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Biodiversity assessment and communication through new approaches to
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ABSTRACT

The valorisation of geo-palaeontological heritage includes both the conservation of physical specimens and the development of communication strategies that make them understandable and meaningful for a wide range of audiences. This requires clear interpretation, accessible narratives, and engaging forms of presentation. In this work, new museological approaches are explored by combining scientific research, interdisciplinary collaboration, and digital innovation. The goal is to strengthen the connection between collections, scientific knowledge, and the public through updated tools and methods.

Virtual palaeontology tools are tested as ways to create new interpretive layers around fossil specimens. These technologies allow fragile or complex objects to be explored in detail, reproduced, and shared beyond physical limitations. They also support the creation of interactive experiences, both virtual and physical, that can adapt to different learning styles and levels of prior knowledge. In this way, digital applications become not a replacement for the original objects, but a complementary resource that enhances their interpretation and visibility.

This work is structured around four case studies, each representing a different approach to integrating virtual palaeontology into museum and exhibition practice. Two case studies focus on specific fossil specimens displayed in the permanent exhibition of the Museum of Geology and Palaeontology of Florence, where digital tools are used to expand interpretation, accessibility, and dissemination. The other two case studies develop around exhibitions as a whole in two different museums, testing digital and immersive solutions that support broader storytelling and visitor engagement rather than focusing on single objects.

Taken together, the results demonstrate that new technologies can effectively support and strengthen the communication and valorisation of biodiversity through the palaeontological heritage preserved in museums, offering practical models for future applications in scientific and cultural institutions.

RIASSUNTO

La valorizzazione del patrimonio geo-paleontologico comprende sia la conservazione dei reperti materiali sia lo sviluppo di strategie comunicative che li rendano comprensibili e significativi per un pubblico ampio e diversificato. Questo richiede interpretazioni chiare, narrazioni accessibili e forme di presentazione coinvolgenti. In questo lavoro vengono esplorati nuovi approcci museologici attraverso l'integrazione di ricerca scientifica, collaborazione interdisciplinare e innovazione digitale. L'obiettivo è rafforzare il legame tra collezioni, conoscenza scientifica e pubblico mediante strumenti e metodi aggiornati.

Strumenti come la scansione tridimensionale, la modellazione digitale, la realtà aumentata e la ricostruzione in ambiente virtuale vengono sperimentati come modalità per creare nuovi livelli di interpretazione attorno ai reperti fossili. Queste tecnologie permettono di analizzare in dettaglio esemplari fragili o complessi, riprodurli e condividerli superando i limiti fisici. Favoriscono inoltre la creazione di esperienze interattive, sia virtuali sia tangibili, capaci di adattarsi a diversi stili di apprendimento e livelli di conoscenza pregressa. In questo modo, le applicazioni digitali non sostituiscono gli oggetti originali, ma ne diventano una risorsa complementare che ne amplia interpretazione e visibilità.

Il lavoro è strutturato attorno a quattro casi studio, ciascuno dei quali rappresenta un diverso approccio all'integrazione della paleontologia virtuale nella pratica museale ed espositiva. Due casi studio si concentrano su specifici reperti fossili esposti nel Museo di Geologia e Paleontologia dell'Università di Firenze, in cui strumenti digitali vengono utilizzati per ampliarne le possibilità di interpretazione, accessibilità e diffusione. Gli altri due casi studio riguardano invece l'esposizione nel suo insieme in due musei differenti, sperimentando soluzioni digitali e immersive a supporto di una narrazione più ampia e del coinvolgimento del pubblico, piuttosto che focalizzarsi su singoli esemplari.

Nel complesso, i risultati dimostrano che le nuove tecnologie possono sostenere e rafforzare in modo efficace la comunicazione e la valorizzazione della biodiversità attraverso il patrimonio paleontologico conservato nei musei, offrendo modelli applicativi per sviluppi futuri in ambito scientifico e culturale.

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1 INTRODUCTION

1.1 Valorisation techniques in museum exhibitions and displays: a state of the art

Museum exhibitions are designed to encourage visitors to engage critically with scientific processes. Natural history institutions have undergone profound transformation over the past several decades. Once primarily repositories of objects accompanied by descriptive panels, solely meant for research purposes aimed at educating students and passionate visitors, have now become dynamic spaces for public engagement, informal learning, and participatory dialogue between science and public (Rössig et al., 2023). The communicative dimension of these institutions now extends well beyond simple transmission of information, encompassing diverse techniques and media that seek to foster curiosity, critical thinking, and engagement with scientific issues.

The museum can be conceptualised as a communication system involving messages, media, and audience (Mason, 2004; Nielsen, 2017). Within this framework, museum communication operates through both verbal and non-verbal means, including exhibition-based and non-exhibition-based modalities, situating the museum as a medium that stands in between scientific knowledge and the public sphere. The broader field of science communication provides additional conceptual grounding through models that describe different orientations toward the public. The deficit model assumes a one-way transmission of expert knowledge to an uninformed audience, while dialogic and participatory models emphasise two-way interaction, co-production, and engagement (Navas Iannini et al., 2023). In recent years, participatory and deliberative models have become increasingly relevant in the museum context, reflecting a shift from dissemination to engagement (Arnaboldi & Lema, 2021; Lazzaretti et al., 2024).

Visitor learning in museums has been extensively studied through the framework proposed by Falk & Dierking (2013), who emphasise that learning is shaped by the interplay of personal, social, and physical contexts. Visitors' prior knowledge, motivations, and social interactions influence how they interpret and internalise scientific content. These contexts also determine

the effectiveness of different communication techniques, reinforcing the notion that museum communication must be designed to accommodate heterogeneity in audiences. Additionally, museums have come to embrace their role in promoting public engagement with science, not merely as sites of education but as arenas for negotiation of societal issues and values related to science and technology (Davies et al., 2017). Traditional communication techniques remain a cornerstone of scientific museums, despite growing diversification in approaches. The most established methods involve the use of object displays accompanied by textual panels or labels. Such techniques, though sometimes perceived as static, continue to serve a critical function in presenting information and contextualising objects within scientific or historical narratives (Rovetta & Rovida, 2017). The physical objects themselves act as non-verbal communicative media; their presence and arrangement convey meaning, authenticity, and authority (Rahadi, 2015). However, purely object-centred communication can limit interpretive depth when unaccompanied by interpretive scaffolds such as texts, guided tours, or multimedia. Studies have shown that traditional displays often fail to provoke substantial shifts in visitors' perceptions of science or encourage critical reflection (Rennie & Williams, 2006). To address such limitations, museums have increasingly incorporated interactive and participatory communication strategies. Hands-on interactive exhibits, often found in science centres, enable visitors to engage directly with scientific phenomena by manipulating variables and observing outcomes. Such exhibits foster active participation, inquiry-based learning, and play, which have been shown to enhance comprehension and retention (Zhao et al., 2022). The use of narrative and storytelling has also gained prominence as an engagement strategy. Storytelling allows complex scientific concepts to be situated within human experiences, connecting abstract knowledge to emotion and meaning (Chakraborty, 2016). By embedding scientific facts within narratives, museums can facilitate deeper cognitive and affective engagement, although such approaches must balance accessibility with scientific rigour.

The integration of digital and media technologies has radically expanded the communicative repertoire of museums. Augmented reality (AR), virtual reality (VR), and mobile applications now allow visitors to experience layered, interactive forms of content that transcend the limitations of physical display. Empirical studies demonstrate that AR in museum environments can

significantly enhance engagement and learning outcomes by rendering content vivid and memorable (Scopigno et al., 2015). Digital visualisation techniques, including cinematic scientific visualisations and planetarium projections, provide powerful means of representing phenomena that are otherwise invisible or abstract (Jensen et al., 2022). Yet, these innovations introduce challenges such as high production costs, technological obsolescence, and the risk that spectacle may overshadow the substance of an exhibition, leaving the user without new knowledge. Furthermore, the digital divide and visitors' varying levels of technological literacy necessitate careful design to ensure inclusivity and accessibility.

Beyond digital enhancement, museums are increasingly adopting participatory and dialogic forms of communication that position visitors as active contributors rather than passive recipients. Public engagement events, citizen science projects, and co-curation initiatives exemplify this participatory turn. Through such initiatives, museums become brokers of participation, facilitating dialogue between scientists and the public, and fostering civic engagement with scientific issues (Bucchi & Trench, 2021). Citizen science projects, for example, invite visitors to contribute data or insights to ongoing research, promoting a sense of ownership and bridging the gap between professional and lay knowledge (Bonney et al., 2016). Co-curation practices, where visitors participate in shaping exhibitions or generating content, further personalise the museum experience and diversify the interpretive voice (Kidd et al., 2020). However, these practices demand significant institutional resources, skilled facilitation, and thoughtful integration into existing curatorial and educational frameworks. Despite the proliferation of new communication techniques, several enduring challenges constrain their effective implementation. Museums must continuously negotiate the tension between scientific accuracy and accessibility, ensuring that content remains both rigorous and comprehensible to varied audiences. Visitor heterogeneity (such as differences in age, background, education, and motivation), requires flexible and layered interpretive strategies (Falk & Dierking, 2013). Moreover, the transition from one-way to interactive communication often necessitates cultural change within institutions, including the development of new skills among staff and a willingness to experiment (Yudhawasthi et al., 2019). The evaluation of communicative effectiveness also remains problematic, as visitor numbers provide limited insight into actual learning or engagement outcomes.

Looking toward the future, several trends appear to be shaping the trajectory of communication in scientific museums. Hybrid physical-digital experiences are likely to become more prevalent, combining tangible exhibits with immersive digital augmentation (Cliffe et al., 2024; Lazzaretti et al., 2024). Visitors’ engagement will continue to drive innovation, enabling adaptive learning experiences tailored to individual preferences and knowledge levels (Lu et al., 2023). Furthermore, the integration of socio-scientific issues (such as climate change, biotechnology, and artificial intelligence) into museum exhibits reflects an emerging commitment to fostering public deliberation around ethically and politically charged topics (Navas Iannini et al., 2023). The ongoing emphasis on inclusivity, accessibility, and sustainability will require institutions to adopt universal design principles and equitable communication practices that reach diverse publics. In conclusion, communication in scientific museums has evolved from object-centred didacticism toward dynamic, participatory, and technologically enriched forms of engagement. Museums now serve as mediators of science in society, i.e. spaces where knowledge, emotion, and dialogue intersect. Their communication techniques must therefore balance intellectual rigor with experiential resonance, ensuring that visitors not only learn about science but also reflect upon its implications for their lives and communities. As museums continue to navigate this transformation, effective communication will remain central to their mission of connecting people with science in a rapidly changing world.

1.2 Virtual palaeontology for museums

Over the past few decades, the study of fossil specimens has undergone a rapid and exponential transformation, driven by technological advancements in digitisation and virtual modelling techniques. Methods such as close-range photogrammetry, surface scanning, and computed tomography (CT) have become increasingly accessible, cost-effective, and efficient. These technologies have catalysed a digital revolution in palaeontological research, enabling the development of new methodologies and analytical approaches (e.g. Davies et al., 2017; Falkingham et al., 2018; Profico et al., 2019; Bartolini-Lucenti & Rook, 2023). This technological shift has led to the emergence of a new sub-discipline known as Virtual Palaeontology, which operates primarily within a digital environment. Here, three-dimensional (3D) digital models of fossil

specimens are utilised for a range of applications, including morphometric analysis, biomechanical simulations, body mass estimates and statistical evaluations. These approaches allow for in-depth investigations into palaeobiology, functional morphology, evolutionary biology, and ecological reconstructions (e.g., Pandolfi et al., 2020).

One significant challenge in traditional palaeontology lies in the taphonomic and diagenetic alterations that often affect fossil remains. These preservation-related artefacts include fractures, disarticulation, compression, fragmentation, and deformation, all of which can obscure the original anatomical features of the organism (Shipman, 1981; Lyman, 1994). Since morphological data form the fundamental stone of palaeontological analysis, such alterations can be the cause of substantial limitations in research. Virtual tools can mitigate these issues by enabling digital restoration techniques, including retro-deformation and target-based deformation, which aim to reconstruct the specimen’s original morphology (Lautenschlager, 2016; Schlager et al., 2018; Cirilli et al., 2020; Bartolini-Lucenti et al., 2024). These digital methods not only enhance the accuracy of morphological reconstructions but also preserve the integrity of the original specimens by avoiding physical intervention. One of the most impactful benefits of virtual palaeontology is the ability to conduct detailed research and analysis without the need for direct manipulation of the original fossil material. After digitisation, fossil specimens can be studied, replicated, and shared in a virtual environment, significantly reducing the risk of damage or degradation.

Natural history museums stand to gain considerably from the integration of digital technologies into their workflows. The digitisation of collections enables the creation of comprehensive online catalogues, which can be managed internally or hosted on open-access platforms that adhere, in the closest possible way, to the FAIR principles (Findable, Accessible, Interoperable and Reusable) (FORCE11, 2014; Wilkinson et al., 2016; Díez Díaz et al., 2026). Popular open access research repositories such as Dryad, Zenodo, and MorphoSource facilitate global access to digital fossil collections, making them available to researchers, educators, and the public without compromising the physical integrity of the originals (Cunningham, 2021). In addition, digital collections serve as powerful tools for science communication, education, and public outreach. High-resolution 3D models allow museums to produce accurate and detailed repro-

ductions of fossil specimens. These models can be explored virtually or physically reproduced through 3D printing. This approach significantly improves accessibility, especially for fragile, oversized, or microscopic specimens that are not suitable for traditional casting techniques. 3D printing also introduces new avenues for inclusive engagement. Tactile replicas of fossils provide educational opportunities for visually impaired individuals, creating a more inclusive learning environment (Reinhardt et al., 2024). Furthermore, scaling replicas - either enlarging microfossils or miniaturising large specimens - allows visitors to engage more meaningfully with palaeontological material, without compromising on anatomical detail or scientific accuracy. Virtual accessibility initiatives, informed by 3D modelling and printing, enable museums to reach remote and underserved audiences. These innovations effectively eliminate geographical and physical barriers, transforming traditional museum experiences and promoting global access to cultural and scientific heritage (Herraiz et al., 2019). The aim is to understand fossils not simply as static objects, but as dynamic elements in ongoing research, and ultimately as a tool to better understand and predict the patterns of evolution of the natural world (Kohlstedt, 2015).

1.3 Aims and Objectives

The aim of this project is to examine the role of virtual palaeontology as a valorisation strategy within museum contexts, with a specific focus on its implications for scientific communication, education, and accessibility. By enhancing practices of communication and public engagement with science and evaluating their impact, this research approaches virtual palaeontological techniques as mediating tools between research, fossil collections, and heterogeneous audiences.

More specifically, the objectives of this study are to: 1. assess the contribution of virtual palaeontological tools to museum communication, particularly in relation to visitor engagement, comprehension of palaeontological processes, and the interpretation of fossil material as active scientific evidence rather than static heritage objects. 2. Examine the capacity of virtual palaeontology to enhance accessibility and inclusivity in museum settings, including the use of digital platforms, three-dimensional visualisation, and physical reproductions such as 3D-printed models. 3. Develop a conceptual framework for the effective employment of virtual

palaeontology as a valorisation tool, integrating research, conservation, education, and public engagement within natural history museums. Through these objectives, the study seeks to contribute to a critical understanding of the potential and limitations of virtual palaeontology in supporting the evolving communicative role of scientific museums and their function as interfaces between science and society, but with an attentive focus on younger generations, hoping to stimulate such audiences to appreciate natural history museums as an active and effective place of entertainment and education.

To address these objectives, the thesis is structured around four different case studies, each exploring the application of virtual palaeontology and museology techniques within different museum and exhibition contexts. The first case study focuses on the valorisation and enhancement of a fossil specimen exhibited in the Museo di Geologia e Paleontologia of the University of Florence (Chapter 2), using tools of virtual palaeontology to test the potential of edutainment activities designed around a 3D-printed copy of the specimen.

The second case study centres on the Farneta Faunal Unit collection housed at the Museo di Geologia e Paleontologia of the University of Florence and adopts a multidisciplinary approach: it combines scientific research (Chapters 3 and 4) and museum valorisation and dissemination strategies through the development of the Linda. website (Chapter 5). This digital platform integrates the scientific outcomes of the research and offers visitors an entirely virtual exploration of the Farneta fossil faunal assemblage, while also addressing the fragmentation of the collection between two institutions by providing a virtual space that unites an otherwise fragmented collection.

The third case study focuses on the development of an ex-novo exhibition at the Urweltsteinbruch Museum in Holzmaden (Chapter 6) and is conceived as a methodological investigation into the full exhibition-making process, from initial concept design to narrative construction and museological strategy, with particular attention to storytelling and visitor experience.

The last case study examines the recontextualisation of selected exhibition items from the main hall of Den Blå Planet aquarium in Copenhagen into its restaurant area (Chapter 7), employing virtual palaeontological techniques to transform a primarily recreational space into an environment of exhibition and edutainment. The aim is to test the potential of digital tools

to extend scientific communication beyond traditional display areas.

2 VALORISATION OF A PERMANENT FOSSIL EXHIBIT: POGGIO ROSSO’S FOSSILIFEROUS BLOCK

2.1 Introduction

2.1.1 The Villafranchian vertebrate collection in the museum of Geology and Palaeontology of Florence

The Museum of Geology and Palaeontology of Florence (IGF, short for the former name of the museum: Istituto Geologico Fiorentino) preserves one of the most comprehensive and scientifically significant collections of Plio-Pleistocene continental vertebrates worldwide, comprising approximately 15,000 catalogued specimens (Fig. 2.1; Monechi & Rook, 2009). The origins of this collection date back to the early seventeenth century, when fossils were first gathered and donated under the patronage of Grand Duke Cosimo III de’ Medici (Monechi & Rook, 2009; Bellucci et al., 2025). Later centuries saw the continuous expansion of the assemblage through systematic excavation campaigns and private donations. A substantial portion of the vertebrate material comes from the Upper Valdarno Basin, an area of exceptional paleontological importance in Central Italy. Fossil recovery from this region was particularly intense during the eighteenth and nineteenth centuries, and today specimens from the Valdarno Basin comprise nearly 70% of the museum’s vertebrate holdings (Bellucci et al., 2025). The collection thus provides an invaluable record of the evolutionary and ecological dynamics that characterised the Upper Valdarno vertebrate fauna during the Villafranchian Mammal Age, between approximately 3.3 and 1.0 million years ago (Azzaroli, 1977, 1998; Cherin et al., 2023).

The Villafranchian represents a crucial interval of faunal communities’ evolution, from the late Pliocene to the end of the Early Pleistocene. It is subdivided into several Faunal Units, each defined by distinctive faunal assemblages and associated climatic regimes, which together reflect the complex interplay of environmental and tectonic factors shaping the region during this time (Azzaroli, 1977; Cherin et al., 2023). In the earliest phases, climatic conditions were predominantly warm and humid, supporting subtropical forest ecosystems inhabited by taxa such as tapirs (*Tapirus arvernensis* Croizet and Jobert, 1828) and mastodons (*Anancus*



Figure 2.1: The Villafranchian gallery of the Museum of Geology and Palaeontology of Florence that hosts Upper and Lower Valdarno specimens. On the left: the Poggio Rosso fossiliferous block.

arvernensis Croizet and Jobert, 1828).

Around 2.6 million years ago, the maximum expansion of the polar arctic cap caused a major global climatic reorganisation that marked the onset of the Quaternary glacial–interglacial cycles, characterised by periodic oscillations of approximately 41,000 years (Mazza et al., 2004). This climatic shift led to the gradual replacement of subtropical forests with more temperate and open habitats, accompanied by the expansion of grasslands and steppe environments. In response, the faunal composition of the Valdarno Basin underwent significant turnover, with the appearance and diversification of taxa adapted to more arid and seasonal conditions, including equids, bovids, cervids, suids, and a diverse assemblage of carnivores (Bartolini-Lucenti & Rook, 2016). Today, the fossil material curated and displayed in the IGF not only provides a comprehensive overview of the faunal succession of the Upper Valdarno but also constitutes a key reference for understanding the palaeoenvironmental and biostratigraphic framework of the Plio-Pleistocene in the Mediterranean region. Through its scientific, educational, and heritage

value, the collection stands as an enduring testament to centuries of research and to the dynamic history of Earth's climatic and ecological transformation.

2.1.2 The Poggio Rosso fossiliferous block and aims of the study

In this study, one specimen of the Villafranchian collection of the IGF was selected to test an innovative approach for museum communication and valorisation. The fossiliferous block of Poggio Rosso (catalogued as IGF 9315V; Fig. 2.2) occupies a prominent position at the entrance of Hall II of the Museum, where vertebrate fossils from the Villafranchian Mammal Age are displayed.

The discovery of the Poggio Rosso site dates to 1995, when the SO.LA.VA brick factory - active in the Matassino clay pit (Arezzo, Tuscany) since the 1950s - accidentally exposed a fossiliferous layer approximately five meters long and one to two meters thick. The site (Fig. 2.3), situated on the right bank of the Arno River on a hill locally known as Poggio Rosso (named for the characteristic reddish paleosols that crop out in the area), yielded an abundant and well-preserved vertebrate assemblage (Napoleone et al., 2001). Excavations were promptly undertaken by the staff of the IGF, in collaboration with SO.LA.VA personnel. Over one thousand bone remains were recovered, alongside numerous coprolites and fossiliferous blocks (Napoleone et al., 2001).

The largest and most significant block (IGF 9315V) was transferred to the palaeontology laboratories of the museum for restoration and conservation. Following its preparation, the specimen was first exhibited temporarily in 1997 and later incorporated into the museum's permanent exhibition in 2003 (Mazza, 2006). Measuring 178 cm in length and reaching a maximum height of 25 cm from the base to the tip of the *Ursus etruscus* Cuvier, 1822 skull, the block has both surfaces exposed. This preparation enables visitors to observe the fossil remains on both sides. In its current display, the lower surface is made visible through mirrors installed beneath the block, enabling a full three-dimensional appreciation of the fossil arrangement (Fig. 2.4). The skeletal content of IGF 9315V consists of a dense concentration of sub-horizontally oriented bones belonging to various vertebrate taxa: *Eucladoceros dicranios* Nesti, 1841, *Pseudodama farnetensis* Azzaroli, 1992, *Homoterium crenatidens* Fabrini, 1890,



Figure 2.2: Picture and coloured sketch of IGF 9315V with the most present taxa bone remains highlighted, displayed in the illustration panel in front of the specimen, courtesy of IGF. The taxa and relative anatomical remains are: *Equus stenonis* (skull, in light blue); *Sus strozzii* (mandible and foot bones, in purple); *Eucladoceros dicranios* (scapula, mandible and limb elements, in green), *Castor plicidens* (two mandible fragments, in orange), *Leptobos etruscus* (femur and tibia, in magenta), *Homotherium crenatidens* (scapula and forelimb, in light orange), *Ursus etruscus* (skull, in brown), *Canis arnensis* (left and right hemimandibles, in yellow), *Pachycrocuta brevirostris* (coprolite, in gray).

Ursus etruscus Cuvier, 1822, *Castor plicidens* Major, 1877, *Sus strozzi* Major, 1881, *Canis arnensis* Del Campana, 1913, *Pachycrocuta brevirostris* Gervais, 1852 (Schematic overview in Fig. 2.2). Many elements are preserved in anatomical connection or close association, including articulated limb bones and skulls with mandibles still attached. The assemblage is mainly characterised by the presence of herbivorous taxa, but displays a particularly rich number of carnivores remains, with an abundance of coprolites attributed to the giant hyena *Pachycrocuta brevirostris*. The bones show limited weathering and frequent evidence of gnawing and bite marks, consistent with scavenging or predatory activity. These taphonomic indicators suggest that Poggio Rosso may represent a kill site or den associated with *P. brevirostris*, although the depositional context also reflects the influence of other sedimentary and post-depositional processes (Mazza et al., 2004; Mazza, 2006).

The Poggio Rosso block constitutes a powerful tool for the communication and valorisation of the Plio-Pleistocene heritage of the Upper Valdarno. Its display in the IGF exemplifies the intersection between scientific research, conservation, and public engagement, transforming a complex palaeontological record into an accessible narrative of evolutionary and environmental change.

To further enhance the dissemination potential of the Poggio Rosso block, we designed educational activities for families and children, based on a 3D-printed model of the block, so that visitors can interact with the replica without compromising the integrity and preservation of the block itself. First, we digitized the specimen using close-range photogrammetry. Once the 3D model was obtained, we proceeded with digital manipulation of the latter, in order to virtually extrapolate each bone individually from the block. Every isolated bone was then 3D printed separately from the block, and the final replica was employed in a series of educational activities designed specifically for the valorisation of the Poggio Rosso fossil block.

2.2 Geological setting

The fossiliferous deposit of Poggio Rosso is located near the locality of Matassino, in the southeastern sector of the Upper Valdarno Basin (Arezzo, Tuscany, Central Italy). This basin forms part of a wider system of extensional intramontane basins of the Northern Apennines

that developed during the Neogene - Quaternary, due to post-orogenic crustal thinning and associated normal faulting of the Africa - Eurasia collision zone (Carmignani et al., 2001; Ghinassi et al., 2025). Structurally, the Upper Valdarno represents a half-graben depression bounded by the Pratomagno fault system and the Chianti mountains. The basin is filled by a thick continental succession, predominantly of lacustrine and fluvio-lacustrine origin, that records the progressive infilling of the basin from the late Pliocene to the early Pleistocene (Fig. 2.3; Benvenuti, 1992; Fidolini et al. 2013).

