93	24.8	-	Early Neolithic
D02_KA91_8	LD1FA42	La Draga	Post	Bos	74.2	24.93	29.77	27.38	-	Early Neolithic
D03_JG88_4	LD1FA39	La Draga	Post	Bos	59	23.64	28.46	24.4	-	Early Neolithic
D03_JH88_2	LD1FA55	La Draga	Post	Bos	63.9	23.33	28.95	24.85	-	Early Neolithic
D15_110041_1535	LD1FA34	La Draga	Post	Bos	64.5	20.77	26.92	23.76	-	Early Neolithic
D15_261_1_12019	LD1FA48	La Draga	Post	Bos	71.7	24.9	31.49	28.27	-	Early Neolithic
D15_261_2_12145	LD1FA49	La Draga	Post	Bos	63.5	22.18	25.25	23.46	-	Early Neolithic
D95_092111	LD1FA38	La Draga	Post	Bos	63.3	25.03	31.33	27.76	-	Early Neolithic
D95_C20_98	LD1FA56	La Draga	Post	Bos	67	23.27	26.81	23.27	-	Early Neolithic
D97_5A82_2	LD1FA46	La Draga	Post	Bos	65.2	23.28	28.15	24.54	-	Early Neolithic
D97_JEE83_6	LD1FA45	La Draga	Post	Bos	69.7	23.46	28.51	25.37	-	Early Neolithic

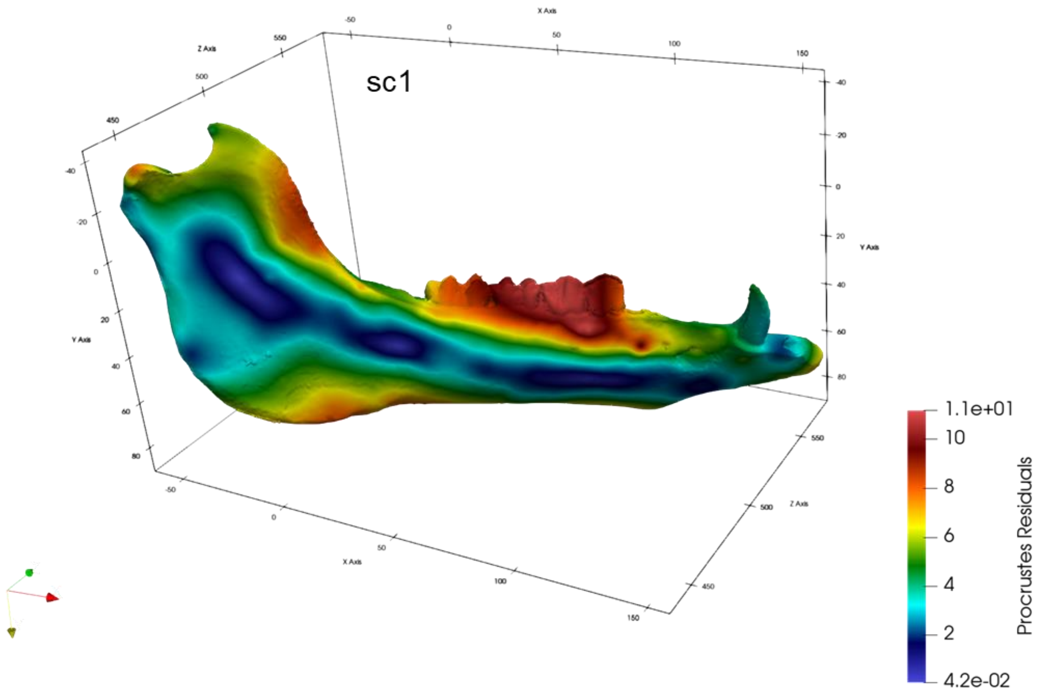
CODE	NAME	SITE	A/P	SPECIES	GL	SD	Bp	Bd	OP	PERIOD
PX_17	PX1FA10	Pixarelles	Ant	Bos	57.47	24.56	29.87	26.72	-	Middle Neolithic
PX_25	PX1FA16	Pixarelles	Ant	Bos	60.54	26.75	32.11	29.21	-	Middle Neolithic
PX_27	PX1FA17	Pixarelles	Ant	Bos	55.96	23.55	27.41	25.8	-	Middle Neolithic
PX_35	PX1FA18	Pixarelles	Ant	Bos	57.79	35.59	37.1	32.99	-	Middle Neolithic
PX_16	PX1FA9	Pixarelles	Post	Bos	59.96	24.83	30.13	28.44	-	Middle Neolithic
PX_19	PX1FA11	Pixarelles	Post	Bos	59.79	26.69	29.66	25.29	-	Middle Neolithic
PX_20	PX1FA12	Pixarelles	Post	Bos	58.83	24.79	28.25	25.62	-	Middle Neolithic
PX_22	PX1FA13	Pixarelles	Post	Bos	58.19	22.01	26.24	24.04	-	Middle Neolithic
PX_23	PX1FA14	Pixarelles	Post	Bos	55.05	20.84	25.54	22.35	-	Middle Neolithic
PX_24	PX1FA15	Pixarelles	Post	Bos	58.44	24.34	27.25	26.28	-	Middle Neolithic

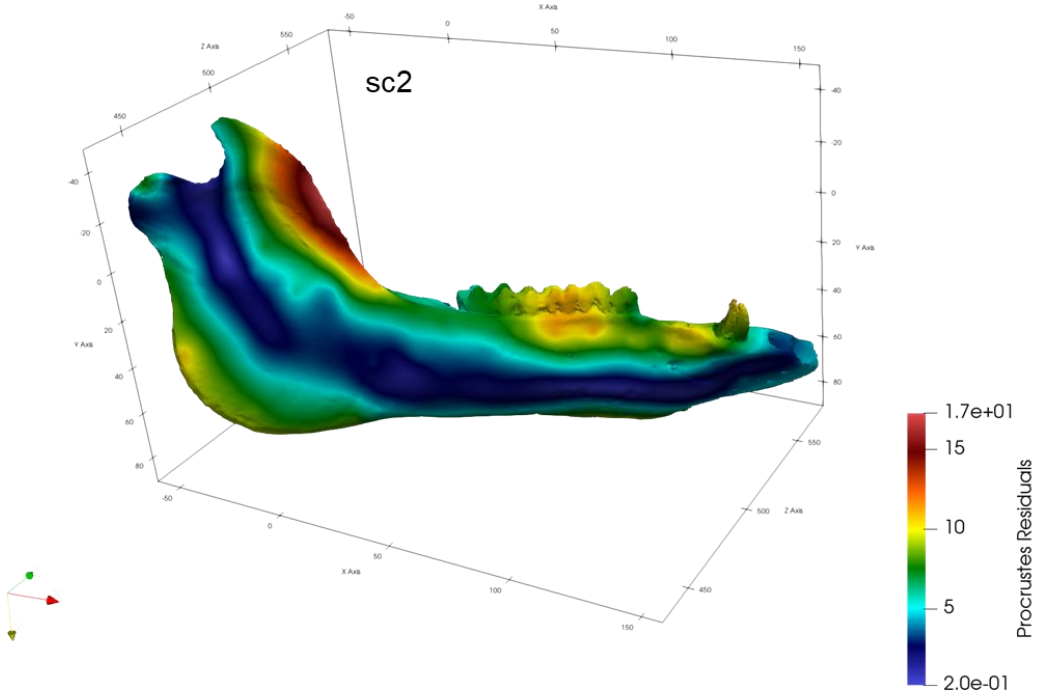
CODE	NAME	SITE	A/P	SPECIES	GL	SD	Bp	Bd	OP	PERIOD
D15_2_261_212196	LD2FA1	La Draga	Post	Bos	41.7	28.58	23.15	21.6	-	Early Neolithic
D15_2_2002_11962	LD2FA10	La Draga	Post	Bos	42.18	28.58	23.42	22.07	-	Early Neolithic
D15_2_2002_11959	LD2FA11	La Draga	Post	Bos	41.99	26.82	22.09	19.98	-	Early Neolithic
D95_0Z_21_18	LD2FA12	La Draga	Post	Bos	43.51	27.84	22.76	21.64	-	Early Neolithic
D10_403	LD2FA13	La Draga	Ant	Bos	41.6	31.28	27.74	25.78	-	Early Neolithic
D15_2_2002_11881	LD2FA14	La Draga	Post	Bos	45.08	30.03	25.63	23.99	-	Early Neolithic
D97_JD8227	LD2FA15	La Draga	Post	Bos	42.02	28.38	23.58	21.49	-	Early Neolithic
D14_1146_81_1	LD2FA16	La Draga	Post	Bos	46.39	32.3	27.25	26.43	-	Early Neolithic
D95_DZ22_2_5	LD2FA17	La Draga	Post	Bos	42.38	26.47	22.95	21.6	-	Early Neolithic
D13_NETJC4_336	LD2FA18	La Draga	Ant	Bos	42.6	28.61	24.82	22.7	-	Early Neolithic
LD97_JE_83_21	LD2FA19	La Draga	Ant	Bos	44.77	32.65	27.26	26.57	-	Early Neolithic
DH24_2J	LD2FA2	La Draga	Post	Bos	41.17	26.9	22.08	20.19	-	Early Neolithic
D13_6541	LD2FA20	La Draga	Ant	Bos	38.37	27.82	24.3	22.69	-	Early Neolithic
D13_JB40_6276	LD2FA21	La Draga	Ant	Bos	41.37	29.49	25.87	23.73	-	Early Neolithic
D13_4_Dr20	LD2FA22	La Draga	Ant	Bos	46.93	35.43	31.34	28.3	-	Early Neolithic
LD	LD2FA23	La Draga	Ant	Bos	41.77	29.6	25.42	23	-	Early Neolithic
D04_JG_92_8	LD2FA24	La Draga	Ant	Bos	41.25	29.28	24.28	23.49	-	Early Neolithic
D_H21	LD2FA25	La Draga	Ant	Bos	41.26	28.79	23.23	21.6	-	Early Neolithic
D_K16_KO_58	LD2FA26	La Draga	Post	Bos	45.46	30.45	28.25	25.32	-	Early Neolithic
D97_J684_4	LD2FA27	La Draga	Post	Bos	41.34	28.84	23.72	23.74	-	Early Neolithic
DNY25_SE4	LD2FA3	La Draga	Ant	Bos	42.96	27.78	22.64	21.69	-	Early Neolithic
LD78_2529	LD2FA30	La Draga	Post	Bos	47.03	34.6	28.83	28.07	-	Early Neolithic
D97_EEY319	LD2FA31	La Draga	Post	Bos	42.5	29.19	24.06	22.92	-	Early Neolithic
D01_J188_2	LD2FA32	La Draga	Ant	Bos	42.92	29.24	26.05	24.26	-	Early Neolithic
DH77_8	LD2FA33	La Draga	Post	Bos	42.92	32.02	26.6	26.85	-	Early Neolithic
D14_JA42_9343	LD2FA4	La Draga	Ant	Bos	42.05	31.12	27.89	25.69	-	Early Neolithic
D95_D22_5	LD2FA5	La Draga	Post	Bos	45.13	29.82	25.63	24.01	-	Early Neolithic
D_G16_NE24	LD2FA6	La Draga	Ant	Bos	42.04	28.38	23.59	21.73	-	Early Neolithic
DF17_38	LD2FA7	La Draga	Post	Bos	46.57	32.18	26.99	26.04	-	Early Neolithic
D15_110041_1650	LD2FA8	La Draga	Ant	Bos	42.37	26.54	22.92	21.26	-	Early Neolithic
D95_C2189	LD2FA9	La Draga	Ant	Bos	42.56	28.45	24.64	22.69	-	Early Neolithic

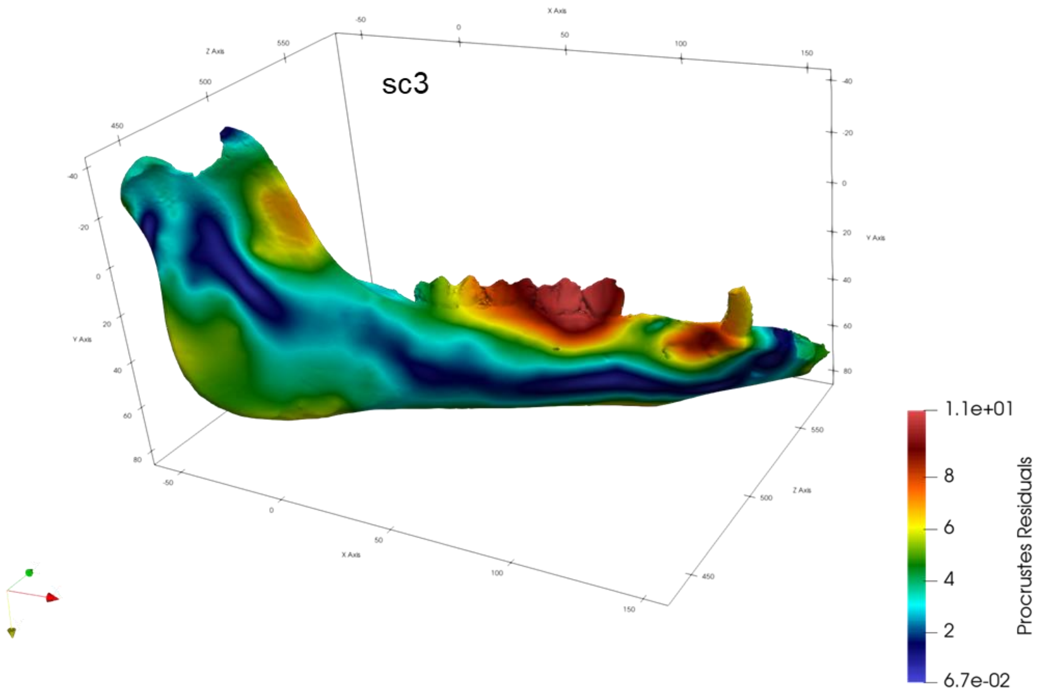
CODE	NAME	SITE	A/P	SPECIES	GL	SD	Bp	Bd	OP	PERIOD
PX31	PX2FA1	Pixarelles	Ant	Bos	42.72	32.22	29.26	26.21	-	Middle Neolithic
PX32	PX2FA2	Pixarelles	Post	Bos	39.4	28.89	23.03	22.6	-	Middle Neolithic
PX33	PX2FA3	Pixarelles	Ant	Bos	38.55	27.27	23.28	21.8	-	Middle Neolithic
PX34	PX2FA4	Pixarelles	Post	Bos	38.71	28.43	24.35	23.79	-	Middle Neolithic
PX21	PX2FA5	Pixarelles	Post	Bos	41.27	30.99	25.76	25.54	-	Middle Neolithic
PX26	PX2FA6	Pixarelles	Post	Bos	37.95	30	25.08	24.28	-	Middle Neolithic
PX28	PX2FA7	Pixarelles	Post	Bos	38.49	26.67	22.06	21.19	-	Middle Neolithic
PX29	PX2FA8	Pixarelles	Post	Bos	38.35	28.42	23.79	23.1	-	Middle Neolithic