The sedimentary succession, exceeding 800 m in thickness, documents a complex alternation of depositional environments reflecting both tectonic subsidence and climatic oscillations, which controlled the stratigraphic architecture of the basin (Bertini et al., 2013). The filling deposits of the Valdarno basin have been extensively studied in the last century (Sestini, 1936; Abbate, 1983), leading to the recognition of three main unconformity-bounded stratigraphic units (Merla & Abbate, 1967; Azzaroli & Lazzeri, 1977; Sagri & Magi, 1992; Ghinassi & Magi, 2004) that characterise the evolution of the basin. More recent works (Fidolini et al., 2013) divide the Valdarno basin succession into four synthems, following the scheme adopted by the CARG project (Sagri et al., 2012): Castelnovo dei Sabbioni (CSB); Montevarchi (VRC) and Fosso Salceto (OLC), and the Torrente Ciuffenna (UFF) Synthems. Sedimentary units were further identified within each synthem and are defined on the basis of their sedimentary facies and lithology (Ghinassi et al., 2025). The first synthem is characterised by fluvial to deltaic deposits, the VRC and OLC synthems are coeval and defined by alluvial to fluvial and palustrine deposits, whereas the Torrente Ciuffenna unit is characterised by fluvial to alluvial fan deposits (Ghinassi et al., 2025 and references therein). Several studies focused on the chronological analysis of the basin succession (Torre et al., 1993; Albanelli et al., 1995), until it was reviewed and refined by Napoleone et al. (2003) and later calibrated by Ghinassi et al. (2004). The Matassino area, on the right bank of the Arno River, lies within the uppermost portion of the fluvio-lacustrine succession, corresponding to deposits attributed to the Tasso Faunal Unit (1.9–1.8 Ma; Napoleone et al., 2001). These sediments consist mainly of fine-grained clayey-silty layers interbedded with sandy lenses and palaeosols, representing the distal facies of a floodplain environment periodically influenced by fluvial and ephemeral lacustrine dynamics (Benvenuti,

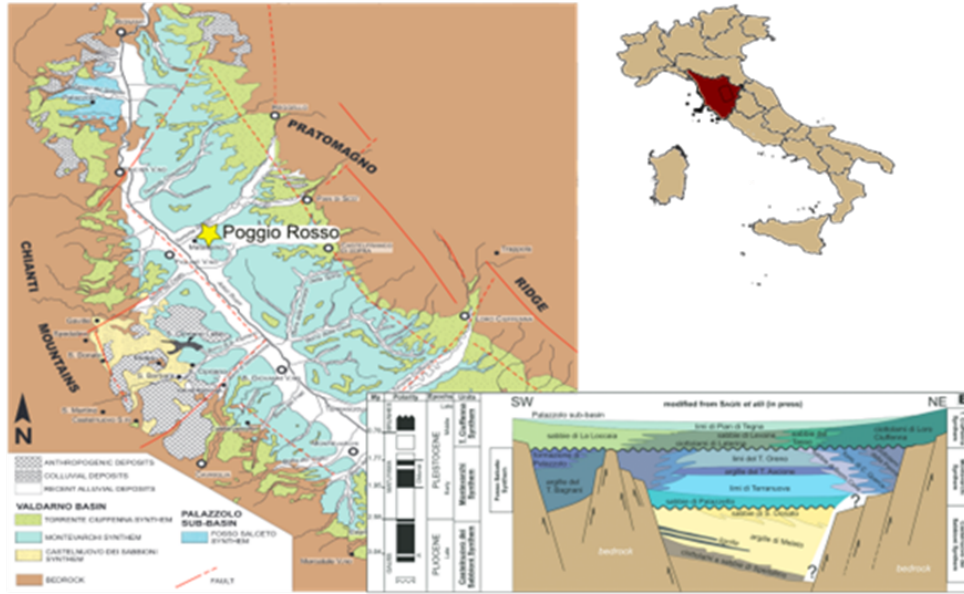


Figure 2.3: Geological map of the Upper Valdarno basin with Poggio Rosso locality highlighted. Modified after Fidolini et al. (2013).

1992). The reddish hue of the local palaeosols, which inspired the toponym “Poggio Rosso,” is the result of pedogenic processes under semi-arid conditions, marked by alternating wet and dry phases that promoted iron oxidation and soil concretion formation (Mazza et al., 2004). Such stratigraphic features are consistent with the climatic transition toward more open and arid landscapes that characterised the late Villafranchian, following the onset of the Quaternary glacial–interglacial cycles (Mazza et al., 2004).

Palaeomagnetic and biostratigraphic correlations have placed the Poggio Rosso fossil-bearing level within the Olduvai subchron, dated between 1.95 and 1.78 Ma (Napoleone et al., 2001). The sedimentological context of the deposit - composed of cohesive silty clays intercalated with sandy levels - favoured the rapid burial and exceptional preservation of vertebrate remains, which are found in a sub-horizontal orientation and frequently in anatomical connection (Mazza et al., 2004).



Figure 2.4: Digitisation attempts through photogrammetry (left) and light-structured scanning (right) of the whole fossiliferous block.

2.3 Methods

2.3.1 Digitisation

The block (Fig. 2.2) is characterised by a complex morphology: highly irregular surface, numerous cavities and undercuts produced by the densely packed fossil bones. For these reasons its digitisation presented several technical challenges. In addition, the bottom side of the block is prepared and displays fossil bones, which are visible to visitors through a fixed reflecting glass placed underneath the block. This setting makes the digitisation of the bottom side of the block particularly challenging. Initially, structured-light scanning was tested using Artec Eva and Artec Micro devices. While these scanners are widely used in heritage digitisation for their accuracy and ease of use (Menna et al., 2016; Bartolini-Lucenti et al., 2024), their performance proved inadequate in this case. The restricted working distance and limited accessibility to the lower surface prevented full coverage, together with the complex geometry of the upper and lower surfaces, resulting in extensive data gaps and errors in the generated mesh. A close-range structure-from-motion (SfM) photogrammetric approach was adopted, following successful precedents in fossil and museum specimen documentation (Wings & Mallison, 2015; Falkingham et al., 2018; Puerta et al., 2020). A Canon EOS 70D DSLR camera equipped with a Canon 10–18 mm STM lens and a continuous LED ring light was used to acquire 1,713 high-

resolution images in JPEG format. The camera settings were optimised for consistent exposure and depth of field, in accordance with best practices for palaeontological photogrammetry (Wings & Mallison, 2015). The upper surface was photographed freehand, while the lower side was captured using an extendable pole, allowing constant focal distance and uniform illumination between the two surfaces. The photogrammetric reconstruction was processed in Agisoft Metashape Professional (v. 2.0.3), which generated a high-fidelity 3D mesh composed of approximately 206.6 million polygons, with an average spatial resolution of 0.25 mm. To optimise the model for interactive and printing purposes, the mesh was down sampled to 10 million polygons without perceptible loss of detail and subsequently exported as a Stanford PLY file. Because the workflow’s objective was to produce a manipulable 3D print rather than a photorealistic rendering, texture mapping was not applied.

2.3.2 Digital manipulation

Digital post-processing was carried out using Autodesk Meshmixer (v. 3.5.474), a software commonly used in palaeontological 3D modeling to prepare meshes for analysis or printing (Peterson et al., 2021). The software "select" and "separate" functions were used to isolate specific skeletal elements from the surrounding matrix. The open surfaces generated during this segmentation were repaired using the "make whole" and "bridge" functions to ensure watertight geometry. To transform the model into an interactive educational tool, a cubic keying system was designed: small cubes were digitally added to the base of each isolated element and subtracted from the block’s corresponding cavities, generating a 3D puzzle that enables physical assembly and disassembly of the parts (Fig. 2.5). To compensate for potential printing tolerances, the cubes on the isolated elements were modelled slightly smaller than the cavities in the block mesh. Because of some Meshmixer limited stability issues and its last update in 2018, some topological errors and processing slowdowns occurred. A final verification was necessary and was carried out together with the mesh correction phase in Blender (v. 3.5), which provided superior control and computational performance.

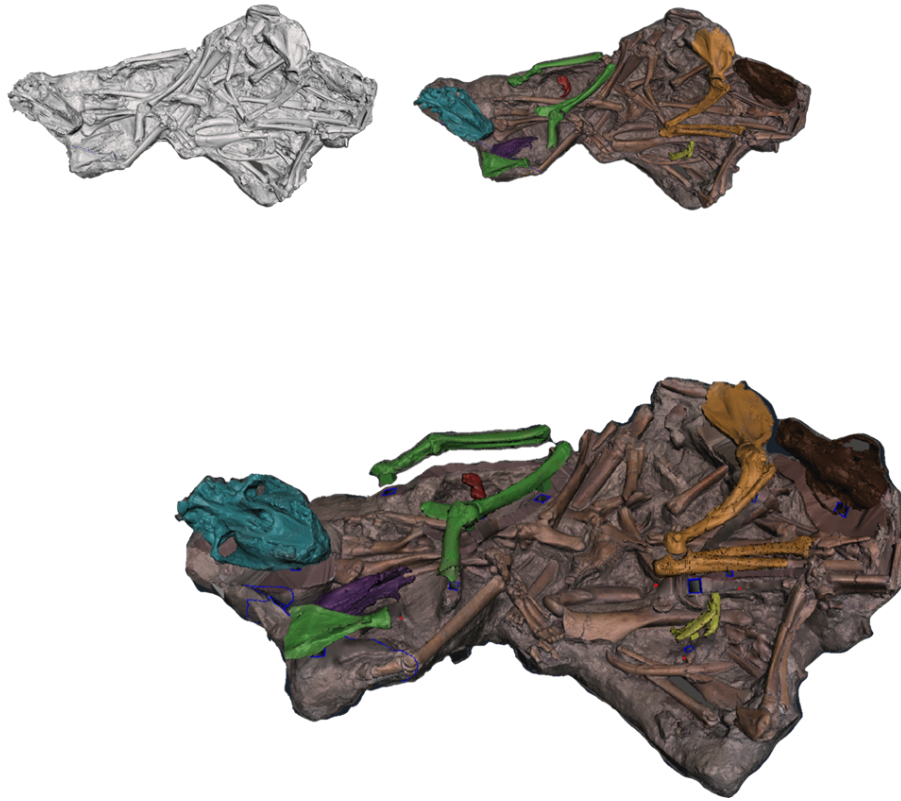


Figure 2.5: Virtual manipulation of the digitised specimen in the MeshMixer workspace. In colour are highlighted the fossil bones selected for “virtual extraction”.

2.3.3 3D printing

Additive manufacturing was performed using a Formlabs Form 3 SLA printer. The final model, scaled to one-sixth of the original (approximately 30 cm in length), accurately reproduces the morphology of the original fossil block, providing a durable and portable replica for educational handling and exhibition (Fig. 2.6). Due to the constraints of the printer’s build volume (145x145x185 mm), the block was divided into three parts, which were subsequently assembled using resin-based adhesive (Fig.2.6). All components were printed with Formlabs Grey Resin and hand-finished with Molotow acrylic paints to enhance visual contrast between the bones and matrix.

2.3.4 Educational activities

To test the potential of dissemination and edutainment of the Poggio Rosso’s block 3D replica, two different activities were designed. These projects involved consultation with museum curators to make sure the planning considered feasibility inside the museum halls and hallways,

with museum educational directors and operators and a palaeo-artist who curated designs and graphics for the material used during the activities.

2.4 Results

2.5 3D printed replica

The results demonstrate that the photogrammetric approach provided a detailed and accurate digital reconstruction of both sides of the Poggio Rosso block. Despite the presence of minor artefacts in the digitally separated bones, mainly affecting non-visible lower surfaces, these did not compromise the overall interpretive or educational value of the model. Future iterations of the workflow may benefit from the integration of computed tomography (CT) scanning to facilitate more precise segmentation of fossil bones from their sedimentary matrix, enhancing both morphological fidelity and potential for scientific study (Mazza et al., 2004; Mazza, 2006; Sutton et al., 2014).

2.5.1 Educational activities

The first application of the 3D Poggio Rosso’s block replica to educational activities took place in December 2023 during the museum’s annual summer camp program. For this activity, five replicas of the Poggio Rosso block were printed and distributed amongst eight children aged 6 to 12 years. The workshop began with an introductory session in the exhibition hall, where participants were presented with the original fossil block and guided through its geological context, age, taphonomic history, and the diversity of vertebrate taxa represented. This phase emphasised direct observation and scientific narration, promoting curiosity and contextual understanding. The activity then moved to the museum’s educational laboratory, where participants were invited to handle the 3D replicas. Using brushes and paint, the children reassembled the bones into their correct positions and subsequently painted each taxon in different colours to visually identify species (Fig. 2.8). This hands-on, multisensory approach stimulated creativity and motor coordination, while reinforcing key palaeontological concepts through play and artistic engagement—an approach aligned with constructivist educational models in informal science learning (Letourneau et al., 2017; Olesen and Holdgaard, 2024).

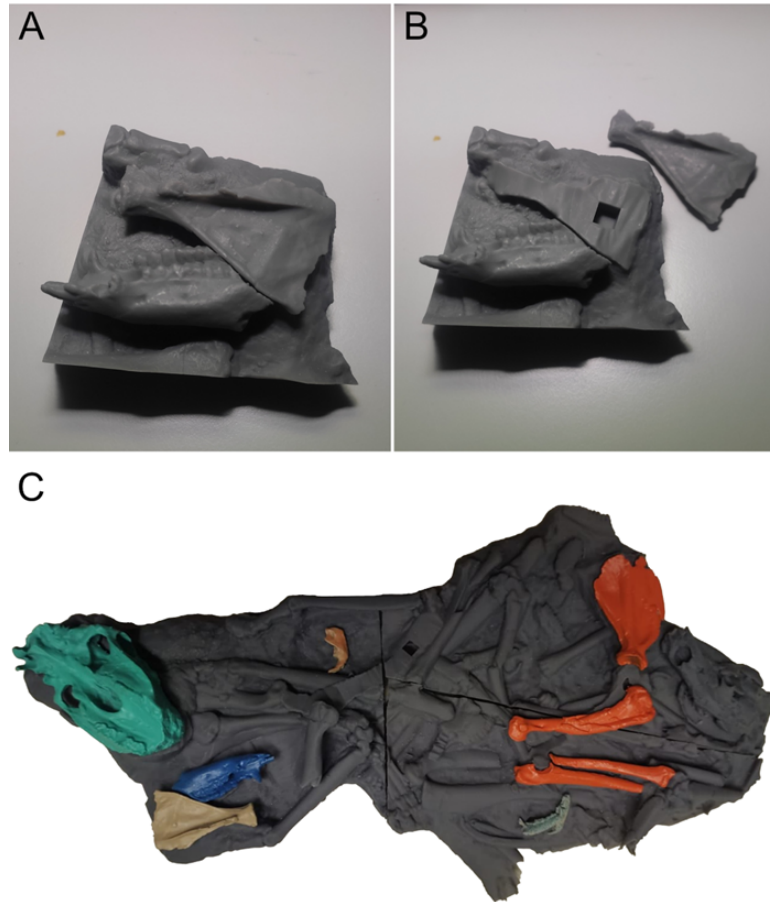


Figure 2.6: Printed small section of the whole fossiliferous block (A), showing the replica of an *Eucladoceros dicranios* scapula as a separate jigsaw piece (B). C) First 1:6 replica of the Poggio Rosso's block 3D- printed, with some of the jigsaw bones coloured based on their taxon.

A second, more complex educational workshop was conducted in May 2024 as part of “Firenze nei Musei” (“Florence in the Museums”) program, a public initiative organised by the Municipality of Florence to promote families’ participation in local cultural institutions. The event, titled “Mystery at the Museum: Let’s Explore the Tuscan Palaeoenvironment of Two Million Years Ago,” was specifically designed to deepen participants’ understanding of fossil accumulation processes and the ecological dynamics of the Villafranchian faunal assemblage. Children aged 6 to 11 were divided into small investigative teams and guided by museum educators in an interactive exploration of the exhibit. The activity required participants to examine both the physical fossil block and its 3D-printed replicas to identify the species represented within the accumulation. By comparing morphological features of the printed bones

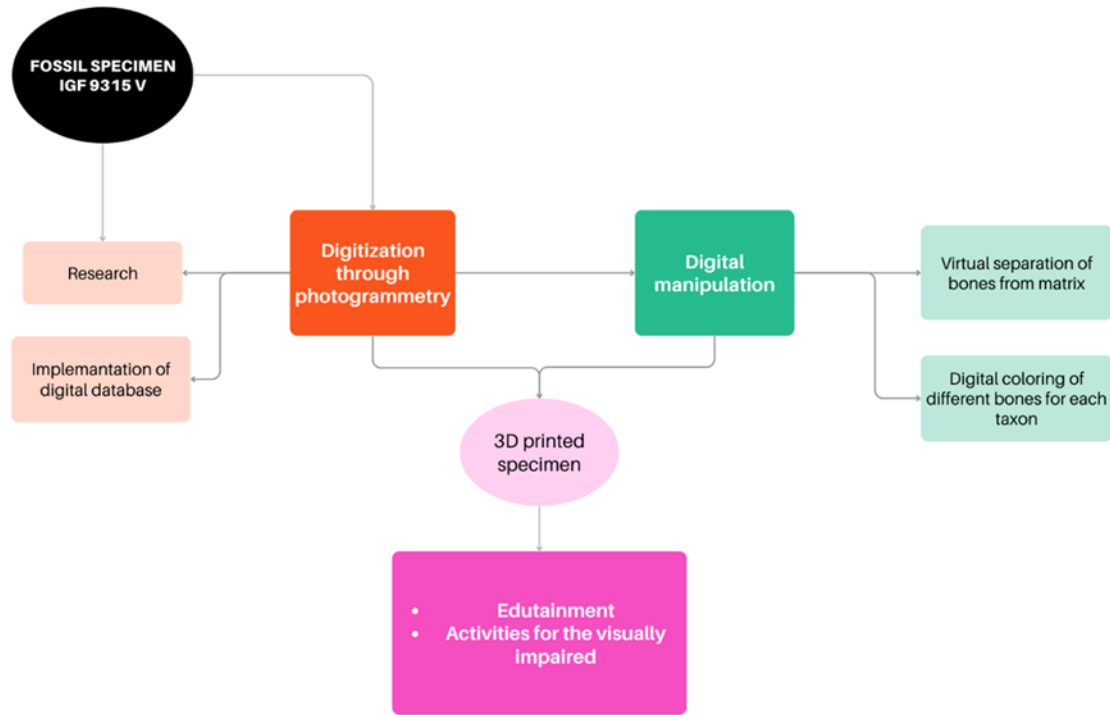


Figure 2.7: Scheme of workflow for the valorisation of the specimen process, starting from digitisation and leading to various outcomes.

with labelled specimens displayed throughout the museum, and following colour-coded clues, participants were encouraged to connect anatomical observation with deductive reasoning. The use of “detective cards” reinforced the investigative aspect of the task, as each group formulated and presented hypotheses on the origin of the fossil deposit, emulating scientific reasoning processes. This format effectively merged inquiry-based learning with storytelling and game design, promoting autonomy, teamwork, and critical thinking. Building upon these positive results, a permanent educational laboratory was developed for the museum’s official school program.

This iteration retained the “mystery-solving” framework but was relocated entirely to the museum’s teaching laboratory, offering an environment better suited for detailed observation and reflection. Participants - guided by educators - used the 3D-printed bones to analyse taphonomic evidence such as bone fractures, bite marks, and coprolites, as well as to compare morphological differences among species. Through these analytical exercises, students reconstructed the ecological and behavioural interactions that led to the formation of the Poggio Rosso fossil assemblage. This activity encouraged scientific learning by immersing students in a simulated research process, bridging the gap between abstract palaeontological knowledge

and experiential understanding (Fig. 2.7).

2.6 Discussion

The outreach potential of the 3D-printed replicas and of the 3D puzzle of the Poggio Rosso fossil block was systematically evaluated through a series of educational initiatives aimed at children and family audiences (Fig. 2.8). These activities were designed to test the pedagogical effectiveness of 3D reproductions as tools for science communication, experiential learning, and cognitive engagement within a museum setting. The underlying premise was that digital fabrication technologies, when integrated into educational design, can enhance the visitor’s sense of discovery and foster a deeper connection with palaeontological heritage through tactile interaction and collaborative problem-solving (Jermstad, 2025). Overall, the integration of 3D-printed replicas into the museum’s educational programs has proven to be an effective tool for enhancing the learning experience of children and families. The combination of tactile interaction, narrative immersion, and visual exploration aligns with current best practices in informal science education and museum pedagogy, fostering long-term interest in Earth sciences and natural history. Preliminary feedback gathered through anonymous forms at the end of each activity indicates a notable increase in visitor engagement and comprehension of complex palaeontological concepts through these participatory activities.

In the near future, further adaptations will focus on accessibility, including the design of tailored activities for visually impaired visitors, thereby extending the inclusivity and social impact of the museum’s educational initiatives. In the case of the Poggio Rosso, the integration of digital fabrication into educational practice exemplifies the pedagogical value of “experiential authenticity,” wherein the tactile interaction with scientifically accurate reproductions allows non-specialists (particularly children) to engage with complex concepts such as taphonomy, stratigraphy, and palaeoecology in a tangible and comprehensible manner. This approach aligns with constructivist learning theories, which show that knowledge construction is most effective when learners physically interact with objects and environments, activating both cognitive and sensory dimensions of understanding (Falk & Dierking, 2018; Kenderdine, 2021). Moreover, such strategies embody a “dialogical museology” (Dysthe, 2021), where the museum



Figure 2.8: The activity that was carried out during the Museum winter camp in December 2023.

ceases to act as a transmitter of static knowledge and becomes a mediator of shared inquiry instead, inviting audiences to participate in scientific reasoning processes. The incorporation of technologies such as 3D printing and virtual modelling further contribute to the accessibility to cultural heritage. By generating high-resolution digital surrogates of fragile or inaccessible specimens, institutions can expand their educational reach beyond the physical museum space, fostering global participation and interdisciplinary collaboration.

The Poggio Rosso project is a testament to how digital museography can transform traditional communication paradigms. Beyond the immediate benefits for public engagement, such practices also contribute to the conservation, documentation, and long-term valorisation of geo-palaeontological heritage, reinforcing the role of Natural History museums as both scientific and societal institutions.

2.7 Conclusions

The Poggio Rosso's block replica outreach activities represent a significant step forward within a broader transformation in museum communication strategies, shifting from object-centred

display models to participatory and experience-based learning frameworks.

Beyond its technical success, the digitisation of IGF 9315V represents a tested model for integrating 3D technologies into museum practice (Fig.2.7). The resulting dataset supports multiple applications: (1) research, including morphometric and taphonomic analysis; (2) digital restoration and conservation planning (Cirilli et al., 2020); (3) database enhancement for the Museum of Geology and Palaeontology's growing 3D archive, which currently includes approximately 300 digital holotypes (Bartolini-Lucenti & Rook, 2023); and (4) educational and interpretive innovation through interactive and augmented reality (AR) visualisation. The implementation of AR platforms has already proven highly effective in enhancing visitor engagement and scientific literacy in museum contexts (Akçayır & Akçayır, 2017; Bartolini-Lucenti et al., 2024), and its future application to the Poggio Rosso block may further bridge the gap between research and public understanding of palaeontological heritage.

3 FAUNAL REVIEW OF THE FARNETA FAUNAL UNIT

3.1 Introduction

3.1.1 Valorisation of the collection of the Farneta Faunal Unit

The Halls V and VI of the Museum of Geology and Palaeontology of the University of Florence exhibit the “giants” of the Plio-Pleistocene of Tuscany. In Hall V visitors find two specimens displayed next to each other. On the left, a partially reconstructed skeleton of *Anancus arvernensis*, recovered in 1886 by Filippo Nesti in the Upper Valdarno basin. On the right, a partial skeleton of a female *Mammuthus meridionalis*, recovered in 1973 in the locality of Farneta (Val di Chiana, Central Italy). This huge - yet incomplete - specimen was found during excavation activities meant to extract sandstone to build the national highway A1 (Autostrada del Sole).

The Farneta village is a rural area where agriculture is the main activity. The continental deposits that cover the area are exceptionally rich in fossils; their recovery was also further enhanced by the numerous sand quarries temporarily exploited for the highway construction, so much so that its corresponding Faunal Unit takes the name from the village: the Farneta F. U. (Gliozzi et al., 1997). The fossil collection is now under the supervision of the Museum of Geology and Palaeontology of Florence, but it is housed in two different locations. To honour the work and dedication of the local priest of the Farneta Abbey on the fossil specimens of the area, part of the collection was transferred to a permanent exhibit in the Farneta village in 2010: the Mostra Paleontologica of Farneta (acronym: Mo.Pa.).

The sand quarry where the remains of the *M. meridionalis* specimens were found (Cava Liberatori) yielded numerous other fossils, although mostly poorly preserved. The fossils recovered include cranial fragments, upper and lower jaws, isolated teeth, as well as post-cranial elements of various species. They were collected and stored in the IGF storage area until they were recently rediscovered. Specimens were stored in a wooden crate, divided into plastic bags, each with its own field note indicating the specimen’s position relative to the *M. meridionalis* skeleton. Nonetheless, no specimen had been catalogued, and in most cases fossil elements were still mostly covered in matrix. Apart from the specimens exposed at the IGF, most of the

collection is kept in the museum storage area and not accessible to the public. This case study is rooted in the idea of unveiling the whole collection to the public and of communicating to the visitors its history and its scientific value. However, since only a few and old studies were available on the fossil assemblage, further investigation about the taphonomy and the faunal assemblage of the locality was needed and is being carried out.

The following chapters are therefore structured: Chapter 3 is dedicated to the review of the faunal assemblage of the Farneta Faunal Unit. In this work, the focus is only on equids, whereas other taxa are currently under review by other members of the research team (see Parparousi et al., 2024). Chapter 4 deals with the taphonomy of the elements recovered from the sand quarry Cava Liberatori. The aim is to shed light on the palaeo-environment and on the nature of the fossil assemblage. Chapter 5 focuses on valorising and unveiling the collection through the “Project Linda.”: a digital platform built to share and communicate with a wider audience the results of the previous works, to shed light on specimens that are not currently on display, and to virtually merge the fossil heritage of two institutions that share fossils from the Farneta area to better valorise the entire fossil assemblage.

3.1.2 The Farneta Faunal Unit

Italian continental deposits and fossil assemblages dated between 3.5 and 1.2 Ma are commonly attributed to the Villafranchian European Land Mammal Age (ELMA; Pareto, 1865; Rook & Martínez-Navarro, 2010), which also encompasses faunal assemblages from numerous other European localities (Cherin et al., 2023). This time interval has been subdivided into Faunal Units (F.U.s), which act as chronological markers for defined faunal assemblages, reflecting specific bioevents that mirror climatic, environmental, and evolutionary changes influencing species’ eco-morphotypes. Since their initial definition (Azzaroli, 1977, 1983) and the formal establishment of 17 Italian F.U.s by Gliozzi et al. (1997), several revisions and refinements have been undertaken. Consequently, while some F.U.s have been extensively studied and temporally constrained, others remain dated only by relative methods, lacking corroboration from independent proxies such as magnetostratigraphy, micropalaeontology, or radiometric dating techniques (Cherin et al., 2023).

The Farneta F.U. is positioned between the older Tasso F.U. (ca. 1.8 Ma) and the younger Pirro Nord F.U. (ca. 1.5–1.2 Ma), with an estimated age range of 1.6–1.4 Ma (Gliozzi et al., 1997). Three Local Faunal Assemblages (LFAs)—Farneta, Selvella, and Pietrafitta—are referred to this unit (Azzaroli, 1977; Gliozzi et al., 1997; Rook & Martínez-Navarro, 2010; Petronio et al., 2011; Martinetto et al., 2014). The fossil assemblages from these sites have been investigated by numerous authors. Early works by Azzaroli & Ambrosetti (1970) and Ambrosetti et al. (1972) documented two distinct faunas in the northern hills surrounding the Farneta Abbey: a Late Villafranchian and a Galerian assemblage. The former was later used by Azzaroli (1977) to define the Farneta F.U.. The original Farneta Local Fauna (LFA), as reported by Azzaroli (1977) and Azzaroli & Ambrosetti (1970), included the following taxa: *Archidiskodon* (= *Mammuthus*) *meridionalis vestinus*, *Equus stehlini*, *Dicerorhinus* (= *Stephanorhinus*) *etruscus*, *Leptobos etruscus*, “*Leptobos*” *vallisarni*, *Dama nestii* (?), *Eucladoceros* sp. (?), and *Homotherium* sp. Additional taxa listed by Azzaroli (1977) for the Farneta F.U. include *Macaca florentina* (?), *Ursus etruscus* (?), Bovidae indet., *Sus strozzii*, *Hippopotamus major* (= *antiquus*), and *Libralces* (= *Cervalces*) *gallicus*. De Giuli (1986) described the Selvella LFA, comprising Elephantidae indet., *Sus* sp., *Lynx issiodorensis*, *Canis etruscus*, *Leptobos* sp., *Eucladoceros* cf. *dicranios*, *Dama* cf. *nestii*, and *Equus* cf. *stenonis*. The Pietrafitta LFA includes *Bison* (*Eobison*) *degiulii*, *Castor fiber plicidens*, *Equus* sp., *Eucladoceros* sp., *Macaca sylvana florentina*, *Mammuthus meridionalis*, *Praemegaceros obscurus*, *Microtus* (*Allophaiomys*) cf. *chalinei*, *Microtus* (*Allophaiomys*) cf. *ruffoi*, *Mimomys pusillus*, *Oryctolagus* cf. *lacosti*, *Pannonictis nestii*, *Pseudodama farnetensis*, *Sciurus* sp., *Sorex* cf. *minutus*, *Stephanorhinus etruscus*, *Talpa* sp., and *Ursus etruscus* (modified after Sorbelli et al., 2021, 2023). In subsequent decades, the Farneta F.U. fauna has undergone multiple taxonomic revisions. Azzaroli (1983) expanded the known assemblage by adding *Equus stenonis*, *Leptobos* sp., and tentatively *Panthera toscana* and *Pachycrocuta brevirostris*. Later, Azzaroli (1992) reviewed Villafranchian cervids from Tuscany, erecting the genus *Pseudodama* and the species *Pseudodama farnetensis* for the specimens previously assigned to “*Dama nestii*” from different sites in the Farneta surroundings (La Villa, Cava Liberatori, and Casa Palazzi) and Selvella.

Among other significant taxa, Abbazzi (1995, 2004) identified *Praemegaceros obscurus* from

Val di Chiana (Cava Liberatori, Farneta) and Pietrafitta. Palombo & Ferretti (2005) re-evaluated *Mammuthus meridionalis vestinus* (Azzaroli, 1972), suggesting that these remains should be included within *M. meridionalis* without subspecific distinction; they also confirmed the occurrence of *M. meridionalis* at Pietrafitta. Following Abbazzi (2004), Rook & Martínez-Navarro (2010) reported the first appearances of *Pr. obscurus* and *Stephanorhinus* cf. *hundsheimensis* (Alberdi et al., 1998) within the Farneta F.U.. However, recent studies (Pandolfi et al., 2017; Pandolfi & Erten, 2017; Cirilli et al., 2020a) indicate that the earliest occurrence of *S. hundsheimensis* in the Italian Peninsula is from Lefte (Jaramillo subchron; Vialli, 1956; Pandolfi & Erten, 2017), and that the rhinocerotid remains from Farneta F.U. localities, including Pietrafitta, are more appropriately attributed to *Stephanorhinus etruscus* (pending further revision).

Masini et al. (2013) documented *Leptobos vallisarni* from Selvella, Casa Palazzi, and Pietrafitta, although more recent analyses have reclassified the Pietrafitta bovid as *Bison (Eobison) degiulii* (Sorbelli et al., 2023). Finally, Alberdi & Palombo (2013a) reported the presence of *Equus suessenbornensis* and *Equus altidens* in the Selvella assemblage.

3.2 The evolution and dispersal of equids during the Pleistocene

The fossil record of European Early Pleistocene equids has been well deciphered during the last decades. Since the early works of the last Century (Azzaroli, 1964, 1982, 1990, 2000, 2003; De Giuli, 1972, 1986; Eisenmann, 1980, 2004; De Giuli & Masini, 1986; De Giuli et al. 1986; Alberdi & Ruiz Bustos, 1985, 1989; Koufos, 1992; Koufos & Kostopoulos, 1993; Alberdi et al., 1997, 1998; Koufos & Vlachou, 1997; Koufos et al., 1997; Forsten, 1999), their biochronology and palaeobiogeography have been constantly updated and revised, allowing to obtain a well-represented scenario through space and time (Petronio et al., 2011; Alberdi & Palombo, 2013a, 2013b; Palombo & Alberdi, 2017; Palombo et al., 2017; Bernor et al., 2018, 2019, 2021; Boulbes & Van Asperen, 2019; Rook et al., 2019; Cherin et al., 2021; Cirilli et al., 2020a, 2020b, 2021a, 2021b, 2021c, 2022, 2023a, 2024a; Cirilli, 2022; Eisenmann, 2022a, 2022b; Eisenmann & Boulbes, 2020; Gkeme et al., 2021; Koufos et al., 2022).

The earliest representatives of *Equus* appeared in Eurasia at the onset of the Quaternary,

following the dispersal wave from North America of the genus (Azzaroli 1982, 2000, 2003; Azzaroli & Voorhies, 1993; Bernor et al., 2019; Cirilli et al., 2021a, 2022, 2024b). These newcomers in Western Eurasia (from the Caucasus to the Iberian Peninsula) are represented by the species *Equus livenzovensis*, a large equid with an estimated body mass of 400–600 kg (Cirilli et al., 2022, 2024a), found at Liventsovka (2.58–2.1 Ma, Russia; Tesakov et al., 2007a, 2007b; Titov, 2008), Roca-Neyra (2.6 ± 0.02 Ma, France; Nomade et al., 2014), Montopoli (2.58 Ma Italy; Bartolini-Lucenti et al., 2022), El-Rincòn 1 (2.6 Ma, Spain; Alberdi et al., 1997) and Fonelas P-1 (Spain) (Alberdi et al., 1997, 1998, 2001; Bernor et al., 2018, 2019, 2021; Cirilli et al., 2021a, 2021b, 2021c, 2022, 2024a). In Roca-Neyra, *E. livenzovensis* shared the palaeoenvironment with one of the last representatives of the three-toed equids which roamed Eurasia and Africa since the Late Miocene, namely *Plesiohipparion rocinantis* (Cirilli et al., 2023b). Slightly later, *Equus major*, a much larger species about 600–800 kg in body mass (Cirilli et al., 2022, 2024a) with browse-to-mixed feeders habits, appeared in Central and Eastern Europe (Cirilli et al., 2024a), with records (from East to West) in the Middle and early Late Villafranchian localities of Liventsovka (Russia), Schernfeld and Erpfinger Hole (Germany), Tegelen (The Netherlands), Pardines, Chagny, and Senèze (France), East Runton and Norwich (England) (Cirilli et al., 2024a).

Equus stenonis is a medium- to large-sized species (ca. 350–500 kg, Cirilli et al., 2024a), first recorded in Western Eurasia at ca. 2.5–2.4 Ma, and it represents the most widespread species during the Middle and early Late Villafranchian (Cirilli et al., 2021b). From East to West, the species has been found in the localities of Dmanisi (Georgia), Guliazy and Sarikol Tepe (Turkey), Sesklo, Dafnero, Volax, Vatera, and Krimni (Greece), Olivola, Pantalla, and Upper Valdarno (Italy), Saint Vallier and Chilhac (France) and La Puebla de Valverde (Spain) (Azzaroli, 1964, 1982; De Giuli 1972, 1986; De Giuli et al., 1986b; Eisenmann, 2004; Bernor et al., 2018, 2019, 2021; Cherin et al., 2020; Cirilli et al., 2020a, 2020b, 2022; Koufos et al., 2022). Late occurrences of *E. stenonis* have been recorded in the late Late Villafranchian sites of Pirro Nord, Italy (Arzarello et al., 2009; De Giuli, 1986; De Giuli et al., 1986), and Ceyssaguet, France (Aouadi, 1999; Aouadi & Bonifay, 2008), but unfortunately these occurrences remain hypothetical pending a revision of the entire collections from these localities (Cirilli et al.,

2021b).

Equus senezensis is a medium-sized equid (ca. 300–400 kg, Cirilli et al., 2024a) occurring at the Middle Villafranchian localities of Senèze (France) and Coste San Giacomo and Vigna Nuova (Italy) (Palombo et al., 2017; Cirilli et al., 2021c, 2022; Azzarà et al., 2022).

E. stehlini is the smallest Early Pleistocene equid (ca. 250–350 kg, Cirilli et al., 2024a), at the present time recovered only in the early Late Villafranchian Italian localities of Upper Valdarno (Cirilli, 2022) and Frattaguida (Petronio & Salari, 2021).

Equus altidens is medium-sized equid (250–400 kg, Cirilli et al., 2024a) widespread in Western Eurasia in the late Early and Middle Pleistocene (Cirilli et al., 2022). The oldest presence of the species was first recognised in the palaeoanthropological site of Dmanisi (Georgia, Bernor et al., 2021), and reported also in the localities of Libakos and Gerakarou (Greece; Gkeme et al., 2017, Koufos et al., 2022), Venta Micena, Atapuerca TD6, Sima de Elefante TE17, Cullar de Baza, Vallparadís, Cueva Victoria, Huescar-1, (Spain; Alberdi, 2010; Alberdi & Palombo, 2013a, 2013b; Alberdi & Piñero, 2015; Alberdi et al., 1988; Bellucci et al., 2021; Madurell-Malapeira et al., 2010; Piñero & Alberdi, 2015; Van der Made, 1999), Sainzelles, Soleilhac, Bois-de-Riquet (France; Palombo & Valli, 2004, Bourguignon et al., 2016), Pirro Nord, Slivia, Venosa-Loreto (Italy; Alberdi & Palombo, 2013a, 2013b; Alberdi et al., 1988), and Süssenborn (Germany; Alberdi & Palombo, 2013a, 2013b; Cirilli et al., 2022). As for *E. stenonis* in previous times, *E. altidens* was the most widespread equid species in the Late Villafranchian - Early Galerian of Western Eurasia. Nevertheless, its systematics is debated, and not all the authors recognise its validity (for a summary see Eisenmann, 2022b).

Equus suessenbornensis is a large-sized equid (ca. 550–750 kg, Cirilli et al., 2024a) closely related to *E. major* (Cirilli et al., 2023a), present in Western Eurasia during the latest Villafranchian, Epivillafranchian, and Early Galerian (Cirilli et al., 2023a). From East to West, it was recovered from the localities of Akhalkalaki (Georgia), Apollonia-1 (Greece), Stranska Skala (Czech Republic), Pirro Nord, Slivia, Il Castello, Soave, Monte Tenda, Bucine, Venosa-Loreto (Italy), Voigtstedt, Süssenborn, Dorn-Dürkheim 3 (Germany), West Runton and Pakefield (England), Barranco León, Fuente Nueva-3, Cueva-Victoria, Quibas, Huescar-1 and Cullar de Baza-1 (Spain) and possibly at Bois-de-Riquet (France) (Alberdi 2010; Alberdi & Piñero, 2015;

Piñero & Alberdi, 2015; Cirilli et al., 2023a).

Equus apolloniensis was recovered only from the latest Villafranchian type locality of Apollo-
nia-1 (Greece; Gkeme et al., 2021) and *Equus wuesti* only from the Epivillafranchian type
locality of Untermassfeld (Germany; Eisenmann & Boulbes, 2020; Eisenmann, 2022b).

3.3 Previous identification of fossil equids from the Farneta F. U.

The identification of the fossil equid remains from the Farneta F.U. is controversial, as resulted
in past publications by different authors. Azzaroli & Ambrosetti (1970) and Azzaroli (1977)
reported the presence of *E. stehlini* whereas, later, Azzaroli (1983, 1992, 1998) identified both
E. stenonis and *E. stehlini* in the Farneta LFA. De Giuli (1986) reported *E. cf. stenonis*
from the Selvella LFA, whereas the same sample was reinterpreted as *E. stenonis* by Forsten
(1999). Caloi & Palombo (1987) reported *E. stenonis* ssp. (i.e., a not identifiable subspecies)
in Selvella, whereas Caloi (1995) ascribed the same sample to *E. aff. altidens*. Palombo et al.
(2003) reported ?*E. stehlini* from Val di Chiana (=Farneta LFA) and *E. altidens* from Selvella,
whereas in the last revision of the Selvella equid sample, Alberdi & Palombo (2013a) recognized
the co-occurrence of *E. altidens* and *E. suessenbornensis*. The fossil samples are compared with
all known Early and early Middle Pleistocene fossil *Equus* species, to assess their systematics
and discuss their position and relevance for the evolution of the Villafranchian faunas in Western
Eurasia.

3.4 Geological context

3.4.1 Val di Chiana

The Plio–Pleistocene continental deposits of the Val di Chiana Synthem extend widely across
the Val di Chiana (Chiana Valley) basin, from the Farneta Abbey (south of Arezzo) to the
Selvella farmhouse (east of Gioiella), reaching westward into Umbria and eastward to Lake
Trasimeno (Azzaroli, 1992). Some discrepancies exist in the nomenclature of the stratigraphic
units between Tuscany and Umbria, primarily reflecting differences in regional geological map-
ping schemes (e.g., Azzarà et al., 2022). Although largely buried beneath the present-day

surface, seismic data indicate that these deposits range in thickness from several hundred to more than one thousand meters (Aruta et al., 2007).

The Val di Chiana Synthem is divided into two principal subsynthem. The lower subsynthem consists of yellow fine sands (De Giuli, 1986), interpreted as deposits formed in alluvial plain and palustrine environments, including alluvial channels, up to the Early Pleistocene. The overlying subsynthem, in contrast, is dominated by fluvial and alluvial fan facies (Aruta et al., 2007). Two distinct faunal assemblages have been recovered from these units. The older assemblage, of Early Pleistocene age, contains the characteristic taxa that define the Farneta Faunal Unit (F.U.; Azzaroli, 1977). The younger assemblage was discovered within small, pebbly lenses at the Borgonovo cemetery—approximately two kilometers northeast of Farneta—and in scattered outcrops further south in the Val di Chiana (Azzaroli, 1977, 1998). This latter assemblage has been interpreted as Galerian in age (Azzaroli, 1977, 1998; De Giuli, 1986; Petronio et al., 2011). However, a preliminary re-examination of the Borgonovo fossil material indicates that further study is required to clarify its faunal composition and chronological attribution. Consequently, the equid specimens from Borgonovo are excluded from the present analysis. As mentioned above, the locality of Farneta has been extensively excavated in the late 20th century during highway construction works (Fig. 3.1). Several temporary quarries were opened around the village of Farneta, including Cava Liberatori, Cava La Rota, and Cava Oppiello, as well as further south near Vaiano, Casa Palazzi (De Giuli, 1986). These excavations yielded numerous fossil specimens representing taxa distinct from those of the older Tasso F.U., yet characteristic of the Late Villafranchian ELMA (Azzaroli, 1977; Gliozzi et al., 1997).

Of particular significance is the co-occurrence of the Epivillafranchian–Galerian genus *Praemegaceros* with the earliest Italian record of *P. obscurus* alongside typical Late Villafranchian taxa such as *Leptobos* and possibly *Eucladoceros* (Azzaroli & Mazza, 1993).

The Selvella locality (IGF n. 87; Fig. 3.1) corresponds to a small sand quarry opened in 1969 near a farmhouse of the same name, located a few kilometres east of Gioiella (De Giuli, 1986). Before excavation, only limited exposures of yellow coarse-grained sands were visible. Fossils were recovered from small, sorted lenses just below the uppermost sandy layer

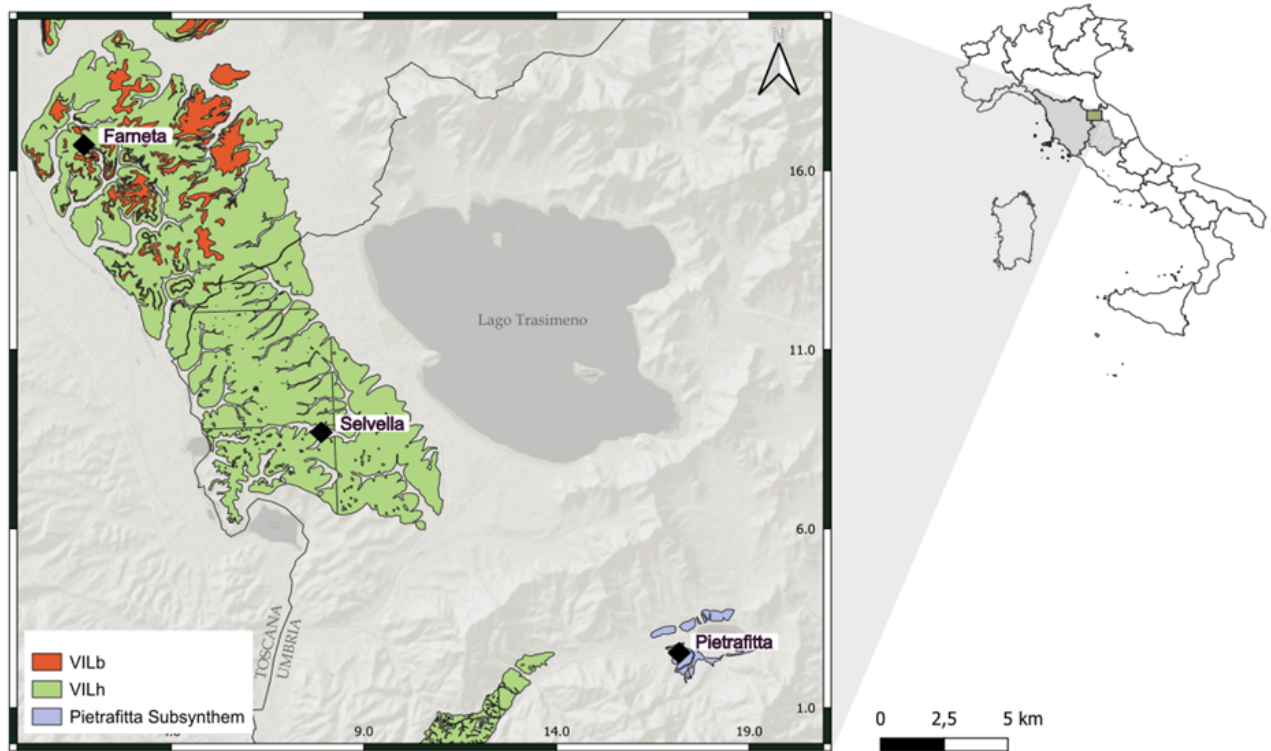


Figure 3.1: Geographical distribution of the Farneta Faunal Unit areas of interest with associated geological formations. Highlighted lithologies are Vilb in orange = Villafranchian b; in green, Vilh: Villafranchian h; in purple, Pietrafitta subsynthem. The map was made using QGIS software and geological data from the Geoportal of the Tuscany Region (after Borchì et al., 2025).

(De Giuli, 1986). The collected material, currently housed in the Natural History Museum of the University of Florence, was initially referred to the Tasso F.U. but was later reassigned to an intermediate position between the Olivola and Pirro F.U.s (De Giuli, 1975, 1986) based on its taxonomic composition. *Equus* and *Dama*-like remains dominate the assemblage, but additional taxa include Elephantidae indet., *Eucladoceros dicranios*, *Canis etruscus* (Cherini et al., 2014), *Lynx issiodorensis* (Cherini et al., 2013), and *Sus* sp.

3.4.2 Pietrafitta

The Pietrafitta fossil locality, named after the nearby village, is situated within the Tavernelle–Pietrafitta Basin, south of Lake Trasimeno in the Umbria region (Fig. 3.1). The site corresponds to a former lignite quarry, active during the mid–late 20th century and is renowned for its exceptionally rich and well-preserved fossil assemblages (Martinetto et al., 2014). Like many intramontane basins of central Italy, the Tavernelle–Pietrafitta Basin exhibits a predom-

inant NE–SW orientation and originated during the phases of Apennine uplift (Ambrosetti et al., 1995).

During parts of the Early Pleistocene, the basin was intermittently connected to the broader Tiberino Basin and experienced alternating depositional phases, characterised by lacustrine–palustrine and alluvial plain environments (Gentili et al., 1998; Cherin et al., 2012; Pazzaglia et al., 2013; Martinetto et al., 2014; Petronio et al., 2020; Sorbelli et al., 2021). The lignite deposits, ranging from 5 to 8.5 m in total thickness, accumulated through the deposition of organic-rich material and subordinate clays under stagnant-water conditions in perilacustrine settings around 1.5 Ma; before basin uplift and its gradual evolution into the present-day fluvial system (Ambrosetti et al., 1989; Martinetto et al., 2014).

Palaeobotanical evidence indicates that the lignite-bearing swamp was bordered by a humid deciduous broad-leaved forest developed under a warm-temperate climate (Martinetto et al., 2014). This paleoenvironmental reconstruction is further corroborated by data from the highly diversified vertebrate assemblage recovered at the site (Martinetto et al., 2014; Cherin et al., 2018; Sorbelli et al., 2021, 2023).

3.5 Material and Methods

3.5.1 Morphometric and statistical analyses

The fossil equids from Farneta, Selvella, and Pietrafitta are housed at the Museum of Geology and Palaeontology of the University of Florence (IGF; Farneta and Selvella localities), at the Mostra Paleontologica Permanente (Mo.Pa., Farneta Abbey) and at the Museo Paleontologico “Luigi Boldrini” of Pietrafitta (Pietrafitta locality). A complete list of the material studied herein is provided in Appendix 1. The assemblages have been compared with a large dataset of Plio-Pleistocene fossil (*E. simplicidens*, *E. livenzovensensis*, *E. major*, *E. stenorionis*, *E. senegensis*, *E. stehlini*, *E. altidens*, *E. suessenbornensis*, and *E. apolloniensis*) and extant (*E. grevyi*) stenonid *Equus* species from North America, Eurasia, and Africa (Table 1) following Cirilli et al. (2023a, 2024a). The Plio-Pleistocene monodactyl equid species are included in the genus *Equus* following the latest cladistic results of Cirilli et al. (2021a), not recognising *Plesippus* and *Allohippus* as distinct genera or subgenera.