CODE	NAME	SITE	A/P	SPECIES	GL	SD	Bp	Bd	OP	PERIOD
HL10	TH1FA13	Tell Halula	Post	Bos	50.9	34.31	30.32	27.96	5	MPPNB
HL92_CALA_SS7_Secl_Estr_A8_52	TH2FA17	Tell Halula	Post	Bos	55.01	35.57	30.87	30.81	20	LPPNB
HL93_S_IV_413_D4c	TH2FA18	Tell Halula	Post	Bos	45.03	30.91	26.56	25.39	6	MPPNB
HL93_4B_A16	TH2FA19	Tell Halula	Ant	Bos	49.46	35.95	30.3	28.06	8	MPPNB
HL2003_4I_132	TH2FA2	Tell Halula	Ant	Bos	54.67	40.11	34.86	33.19	8	MPPNB
HL2003_4J_A40_s10	TH2FA21	Tell Halula	Post	Bos	56.39	37.91	31.65	30.17	13	LPPNB
HL_4B_D2c_50	TH2FA22	Tell Halula	Post	Bos	46.65	29.88	25.99	24.83	7	MPPNB
HL93_4B_A31_42	TH2FA23	Tell Halula	Post	Bos	50.5	35.3	29.03	27.73	7	MPPNB
HL_int	TH2FA24	Tell Halula	Post	Bos	53.59	38.66	35.34	33.07	6	MPPNB
HL_4B_D5a_48	TH2FA25	Tell Halula	Ant	Bos	42.09	31.92	27.51	26.6	6	MPPNB
HL93_4B_A16_s9	TH2FA26	Tell Halula	Ant	Bos	50.37	37.63	34.06	30.37	8	MPPNB
HL_2D_E49_61	TH2FA29	Tell Halula	Ant	Bos	44.44	32.28	27.79	26.36	14	LPPNB
HL92_SS7_A10_Qs10_17	TH2FA3	Tell Halula	Ant	Bos	50.48	40.73	35.42	35.07	20	LPPNB
HL_4BE18_27	TH2FA30	Tell Halula	Post	Bos	46.16	30.69	25.24	25.88	8	MPPNB
HL93_4BE35_19	TH2FA31	Tell Halula	Post	Bos	49.72	35.59	29.73	29.55	8	MPPNB
HL93_4B_D6C_15	TH2FA32	Tell Halula	Ant	Bos	52.07	39.2	35.74	32.4	6	MPPNB
H91_CALAIV_Superficial	TH2FA33	Tell Halula	Post	Bos	42.1	27.91	24.75	22.91	25	Pre-Halaf
H91_CALAIV_superficial_34	TH2FA34	Tell Halula	Ant	Bos	52.59	38.93	36	31.7	5	MPPNB
HL93_4C_C3E_36	TH2FA35	Tell Halula	Post	Bos	51.05	33.44	31.21	28.07	6	MPPNB
HL2000_4D_A7_18	TH2FA36	Tell Halula	Ant	Bos	54.46	40.56	36.81	34.18	8	MPPNB
HL14	TH2FA37	Tell Halula	Post	Bos	50.96	32.31	27.67	26.44	7	MPPNB
HL93_4B_D5A_58	TH2FA38	Tell Halula	Post	Bos	52.68	35.3	29.92	28.18	6	MPPNB
HL93_CALA4C_C3e_22	TH2FA39	Tell Halula	Post	Bos	46.31	30.77	27.61	25.32	6	MPPNB
HL93_4B_D97_26	TH2FA4	Tell Halula	Post	Bos	46.54	29.1	25.4	22.46	6	MPPNB
HL93_4B_A31_43	TH2FA40	Tell Halula	Post	Bos	52.02	34.51	29.61	29.05	7	MPPNB
HL_4B_D12_30	TH2FA41	Tell Halula	Post	Bos	51.96	36.59	29.75	29.45	5	MPPNB
HL93_SIV_4B_D5a1_12	TH2FA42	Tell Halula	Ant	Bos	50.51	36.01	31.45	29.92	6	MPPNB
HL2003_4J_A40	TH2FA43	Tell Halula	Post	Bos	51.46	36.3	31.09	30.52	13	LPPNB
HL93_4B_E15d_49	TH2FA5	Tell Halula	Post	Bos	50.03	31.96	26.92	27.07	8	MPPNB
HL_4C_C2e	TH2FA50	Tell Halula	Post	Bos	45.86	29.97	25.62	24.86	6	MPPNB
HL93_SIV413_D6c	TH2FA51	Tell Halula	Post	Bos	48.96	32.9	28.02	26.79	6	MPPNB
HL63	TH2FA52	Tell Halula	Ant	Bos	52.96	38.09	33.2	32.21	4	MPPNB
HL93_4B_D1C_52	TH2FA53	Tell Halula	Ant	Bos	52.7	37.7	35.12	30.81	7	MPPNB
HL93_4C_B8eB	TH2FA54	Tell Halula	Ant	Bos	46.7	33.45	29.53	27.39	7	MPPNB
HL93_SIV_4B_D6C	TH2FA55	Tell Halula	Post	Bos	43.31	30.67	25.5	25.57	7	MPPNB
HL93_4B_C1F	TH2FA56	Tell Halula	Ant	Bos	41.43	29.86	27	25.66	8	MPPNB
HL93_CALA4B_superficial_b	TH2FA57	Tell Halula	Ant	Bos	46.96	33.67	29.16	26.93	6	MPPNB
HL93_CALA4B_superficial	TH2FA58	Tell Halula	Ant	Bos	44.86	32.57	27.62	26.28	5	MPPNB
HL2002_4J_A10_2	TH2FA59	Tell Halula	Ant	Bos	49.71	38.64	32.76	30.52	14	LPPNB
HL	TH2FA6	Tell Halula	Post	Bos	54.73	35.43	31.57	29.15	7	MPPNB
HL93_4C_C3E_37	TH2FA60	Tell Halula	Ant	Bos	50.2	39.44	35.54	32.85	6	MPPNB
HL_93_4C_B8eA	TH2FA61	Tell Halula	Post	Bos	52.18	38.55	33.31	31.33	7	MPPNB
HL_62	TH2FA62	Tell Halula	Post	Bos	47.4	33.43	27.7	25.51	27	Pre-Halaf
HL93_CALA4B_superficial_c	TH2FA63	Tell Halula	Post	Bos	51.27	33.01	28.13	26.61	3	MPPNB
HL93_4B_D79_24	TH2FA7	Tell Halula	Ant	Bos	47.49	36.12	31.49	29.72	6	MPPNB
HL93_4B_D3a	TH2FA8	Tell Halula	Ant	Bos	44.46	33.72	29.19	26.62	7	MPPNB

Annex IV: Finite element analysis of Sus scrofa mandibles


sc1
X Axis
Y Axis
Z Axis
1.1e+01
10
8
6
4
2
4.2e-02
Procrustes Residuals


sc2
X Axis
Y Axis
Z Axis
1.7e+01
15
10
5
2.0e-01
Procrustes Residuals


sc3
X Axis
Y Axis
Z Axis
1.1e+01
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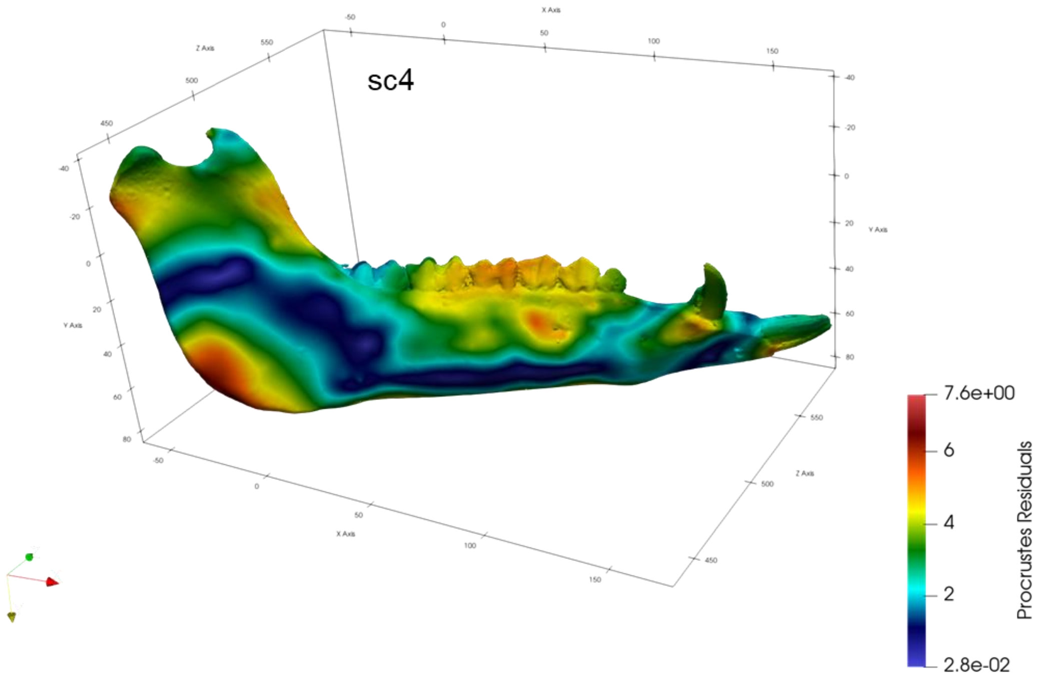
6
4
2
6.7e-02
Procrustes Residuals


sc4
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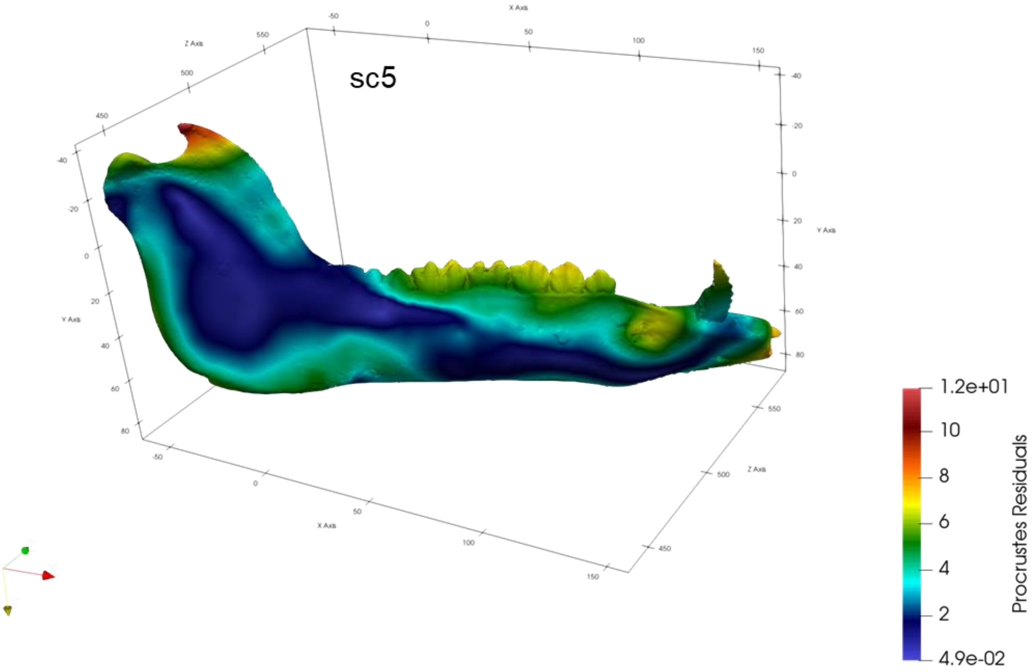
Y Axis
Z Axis
7.6e+00
6
4
2
2.8e-02
Procrustes Residuals


sc5
X Axis
-50
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100
150
Z Axis
450
500
550
Y Axis
-40
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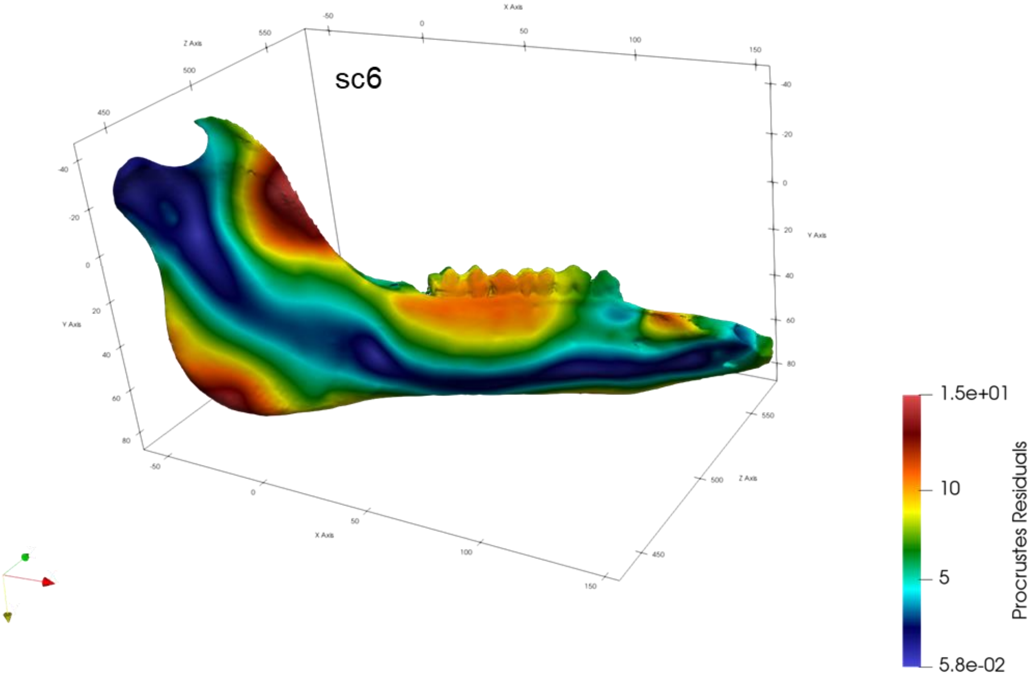
60
80
1.2e+01
10
8
6
4
2
4.9e-02
Procrustes Residuals