Species	Locality	Age (Ma)	Data source
<i>Equus simplicidens</i>	Hagerman Horse Quarry, Idaho	3.3–3.1	Own
<i>Equus livezovens</i>	Roca-Neyra, France	2.6 ± 0.02	Nomade et al., 2014
<i>Equus livezovens</i>	Liventsovka, Russia	2.58–2.2	Forsten, 1997; Eisenmann, 2022b
<i>Equus livezovens</i>	El Rincon-1, Spain	2.6	Alberdi et al., 1997
<i>Equus major</i>	Liventsovka, Russia	2.58–2.2	Forsten, 1997; Eisenmann, 2022b
<i>Equus livezovens</i>	Montopoli, Italy	2.58	Bernor et al., 2018
<i>Equus major</i>	Pardines, France	ca. 2.5	Cirilli et al., 2024b
<i>Equus major</i>	Chagny, France	ca. 2.5	Cirilli et al., 2024b
<i>Equus stenor</i>	Saint-Vallier, France	ca. 2.45	Own; Cirilli et al., 2021a
<i>Equus senezensis</i>	Senèze, France	2.2–2.0	Own
<i>Equus major</i>	Senèze, France	2.2–2.0	Own; Cirilli et al., 2024a
<i>Equus senezensis</i>	Vigna Nuova, Italy	2.2–2.1	Azzarà et al., 2022
<i>Equus major</i>	Schernfeld, Germany	2.1–1.9	Musil, 1992; Cirilli et al., 2024b
<i>Equus livezovens</i>	Fonelas P-1, Spain	2.0	Garrido, 2008
<i>Equus stenor</i>	Pantalla, Italy	ca. 2.2	Cherin et al., 2021
<i>Equus stenor</i>	Olivola, Italy	2.0–1.9	Own; Cirilli et al., 2021a
<i>Equus stenor</i>	Upper Valdarno Basin, Italy	1.9–1.77	Own; Cirilli et al., 2021a
<i>Equus stehlini</i>	Upper Valdarno Basin, Italy	1.9–1.77	Own; Cirilli, 2022
<i>Equus 'stenor mygdoniensis'</i>	Gerakarou, Greece	ca. 1.8	Koufos, 1992
<i>Equus stenor</i>	Dmanisi, Georgia	1.85–1.77	Own; Bernor et al., 2021
<i>Equus altidens</i>	Dmanisi, Georgia	1.85–1.77	Own; Bernor et al., 2021
<i>Equus altidens</i>	Venta Micena, Spain	1.6–1.4	Guerrero-Alba, 1997
<i>Equus altidens</i>	Pirro Nord, Italy	1.5–1.2	Own; Alberdi and Palombo, 2013a; 2013b
<i>Equus suessenbornensis</i>	Pirro Nord, Italy	1.5–1.2	Own; Alberdi and Palombo, 2013a; 2013b
<i>Equus apolloniensis</i>	Apollonia-1, Greece	1.5–1.2	Gkeme et al., 2021
<i>Equus suessenbornensis</i>	Akhalkalaki, Georgia	0.98–0.78	Cirilli et al., 2023b
<i>Equus suessenbornensis</i>	Cueva Victoria, Spain	0.9–0.8	Alberdi and Piñero, 2015
<i>Equus suessenbornensis</i>	Süssenborn, Germany	0.64–0.62	Own; Musil, 1969; V. Eisenmann website
<i>Equus altidens</i>	Süssenborn, Germany	0.64–0.62	Own; V. Eisenmann website
<i>Equus grevyi</i>	East Africa	0.0	Own; V. Eisenmann website

Table 3.1: Complete list of the Plio-Pleistocene and extant *Equus* species used for comparative analyses in the present work listed by age, from older to younger.

Upper and lower cheek teeth and postcranial elements (third metacarpals, third metatarsals, anterior and posterior first phalanges of the central digit) are described and compared with the species mentioned above. No complete crania are available in the studied collections. The measurements and anatomical nomenclature follow the international standards for studying fossil equids by Eisenmann et al. (1988) for postcranial elements and Bernor et al. (1997) for upper and lower teeth. Morphometric and statistical analyses implemented herein include: bivariate plots, principal component analysis (PCA), Log10 ratio diagrams, and a permutational multivariate analysis of variance (PERMANOVA).

In upper and lower cheek teeth, the bivariate plots compare the maximum length (M1) and maximum width (M3 in the upper dentition, M6 in the lower) at the occlusal level. On postcranial elements, the bivariate plots include the maximum length (M1) versus the distal maximum articular width (M11 in third metapodials and M6 in the anterior first phalanges of the central digit). PCAs were computed on the third metacarpals, third metatarsals, and first phalanges of the central digit.

The variables used to build the PCAs on third metapodials include maximum length (M1), minimum width of the diaphysis (M3), depth of the diaphysis at level of M3 (M4), proximal articular width (M5), proximal articular depth (M6), distal maximum supra-articular width (M10), distal maximum articular width (M11), distal maximum depth of the crista sagittalis (M12), and the distal maximum depth of the medial condyle (M14), whereas those used to build the PCA on the first phalanges of the central digit include maximum length (M1), minimal breadth (M3), proximal breadth (M4), proximal depth (M5), and distal breadth at the tuberosities (M6).

To compare the single incomplete metacarpal from Pietrafitta, Log10 ratio diagrams were performed on the Log-transformed mean values of the Höwenegg *Hippotherium primigenium* (Bernor et al. 1997). Considering the present work on the genus *Equus*, the Höwenegg *H. primigenium* represents an ideal fossil sample from a single fossil equine species from a well studied, homogeneous stratigraphic context, for which the full range of descriptive statistics (mean, standard deviation, confidence limits, and minimum, maximum, and median values) are available for each bone, including the cranium, mandible, dentition, and postcranial elements.

Furthermore, the method has the advantage of being referred to a different genus and tribe (Hipparionini, not Equini) allowing an analysis of all species of the genus *Equus*. In addition to the same measurements used in the PCAs, the Log10 ratio diagrams include the diameter of the articular facet for the third carpal/tarsal (M7), maximum diameter for the anterior facet for the fourth carpal/tarsal (M8), and distal maximum depth of the lateral condyle (M13).

Bivariate plots, PCAs and PERMANOVA were computed in the R Environment v. 1.4.1103 (R Core Team, 2025) using the function `prcomp()` v. 3.6.2 (Venables and Ripley, 2008) and the package ‘`ggplot2`’ v. 3.3.3 (Wickham, 2016). PCAs have been built using the parameter `scale = T` to have a unit variance before starting the analyses in R.

The PERMANOVA analyses were performed on the PC values of third metapodials using the ‘`pairwiseAdonis`’ package v. 0.4 (Martinez-Arbizu, 2020), which includes the Bonferroni adjustment method (`p.adjust`). Third metapodials were chosen because they represent the most discriminant postcranial elements to evaluate similarities or differences in morphology among *Equus* species. These analyses are aimed at quantifying and identifying the intra- and interspecific variability in extant and fossil (sub)species and calculating body mass (Bernor et al., 2021; Cirilli et al. 2021c, 2022, 2023a, 2024a; Cirilli 2022; Saarinen et al., 2021).

3.5.2 Anatomical abbreviations

UTR, upper cheek tooth row; **LTR**, lower cheek tooth row; **P2**, maxillary second premolar; **P3**, maxillary third premolar; **P4**, maxillary fourth premolar; **M1**, maxillary first molar; **M2**, maxillary second molar; **M3**, maxillary third molar; **p2**, mandibular second premolar; **p3**, mandibular third premolar; **p4**, mandibular fourth premolar; **m1**, mandibular first molar; **m2**, mandibular second molar; **m3**, mandibular third molar; **mc3**, third metacarpal; **a1ph3**, anterior first phalanx of the central digit; **mt3**, third metatarsal; **p1ph3**, posterior first phalanx of the central digit.

3.5.3 Institutional abbreviations

IGF, Museo di Geologia e Paleontologia, Università degli Studi di Firenze (Italy); **MPLBP**, Museo Paleontologico “Luigi Boldrini” di Pietrafitta (Italy).

3.5.4 Systematic Palaeontology

Class Mammalia Linnaeus, 1758.

Order Perissodactyla Owen, 1848.

Subfamily Equinae Gray, 1821.

Genus *Equus* Linnaeus, 1758.

Equus stenonis Cocchi, 1867

Holotype. The skull, IGF560, is housed in the Museo di Geologia e Paleontologia, Florence, Italy. Originally described by Cocchi (1867) and figured in Azzaroli (1964: Pl. I fig. 3, Pl. II figs. 1, 1a, Pl. IV figs. 1, 1a, Pl. V fig. 1, 1a).

Type locality. Terranuova Bracciolini, Upper Valdarno Basin (Italy), ca. 1.9–1.77 Ma (Cirilli et al., 2021c).

Age range ca. 2.5–1.3 Ma (Cirilli et al., 2021b, 2022).

Geographic range. From East to West: Georgia, Turkey, Greece, Italy, France, and Spain (Cirilli et al., 2021b, 2022).

Referred material. See Appendix 1 and 2.

Description. Cranium - No complete *E. stenonis* crania were recovered from Farneta, Selvella, or Pietrafitta. Therefore, our description of the cranial features will comprise characteristics of the maxillary teeth, retrieved only in the first two localities.

Maxillary teeth - Figure 3.2A-F shows five isolated upper teeth ascribed to *E. stenonis*. All teeth show a high crown and a medium stage of wear except for IGF14343 (Fig. 3.2C) that has a lower, partially broken crown in labial view, but preserves all morphological features in occlusal view. In occlusal view, all teeth show a squared mesostyle, which is thicker in premolars and compressed mesio-distally in molars. Similarly, the labial ridge of the mesostyle shows a slight depression which is more pronounced in P3-P4 than in M1-M3. The protocone differs slightly in shape between the specimens: compressed labio-lingually in IGF14337 (Fig. 3.2A), IGF14343 (Fig. 3.2C), IGF14339 (Fig. 3.2D) and IGF14340 (Fig. 3.2E), while more rounded in IGF14338 (Fig. 3.2B). The lingual margin of the protocone shows a slight concavity in all specimens except for IGF14341 (Fig. 3.2B). The protocone is always connected to the protoloph by a sharp, single-pointed isthmus. The pli caballin is visible in all teeth except in IGF14337

(Fig. 3.2A) and IGF14341 (Fig. 3.2E). When present, it is single and well developed. The hypocone is well developed except in M3 (Fig. 3.2E) and distally pointed. The fossettes have ornamentation in all teeth but show a higher complexity in the premolars (Fig. 3.2A-3.2B).

Third metatarsal – Figure 3.2G-I illustrates third metatarsals IGF14185, IGF14186, and IGF14190 from Selvella. The mt3s are characterised by an elongated morphology with a circular section diaphysis and by wide proximal and distal epiphyses. The supra-articular tuberosities (M10) are more developed than the distal articular processes (M11) in all three specimens. The lateral condyle (M13) is less developed than the medial condyle (M14). The mt3s have a well-developed crista sagittalis.

First anterior phalanx of the central digit – Figure 3.2J–K illustrates IGF 14171 and IGF14324 from Selvella, two anterior first phalanges. The a1ph3s are large and elongated with the proximal epiphysis being more laterally developed than the distal epiphysis. In dorsal view, the proximal epiphysis shows a light concavity in the midline towards the sagittal plane. In palmar view, the midline concavity is deep and well developed, and it is connected to the V-shaped, proximal-distally deep surface of the trigonum phalangis proximalis. The lateral glenoid cavity is more pronounced than the medial one. The distal supra-articular protuberances are as laterally developed as the medial and lateral trochleae.

First posterior phalanx of the central digit - Figure 3.2L illustrates IGF 14325 from Selvella. It shows the same morphologies of the anterior phalanges (Fig. 3.2J-K), but the distal supra-articular protuberances are wider than the medial and lateral trochleae.

Equus altidens von Reichenau, 1915

Lectotype. Right P2, housed at the Universitat Halle a.d. Saale Collection, Germany. Figured in von Reichenau (1915: Pl. 6 fig. 17) and designated by Schwarz (1928).

Type locality. Süssenborn, Germany; ca. 0.64–.62 Ma (Kahlke 2014).

Age range. ca. 1.85–0.60 Ma (Alberdi & Palombo 2013a; Bernor et al. 2021; Cirilli et al. 2022).

Geographic range. From West to East: Georgia, Greece, Italy, Germany, France, England, and Spain (Alberdi & Palombo, 2013a; Cirilli et al. 2022).

Referred material. See Appendix 1

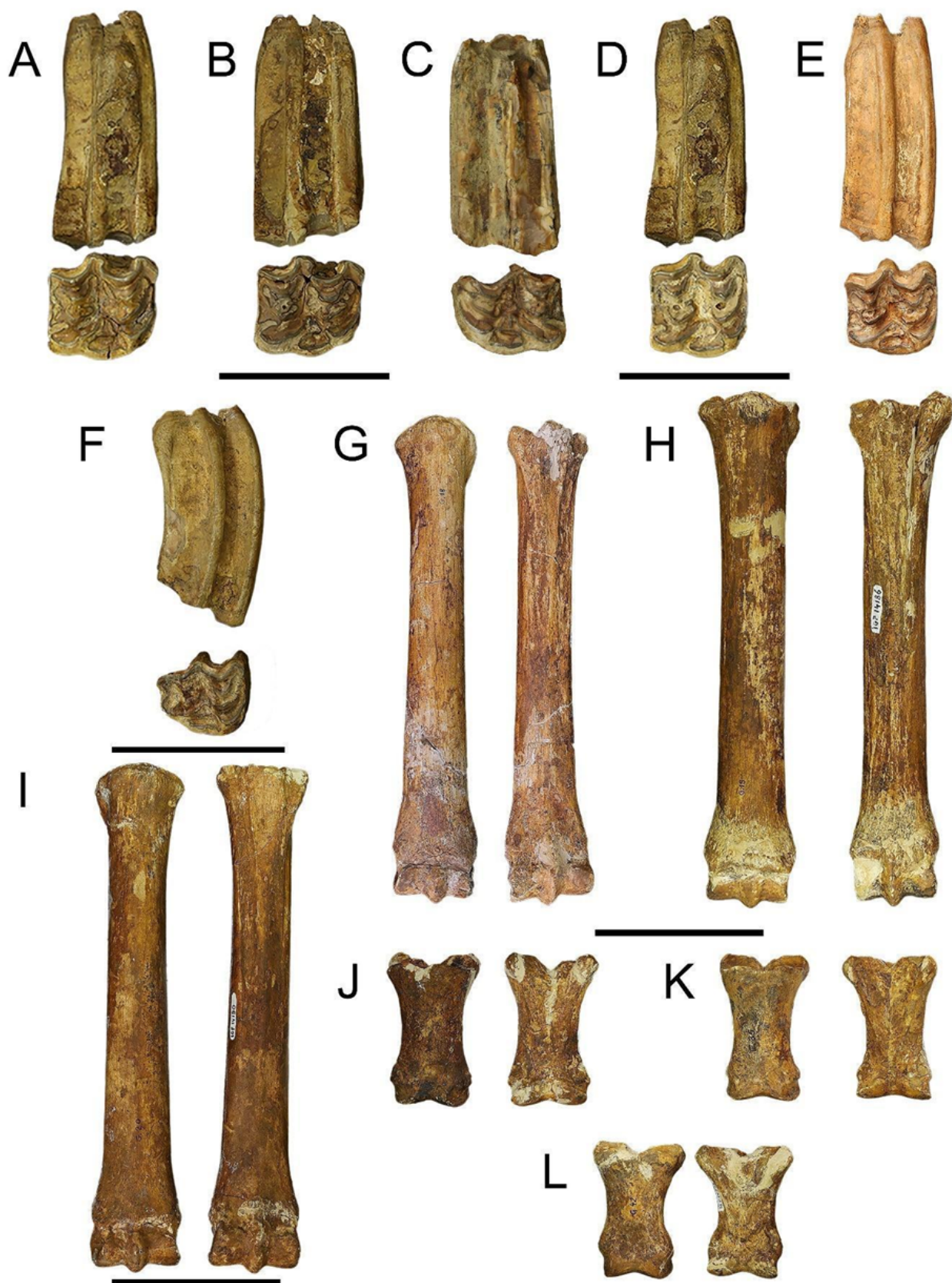


Figure 3.2: *Equus stenonis* isolated maxillary teeth (A-F), third metatarsals (G-I), first anterior (J-K) and posterior (L) phalanges of the central digit in dorsal and palmar view. A) IGF 14337, B) IGF 14338, C) IGF 14343, D) IGF 14339, E) IGF 14340, F) IGF 14341, G) IGF 14185, H) IGF 14186, I) IGF 14190, J) IGF 14171, K) IGF 14324, L) IGF 14325. Scale bar 5 cm for cranial elements, 10 cm for postcranial elements (after Borch et al., 2025).

Description. Cranium - No complete *E. altidens* crania were recovered from Farneta, Selvella, and Pietrafitta. Therefore, our description of the cranial features is limited to characteristics of the maxillary teeth. Maxillary tooth row - Figure 3.3A-B illustrates the right and left complete UTRs of IGF 4022v. The UTRs are low crowned suggesting a late stage of wear and the anatomical features of the occlusal morphology are faintly preserved. The anterostyle on P2 is short and subtriangular. The mesostyle is mesio-distally narrow on all teeth, with a labial tip pointed distally. The protocone is always connected to the protoloph. From P2 to M3, the shape of the protocone gradually shifts from rounded to labio-lingually flattened, with a progressive ornamentation development on the lingual ridge. The pli caballin is absent in all teeth of the UTRs. Pre- and post-fossettes are similar in size and appearance, resembling a U shape and bearing little to no ornamentation.

Mandible and mandibular cheek tooth row - Figure 3.3C-E shows three LTRs of *E. altidens* from Selvella. IGF 14312 (Fig. 3.3C) is an almost complete mandible with right and left sides completely preserved, with the only exception of left m3 which is missing. All incisors are preserved; the right canine is broken; the left canine has been restored but is still incomplete. In occlusal view, the teeth show the following features: in p2 the anterostylid is wide and rounded; the metaconid is rounded in all teeth, and thicker than the metastylid, which is narrow and flattened labio-lingually; the metaconid is always connected to the preflexid, which is faintly developed in left p4 and nearly absent in left p2, p3, m1, m2; on the right side, the preflexid is not always visible due to the late stage of wear; the metastylid is pointed lingually in all teeth, but thicker in left and right p2 than in p3-m3; the linguaeflexid is V-shaped in all teeth, deeper and wider in p3-m3 than in p2; the ectoflexid is short in p2, and progressively more developed in premolars and molars; the preflexid is poorly developed to nearly absent, while the postflexid is flat and mesio-distally elongated in premolars, less developed in molars, with little to no ornamentation; the pli caballinid is absent.

IGF 14314a (Fig. 3.3D) is a partially preserved left LTR. In labial view, it shows high crowns and in occlusal view the dental morphology is well preserved, suggesting an early-adult stage of wear. The morphological features slightly differ from those of IGF 14312. The metastylid is still less developed than the metaconid, but it is rounded rather than flattened. The preflexid

is visible in p4-m3, though poorly developed. IGF14313 (Fig. 3.3E) is a mandible with the right ramus completely preserved, and the left ramus bearing only p2 and p3. The canines are preserved as well as the incisor arcade which is curved rather than horizontal. All teeth show an advanced stage of wear that hides the majority of morphological features. The anterostylid is wide and round in p2. The metaconid is slightly larger than the metasyloid, which is lingually pointed. The linguaeflexid is V-shaped and wider in p3-p4 than p2.

Third metacarpal - Figure 3.4 illustrates the *E. altidens* mc3 from Farneta (Fig. 3.4A), Pietrafitta (Fig. 3.4B), and Selvella (Gioiella) (Fig. 3.4C-L). All third metacarpals are complete except for MPLBP EQ-0001 (Fig. 3.4B) which lacks the proximal end and the proximal half of the medial side of diaphysis. All specimens show an elongated, massive morphology with well-developed proximal and distal epiphyses which are wider than the diaphysis. On the distal epiphysis, the supra-articular tuberosities are well developed, with the medial side being more pronounced than the lateral side. The same symmetry can be observed for the medial and lateral trochleae, which are separated by a marked crista sagittalis.

Third metatarsal - Figure 3.4 shows the *E. altidens* mt3s IGF 9108v, IGF 785v and IGF 9019v from Farneta (Fig. 3.4M-O) and Selvella (Gioiella) (Fig. 3.4P-Q). The mt3s are characterised by elongated and slender morphology, with long, circular-sectioned diaphysis and by large proximal and distal epiphyses. The supra-articular tuberosities are as laterally prominent as the distal articular processes in all specimens, except for IGF 9109v, where the tuberosities are more pronounced than the lateral and medial trochleae. The mt3s have a well-developed crista sagittalis.

First anterior phalanx of the central digit - Figure 3.4R-S shows two a1ph3s (IGF 14323 and IGF 14326) of *E. altidens* from Selvella. The proximal end is broad and wide, the diaphysis is elongated and slightly asymmetrical, with the medial side more developed than the lateral one. In palmar view, the V-shaped trigonum phalangis proximalis is well developed and deep, reaching the distal end of the diaphysis. The distal end is slenderer than the proximal end, with the supra-articular protuberances being the same size as the trochleae, which are symmetrical.

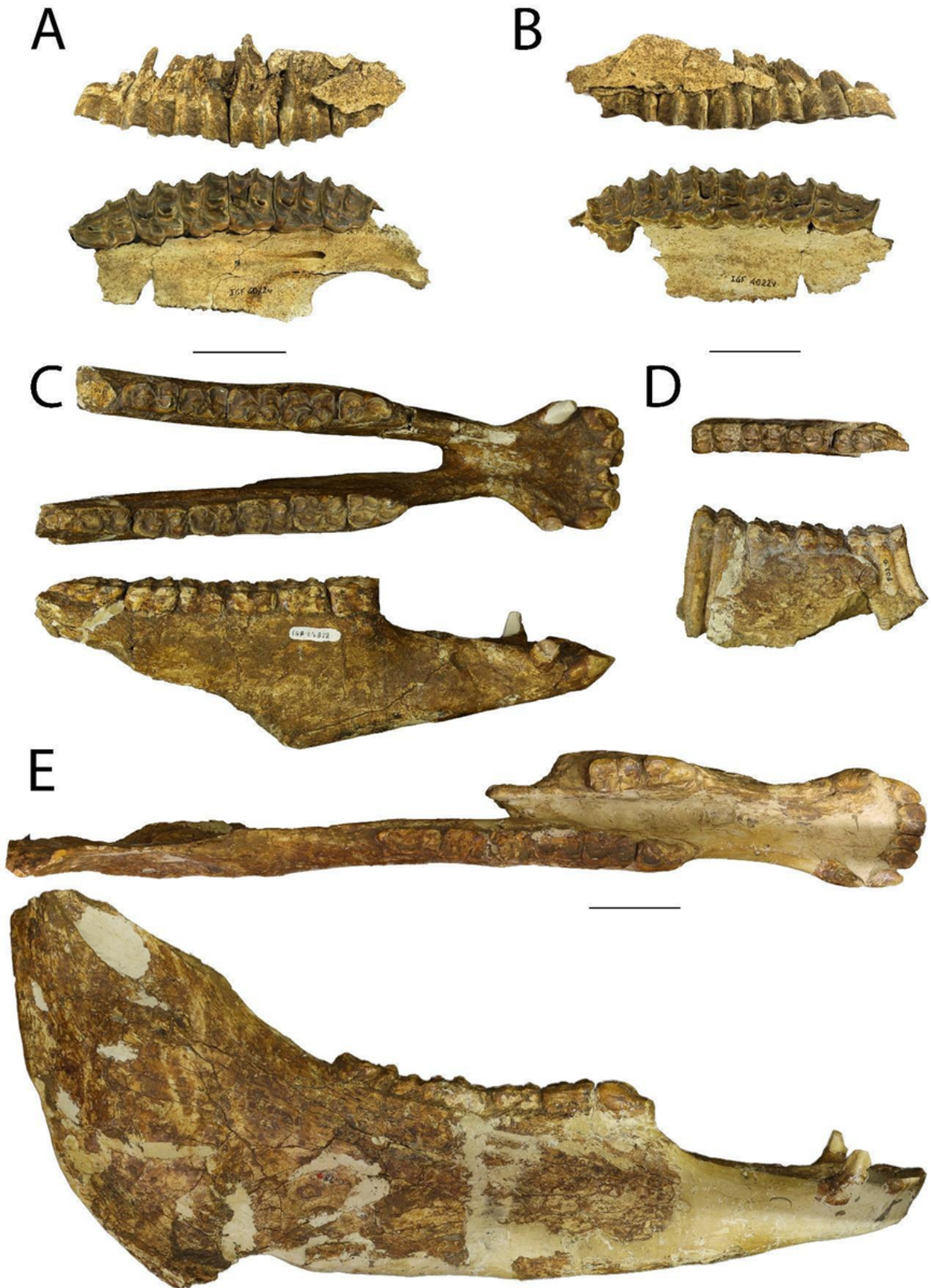


Figure 3.3: *Equus altidens* upper and lower cheek tooth rows in labial and occlusal view. A) right IGF 4022v, B) left IGF 4022v, C) IGF14312, D) IGF 14314a, E) IGF 14313. Scale bar 5 cm (after Borch et al., 2025).