sc6
X Axis
-50
0
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100
150
Z Axis
450
500
550
Y Axis
-40
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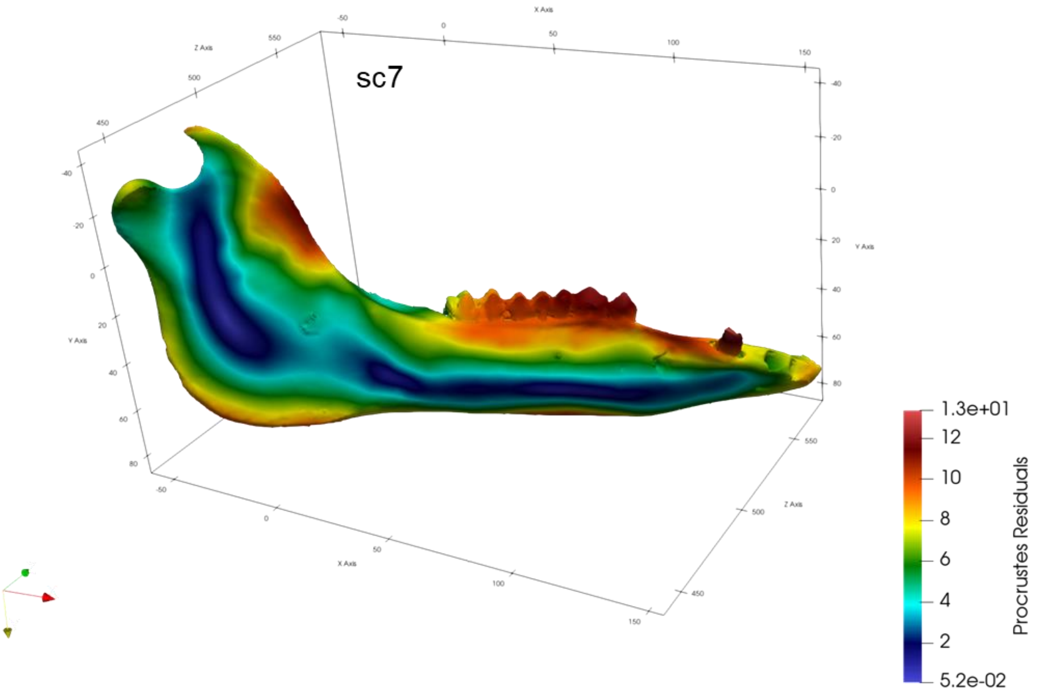
0
20
40
60
80
1.5e+01
10
5
5.8e-02
Procrustes Residuals


sc7
X Axis
Y Axis
Z Axis
-50
0
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100
150
450
500
550
-40
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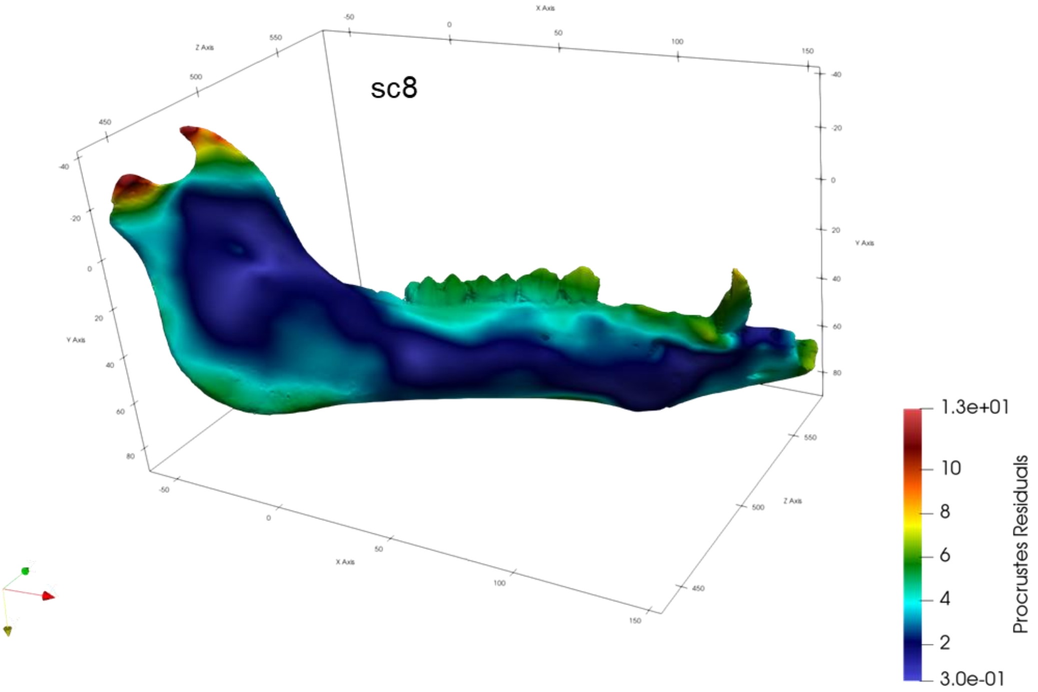
80
1.3e+01
12
10
8
6
4
2
5.2e-02
Procrustes Residuals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Y Axis
Z Axis
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-40
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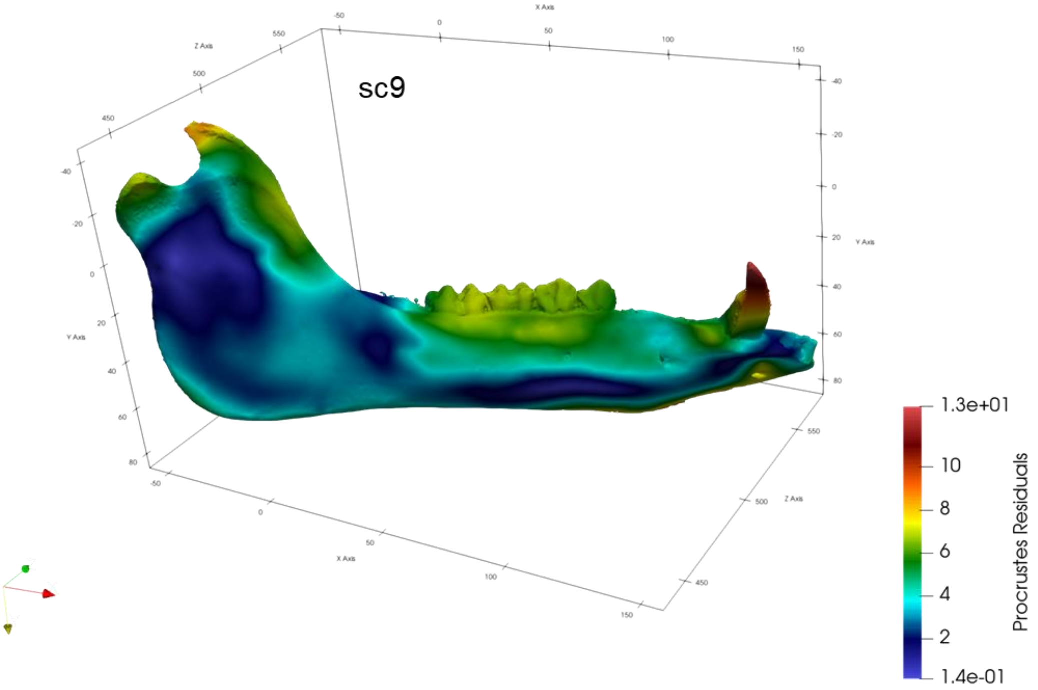
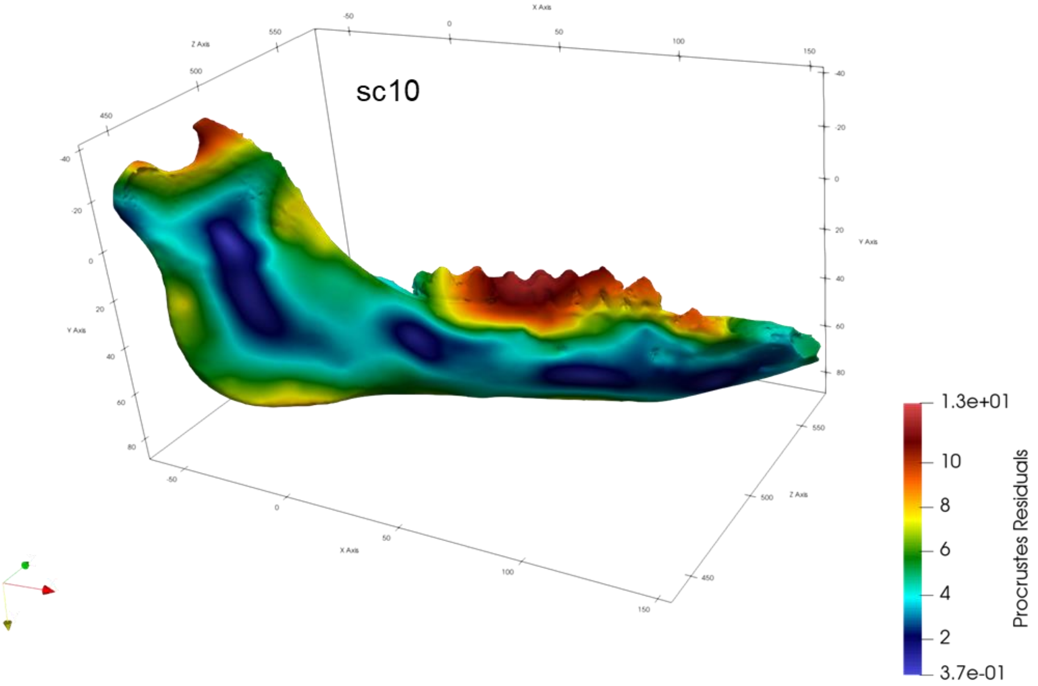
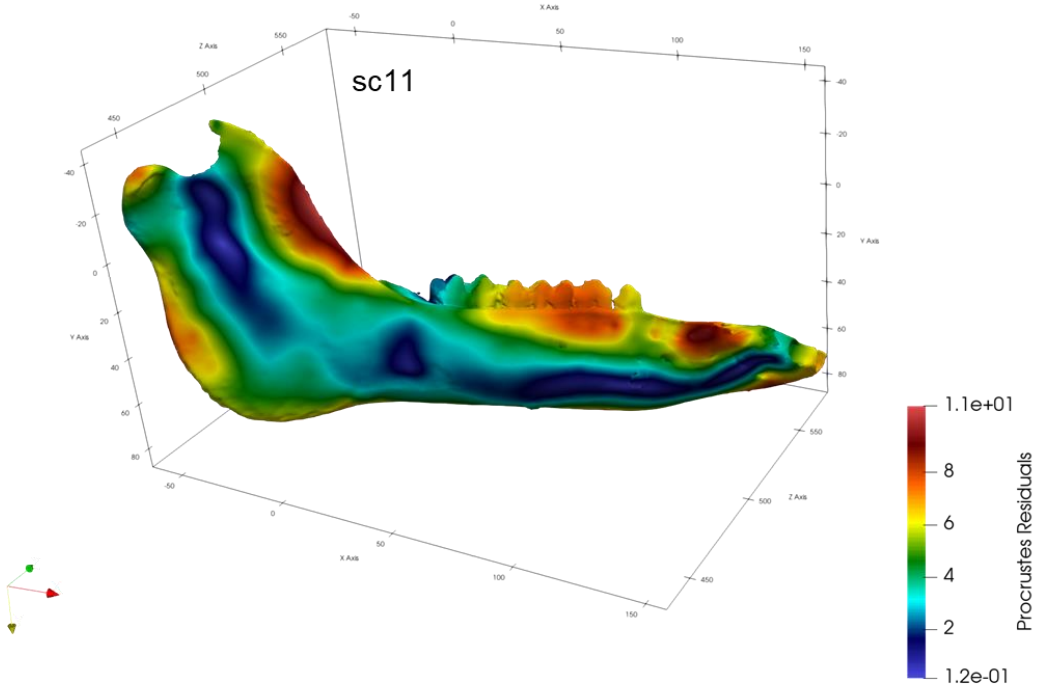
60
80
1.3e+01
10
8
6
4
2
3.0e-01
Procrustes Residuals