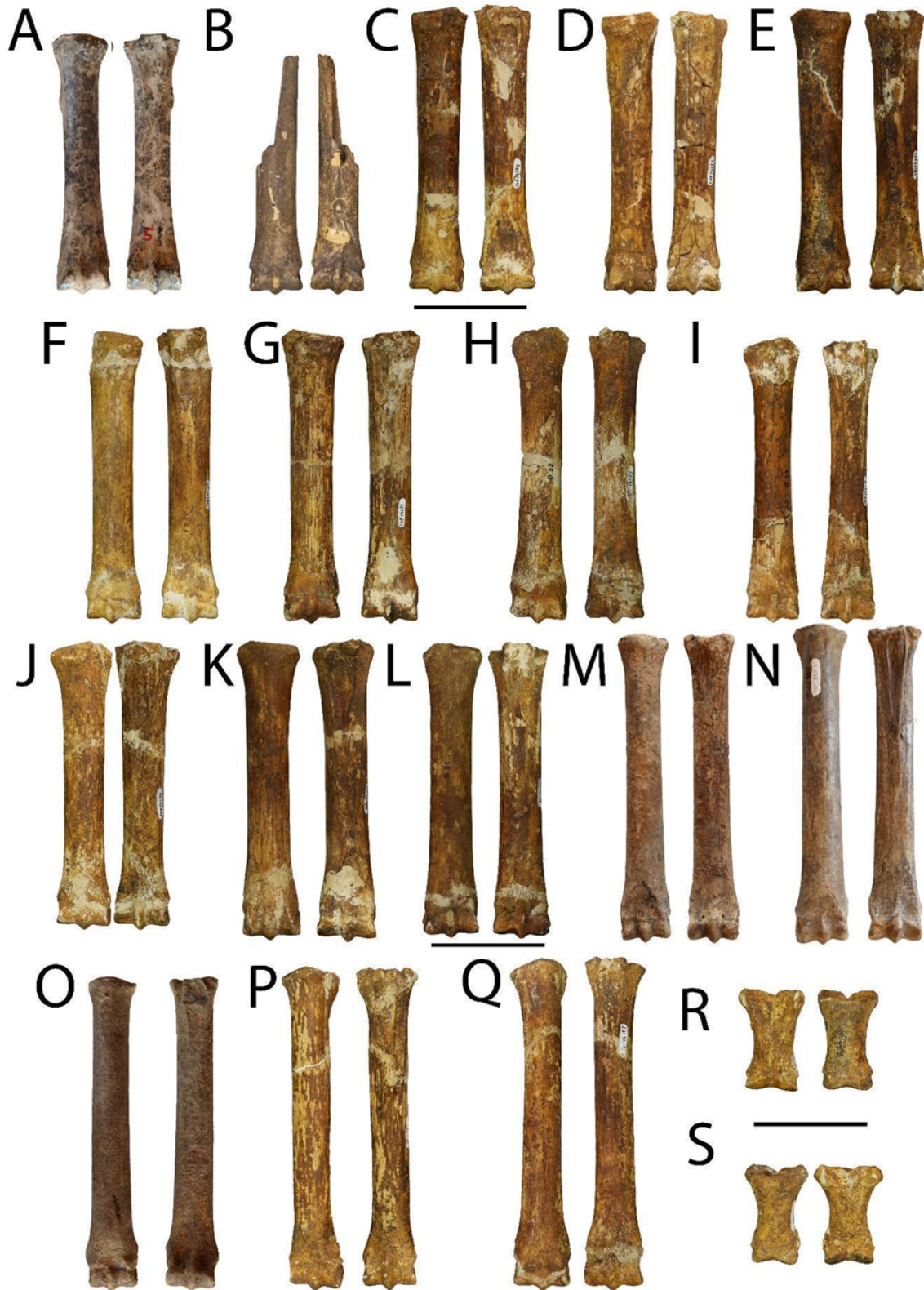


Figure 3.4: *Equus altidens* third metacarpals (A-L), third metatarsals (M-Q) and first anterior phalanges of the central digit in dorsal and palmar view (R-S) from Farneta, Pietrafitta and Selvella. A) IGF 9114v, B) MPLBP EQ-0001, C) IGF 14171, D) IGF 14172, E) IGF 14173, F) IGF 14174, G) IGF 14175, H) IGF 14176, I) IGF 14177, J) IGF 14180, K) IGF 14181, L) IGF 14182, M) IGF 9108v, N) IGF 785v, O) IGF 9019v, P) IGF 14184, Q) IGF 14187, R) IGF 14323, S) IGF 14326. Scale bar 10 cm (after Borchì et al., 2025).

3.6 Morphometric and statistical analyses

3.6.1 Morphometric analyses of the Farneta F.U. equids compared with the European Early and early Middle Pleistocene stenonid *Equus*

The morphometric comparisons of the Farneta equids with the European Early and early Middle Pleistocene *Equus* species are shown in Figures 3.5-3.10 for cranial and selected postcranial elements. Due to the absence of complete crania, the morphometric comparisons on cranial elements are limited to upper and lower cheek teeth. In Figure 5, the P3/4, M1/2, p3/4, and m1/2 are analysed together due to their similar morphology and morphometrics, to increase the comparative sample size. Appendix 1 reports all the measurements taken for each specimen; Appendix 3 illustrates all variance components and the loadings' distribution of PCA analyses; Appendix 4 shows MANOVA results performed on the PC values of the third metacarpals and third metatarsals.

Figure 3.5A-C illustrates bivariate plots comparing the maximum length vs maximum width at the occlusal level of upper dentitions (M1 vs M3 of Bernor et al. 1997). The Farneta and Selvella samples are included in the variability of *E. altidens* and *E. stenonis*. In Figure 3.5A, the two specimens IGF 4022V (right and left P2 of the same individual) are plotted close to the smallest *E. altidens* individuals from Süssenborn, Dmanisi, Pirro Nord, and Venta Micena. This result is an effect of the late stage of wear of IGF4022V, as shown in Figure 3.3. Figure 3.5B shows the comparisons of the P3/4. Here, the sample from Farneta is included in the *E. altidens* range of variability, larger than *E. stehlini* from Upper Valdarno (Cirilli 2022), whereas three specimens from Selvella (IGF 14337, IGF 14338, and IGF 14343) are plotted in the range of variability of *E. stenonis* from Saint Vallier and Upper Valdarno Basin. In Figure 3.5C (M1/2), the sample from Farneta is included in the range of variability of European *E. altidens*, whereas two specimens from Selvella (IGF 14339 and IGF 14340) show larger dimensions comparable with those of *E. stenonis*.

Figure 3.6A-C shows bivariate plots comparing the maximum length vs maximum width at the occlusal level of upper dentitions (M1 vs M6 of Bernor et al. 1997). In Figure 3.6A (p2), one specimen from Farneta (IGF 105313) and the Selvella sample (IGF 14312 [right and left], IGF

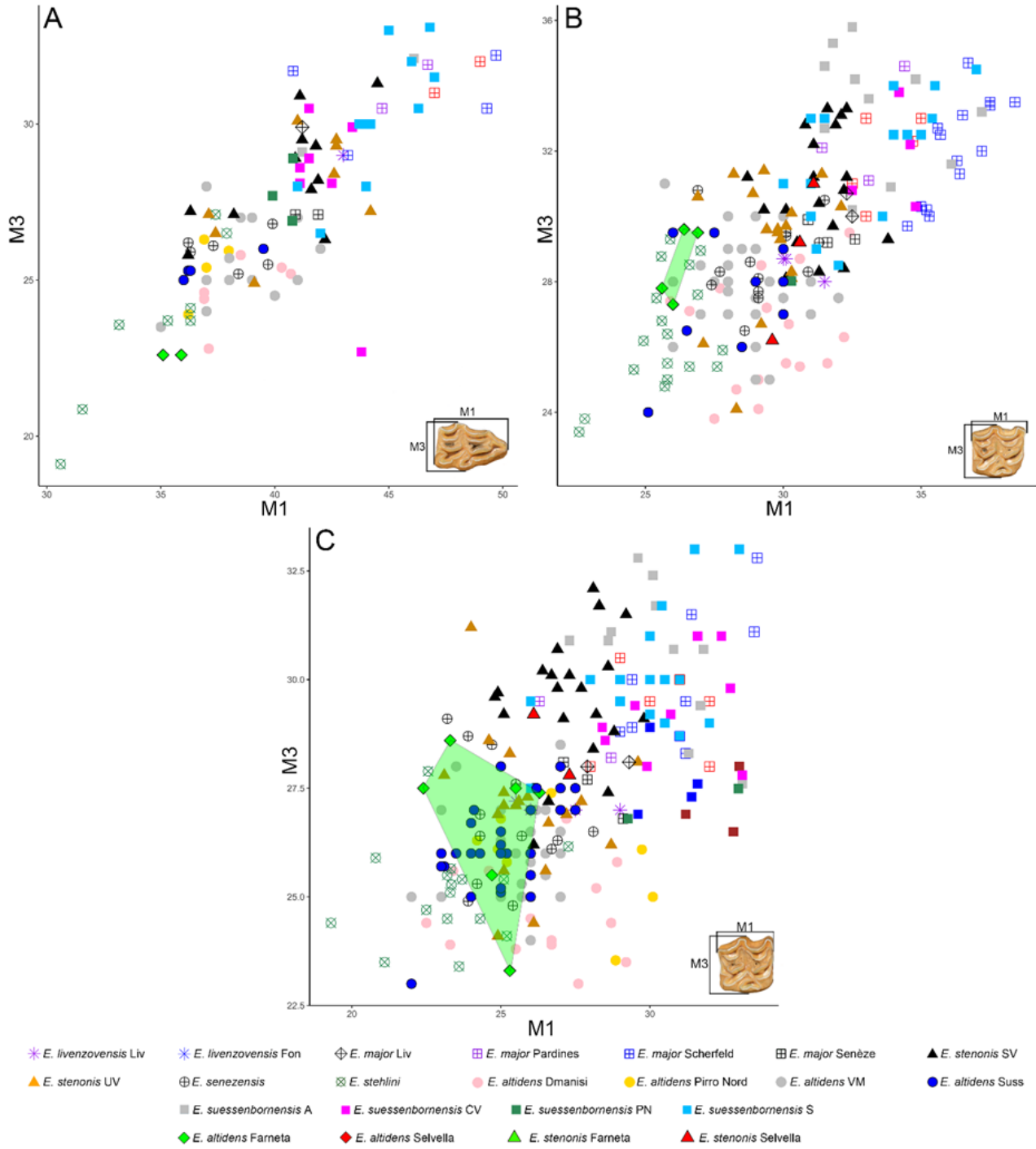


Figure 3.5: Bivariate plots comparing the *E. stenonis* and *E. altidens* upper cheek teeth with the European Early Pleistocene *Equus* species in maximal length versus maximal width. A) P2; B) P3 and P4; C) M1 and M2. Abbreviations: A: Akhalkalaki; CV: Cueva Victoria; Fon: Fonelas P-1; Liv: Liventsovka; UV: Upper Valdarno; PR: Pirro Nord; SV: Saint Vallier; S: Süssenborn; VM: Venta Micena (after Borchì et al., 2025).

14313 [right and left], IGF 14348) are included in the range of variability of *E. altidens*. In Figure 3.6B, the Selvella sample of p3/4 (IGF 105129, IGF 14312 [right and left], IGF 14313 [right and left], IGF 14314, IGF 14349) is plotted between the range of variability of *E. altidens* and that of *E. stehlini*, whereas three specimens from Farneta (IGF 105129, IGF 105314, IGF 105316) fall close to the range of variability of *E. altidens*. In Figure 3.6C (m1/2) the sample from Farneta (IGF 14282, IGF 2842V) and from Selvella (IGF 14312 [right and left], IGF 14313 [right and left], IGF 14314 [right and left], IGF 14350) are plotted within the variability of *E. altidens* from Süssenborn, Dmanisi, Pirro Nord, and Venta Micena.

Overall, these plots on upper and lower cheek teeth reflect the previous reports by Cirilli et al. (2023a, 2024a), where *E. major* shows similar dimensions than *E. suessenbornensis*, representing the largest species in the European Early Pleistocene equid record. *Equus livenzovens* from Liventsovka and Fonelas P-1 are included in the *E. stenonis* populations from Saint Valier and Upper Valdarno Basin, being smaller than *E. major* and *E. suessenbornensis*. *Equus senezensis*, *E. altidens*, and *E. stehlini* are the smallest of the Early Pleistocene species, with the latter being the smallest of them. All these species show a remarkable overlap in their range of variability, reflecting the different stages of wear of the specimens considered in the analyses. The same output might be recognised also with some specimens of *E. suessenbornensis* from Akhalkalaki and Süssenborn, plotted close to the *E. stenonis* variability, although preserving the different occlusal enamel morphology (Cirilli et al. 2023a). This confirms the importance of recognising morphology over morphometry in analysing the upper and lower cheek teeth of the fossil equids, as previously reported (Cirilli et al. 2023a, 2024a).

Figure 3.7 illustrates the PCA results and bivariate plots for mc3s and mt3s. The summary of the variance components and the loadings' distribution are reported in Appendix 3. In the PCA of the mc3s (Fig. 3.7A), PC1 and PC2 account for 88.0% of the total variance (PC1 = 82.88%; PC2 = 5.12%). PC1 separates species by size from negative to positive values (larger to smaller). Negative PC2 values indicate a shorter morphology and more robust shape, whereas positive PC2 values indicate a more elongated shape. Here, the samples from Farneta and Selvella are included in the range of variability shown by *E. altidens* from Süssenborn, Dmanisi, Pirro Nord, and Venta Micena, being well distinct from the other two small species

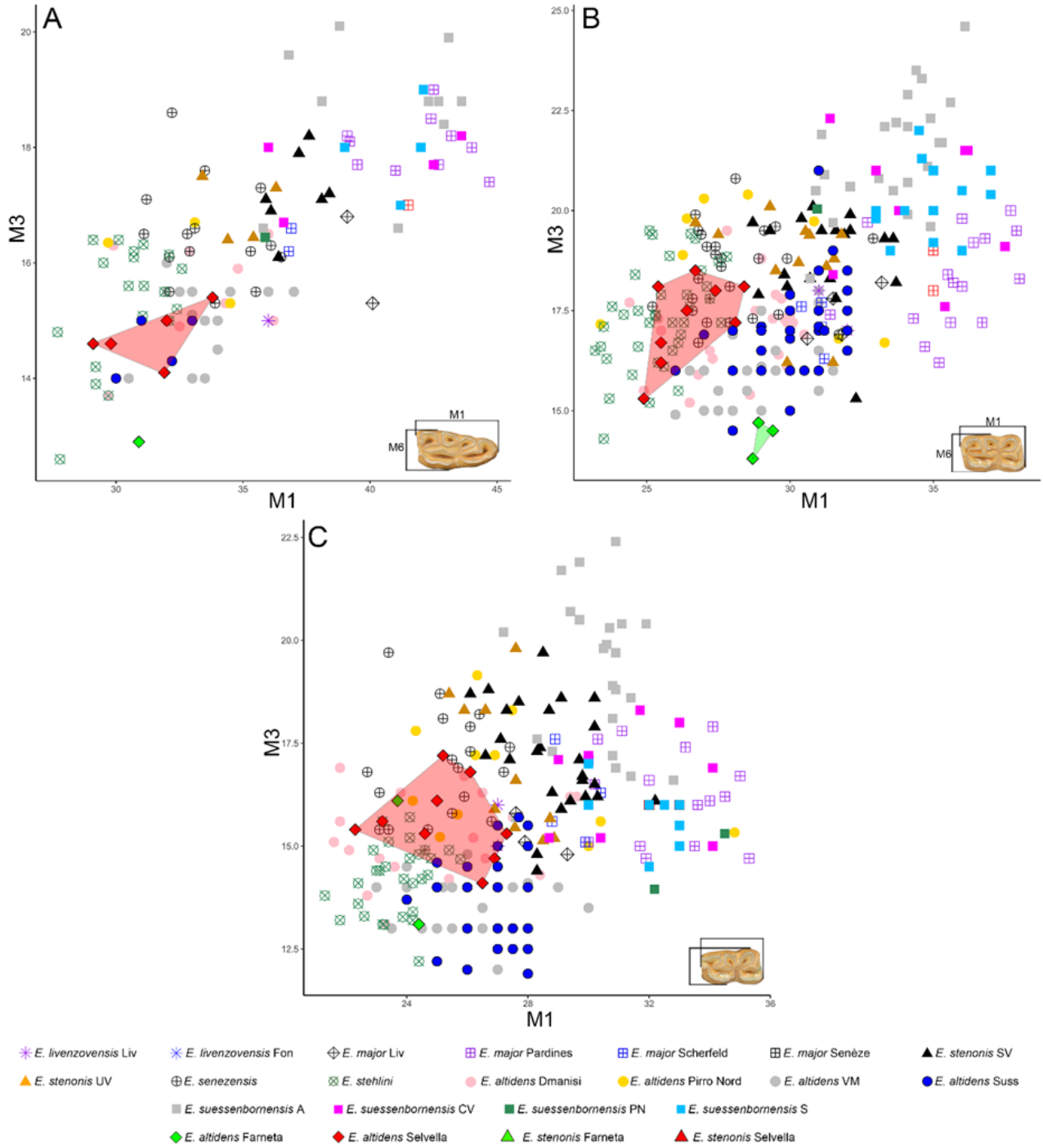


Figure 3.6: Bivariate plots comparing the *E. stenonis* and *E. altidens* lower cheek teeth with the European Early Pleistocene *Equus* species in maximal length versus maximal width. D) p2; E) p3 and p4; F) m1 and m2. Measurements are referred to Bernor et al. (1997). Abbreviations: A: Akhalkalaki; CV: Cueva Victoria; Fon: Fonelas P-1; Liv: Liventsovka; UV: Upper Valdarno; PR: Pirro Nord; SV: Saint Vallier; S: Süssenborn; VM: Venta Micena (after Borch et al. 2025).

E. senezensis (Senèze) and *E. stehlini* (Upper Valdarno Basin).

The range of variability of *E. altidens* includes *E. 'stenonis mygdoniensis'* from Gerakarou-1, as well as the North American *E. simplicidens* and the living *E. grevyi*. The mc3s from Farneta and Selvella are more slender than those of *E. stenonis* from Upper Valdarno Basin and Saint Vallier, and overall smaller than those of *E. livenzovensisi*, *E. major*, and *E. suessenbornensis* which show a larger and massive morphology. Analogous results are depicted in Figure 3.7B. The equids from Farneta and Selvella are included in the range of variability of *E. altidens*, larger than *E. senezensis* and *E. stehlini*, less robust than *E. stenonis*, and much smaller than *E. livenzovensisi*, *E. major*, and *E. suessenbornensis*.

In Figure 3.7C (mt3 PCA), PC1 and PC2 account for 85.8% of the variance (PC1 = 80.68%; PC2 = 5.19%). PC1 separates species by size from negative to positive values (smaller to larger). Positive PC2 values indicate a more elongated morphology, whereas negative PC2 values show a shorter and more robust shape. The results confirm the previous outcomes on mc3s with new insights about the Selvella sample. The Farneta sample (IGF 785v, IGF 9108v, IGF 9109v) and the specimens from Selvella (IGF 14184, IGF 14187, IGF 14191) are included in the range of variability of *E. altidens* from Süssenborn, Dmanisi, Pirro Nord, and Venta Micena, more elongated and larger than the mt3s of *E. senezensis* (Senèze and Vigna Nuova) and *E. stehlini* (Upper Valdarno Basin). However, three specimens from Selvella (IGF 14185, IGF 14186, IGF 14190), previously identified as *Equus* cf. *stenonis* by De Giuli (1986) and later as *E. suessenbornensis* (Alberdi and Palombo, 2013a) are plotted close to the *E. stenonis* samples from Upper Valdarno Basin, Saint Vallier, Pantalla and Olivola, being different from the larger *E. livenzovensisi*, *E. major*, and *E. suessenbornensis*. *Equus 'stenonis mygdoniensis'* from Gerakarou-1 is still included in the *E. altidens* range of variability, whereas *E. apolloniensis* from Apollonia-1 shows a larger and more elongated shape than *E. altidens*. More insights come also from the comparison of the *E. suessenbornensis* mt3s reported in Alberdi and Palombo (2013a, 2013b). In our analysis, these specimens are distributed over the range of variability of *E. altidens* and *E. stenonis*, showing a different shape and size compared to those of *E. suessenbornensis*. These results support the preliminary insights reported by Cirilli et al. (2023a) about the questionable presence of *E. suessenbornensis* in the Italian Farneta

and Pirro Nord F.U.s based on postcranial elements.

Similar results are shown in Figure 3.7D. The medium-sized equids from Farneta and Selvella are plotted with the European *E. altidens* samples, distinct from *E. senezensis* and *E. stehlini*, less robust than *E. stenonis* and much smaller than *E. livenzovensisi*, *E. major*, and *E. suessenbornensis*. The *E. stenonis* remains from Selvella are plotted close to those of *E. stenonis* from Olivola, being slightly more elongated than the those from Upper Valdarno and Saint Vallier, but with the M11 values fitting into the variability of *E. stenonis* from Upper Valdarno. However, they are much smaller than the typical *E. suessenbornensis* from Akhalkalaki and Süssenborn. Furthermore, the Pirro Nord *E. suessenbornensis* reported in Alberdi and Palombo (2013a, 2013b) is plotted over the range of variability of the European *E. altidens* and *E. stenonis*, being in fact, distinct from *E. suessenbornensis*.

Figure 3.8A plots the results for the a1ph3 PCA with PC1 and PC2 accounting for 93.0% of the total variance (PC1 = 87.3%; PC2 = 5.7%). Summary of the variance components and the loadings' distribution are reported in Appendix 3. PC1 separates species by size from negative to positive values (smaller to larger), whereas PC2 is indicative of relative slenderness from negative to positive values (more to less slender). The results of the a1ph3 concur with the previous outcomes on mc3s and mt3s. The Selvella equids are included in the range of variability of *E. altidens* (IGF 14323, IGF 14326) and *E. stenonis* (IGF 14171, IGF 14324, IGF 14325). The *E. altidens* samples of Süssenborn, Dmanisi, Pirro Nord, and Venta Micena overlap extensively, and show a slenderer morphology than those of *E. senezensis* and *E. stehlini*. Overall, the Selvella equids are well separated from the large-sized species, namely *E. livenzovensisi*, *E. major*, and *E. suessenbornensis*.

Figure 3.8B plots the maximal length (M1) versus the maximal distal width (M6) of the a1ph3. The results concur with those of Figure 3.8A, with the Selvella equid sample included in the *E. altidens* and *E. stenonis* range of variability, well separated from the smaller *E. senezensis* and *E. stehlini* on one side, and from the larger *E. livenzovensisi*, *E. major*, and *E. suessenbornensis* on the other.