sc9
X Axis
Y Axis
Z Axis
1.3e+01
10
8
6
4
2
1.4e-01
Procrustes Residuals


sc10
X Axis
Y Axis
Z Axis
1.3e+01
10
8
6
4
2
3.7e-01
Procrustes Residuals


sc11
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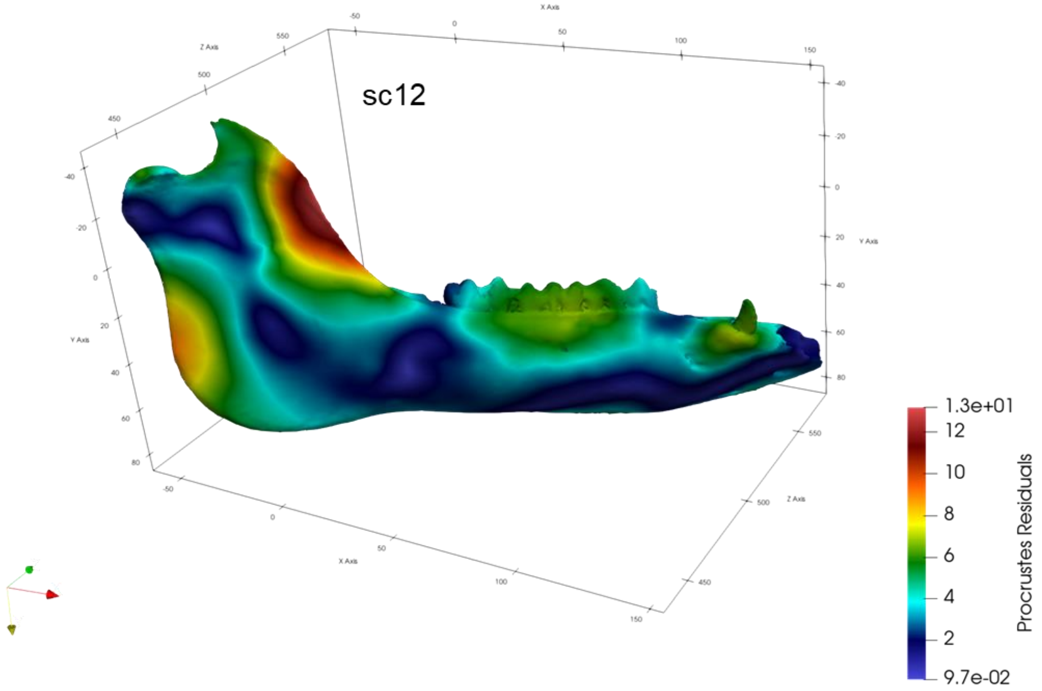
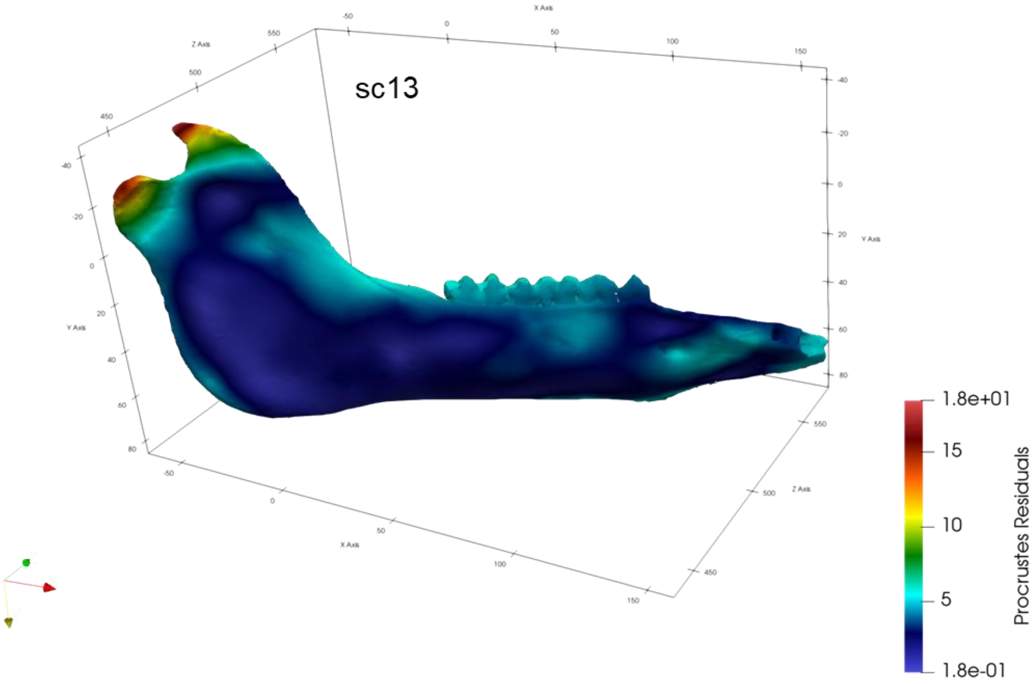
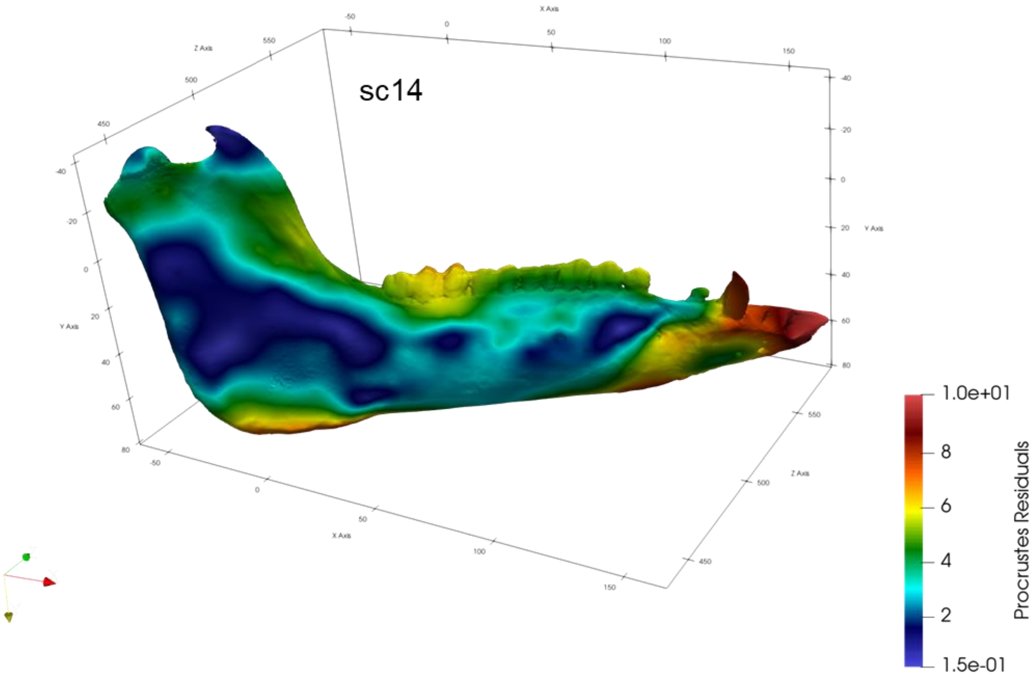
Y Axis
Z Axis
1.1e+01
8
6
4
2
1.2e-01
Procrustes Residuals


sc12
X Axis
Y Axis
Z Axis
1.3e+01
12
10
8
6
4
2
9.7e-02
Procrustes Residuals


sc13
X Axis
Y Axis
Z Axis
1.8e+01
15
10
5
1.8e-01
Procrustes Residuals


sc14
X Axis
Y Axis
Z Axis
1.0e+01
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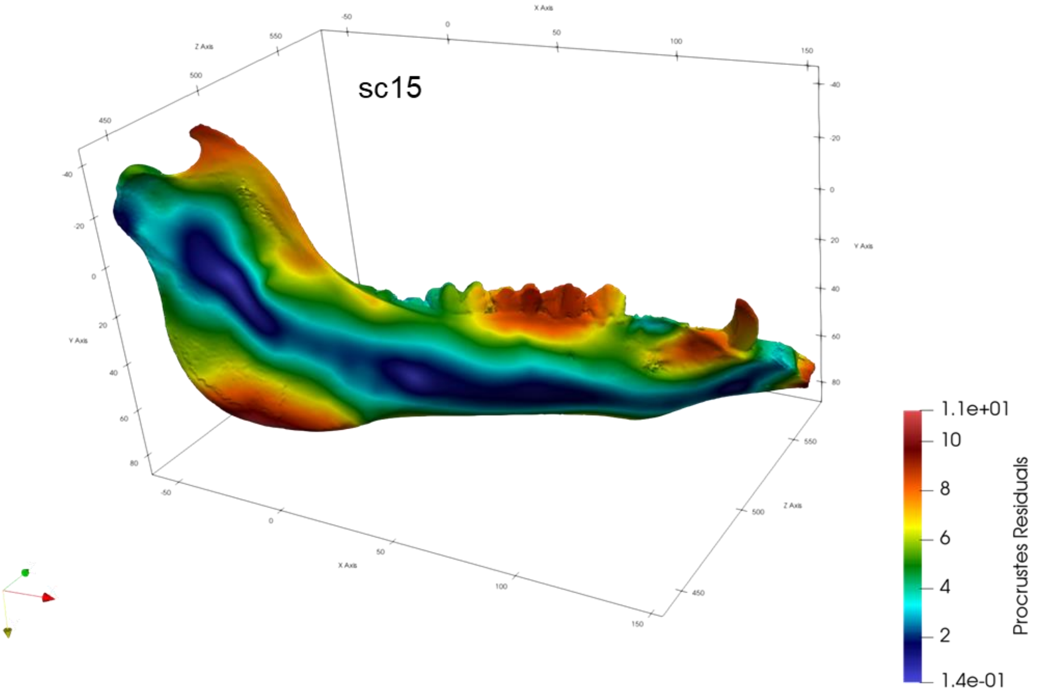
6
4
2
1.5e-01
Procrustes Residuals


sc15
X Axis
Y Axis
Z Axis
-50
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50
100
150
450
500
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-40
-20
0
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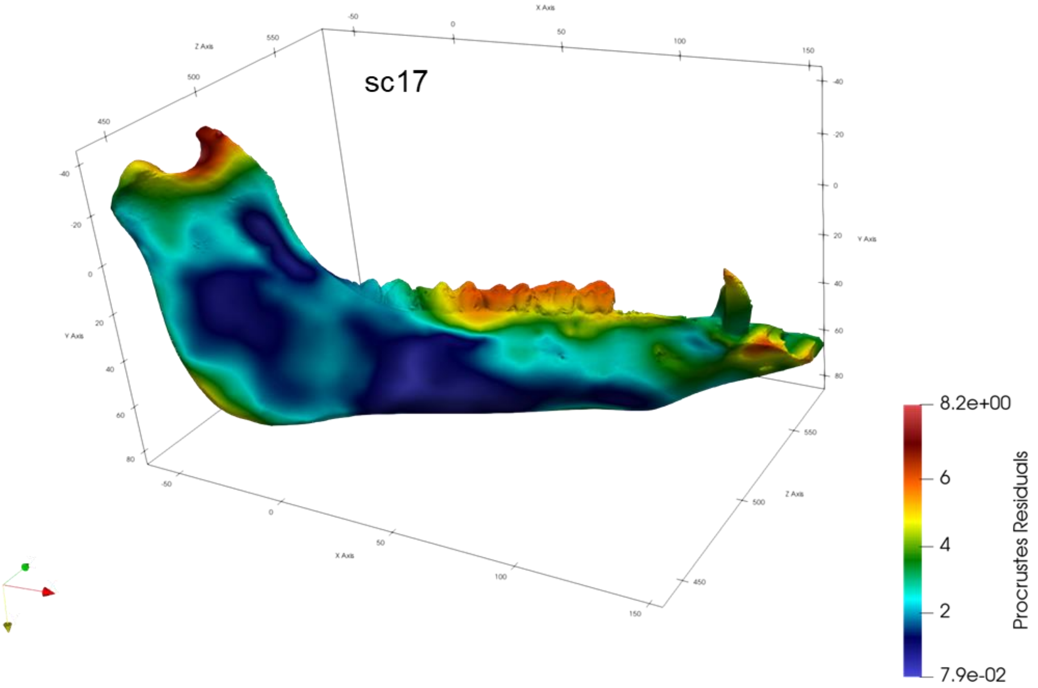
40
60
80
1.1e+01
10
8
6
4
2
1.4e-01
Procrustes Residuals


sc17
X Axis
Y Axis
Z Axis
-50
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100
150
450
500
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-40
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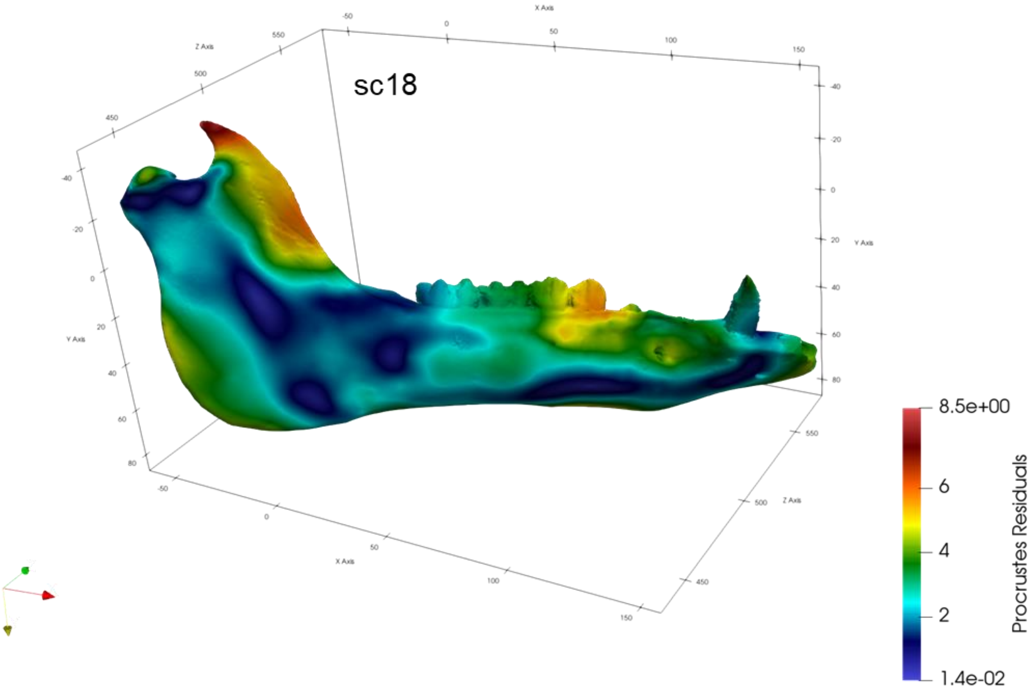
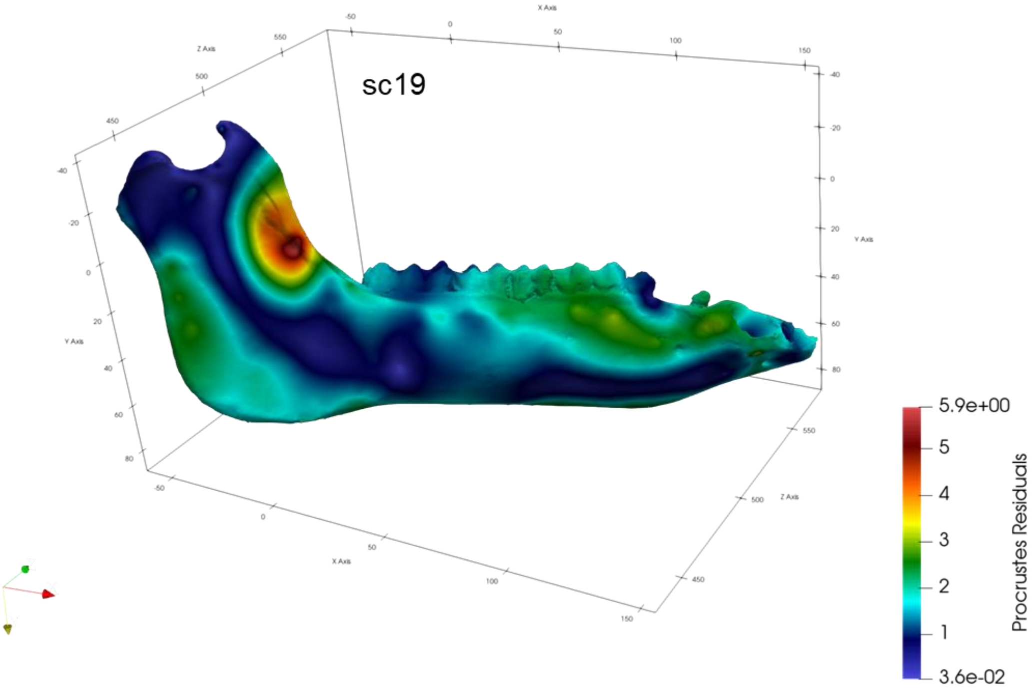
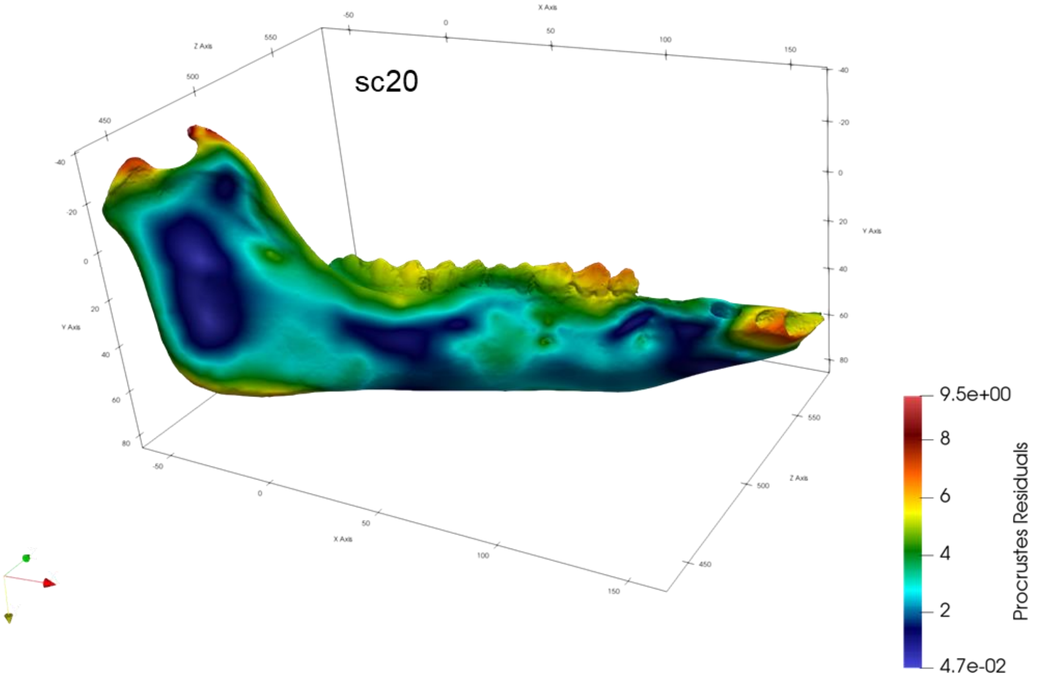
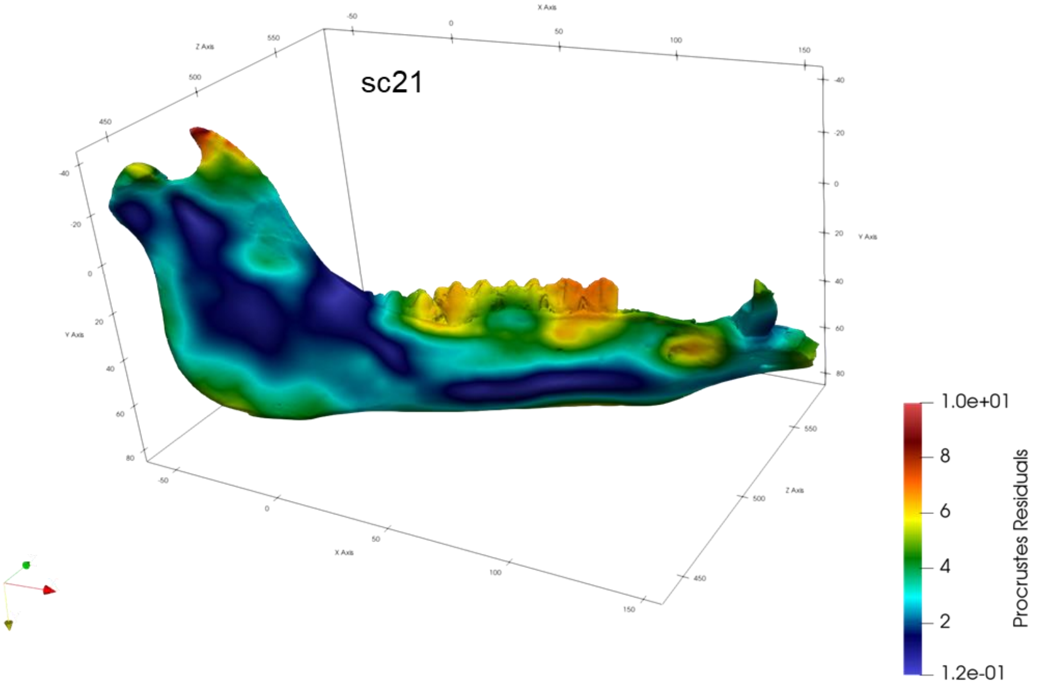
20
40
60
80
8.2e+00
6
4
2
7.9e-02
Procrustes Residuals