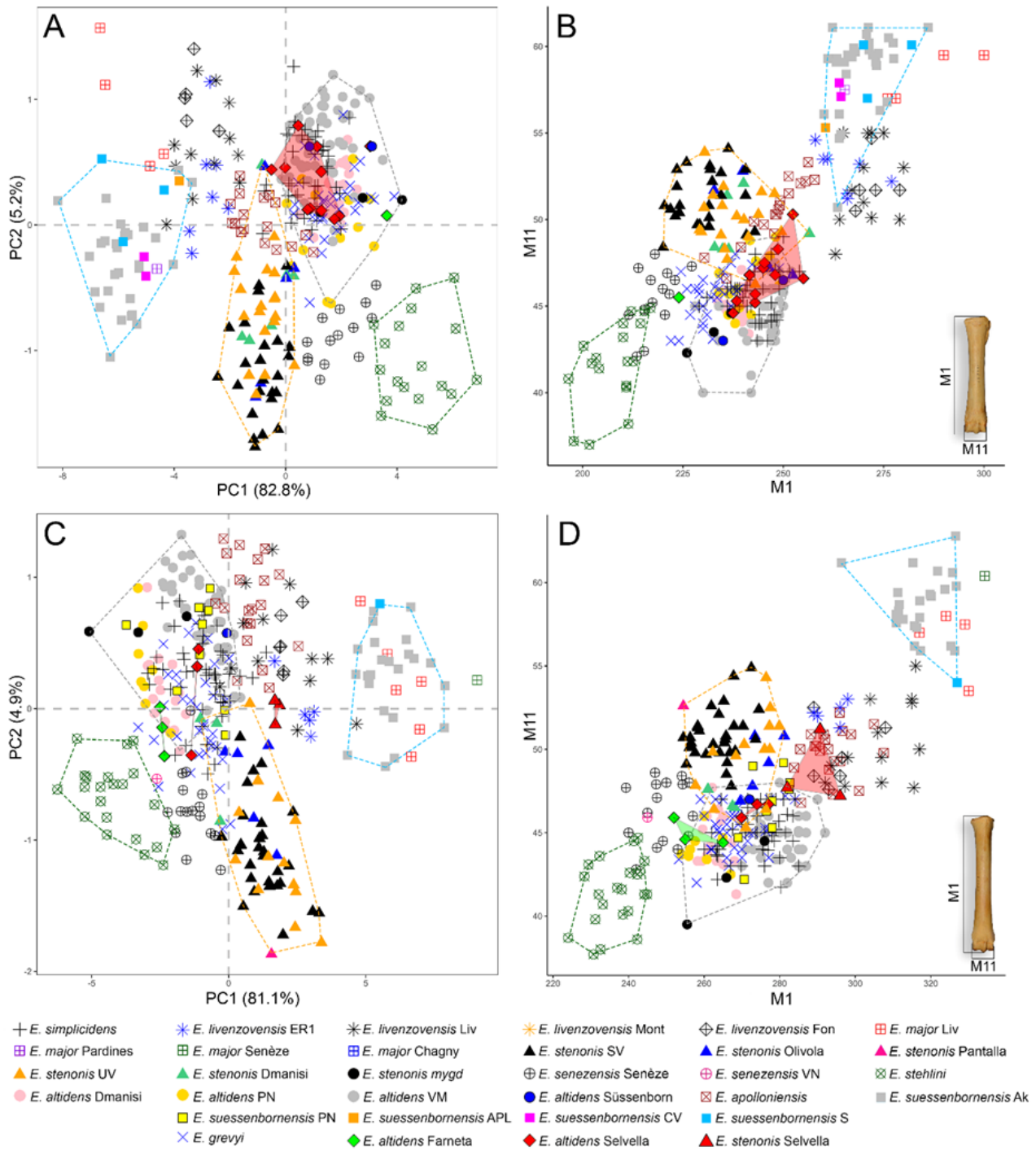


Figure 3.7: Principal component analysis (A, C) and bivariate plots (B, D) on third metacarpals and third metatarsals respectively, comparing *E. altidens* and *E. stenonis* from Farneta and Selvella with a wide sample of fossil Pliocene, Pleistocene and extant *Equus* species. For each PCA, the loadings distribution is shown as an inset in the diagrams. Complete PC components are reported in Appendix 3. Measurements are referred to Eisenmann et al. (1988) and Bernor et al. (1997). Abbreviations: Ak: Akhalkalaki; APL: Apollonia; CV: Cueva Victoria; ER-1: El Rincon -1; Fon: Fonelas; Liv: Liventsovka; mygd: mygdoniensis; Mont: Montopoli; PN: Pirro Nord; S: Süssenborn; SV: Saint Vallier; UV: Upper Valdarno; VM: Venta Micena; VN: Vigna Nuova (after Borch et al., 2025).

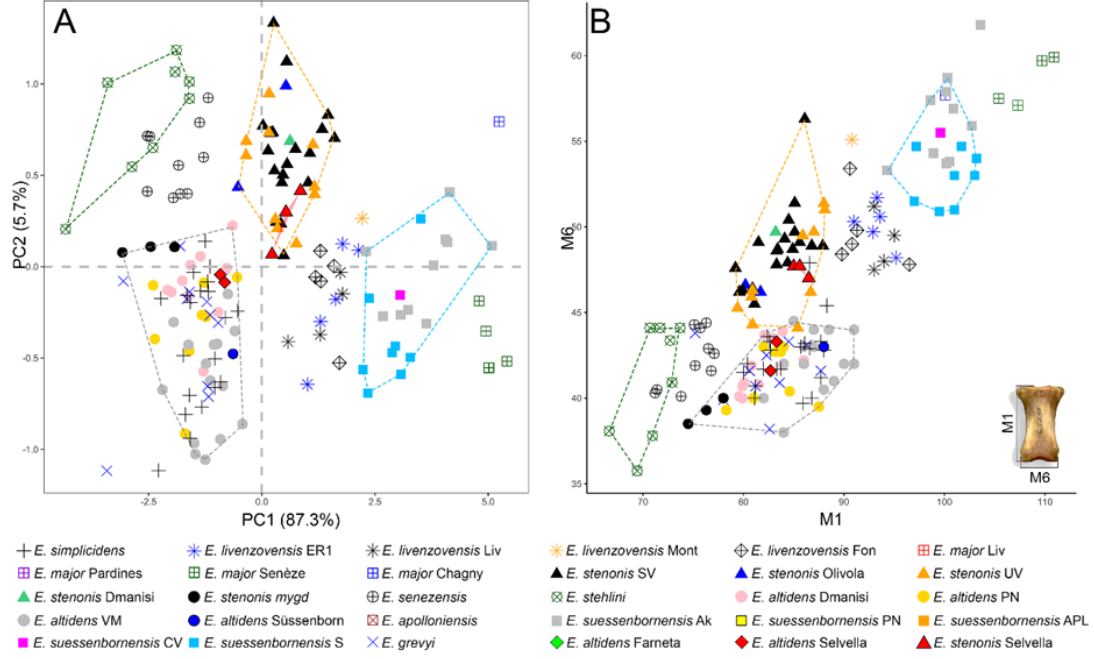


Figure 3.8: Principal component analysis (A) and bivariate plot (B) on first anterior phalanges of the central digit, comparing *E. altidens* and *E. stenonis* from Farneta and Selvella with a wide sample of fossil Pliocene, Pleistocene and extant *Equus* species. For the PCA, loadings distribution is shown as an inset in the diagrams. Complete PC components are reported in Appendix 3. Measurements are referred to Eisenmann et al. (1988) and Bernor et al. (1997). Abbreviations: Ak: Akhalkalaki; APL: Apollonia; CV: Cueva Victoria; ER-1: El Rincon-1; Fon: Fonelas; Liv: Liventsovka; mygd: mygdoniensis; Mont: Montopoli; PN: Pirro Nord; S: Süssenborn; SV: Saint Vallier; UV: Upper Valdarno; VM: Venta Micena; VN: Vigna Nuova (after Borchì et al., 2025).

The Log10 ratio diagrams on mc3s and mt3s provide additional information about the equid assemblage from the Farneta F.U. compared to the other European Early Pleistocene stenonid *Equus*.

Figure 3.9A (mc3) illustrates the range of variability with maximum, mean, and minimum values for the Selvella *E. altidens* with the *E. altidens* specimens from Farneta (IGF 9114v) and with the incomplete mc3 from Pietrafitta (MPLBP EQ-0001). As shown in the diagram, the Selvella sample includes the Farneta and Pietrafitta ones, characterised by a slender morphology represented by an elongated M1 and medium-sized M3, larger than *E. senezensis* and *E. stehlini* (Fig. 3.9B), and with a pattern similar to the other *E. altidens* samples from Dmanisi, Gerakarou (*E. ‘stenonis mygdoniensis’*), Pirro Nord, Venta Micena, and Süssenborn (Fig. 3.9C). The specimen from Pietrafitta plots closely with the mean of the Selvella sample, supporting its attribution to *E. altidens*.

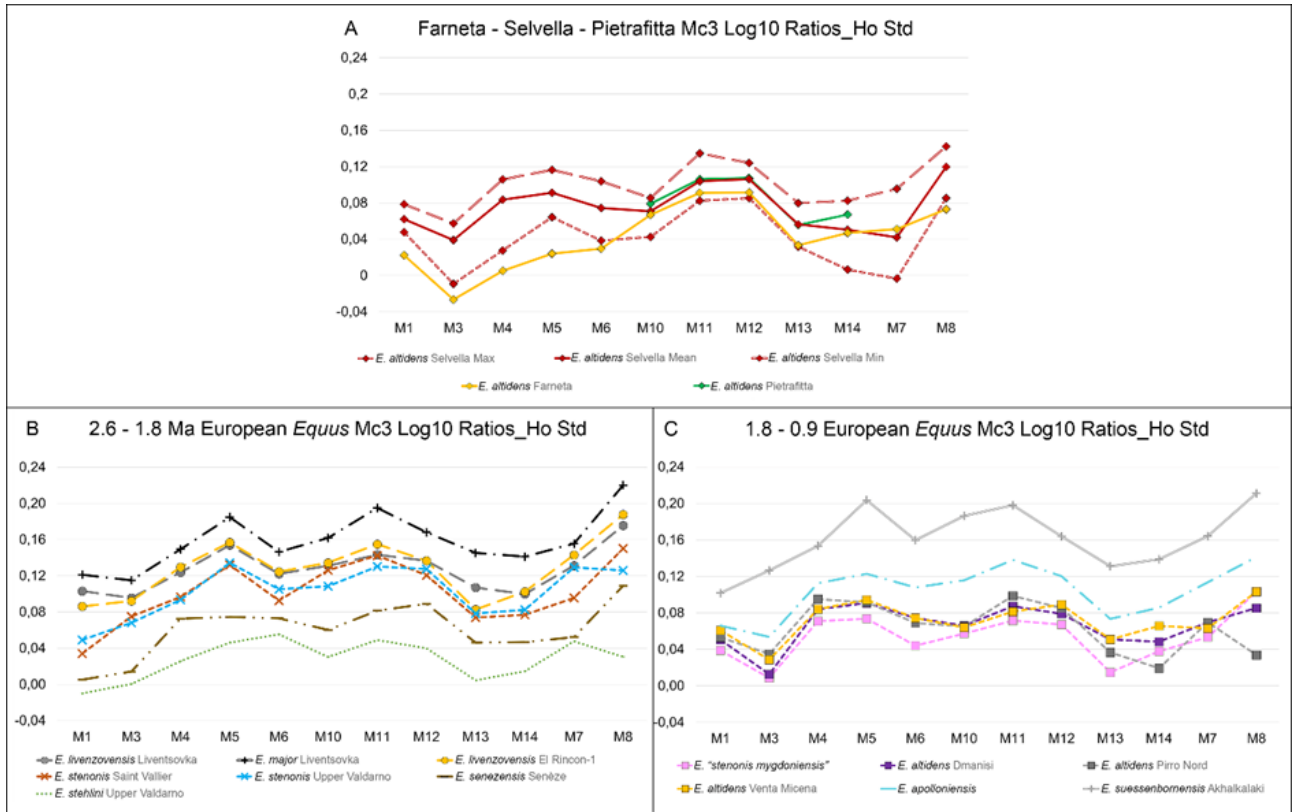


Figure 3.9: Log10 ratio diagrams in third metacarpal based on the Log10 transformed mean of the *Hippotherium primigenium* sample from Höwenegg (Germany, Late Miocene). A) *Equus altidens* mc3 variability from Selvella (maximum, mean and minimum values) compared with the mean values of *E. altidens* from Farneta and Pietrafitta. B) Mean values of mc3 variability of *Equus* fossil species from 2.6 – 1.8 Ma. C) Mean values of mc3 variability of *Equus* fossil species from 1.8 – 0.9 Ma. Measurements are referred to Eisenmann et al. (1988) and Bernor et al. (1997) (after Borch et al., 2025).

Figure 3.10A (mt3) shows the Log10 patterns for the Farneta and Selvella *E. altidens* samples and for the Selvella *E. stenonis* sample, with maximum, mean, and minimum values. As for the mc3s, the Farneta and Selvella *E. altidens* have a pattern similar to the other *E. altidens* samples from Dmanisi, Gerakarou (*E. 'stenonis mygdoniensis'*), Pirro Nord, Venta Micena, and Süssenborn (Fig. 3.10C), with slender proportions (M1-M3), and medium-sized diaphysis, proximal, and distal epiphysis (M3-M4, M5-M6, and M10-M14, respectively). As in Figure 3.9, the Farneta and Selvella *E. altidens* populations differ from *E. senezensis* and *E. stehlini* (Fig. 3.10B) for a more elongated M1 and general larger size of their extremities. On the other hand, the range of variability of *E. stenonis* from Selvella is more similar to the mean values of the *E. stenonis* samples from Saint Vallier and Upper Valdarno (Matassino, Poggio Rosso; Fig. 3.10B), rather than *E. suessenbornensis* (Fig. 10C). Despite having a longer M1, the Selvella

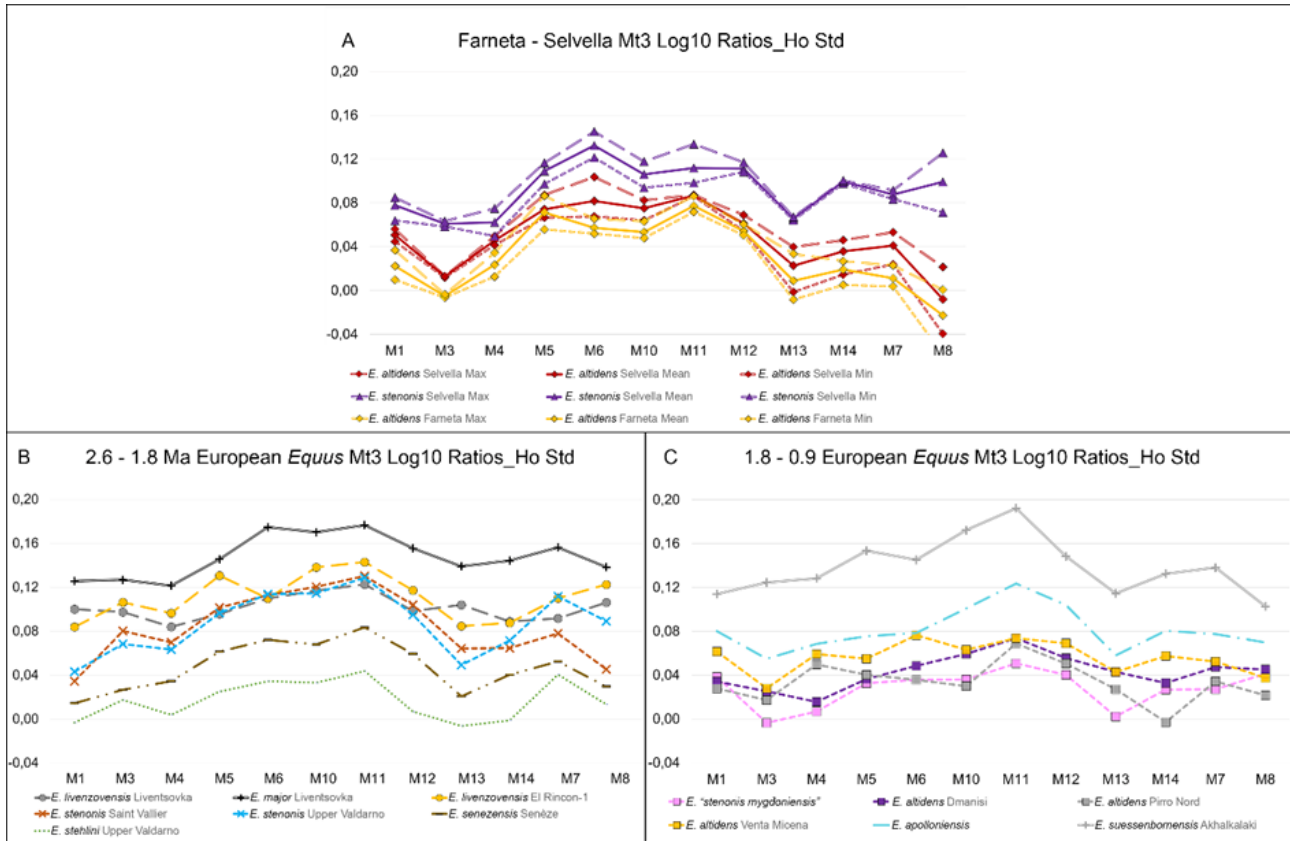


Figure 3.10: Log10 ratio diagrams in the third metatarsal based on the Log10 transformed mean of the *Hippotherium primigenium* sample from Höwenegg (Germany, Late Miocene). A) *Equus altidens* and *Equus stenorion* mt3 variability from Selvella and Farneta in maximum, mean and minimum values compared. B) Mean values of mt3 variability of *Equus* fossil species from 2.6 – 1.8 Ma. C) Mean values of mt3 variability of *Equus* fossil species from 1.8 – 0.9 Ma. Measurements are referred to Eisenmann et al. (1988) and Bernor et al. (1997) (after Borch et al., 2025).

E. stenorion has a smaller diaphysis (M3-M4), and less robust proximal (M5-M6) and distal epiphyses (M10-M14) if compared to *E. suessenbornensis* (Fig. 10C).

Overall, these results concur with the previous comparison of the upper and lower dentition and with the PCAs on postcranial elements, supporting the attribution to *E. stenorion* and *E. altidens* for the fossil equids of the Farneta F.U..

3.6.2 Analysis of the variance of the Farneta F.U. equids compared with the European Early and early Middle Pleistocene stenonid *Equus*

To test for significant differences between the fossil equids from the Farneta F.U. and other European *Equus* species, a permutational multivariate analysis of variance (PERMANOVA) was undertaken on the PC values on mc3s and mt3s (Table 3.2). Unfortunately, given the reduced sample in the mt3s (three mt3s from each sample), the best results were obtained for

mc3s for the Selvella sample, which includes 10 specimens. These results are reported in Table 3.2.

The PERMANOVA results indicate significant differences between *E. altidens* from Selvella and *E. livenzovens* (El Rincon-1, Liventsovka), *E. stenonis* (Saint Vallier, Upper Valdarno), *E. stehlini*, *E. apolloniensis*, and *E. suessenbornensis* (Akhalkalaki) ($p. = 0.0297$), as well as with *E. senezensis* ($p. = 0.0594$). On the other hand, the Selvella *E. altidens* does not show any significant differences with the other *E. altidens* samples (Dmanisi, Pirro Nord, and Venta Micena), thus far supporting the results of the PCAs and of the Log10 Ratio Diagrams mentioned above. These results are better supported by pairwise large sample comparison (with at least 10 specimens), which helps to better evaluate their range of variability. The not significant results obtained with *E. major* (Liventsovka, Pardines), *E. stenonis* (Dmanisi, Olivola), and *E. suessenbornensis* (Cueva Victoria, Süssenborn) are related to the limited complete specimens retrieved in these samples used for the PCA. Nevertheless, the results shown in Figure 3.7 help to distinguish these samples from the Selvella *E. altidens*.

3.7 Discussion

3.7.1 *Equus stenonis* and *Equus altidens* from the Farneta F.U.: new results compared to previous findings

This review of the samples from Farneta, Selvella, and Pietrafitta LFAs provides a new perspective on the large- and middle-sized horses occurring in the Farneta F.U. The results partially agree with previous interpretations, and do not support others. Specifically, the presence of *E. stenonis* in Selvella is in agreement with the previous identifications by De Giuli (1986), Forsten (1999), and partially Caloi & Palombo (1987). As preliminary suggested in Cirilli et al. (2023a), the large-sized equids from Selvella are not comparable with the typical *E. suessenbornensis* from Akhalkalaki and Süssenborn, characterised by a larger size of the cranial and postcranial elements (Figs. 3.5-10), and by a much more complex occlusal enamel morphology of the upper and lower cheek (Cirilli et al. 2023a: figs. 2, 3, 10).

For the medium- to small-sized equids, results agree with the previous identifications of *E. altidens* (Alberdi & Palombo, 2013a, 2013b), and do not support the presence of *E. stehlini* in

Farneta, Selvella, and Pietrafitta. Although in the comparisons of the upper and lower teeth a certain overlap with *E. stehlini* from Upper Valdarno can be observed, the results on the postcranial elements show a remarkable difference with that sample and, on the other hand, exhibit a striking similarity with the early *E. altidens* samples from Dmanisi, Pirro Nord, and Venta Micena. These results are also in agreement with the hypothesis of Gkeme et al. (2017), Bernor et al. (2021), Cirilli et al. (2021b) and Koufos et al. (2022) in considering also the sample from Gerakarou as comparable with these early *E. altidens* samples, although a detailed study on the collection is missing since Koufos (1992). We also show that *E. altidens* from Süssenborn (type locality of the species) is included in the range of variability defined by the samples from Dmanisi, Farneta, Selvella, Pietrafitta, Pirro Nord, and Venta Micena.

Moreover, this study highlights the presence of two equid species in the Selvella LFA: *E. stenonis* and *E. altidens*, with the latter more abundant in terms of the number of specimens retrieved. The greater abundance of the latter species over the former could explain its failure to be recognised in the almost coeval sites of Farneta and Pietrafitta, where a relatively smaller number of horse remains were recovered (especially in the second; Appendix 1).

3.7.2 Implications for the biochronology of Early Pleistocene *Equus* species in Western Eurasia

The review of the Farneta F.U. equids allows us to shed new insights on the biochronology of the Early Pleistocene *Equus* species in Western Eurasia, especially for the latest occurrence of *E. stenonis* and the earliest of *E. altidens*. As reported by Cirilli et al. (2021b), *E. stenonis* is the most widespread species in the middle and early-late Villafranchian in Western Eurasia. The species has been reported in several fossil localities dated between ca. 2.5–1.8 Ma (Cirilli et al. 2021b), but its last occurrences are still controversial and not well defined. De Giuli & Torre (1984) reported the occurrence of *E. ex gr. stenonis* from Pirro Nord, later changed in *E. cf. altidens* (De Giuli et al. 1986b). More recently, the fossil equids from Pirro Nord have been ascribed to *E. altidens* and *E. suessenbornensis* (Alberdi and Palombo 2013a, 2013b), although this identification has been partially challenged by Cirilli et al. (2023a).

As shown in Figure 3.8C-D, and in Cirilli et al. (2023a), the mt3s from Pirro Nord previously

Pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted
<i>E. simplicidens</i> vs <i>E. altidens</i> Selvella	1	0.899183699	1.30269	0.02539	0.257574243	1.0000
<i>E. livenzovensis</i> Liventsovka vs <i>E. altidens</i> Selvella	1	90.85630012	90.8231	0.81220	0.00009999	0.0297
<i>E. livenzovensis</i> Fonelas P1 vs <i>E. altidens</i> Selvella	1	67.25493345	83.0015	0.85567	0.00019998	0.0594
<i>E. livenzovensis</i> El Rincon-1 vs <i>E. altidens</i> Selvella	1	64.35461799	81.543304	0.83597	0.00009999	0.0297
<i>E. major</i> Liventsovka vs <i>E. altidens</i> Selvella	1	131.9336846	116.5601	0.899660	0.00119988	0.3564
<i>E. major</i> Pardines vs <i>E. altidens</i> Selvella	1	30.31998957	30.30389	0.751885	0.079492051	1.0000
<i>E. stenonis</i> Saint Vallier vs <i>E. altidens</i> Selvella	1	45.59070431	64.65555	0.662077	0.00009999	0.0297
<i>E. stenonis</i> Upper Valdarno vs <i>E. altidens</i> Selvella	1	32.7806055	49.73345	0.648132	0.00009999	0.0297
<i>E. stenonis</i> Dmanisi vs <i>E. altidens</i> Selvella	1	14.48411432	15.44021	0.507230	0.00069993	0.2079
<i>E. stenonis</i> Olivola vs <i>E. altidens</i> Selvella	1	12.57350515	13.45671	0.456830	0.00039996	0.1188
<i>E. stenonis</i> mygdoniensis vs <i>E. altidens</i> Selvella	1	6.376269243	5.342979	0.308077	0.0409959	1.0000
<i>E. senezensis</i> vs <i>E. altidens</i> Selvella	1	12.94702315	14.57340	0.387864	0.00019998	0.0594
<i>E. stehlini</i> vs <i>E. altidens</i> Selvella	1	101.785171	84.57230	0.758004	0.00009999	0.0297
<i>E. apolloniensis</i> vs <i>E. altidens</i> Selvella	1	26.84970606	28.83399	0.525841	0.00009999	0.0297
<i>E. altidens</i> Dmanisi vs <i>E. altidens</i> Selvella	1	3.256489659	6.355537	0.161490	0.01259874	1.0000
<i>E. altidens</i> Pirro Nord vs <i>E. altidens</i> Selvella	1	2.530867097	2.24329	0.092532	0.135786421	1.0000
<i>E. altidens</i> Venta Micena vs <i>E. altidens</i> Selvella	1	1.475583307	1.903267	0.03344	0.163983602	1.0000
<i>E. altidens</i> Selvella vs <i>E. altidens</i> Sussenborn	1	1.447218439	1.272130	0.103660	0.312468753	1.0000
<i>E. suessenbornensis</i> Akhal-kalaki vs <i>E. altidens</i> Selvella	1	379.2931519	353.7136	0.902990	0.00009999	0.0297
<i>E. suessenbornensis</i> Cueva Victoria vs <i>E. altidens</i> Selvella	1	64.49076392	70.80228	0.865529	0.01239876	1.0000
<i>E. suessenbornensis</i> Sussenborn vs <i>E. altidens</i> Selvella	1	105.3566546	98.68140	0.891580	0.00219978	0.6533
<i>E. grevyi</i> vs <i>E. altidens</i> Selvella	1	3.135131716	3.831931	0.08011	0.04979502	1.0000

Table 3.2: PERMANOVA results performed on third metacarpal PC values comparing *Equus stehlini* with the European Early and early Middle Pleistocene *Equus* species.

ascribed to *E. suessenbornensis* from Alberdi & Palombo (2013a, 2013b) extensively overlap the range of variability shown by the *E. altidens* samples, remarkably different from the large-sized *E. suessenbornensis* from Akhalkalaki and Süssenborn. On the other hand, *E. suessenbornensis* from Pirro Nord is better reported by isolated teeth (Cirilli et al. 2023a: fig. 3.10), which show an identical morphology with the Akhalkalaki and Süssenborn fossils. Moreover, Aouadi (1999) and Aouadi & Bonifay (2008) reported *E. stenonis* from Ceyssaguet (France). The measurements provided by these authors (including only maximal, mean, and minimal values) for the species identified in Ceyssaguet, *E. stenonis* and *E. bressanus* (= *E. major*), show a great range of variability, making it difficult to use them for comparative analyses with other Early and early Middle Pleistocene European *Equus* species as provided herein. In Eastern Europe, the best-known record of *E. stenonis* is from Greece. Koufos (1992) and Koufos et al. (2022) reported *E. stenonis* latest known record comes from the localities of Krimni1 and Riza-1, ca. 1.8–1.6 Ma (Konidaris & Kostopoulos, 2024). *E. stenonis* is not reported from Tsiotra Vryssi, where at the present time *Equus* ex gr. *apolloniensis* has been identified (Konidaris et al. 2015; Konidaris & Kostopoulos, 2024), or from Apollonia-1, where *E. apolloniensis* and *E. suessenbornensis* have been identified (Gkeme et al., 2021; Cirilli et al., 2023a; Konidaris & Kostopoulos, 2024). On the other hand, the latest record of *E. stenonis* in the Iberian Peninsula is known from La Puebla de Valverde (Cirilli et al. 2021b), ca. 2.1–1.95 Ma (Sinusia et al., 2004), while *E. stenonis* is not reported from the locality of Venta Micena (ca. 1.5 Ma), where only *E. altidens* is known (Alberdi & Ruiz Bustos, 1985, 1989; Guerrero-Alba & Palmqvist, 1997; Alberdi & Palombo 2013a). The results reported in the present work allow to extend the biochronologic range of *E. stenonis* into the Farneta F.U. (i.e., until ca. 1.6–1.5 Ma), pending the revision of the equid collections from Pirro Nord, Ceyssaguet, and the aforementioned Greek localities.

The taxonomy and biochronology of *E. altidens* are highly debated by different scholars. The species was erected for the Middle Pleistocene sample of Süssenborn, but in the last decades it has been reported in several sites from the late Early and early Middle Pleistocene. Most of the controversy regards its taxonomic status. Some scholars (Alberdi et al., 1998; Alberdi & Palombo, 2013a, 2013b; Palombo et al., 2017; Gkeme et al., 2017; Bernor et al. 2021;

Cirilli et al., 2020a, 2021b, 2023a, 2024a; Koufos et al., 2022; Konidaris & Kostopoulos, 2024) recognise the validity of the species, whereas others (Eisenmann & Boulbes, 2020; Eisenmann 2022b) question it, suggesting to split the middle-sized equid samples ascribed to *E. altidens* in a variety of species as *Equus vekuae* (Dmanisi), *Equus mygdoniensis* (Gerakarou), *Equus granatensis* (Venta Micena), and *Equus* aff. *granatensis* (Pirro Nord), and to restrict *E. altidens* to the only sample of Süssenborn or even questioning its validity as a distinct taxon. Here, analyses on multiple skeletal elements have shown no morphological, morphometric, or even statistical differences between the samples ascribed to *E. altidens* (Figs. 3.5-10, Table 2). Moreover, the specimens from the type sample of Süssenborn are always included within the range of variability shown by the other samples here analysed, making it unlikely to refer these samples to separate taxa. Furthermore, the range of variability shown by the samples from Dmanisi, Gerakarou, central Italy (including Farneta, Selvella, and Pietrafitta), Pirro Nord, Venta Micena, and Süssenborn is similar to the one shown by the European samples of *E. stenorhis* (see Cirilli et al., 2021b), *E. suessenbornensis* (Cirilli et al. 2023a), *E. livenzovens*, and *E. major* (Cirilli et al. 2024a). The range of variability shown by the studied samples is similar to that shown by *E. stehlini* from Upper Valdarno Basin, which includes specimens from different localities of a single basin with a well-constrained age (Cirilli, 2022). These results indicate a remarkable similarity between the populations of these middle-sized equids, not providing compelling evidence to support the hypothesis of splitting them into different species or subspecies. In this regard, the most parsimonious hypothesis is to consider *E. altidens* as a monotypic and polymorphic species and, as *E. stenorhis*, the purported species/subspecies proposed in the past years do not warrant taxonomic distinction at the species or subspecies rank and could represent local eco-morphotypes of a single widespread species.

Nevertheless, this hypothesis needs to be tested with large samples from other Western Eurasian sites where these middle-sized equids have been reported and, at the present time, it needs to be considered as preliminary rather than conclusive, not disregarding the chance that local speciation events could have occurred leading to the origin of different species (e.g., *E. wuesti* from Untermassfeld).

This study supports the identification of a middle-sized equid from the Farneta F.U. different

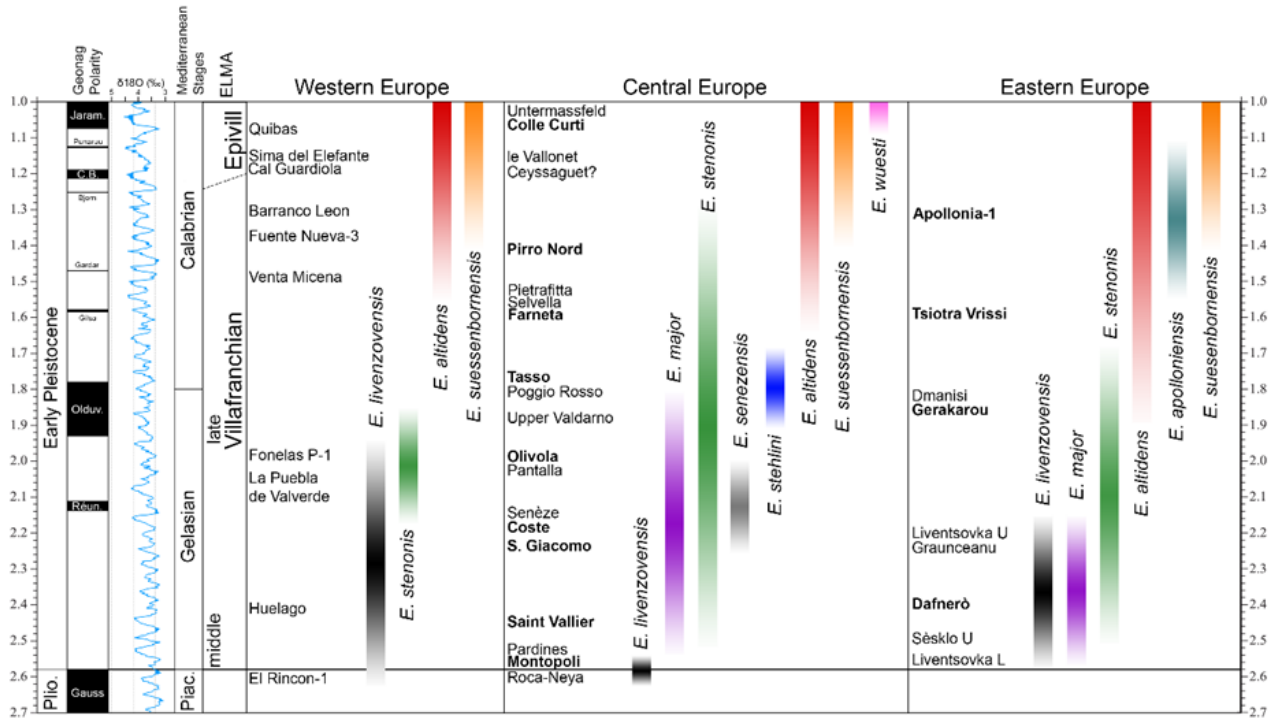


Figure 3.11: Updated biochronological scheme of European *Equus* fossils species of the Late Pliocene and Early Pleistocene. Each *Equus* species biochronology is represented in each locality with its age range. The Quaternary chronology refers to Head & Gibbard (2015) and Gibbard & Head (2020) (after Borchi et al., 2025).

from *E. stehlini* which we refer to as *E. altidens*, supporting the previous identification of Alberdi & Palombo (2013a, 2013b). This is also in agreement with the hypothesis provided by Gkeme et al. (2017), Bernor et al. (2021), Cirilli et al. (2022), and Koufos et al. (2022), to consider the first occurrence of *E. altidens* in the Caucasus and Greece at ca. 1.8 Ma (Dmanisi, Gerakarou), with a subsequent dispersal of the species toward Central and Western Europe during the Farneta F.U. (cf. central Italian sites studied herein, Venta Micena). An updated biochronological scheme of Early Pleistocene *Equus* species is reported in Figure 3.11.

3.8 Conclusions

The review of the fossil equids from the Farneta F.U. allows for better clarification of their taxonomy and provides new insights on the palaeobiogeography and biochronology of *Equus* species of Western Eurasia. The presence of *E. stenonis* remarks a continuity with the Tasso F.U., and it allows for a better frame the occurrence of this species to date. Moreover, these results support the oldest occurrence of *E. suessenbornensis* in the locality of Pirro Nord in



Figure 3.12: Palaeoartistic representation of the Early Pleistocene locality of Farneta with the presence of two *Equus* fossil species. On the left: *Equus stenonis*, on the right: *Equus altidens*. Artwork by Isacco Alberti (after Borchì et al., 2025).

the Italian fossil record, as recently reported (Arzarello et al., 2009; Cirilli et al., 2023a). On the other hand, the recognition of *E. altidens* marks a renewal in the Italian fossil record of the latest Villafranchian. This, combined with the first occurrences of *Ps. farnetensis*, *Pr. obscurus*, and *B.(Eobison) degiulii*, highlights the importance of the Farneta F.U. in the Italian (and Western Eurasian) biochronological record, being placed in a timeframe (ca. 1.6–1.5) where few localities have been reported in Western Eurasia (Rook & Martínez-Navarro, 2010; Kahlke et al., 2011). An artistic representation of the co-occurrence of *E. stenonis* and *E. altidens* in Farneta is given in Figure 3.12.

4 TAPHONOMY OF CAVA LIBERATORI

4.1 Introduction

4.1.1 State of the art on the taphonomy of the fossil locality of Farneta (Val di Chiana, Arezzo).

Despite its biostratigraphic significance, the taphonomic framework of the Farneta assemblage remains poorly understood. While previous studies have primarily focused on taxonomy, biochronology, and stratigraphic correlations (Ambrosetti et al., 1972; Rook, 2010), relatively little attention has been given to the depositional history, post-mortem modification, and accumulation processes of the fossils. Until less than a century ago, it was common practice to recover fossil specimens using basic excavation tools, under the supervision of a palaeontologist who would decide which specimens were suitable for museum collection and exhibition, and which could skip the preparation phase and be sent straight to the museum deposits (Fernández-Jalvo et al., 2011). Most fossil bones recovered from the area of Farneta (Val di Chiana, Arezzo) were recovered over the last century, following the common practice mentioned above.

Through the examination of bone surface modifications, skeletal part representation, breakage patterns, and spatial distribution, taphonomic analysis provides critical insights into the formation processes of the assemblage, allowing the differentiation between biogenic and abio-genic agents and the reconstruction of the palaeoenvironmental context (Lyman, 1994; Behrens-meyer et al., 2000; Domínguez-Rodrigo et al., 2012). Taphonomic observations start from the moment a fossil is discovered, as the contextual information recorded in the field constitutes a fundamental component of any palaeoecological reconstruction. Observations made directly at the excavation site allow researchers to document the spatial, sedimentological, and stratigraphic relationships of fossil remains, providing essential data for understanding the processes that governed their accumulation, modification, and preservation (Behrensmeyer, 1978; Lyman, 1994; Andrews, 1995).

The field phase of a taphonomic study should therefore not be limited to fossil recovery but should involve a systematic recording of depositional and post-depositional evidence that

may later be lost or altered during collection and preparation (Fernández-Jalvo & Andrews, 2003; Eberth et al., 2007). At the excavation site, primary taphonomic information includes the orientation, articulation, and anatomical association of skeletal elements, which can indicate the degree of post-mortem disturbance and transport before burial (Voorhies, 1969; Behrensmeyer, 1978). Measurements of fragmentation patterns and spatial clustering can further help infer the influence of hydrodynamic sorting, trampling, or biotic modification (Dodson, 1973; Eberth & Currie, 2005). Unfortunately, none of these features was recorded when the fossil bones were recovered from Cava Liberatori. The only information available from field observations are those present on labels associated with the original plastic envelopes in which the fossil bones from Cava Liberatori, which were rediscovered in 2022. The specimens were excavated between 1973 and 1974 by the museum staff with the help of the local community. The gathered material was collected at the site and kept in 26 different envelopes with an associated field note (Fig. 4.1), and it is now housed in the Museum of Geology and Palaeontology of Florence. Except for two specimens – the *Mammuthus meridionalis* skeleton informally known as “Linda” (IGF 14838) and the holotype of *Pseudodama farnetensis* (IGF 194 V), the material is not currently exhibited and lacks an official catalogue number, due to their isolated and mostly fragmentary nature.

4.1.2 Aims of this study

The present study conducts a qualitative and quantitative taphonomic analysis of the fossil assemblage from the Cava Liberatori quarry in Farneta. The *Mammuthus meridionalis* (IGF 14838; “Linda”; Azzaroli 1977) is the only articulated skeleton recovered in the quarry in 1973, around 65% to 70% complete (Mazza & Cioppi, 2010). The main objectives of this chapter are: (1) to identify the principal taphonomic agents responsible for bone accumulation and modification such as weathering stages, root etching, or evidence of carnivore activity; (2) to infer the depositional and post-depositional history of the assemblage, taking into account exposure time, subaerial conditions, and biotic interactions before final burial.

4.2 Materials and Methods

To evaluate the nature of the fossil accumulation, all the isolated fossil elements recovered from 1973 and 1974 in Cava Liberatori were taken into consideration (n=44, Appendix 5). All the fossil elements recovered from Cava Liberatori are isolated bones, except for the partial skeleton IGF 14838. As mentioned before, the skeleton is exhibited in the IGF museum and has been overprepared. For these reasons IGF 14838 is not considered for the following analyses, but it will be considered in the discussion section for an overall overview of the taphonomy of the assemblage. The fossil assemblage includes cranial and postcranial bones, as well as upper and lower teeth. For each specimen, information on the taphonomy of the fossil bones was collected (Table 4.2). Measured taphonomic data include (a) bone completeness, (b) weathering stage, (c) element size, (d) predation marks, (e) bioturbation marks. In addition, the colour and oxidation of bone surface were taken into account.

Bone completeness was classified “high” when the element is complete or only lacking articular surfaces, “medium” when the distal and proximal epiphyses are missing in long bones, “low” when only the epiphysis present or the element consists of fragments lacking surfaces that allow for taxonomical identification. The weathering stage is evaluated after Behrensmeyer’s (1978) taphonomic scale and subsequent refinements (Andrews 1995; Lyman 1994; Table 4.2).

Element size refers to the maximum length of the specimens measured in centimetres. Three classes of element size were considered: ‘small’ when the element is <10 cm, medium when the element is over 10 cm and less than 30 cm, and ‘large’ when the length exceeds 30 cm.

When fossil bones are broken into multiple matching parts, the size of each element is considered as the total maximum length of all the parts combined. Predation marks and bioturbation marks - such as root marks - are classified as ‘present’ / ‘absent’. All these variables are considered following direct observation. The bone surface colour and manganese oxidation coverage were qualitatively assessed, in order to spot significant differences between the surface appearance of specimens in the fossil assemblage. In addition, the distance of each fossil bone from IGF 14838 was taken into account using information retrieved from field labels, in an effort to identify different possible deposition events. To analyse sedimentological aspects of the fossil assemblage, pictures taken at the dig site at the time of the excavation

Taphonomy	Category	Description
a	Bone completeness	low; medium; high
b	Weathering stage	0–5
c	Element size	small; medium; large
d	Predation marks	absent; present
e	Bioturbation marks	absent; present

Table 4.1: List of the taphonomic variables considered.

Stage	Surface Characteristics	Charac- teristics	Structural Changes	Approximate Ex- posure Time	Taphonomic In- terpretation
0	Bone smooth, periosteum intact; natural ivory or yellowish color.	surface greasy, intact;	No cracking or flaking; bone retains fresh appearance.	0 – few months	Recently deceased or rapidly buried individual; no subaerial exposure.
1	Surface dulls; fine longitudinal cracks form on exposed areas; surface remains compact.		Cortex intact; no exfoliation or deep cracking.	0.5 – 3 years	Initial stage of weathering; short subaerial exposure before burial.
2	Cracks deepen and widen; first signs of flaking, especially near epiphyses; rougher texture.		Partial exfoliation of outer cortex; early loss of compactness.	2 – 5 years	Moderate exposure; limited mechanical degradation.
3	Extensive flaking; fibrous, rough surface; deeper cracks penetrate subsurface layers.		Outer surface largely exfoliated; increased porosity and brittleness.	4 – 10 years	Advanced weathering; prolonged exposure before burial.
4	Deep cracking and splintering; large cortical areas missing; cancellous tissue exposed.		Severe loss of structural integrity; cortex heavily eroded.	6 – 15 years	Strong physical and chemical alteration due to long exposure.
5	Bone reduced to splinters and powder; shape barely preserved.		Cortical and cancellous bone disintegrated.	10+ years	Extremely prolonged exposure; final stage before total disintegration.

Table 4.2: Weathering stages following Behrensmeyer (1978).

were inspected (Fig 5.1), since no information about the stratigraphy or sedimentology of the quarry was collected at the time, and it has been fully excavated. In addition, the nature of the matrix still attached to some of the fossil bones was also taken into account.



Figure 4.1: Two of the recovered envelopes with their relative fossil elements and field notes. Picture A) Right tibia of *Pantnera* cf. *toscana* recovered under the humerus of IGF 14838. Picture B) *Equus stenonis* p3-4 tooth, recovered under IGF 14838's vertebra

4.3 Results

4.3.1 Taphonomy of Cava Liberatori

Referred material in Fig. 4.4 and Figures in Appendices 7 to 11. A total of 44 specimens were analysed (Table 4.3; Appendix 5), including the holotype of *Pseudodama farnetensis* (Azzaroli, 1992). 28,9% of specimens scored “low” on bone completeness, 42,2% scored medium, and 28,9% scored high. Of all the elements, 42,2% fall into the class size 1 (maximum length 10 cm), 42,2% fall into class 2 (length between 10 and 30 cm), and only 15,6% exceed 30 cm (class 3). The most abundant weathering stage is Stage 3, identified in 28,9% of elements analysed, followed by Stage 2 (24,4%), Stage 4 (20%), Stage 1 (17,8%), and finally Stage 5 (8,9%). Predation marks and bioturbation marks are absent in most of the specimens analysed (presence percentage 13,3% and 31,3%, respectively; Fig. 4.2).

Bone colour and oxidation. All fossil elements show the same light to dark yellow colour preservation, with the exception of specimen 11A (Appendix 8I), which shows a white surface colour and is heavily covered in black manganese oxidation. Manganese occurs mildly in some other fossils, where it evenly covers the shaft and the articular ends. In some elements, oxidation is completely absent.

Predation marks. Carnivore damage occurs most frequently on the shafts of limb bones, on their articular ends, and on spiral breaks (Andrews and Jalvo, 1997). It is present in 13,3% of the specimens. Specimen 1A (Fig. 4.4D) – a lower jaw of a herbivore, possibly a cervid

Family or higher taxa	Number of specimens
Equidae	3
Bovidae	2
Cervidae	14
Rhinocerotidae	1
Canidae	1
Felidae	1
Other Artiodactyla	6
Pectinidae	1
Mammalia indet.	15

Table 4.3: Taxonomic composition of the analyzed assemblage.

– shows gnawing damage on both proximal and distal ends. The edges are broken in sharp fractures, and the surface of the cut bone shows the same mineralisation colour as the rest of the fossil bone. Specimen 6A (Fig. 4.4G), a juvenile cervid scapula, shows a deep pit near the distal end of the ventral surface. The hole is round in shape and deeply perforates the cortical bone. Its edges are smooth and rounded on one side and sharp on the other. Overall, the shape and size of the pit are consistent with a bite mark of a large carnivore (Beherensmeyer et al., 2000). Specimen 12C (Appendix 9G) – a small mammal tibia – shows both proximal and distal epiphyses heavily damaged by gnawing. The tibia is broken in three parts, lacking the medullary cavity and showing the same oxidation pattern both on the inside and outside of the cortical bone. Traces of bite marks are evident in specimen 16A (Fig 4.4E; Appendix 10B) – a tibia of *Panthera toscana* - along the margins of the distal and proximal epiphysis. In the proximal epiphysis two small pits are present as puncture marks made by two small (possibly rodent) incisors, whereas on the distal epiphysis three pit perforations on the bone surface were made by multi-cusped teeth.

Bioturbation marks. Bioturbation marks are present in the form of root etching or scavenger/necrophagous invertebrates. Root etching is present in fossil bones 8B, 10A, 13A, 16A, 17A, 19A, 24A, 26A in the form of shallow, sinuous lines or shallow ramifications (Appendix 10). Bioturbation marks are present in fossil bones 1C, 3A, 5B, 6A, 12C, 24B in the form of small, irregularly distributed, shallow round pits (Appendix 10).

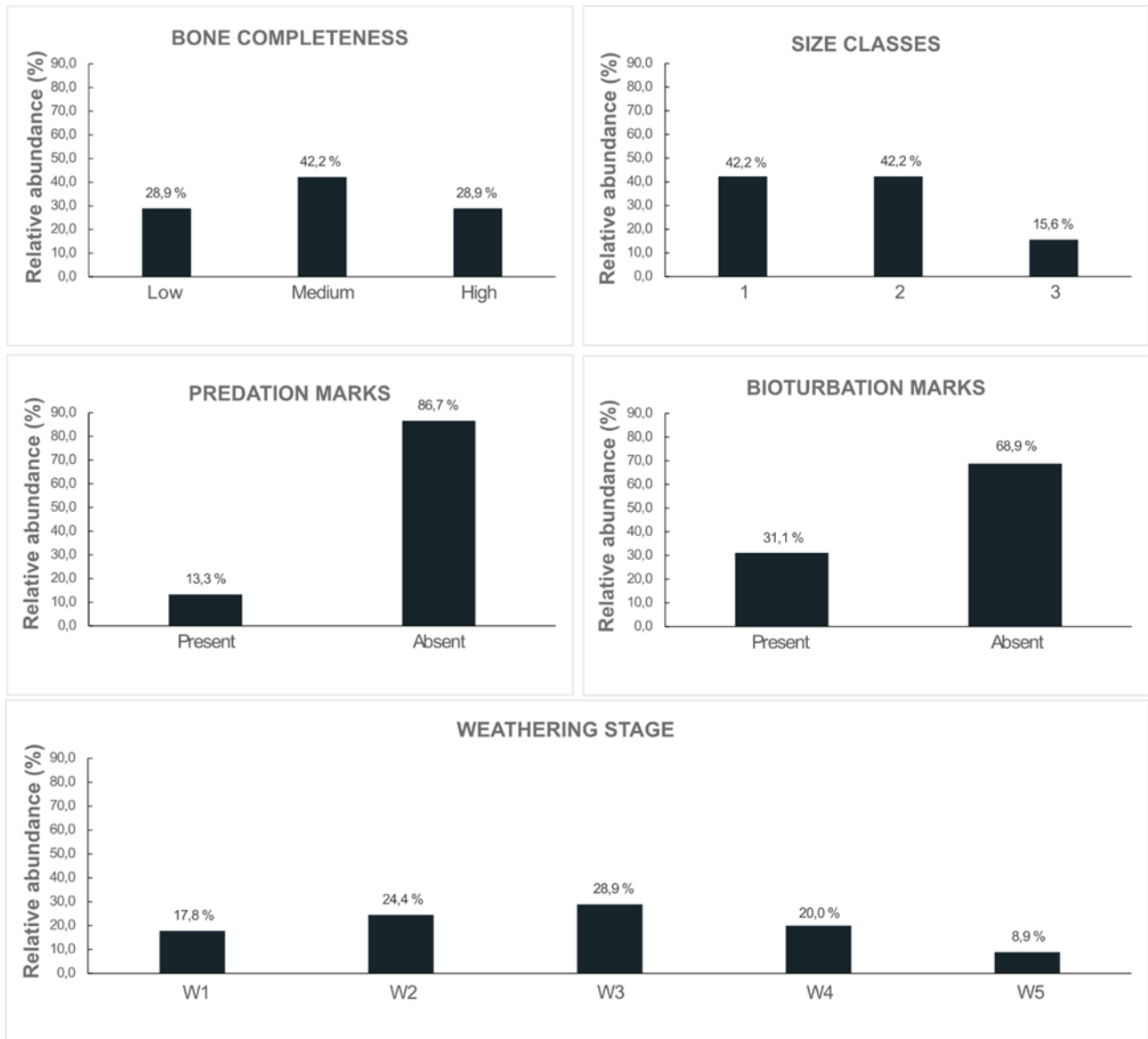


Figure 4.2: Taphonomical analyses performed on the fossil assemblage of Cava Liberatori.