sc18
X Axis
Y Axis
Z Axis
8.5e+00
6
4
2
1.4e-02
Procrustes Residuals


sc19
X Axis
Y Axis
Z Axis
5.9e+00
5
4
3
2
1
3.6e-02
Procrustes Residuals


sc20
X Axis
Y Axis
Z Axis
-50
0
50
100
150
-40
-20
0
20
40
60
80
450
500
550
9.5e+00
8
6
4
2
4.7e-02
Procrustes Residuals


sc21
X Axis
Y Axis
Z Axis
-50
0
50
100
150
-40
-20
0
20
40
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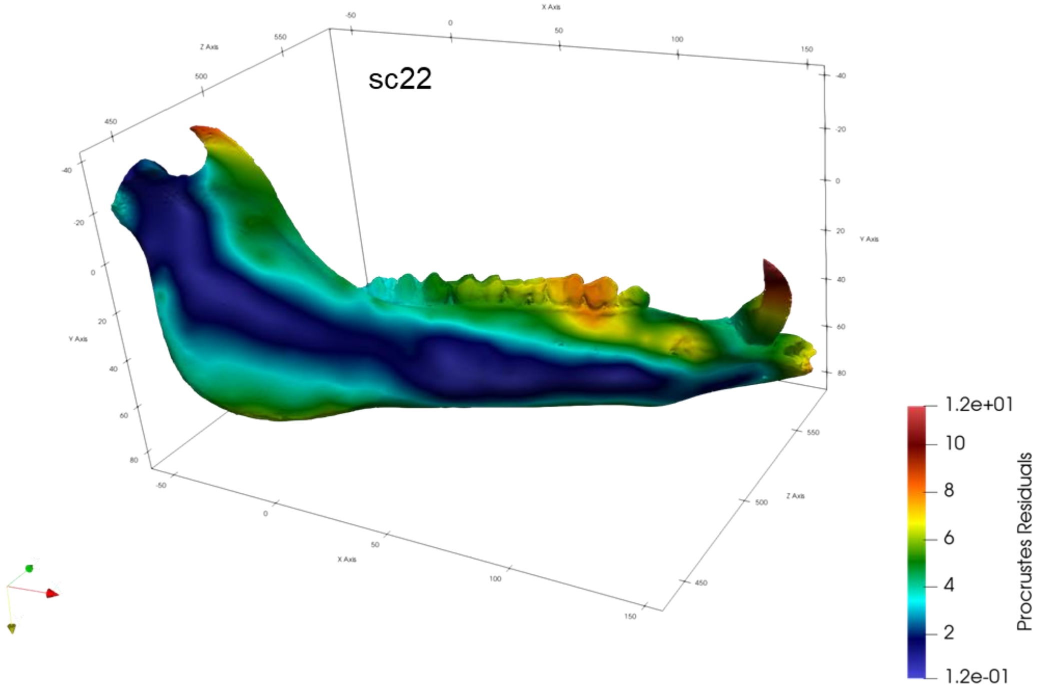
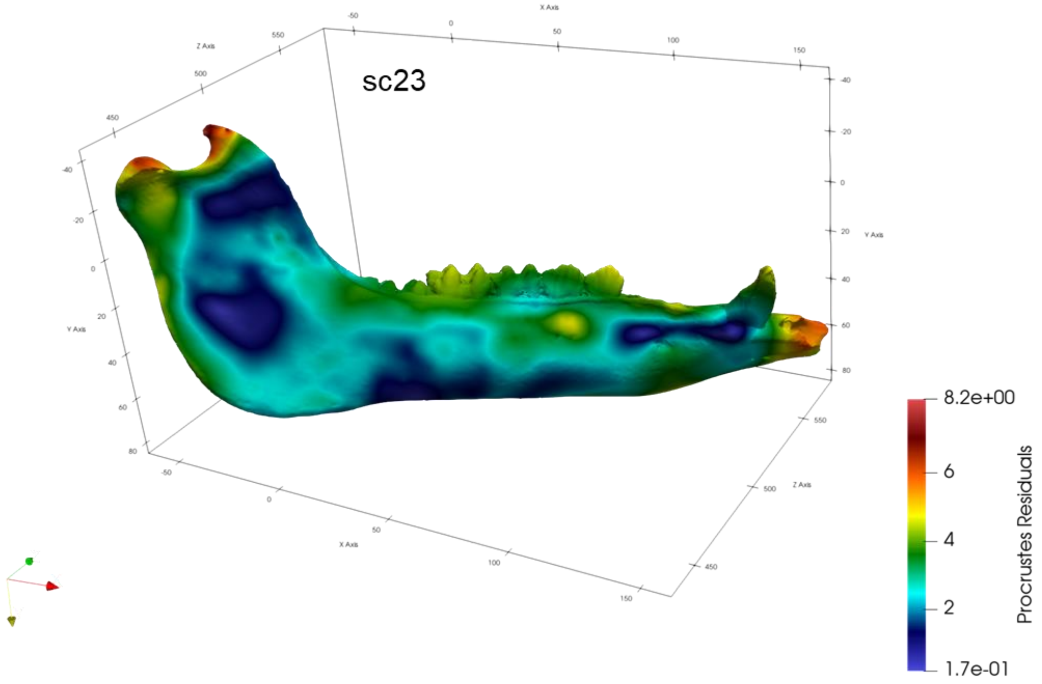
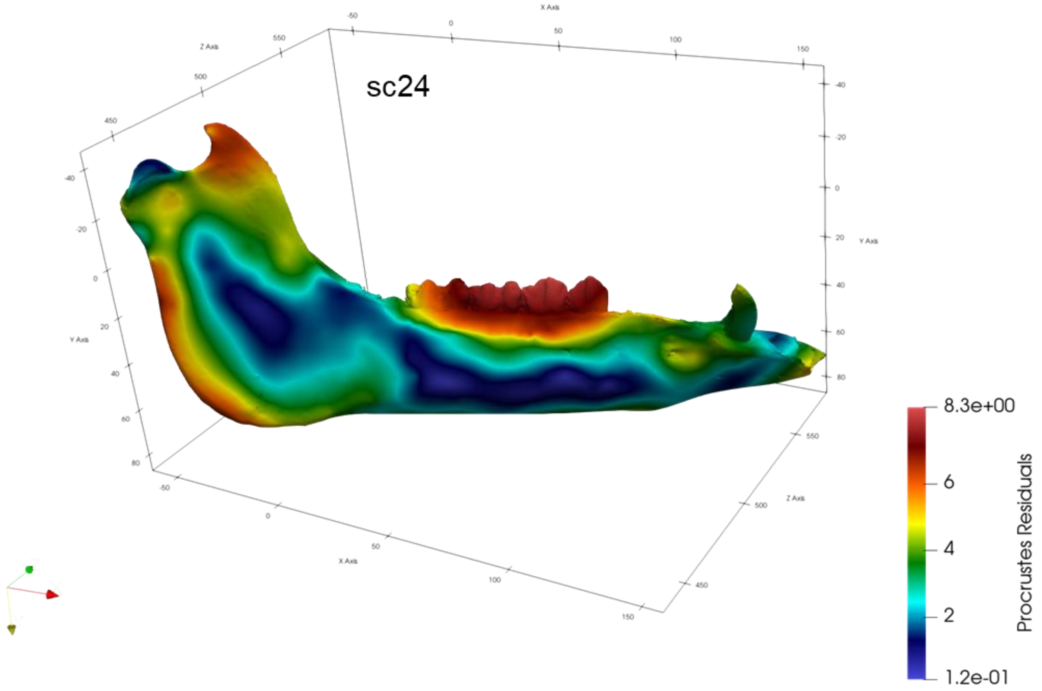
80
450
500
550
1.0e+01
8
6
4
2
1.2e-01
Procrustes Residuals


sc22
X Axis
Y Axis
Z Axis
1.2e+01
10
8
6
4
2
1.2e-01
Procrustes Residuals


sc23
X Axis
Y Axis
Z Axis
8.2e+00
6
4
2
1.7e-01
Procrustes Residuals


sc24
X Axis
-50
0
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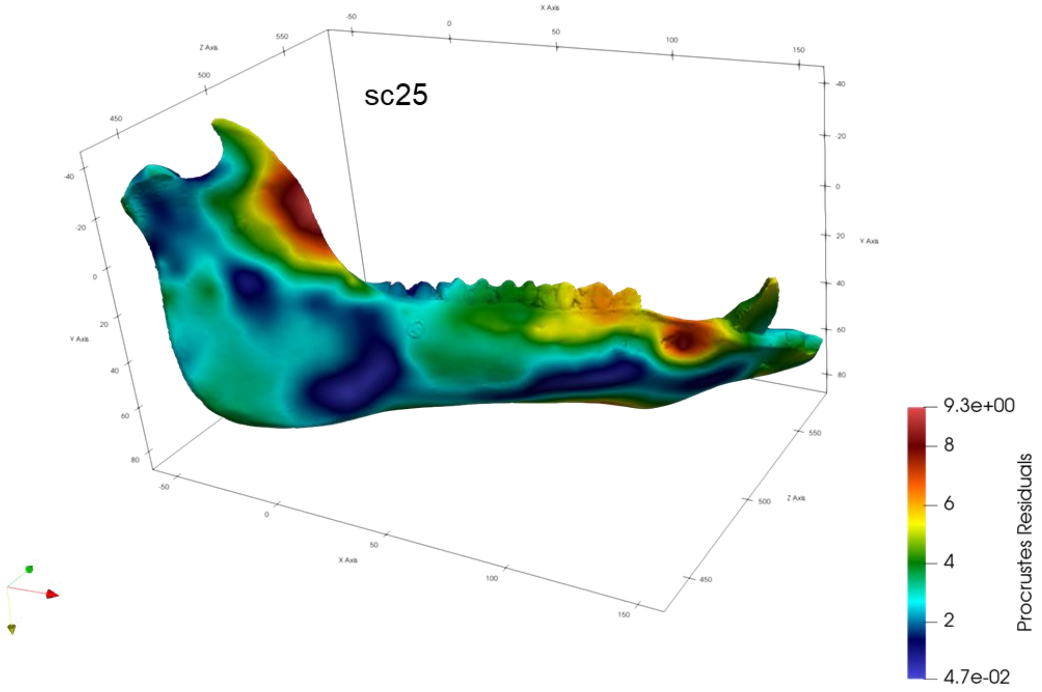
100
150
Z Axis
450
500
550
Y Axis
-40
-20
0
20
40
60
80
8.3e+00
6
4
2
1.2e-01
Procrustes Residuals


sc25
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-50
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100
150
Z Axis
450
500
550
Y Axis
-40
-20
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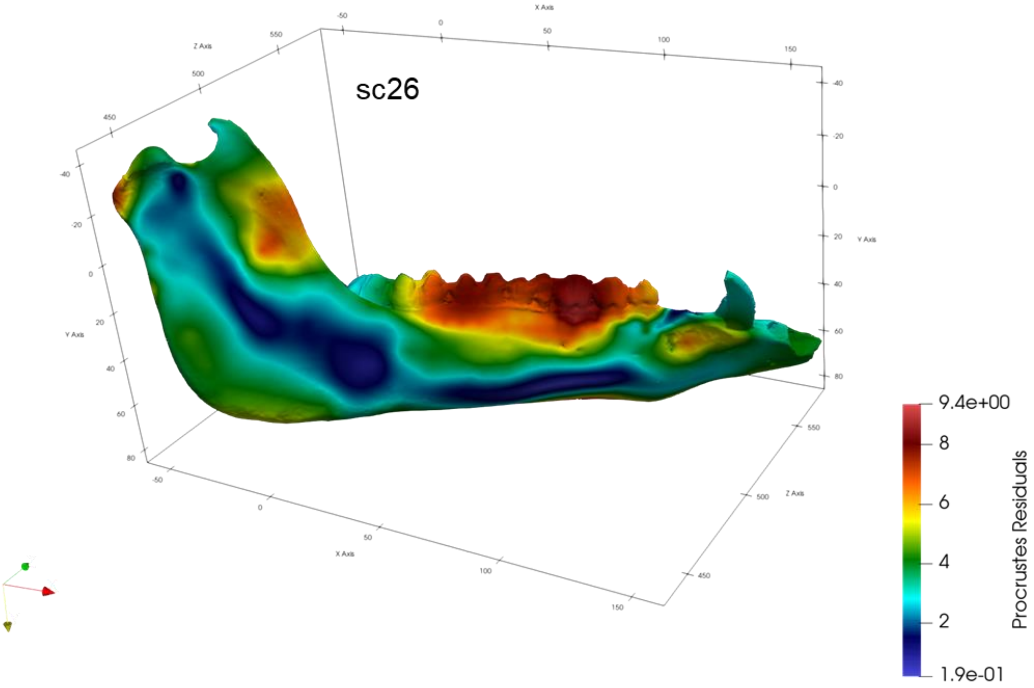
20
40
60
80
9.3e+00
8
6
4
2
4.7e-02
Procrustes Residuals


sc26
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0
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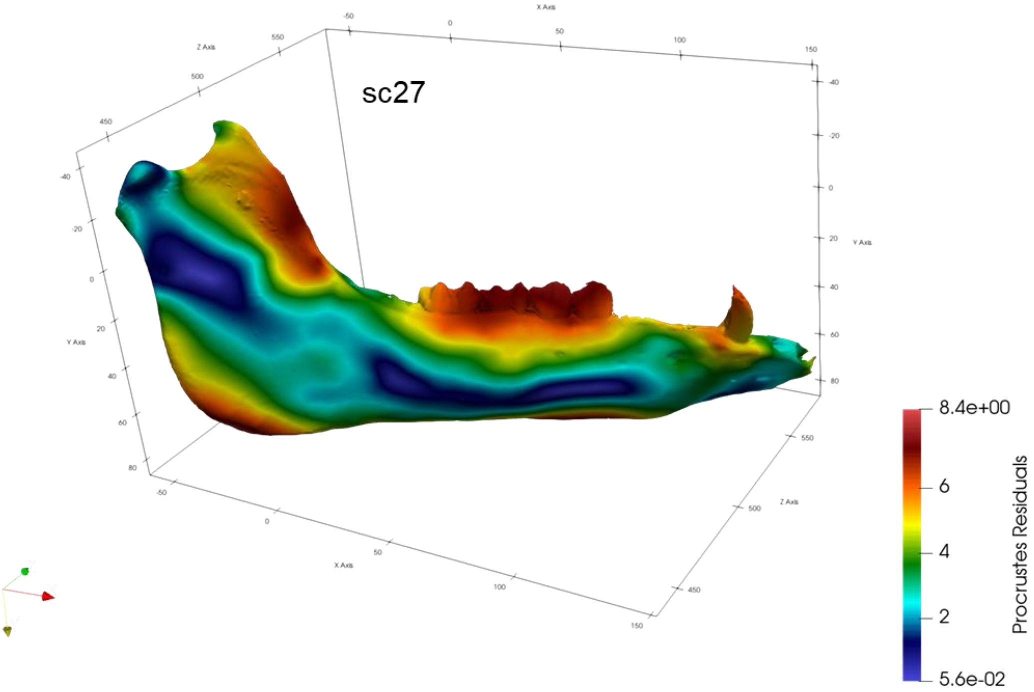
100
150
Y Axis
-40
-20
0
20
40
60
80
Z Axis
450
500
550
9.4e+00
8
6
4
2
1.9e-01
Procrustes Residuals


sc27
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100
150
Y Axis
-40
-20
0
20
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60
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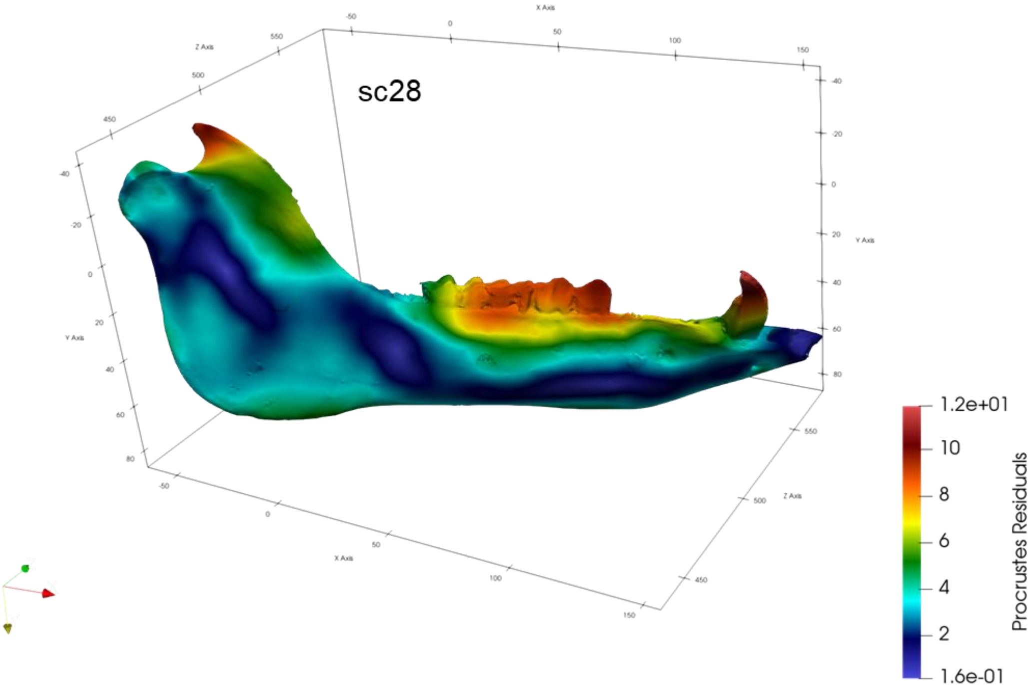
Z Axis
450
500
550
8.4e+00
6
4
2
5.6e-02
Procrustes Residuals


sc28
X Axis
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100
150
Y Axis
-40
-20
0
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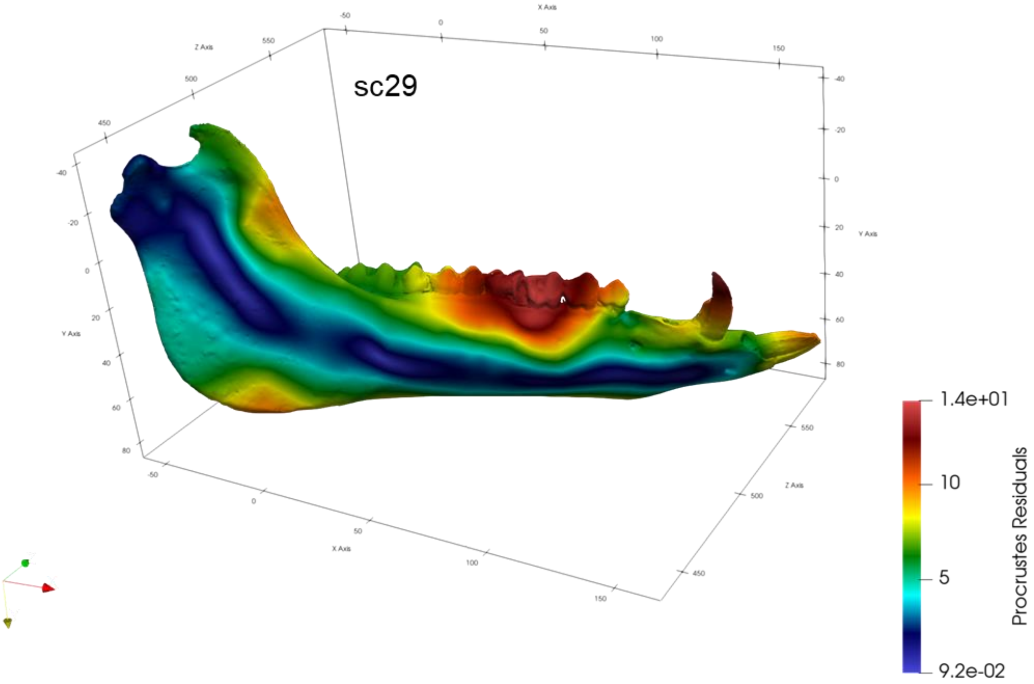
40
60
80
Z Axis
450
500
550
1.2e+01
10
8
6
4
2
1.6e-01
Procrustes Residuals


sc29
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100
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Y Axis
-40
-20
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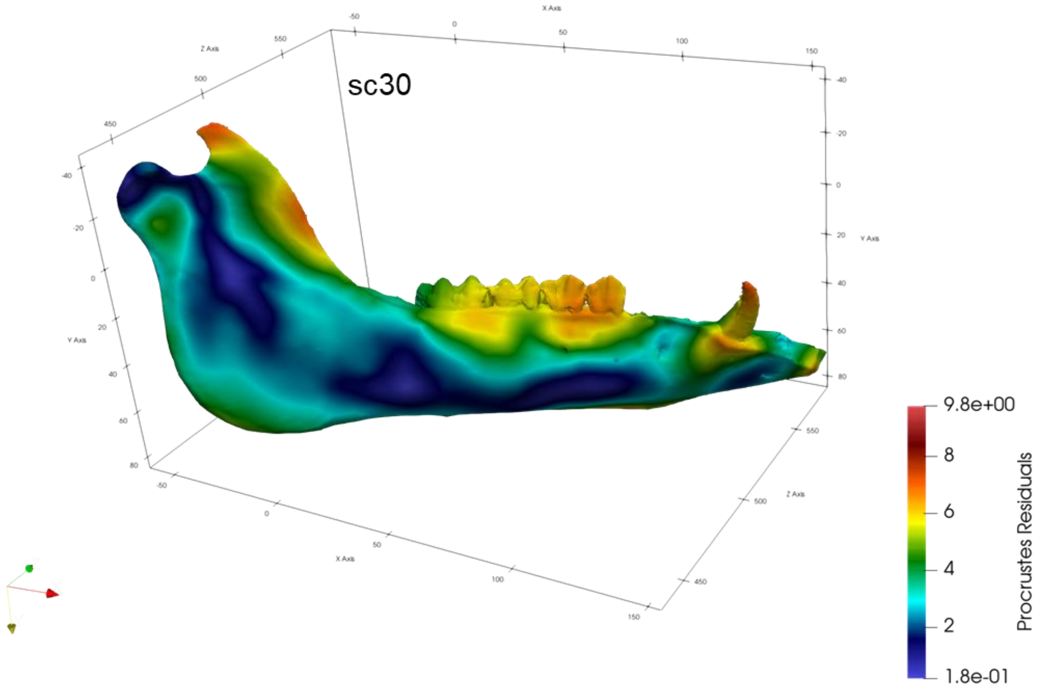
Z Axis
450
500
550
1.4e+01
10
5
9.2e-02
Procrustes Residuals


sc30
X Axis
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Z Axis
450
500
550
Y Axis
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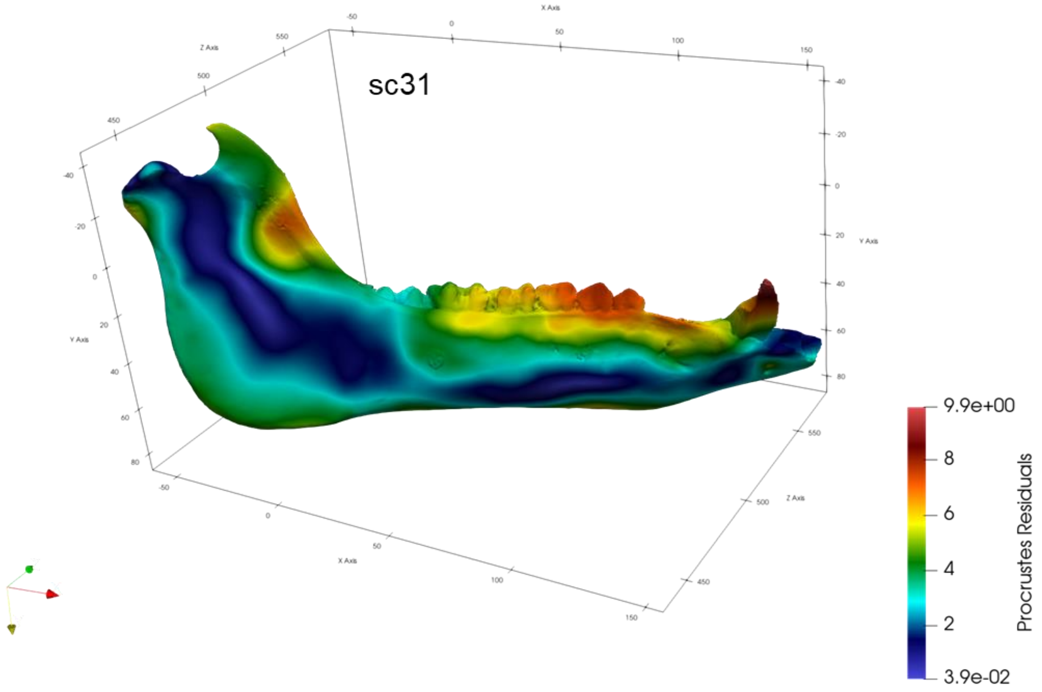
40
60
80
9.8e+00
8
6
4
2
1.8e-01
Procrustes Residuals


sc31
X Axis
-50
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100
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Z Axis
450
500
550
Y Axis
-40
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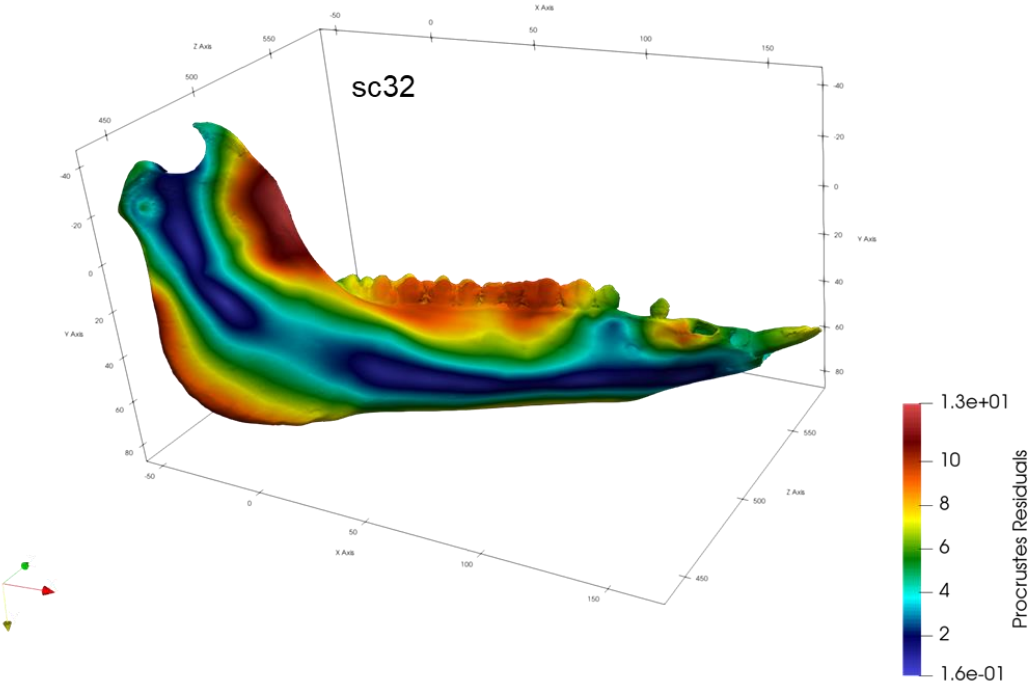
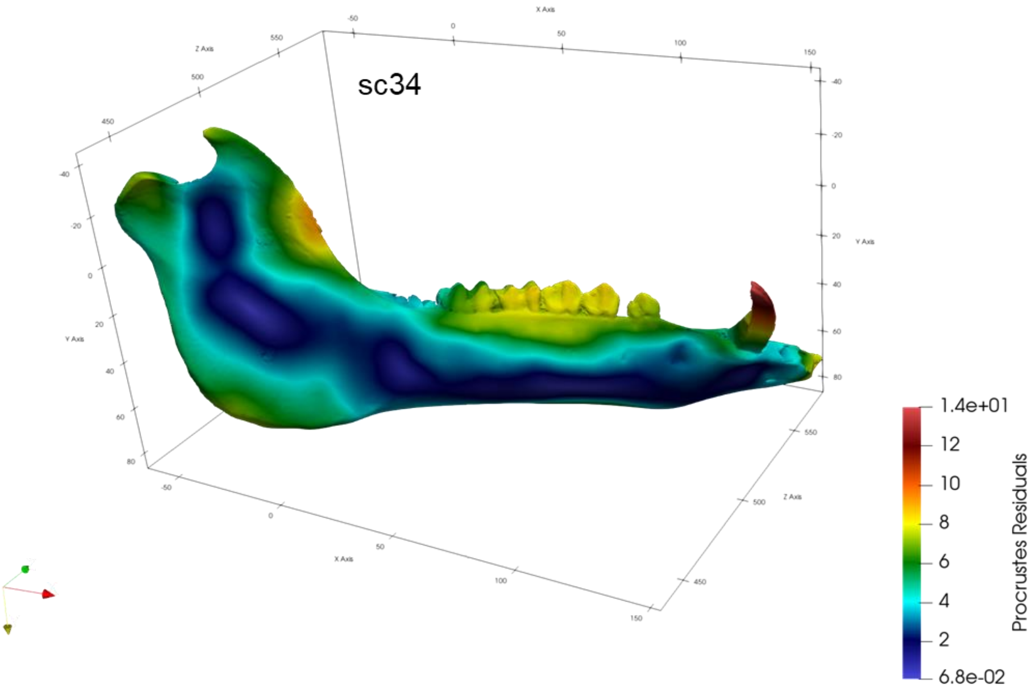
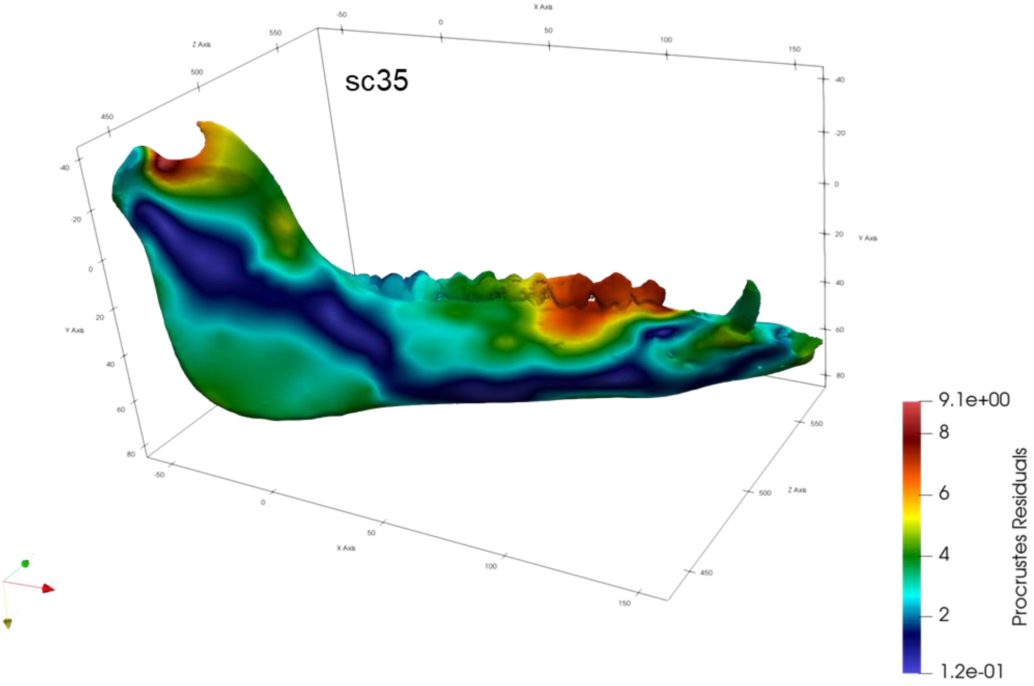
40
60
80
9.9e+00
8
6
4
2
3.9e-02
Procrustes Residuals

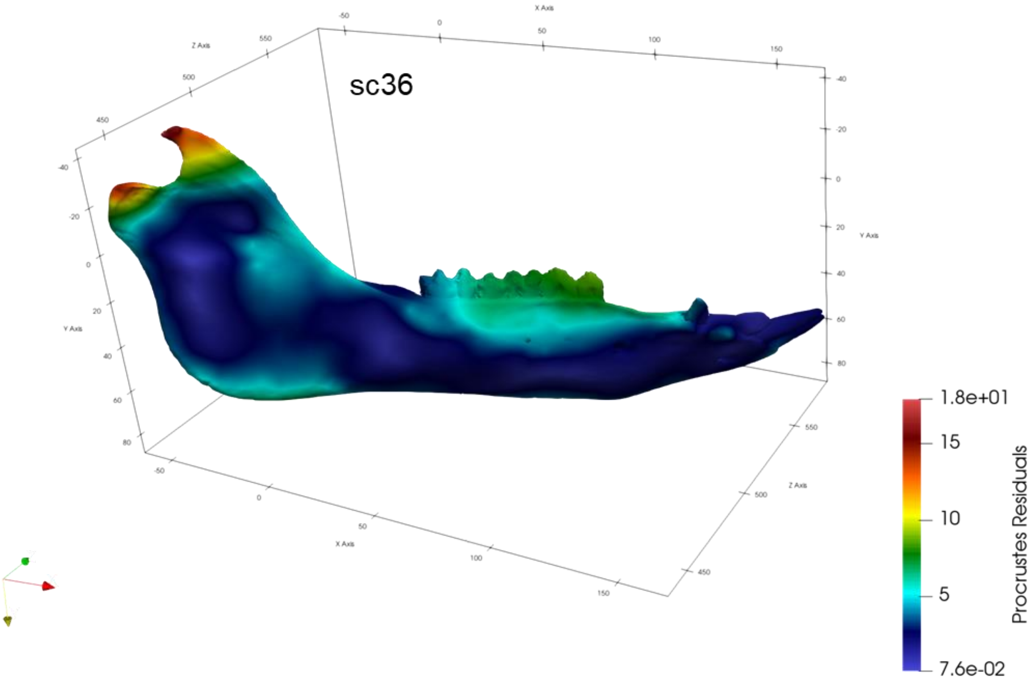


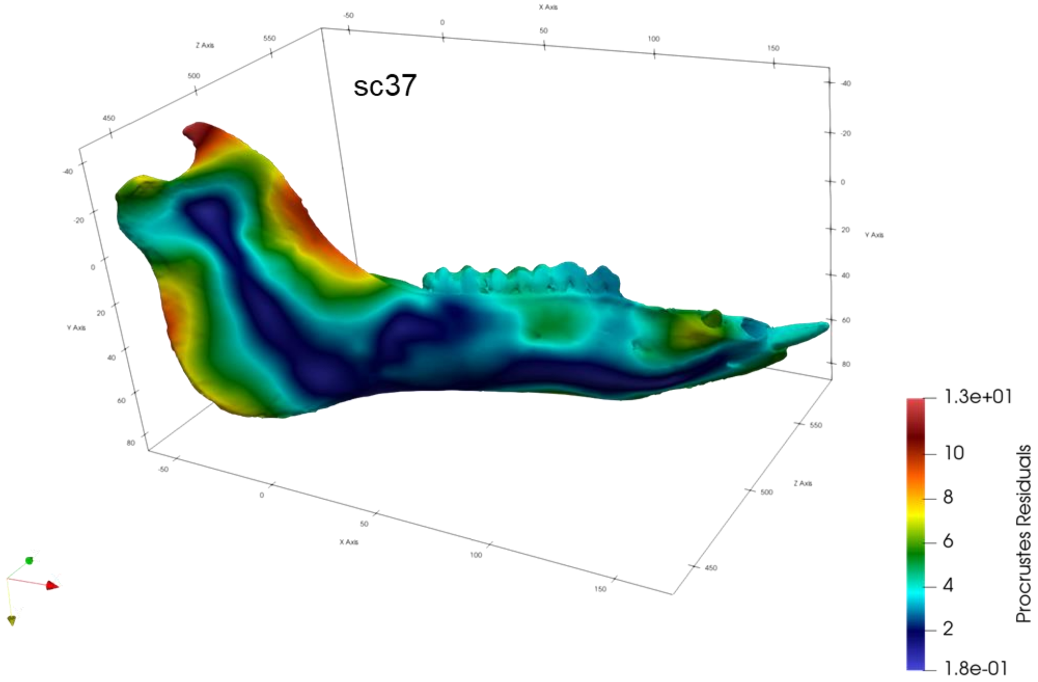
sc32
X Axis
Y Axis
Z Axis
1.3e+01
10
8
6
4
2
1.6e-01
Procrustes Residuals

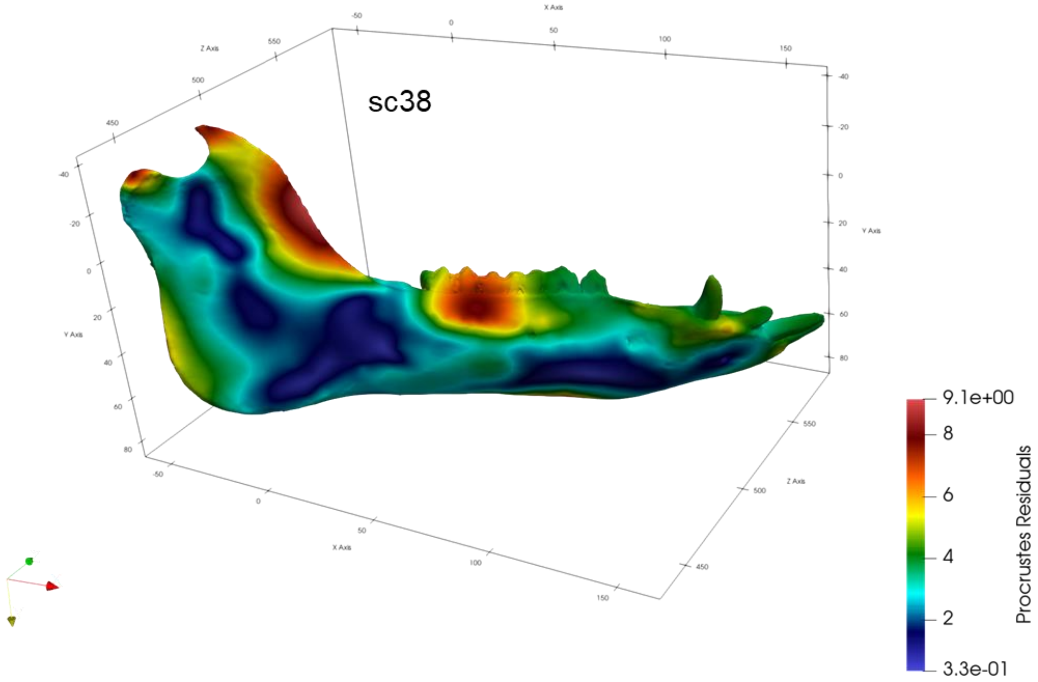


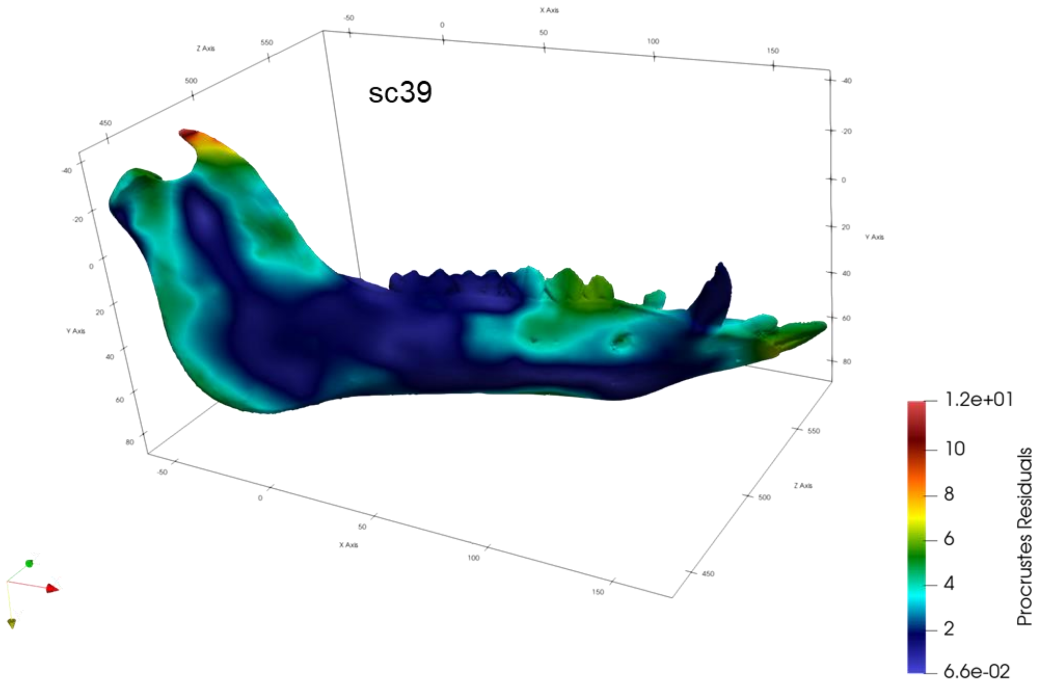
sc34
X Axis
Y Axis
Z Axis
1.4e+01
12
10
8
6
4
2
6.8e-02
Procrustes Residuals

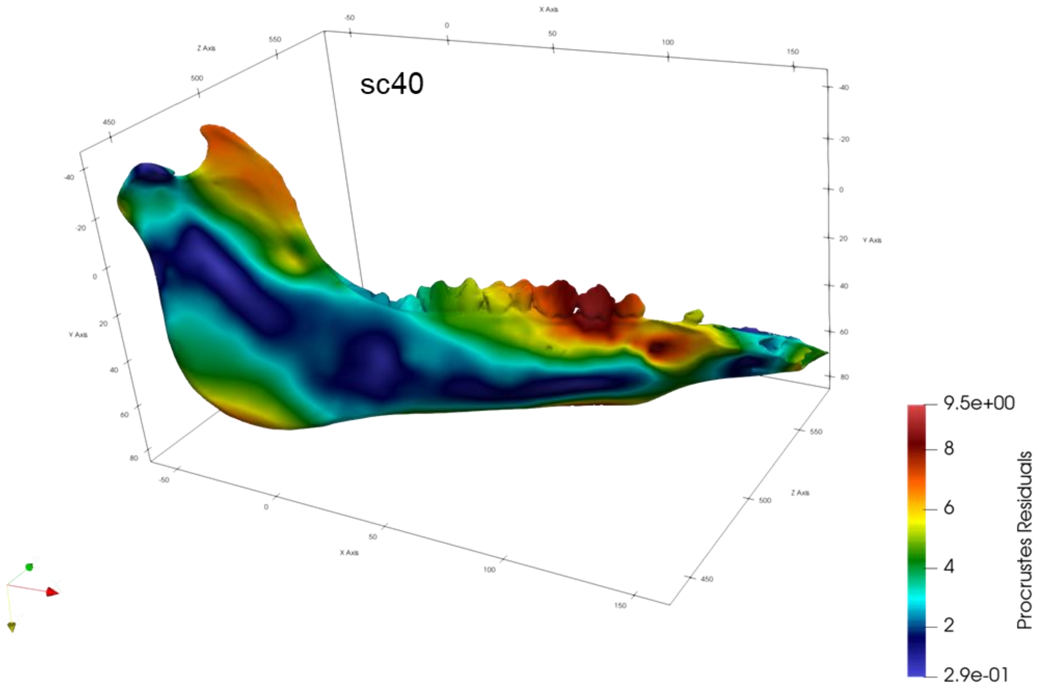

sc35
X Axis
Y Axis
Z Axis
9.1e+00
8
6
4
2
1.2e-01
Procrustes Residuals

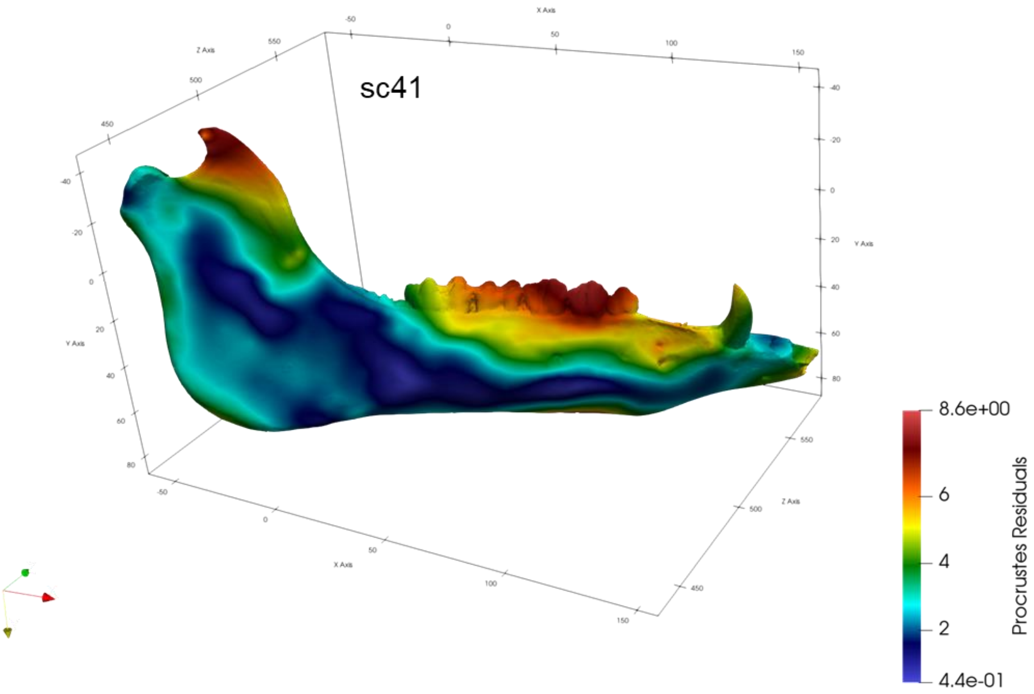

sc36
X Axis
Y Axis
Z Axis
1.8e+01
15
10
5
7.6e-02
Procrustes Residuals


sc37
X Axis
Y Axis
Z Axis
1.3e+01
10
8
6
4
2
1.8e-01
Procrustes Residuals


sc38
X Axis
Y Axis
Z Axis
9.1e+00
8
6
4
2
3.3e-01
Procrustes Residuals


sc39
X Axis
Y Axis
Z Axis
1.2e+01
10
8
6
4
2
6.6e-02
Procrustes Residuals


sc40
X Axis
Y Axis
Z Axis
9.5e+00
8
6
4
2
2.9e-01
Procrustes Residuals


sc41
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Y Axis
Z Axis
8.6e+00
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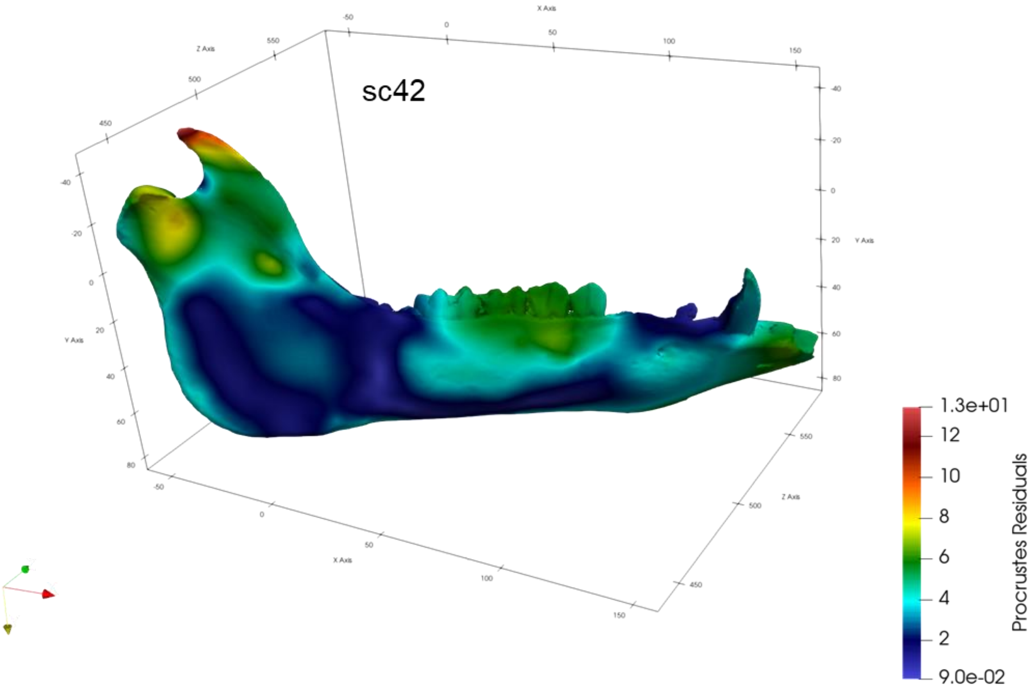
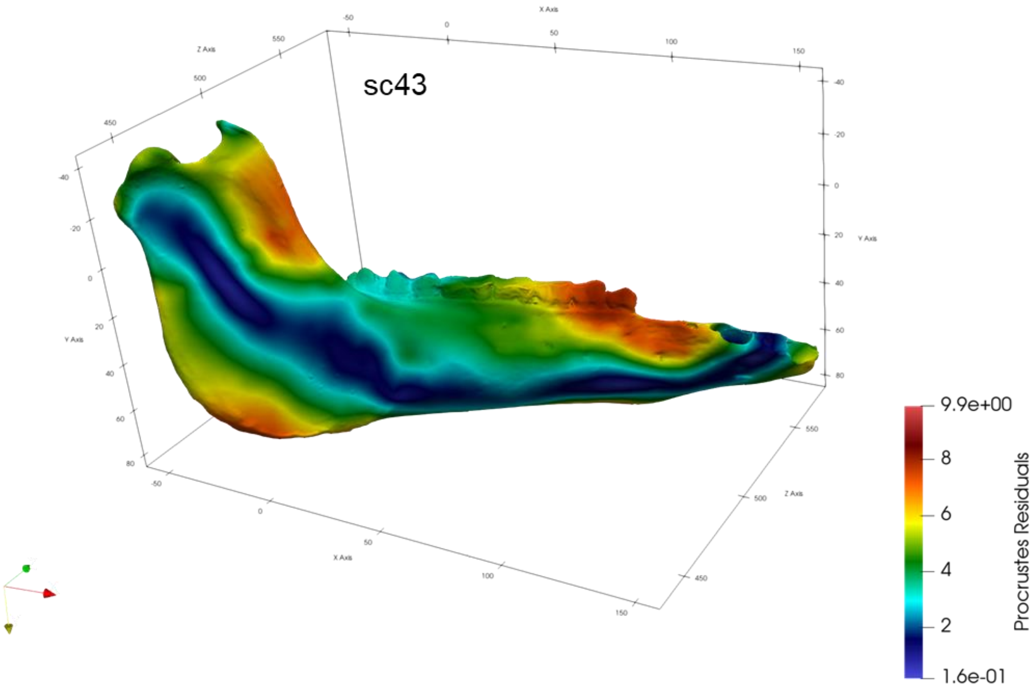
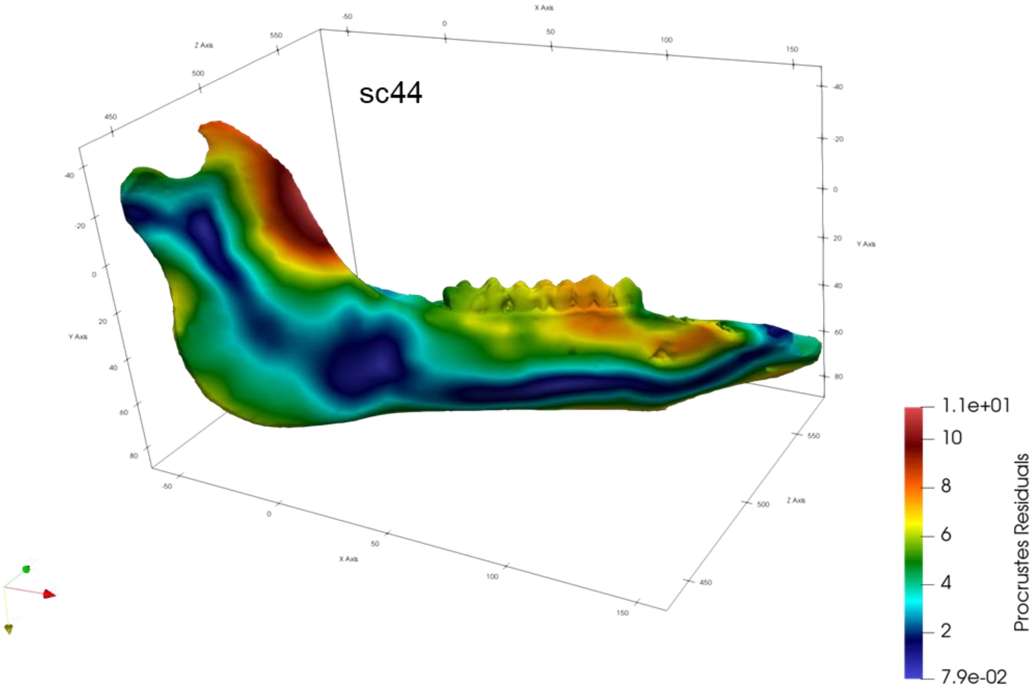
4
2
4.4e-01
Procrustes Residuals


sc42
X Axis
Y Axis
Z Axis
1.3e+01
12
10
8
6
4
2
9.0e-02
Procrustes Residuals


sc43
X Axis
Y Axis
Z Axis
9.9e+00
8
6
4
2
1.6e-01
Procrustes Residuals


sc44
X Axis
Y Axis
Z Axis
1.1e+01
10
8
6
4
2
7.9e-02
Procrustes Residuals