4.3.2 Element distribution

The field notes associated with the recovered material include an indication of their spatial distribution in the quarry relative to IGF 14838, allowing a tentative reconstruction (Fig. 4.3) of the fossil assemblage distribution. The recovery date on all the field notes suggests that all the material with such information was recovered during the removal of IGF 14838. Taking into account the distance from the IGF 14838 as reported in the field labels, three spatial ranges were identified: the first one comprises elements found within 2 m from the skeleton (31,7 %), the second from 2 to 5 meters (12,2 %), and the third comprises all fossil bones recovered at larger distance (56,1 %).

Of the overall 26 envelopes, seven can be confidently attributed to the same stratigraphic level of the *M. meridionalis* skeleton, because their relative field notes indicate a short proximity to the skeleton. The seven envelopes are n.1, 3, 6, 16, 22, 23, 25 (Appendix 5).

Envelops n. 2, 4, 18, 21 report the same field note that states “5 m west from Linda”. Envelops n. 5 and 17 report their relative location as “2 m East of the skeleton”. Envelops n. 7, 14, 15, 24 all contain references of specimens recovered from “petrischio”. Envelops n. 8 and 12 are referred to as recovered from the “scarico”. Envelops n. 10 and 19 are referred to as recovered from the “scasso”. Envelops n. 13 and 21 include material recovered 50 m west from the *M. meridionalis* skeleton. Envelope n. 11 contains fossil bones recovered 30 m from the dig site. Envelops n. 9, 20 and 26 do not retain information regarding their position relative to IGF 14838. The taphonomy of the assemblage was therefore reconsidered following the spatial range distribution of the fossil elements, to test whether different locations resulted in different taphonomical results (Fig. 4.5).

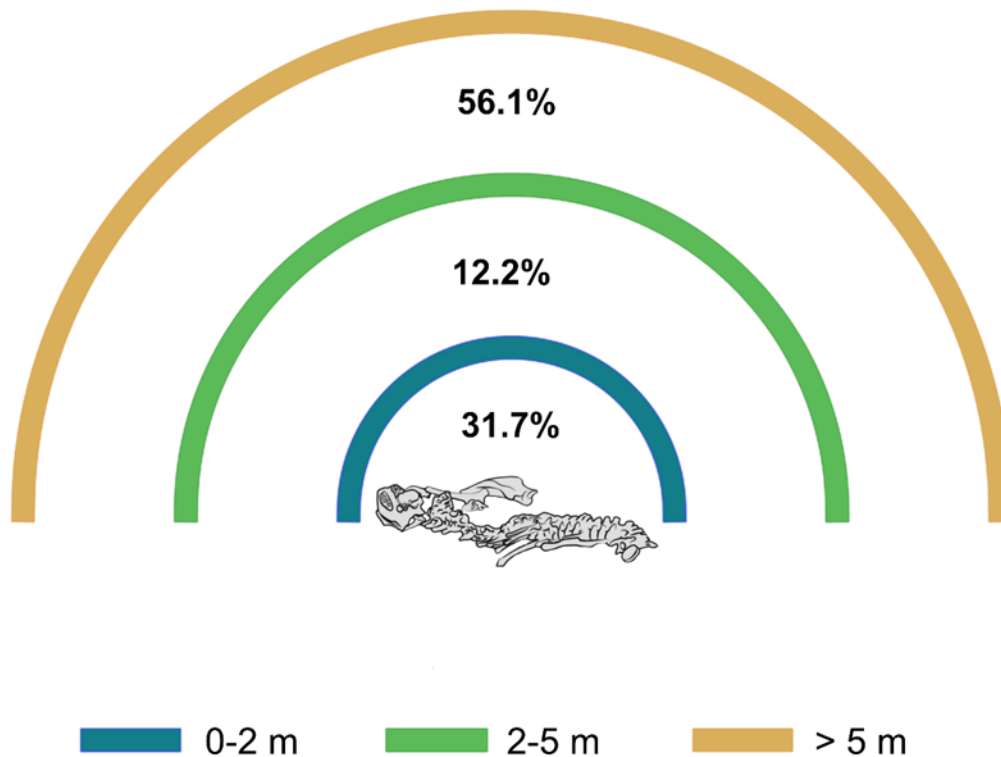


Figure 4.3: Spatial distribution of fossil elements found at Cava Liberatori in relation to their distance from the *M. meridionalis* skeleton, as indicated in the field labels.

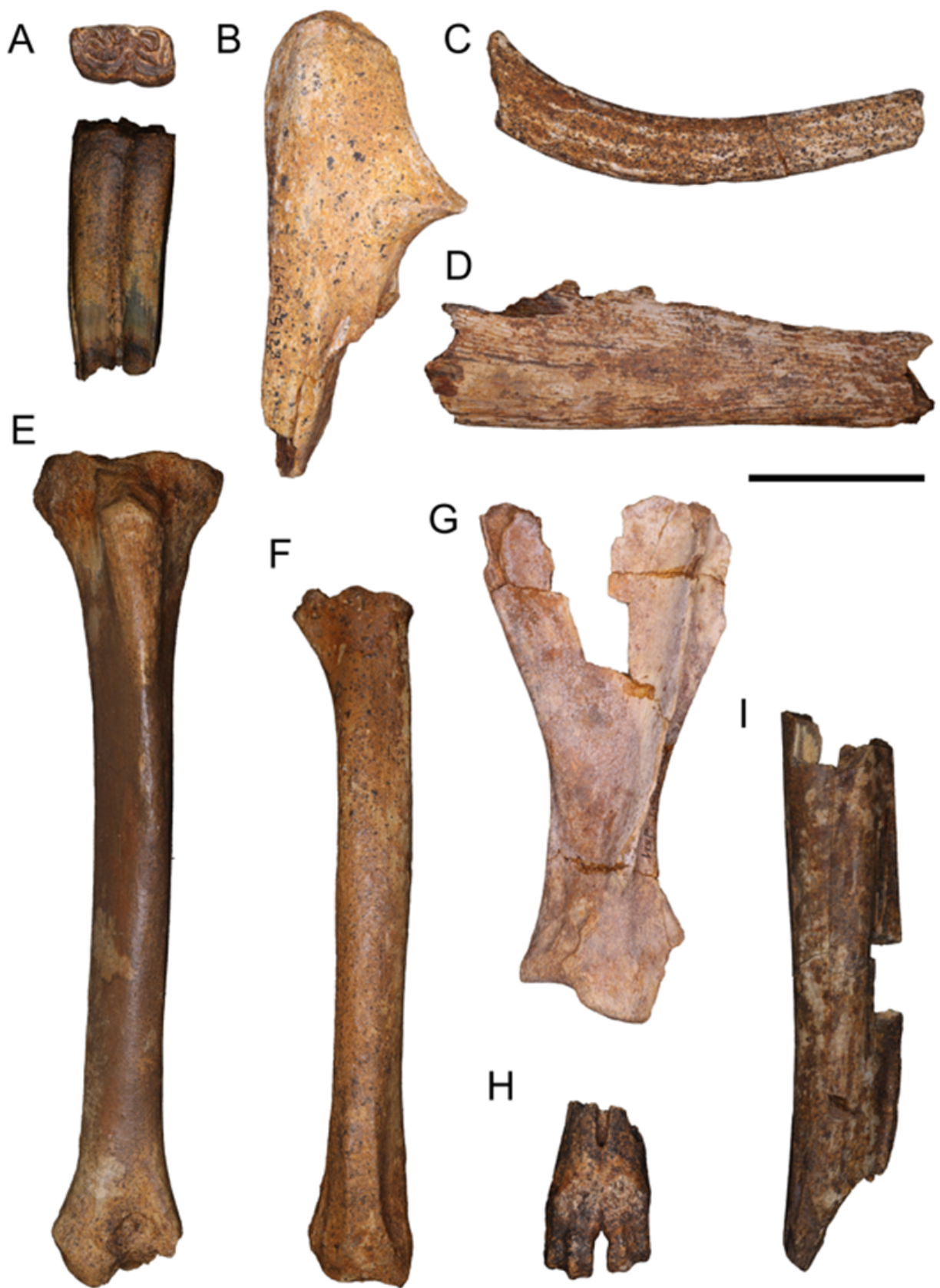


Figure 4.4: Fossil bones recovered in the same stratigraphic level of IGF 14838 as reported in the field labels. A) 22A, B) 3A, C) 1C, D) 1A, E) 16A, F) 17A, G) 6A, H) 1B, I) 23A. Scale bar = 5 cm.

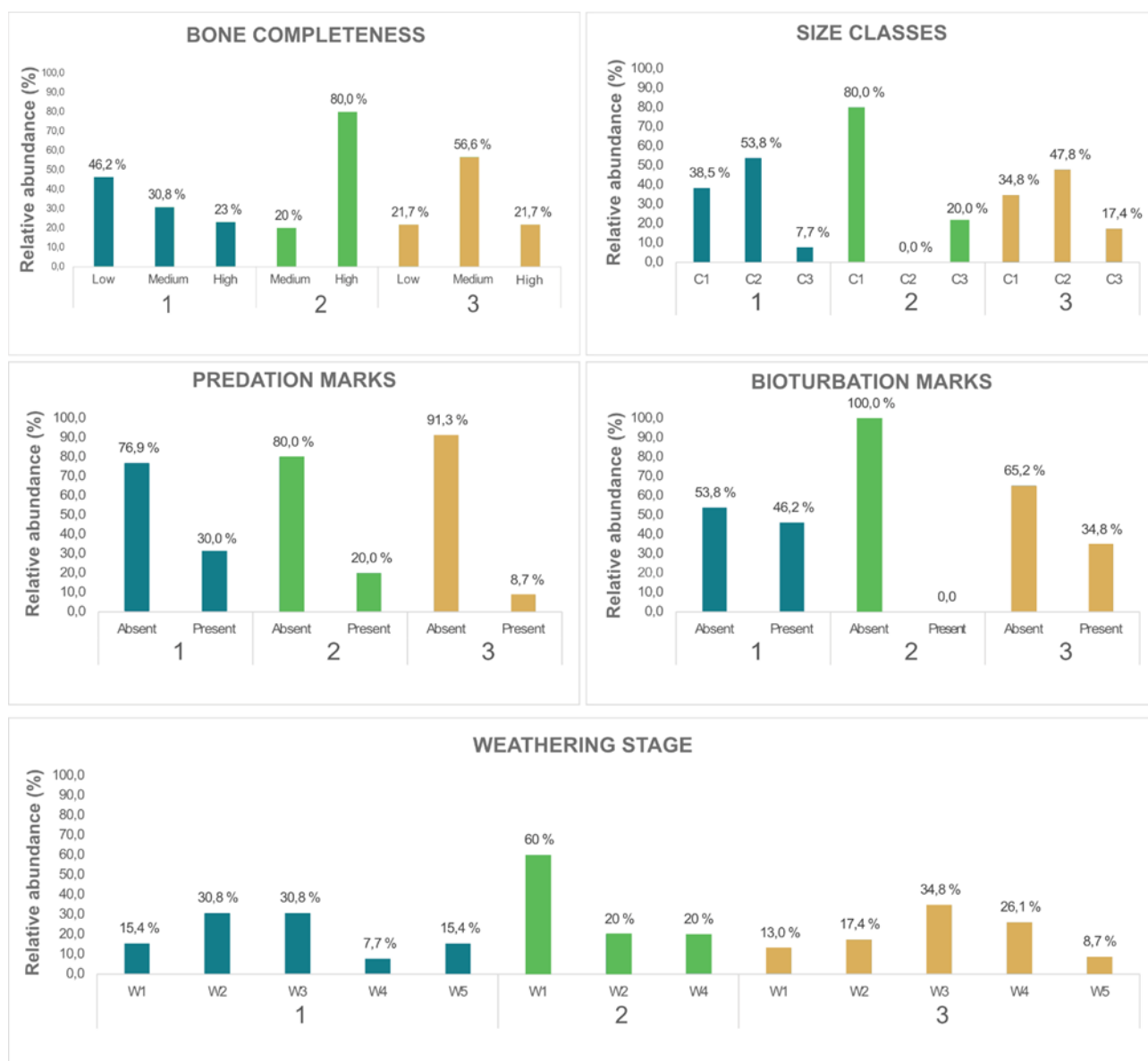


Figure 4.5: Taphonomical analyses reconsidered in regards of the three proximity ranges relative to the spatial distance from IGF 14838.

4.3.3 Sedimentological analysis

The excavation photographs from Cava Liberatori (see Fig. 5.1) show a partial skeleton of *Mammuthus meridionalis* and an associated *Pseudodama farnetensis* skull with antlers attached, both preserved within a homogeneous fine-grained sandy to silty sediment. The fossils occur within a single stratigraphic horizon, lacking visible sedimentary structures. In the matrix surrounding some of the fossil bones of the assemblage quartz pebbles are frequent, and range in diameter from 1 to 3 mm. In all fossil bones that preserve matrix, sediment is present both on the outer surface and in the inner part of the bone.

4.4 Discussion

4.4.1 Taphonomical aspects regarding the overall fossil assemblage

Bone completeness is evenly distributed across low (28.9%), medium (42.2%), and high (28.9%) categories (Fig. 4.4), suggesting that, although fragmentation occurred, it was neither extreme nor preferential. This pattern is consistent with a depositional context where mechanical weathering and trampling may have acted occasionally, but without prolonged or intense physical reworking (Badgley, 1986; Eberth et al., 2007). The balanced completeness profile also implies that hydraulic sorting was minimal, as no clear preferential accumulation of either highly fragmented or near-complete elements is evident. Size class distribution is similarly dominated by small to medium-sized remains (42.2% each), with larger elements comprising only 15.6% of the assemblage. This pattern can reflect several accumulation processes: (1) preferential preservation of smaller, denser fragments following breakage of originally larger bones (Lyman, 1984); (2) selective transport or winnowing in a low-energy continental setting (Behrensmeyer, 1978; Voorhies, 1969; Pante et al., 2010); or (3) a biologically mediated bias related to the fauna present or predators/scavengers targeting individuals of relatively small size (Marean & Spencer, 1991; Palmqvist et al., 2011). The third hypothesis is discarded due to the relatively near absence of predation marks (only 13.3% of identifiable bones bear such traces), which indicates limited vertebrate scavenger involvement. This may suggest that carcasses were not exposed on the landscape long enough to undergo extensive gnawing or that scavenger communities in the environment were sparse.

Importantly, the low frequency of predation marks aligns with moderate weathering stages, implying that exposure times were sufficient for abiotic degradation but not prolonged enough to encourage extensive scavenging. Considering the presence of the large *M. meridionalis* skeleton, with the bones in anatomical association, as part of the assemblage, no selective hydraulic transport played part in the accumulation of the fossil assemblage, but rather fragmentation of fossil bones took place at, or near, the site of accumulation. Evidence of bioturbation is also limited, with only 31.1% of bones showing trace modifications. This suggests that post-burial disturbance by invertebrates or small burrowing vertebrates was moderate and did not

substantially alter the original spatial patterning of the assemblage. The predominance of undisturbed specimens (68.9%) strengthens the interpretation of relatively rapid burial or stable post-depositional conditions. Weathering stages range broadly from W1 to W5, with the greatest representation in intermediate categories (W2–W4: 24.4%–28.9%). This distribution indicates that bones experienced variable durations of subaerial exposure before burial. The presence of advanced weathering (W5: 8.9%) suggests that at least some elements underwent prolonged desiccation or surface exposure, potentially reflecting episodic sedimentation in a fluctuating continental environment (Behrensmeyer, 1982; Boessenecker et al., 2014; Lyman, 2017). Nonetheless, the presence of lightly weathered elements (W1: 17.8%) points to rapid incorporation into the sedimentary record following deposition. Taken together, the weathering profile possibly indicates time-averaging, consistent with multiple depositional episodes. Oxidation patterns when present suggest that when burial of fossil bones took place, the element was already disarticulated, as indicated by manganese oxidation covering both the shaft and the articular surfaces of the fossil bones (López-González et al. 2006).

Colour of the surface does not discriminate the assemblage except for element 11A (a long, broken rib; Appendix 8) which shows a significant colour variation from the rest of the assemblage. This may suggest that the deposition of this element took place as an isolated event, or that during the burial the element was subject to interstitial waters of different geochemical conditions.

4.4.2 Discussion relative to the distribution of fossil elements

When the taphonomic parameters of the assemblage are examined altogether (Fig. 4.5), the fossil sample reflects a moderately time-averaged accumulation shaped by intermittent subaerial exposure, limited biological disturbance, and largely autochthonous to parautochthonous deposition in a low-energy continental setting. However, the spatial subdivision of the same specimens into three distance ranges from the specimen IGF 14838 reveals important local-scale taphonomic heterogeneity that allows for further interpretations.

The spatial distribution of elements shows a marked contrast among the three distance classes. Proximity class 2, representing distances between 2 and 5 meters from IGF 14838, is

dominated by highly complete elements (80%), whereas both class 1 (0-2 meters) and class 3 (over 5 meters) contain substantially higher proportions of low and medium completeness. This pattern suggests that the central zone around IGF 14838 might have acted as a taphonomic ‘quiet’ area, where bones experienced less post-depositional mechanical stress and remained relatively intact. Conversely, the peripheral zones appear to have been more susceptible to fragmentation, possibly due to trampling, localised transport, or differential depositional events.

The dominance of small and medium-sized classes (C1–C2) in the first range of proximity to IGF 14838, contrasted with the overwhelming presence of C1 (80%) in proximity range 2, indicates a spatially selective process. The absence of large elements in class 2 suggests limited transport competence or selective retention in this zone, reinforcing the idea of a localised low-energy depositional microenvironment.

Proximity class 3, in contrast, exhibits a more balanced size distribution, including a non-negligible percentage of larger fragments. This may indicate either greater post-depositional dispersal or heterogeneous sedimentary conditions in the outermost areas. Predation and scavenging traces remain rare throughout the assemblage, but their spatial distribution shows notable variation: proximity class 1 contains the highest proportion of marked specimens (30%), whereas proximity class 3 shows the lowest (8.7%). The concentration of predation marks near IGF 14838 could imply that the *M. meridionalis* specimen itself attracted initial scavenging activity, generating localised bone modification. At greater distances, the relative absence of such marks supports the hypothesis of limited vertebrate scavenger involvement across most of the depositional surface, however, considering their overall higher rates of advanced weathering stages, it might be that bioturbation obliterated possible previously visible predation marks.

Bioturbation shows extreme spatial heterogeneity. Proximity class 2 exhibits no evidence of bioturbation (0% presence), whereas proximity classes 1 and 3 show appreciable levels (46.2% and 34.8%, respectively). This reinforces the interpretation that the intermediate zone around IGF 14838 experienced particularly stable burial conditions, with limited soil turnover and low activity from burrowing organisms. The higher disturbance in classes 1 and 3 suggests that either the fossil accumulation extended across zones with differing substrate stability, where peripheral areas may have been more exposed to root activity, burrowing fauna, or soil

reworking processes, or that more than one depositional event is present.

Weathering data exhibit meaningful spatial trends. Proximity class 2 is strongly dominated by lightly weathered specimens (W1: 60%), whereas class 1 and class 3 include higher proportions of intermediate and advanced stages (W3–W5). These differences indicate that bones in proximity class 2 were buried more rapidly or shielded from prolonged surface exposure, further supporting the interpretation of a localized depositional events with favourable preservation conditions. Proximity class 3, which displays relatively elevated W3 and W4 frequencies, may represent areas where remains were exposed for longer intervals before burial, consistent with greater taphonomic disturbance and the presence of larger and more variable size classes.

4.4.3 Short note on the presence of a fragment of the bivalve *Pecten jacobaeus*

It is peculiar to note the presence of element 12A, a shell fragment of *Pecten jacobaeus*, which is an extant bivalve typical of marine environments that shows two round holes of changing diameter (wider on the outside of the shell, thinner on the inside; Appendix 11), consistent with predation marks made by gastropod *Oichnus* cf. *paraboloides*.

One might consider the presence of this element, found in envelope 12 along with 3 other fossil bones as allochthonous, possibly related to a human contamination that occurred during the 50+ years of manipulation of the fossil elements following their initial recovery in 1973. However, it is a fossil shell, not extant. Furthermore, the specimen shows dendritic patterns of manganese oxidation, which is consistent with the oxidation pattern of numerous fossil bones from the assemblage. In addition, the fragment shows two holes referable to predation marks, but two others consistent with bioturbation due to the action of invertebrate larvae or beetles, which again strengthens the hypothesis that the specimen was in fact buried at the Cava Liberatori site along with the rest of the assemblage (Appendix 11). Because of the challenging implications of this hypothesis, this element will not be further discussed in this chapter.

4.5 Conclusions

The spatial distribution of taphonomic features highlights the presence of local variability within what initially appears to be a relatively homogeneous continental assemblage. IGF 14838 occu-

pies a central position within a preferential preservation zone, characterised by higher bone completeness, dominance of small, intact elements, minimal bioturbation, low weathering stages, and limited predation evidence. This suggests that the specimen was deposited in a localized low-energy sedimentary pocket, potentially representing a shallow depression, abandoned channel margin, or temporarily wetted surface conducive to rapid burial (Behrensmeyer, 1988, 1982). Given the size of the IGF 14838 skeleton and its anatomical association, it is possible to interpret the proximity range 2 as a depositional event that rapidly buried the fossil specimens with little to no transportation (Behrensmeyer, 1978, 1988). In contrast, both the proximal (class 1) and distal (class 3) areas show signs of elevated fragmentation, broader size distributions, higher weathering stages, and greater bioturbation. These zones likely experienced more intense subaerial exposure and post-depositional modification, pointing to episodic sedimentation, pedogenic activity, and possible minor transport or trampling outside the central preservation zone (Behrensmeyer, 1988).

Taken together, the field evidence from Cava Liberatori indicates that remains were deposited within a low-energy, fine-grained depositional setting, likely a floodplain in a temperate environment which favoured slow weathering (Behrensmeyer, 1982, 1988; Fernández-Jalvo et al., 2010). The partial disarticulation of the proboscidean skeleton, coupled with the preservation of small, fragile elements in anatomical proximity, suggests minimal transport and rapid burial following partial decay. The taphonomic features observed are consistent with time-averaged, autochthonous to parautochthonous accumulation (Behrensmeyer, 1982; Staff and Powell, 1990; Eberth, 2007; Behrensmeyer, 2009; Fernández-Jalvo et al., 2010), characterised by limited scavenger activity, moderate bioturbation, and variable but not extreme weathering, where fossils largely represent local mortality rather than long-distance transport or reworking. The scarcity of biological modification (predation and bioturbation) implies relatively low ecological disturbance, whereas the fragmentation and size distribution point to localized breakage rather than extensive transport (Behrensmeyer, 1988, 1978; Fernández-Jalvo et al., 2011; Boessenecker et al., 2014; Lyman, 2017).

This chapter conducts the first taphonomical analysis on the continental deposits of the Farneta Faunal Unit from one of the quarries in the locality of Farneta. The lack of sedimen-

tological analysis conducted in the area, followed by the absence of stratigraphic records of the fossil elements recovered from Cava Liberatori and the complete exhaustion of the quarry itself make the study a challenging one, and only partial information can be retrieved from the quantitative and qualitative observation of taphonomic features on fossil bones. For future research, it would be of great interest to conduct further palaeontological digs in the area to test and further implement these results.

5 LINDA. PLATFORM

5.1 Introduction

5.1.1 The “hidden” collection found in the IGF storage unit

In 2022, while carrying out a project of reorganisation of the IGF storage unit located in the area known as “Ex-Macelli”, a wooden crate was found. Inside there were numerous fossil bones organised in 26 plastic envelopes, each containing a paper label with notes about the date (March 1973) and place of discovery (Cava Liberatori, Farneta; Fig. 5.1). It became clear that the fossil material was collected in the same quarry from where the partial skeleton of the *Mammuthus meridionalis* (IGF 14838) nicknamed “Linda” comes from. The skeleton is nowadays on permanent exhibition in the IGF museum. The material was left in the storage following the museology views of the last century that prioritised appearance over scientific value. Though this view has now changed, the exposition of the new material, is, at the moment, not scheduled, also because the material needs further preparation and cleaning from the yellowish 50-year-old glue.

5.1.2 The Mostra Paleontologia (Mo.Pa.)

The Farneta Faunal Unit collection of the IGF is spread among different institutions. Most of the fossil material is housed, on permanent loan from the IGF, at the Mostra Paleontologica (Mo.Pa.) next to the Farneta Abbey; it is a small, volunteer-run institution founded in 2006 that aims at valorising the palaeontological value of the Farneta area with a permanent exhibition that can be visited upon request. Most of the collection is though not displayed, and it is housed in the Farneta Abbey’s “Antiquarium”, a cellar where the late priest of the Abbey collected all sorts of “mirabilia” from the recent to the ancient past. Don Sante Felici was an enthusiastic amateur palaeontologist active from the 1940s to the first 2000s, who used to collect fossils found in the Farneta surroundings either by himself or by the local community, and kept a close correspondence with the then palaeontology professor at the University of Florence, Prof. Augusto Azzaroli. Before his passing, Don Sante Felici assembled in the “Antiquarium”

a small exhibit of fossils from Farneta and expressed his wish to keep the collection altogether in Farneta, thinking that if moved elsewhere, it would lose significance.

5.1.3 Web Platforms as accessibility and visitors’ engagement tools for museums

Museum web platforms include a broad range of digital solutions, including institutional websites, online collections, virtual exhibitions, educational portals, and interactive services (Taormina et al., 2022). These platforms enable museums to provide access to scientific content regardless of geographical location, opening new possibilities for audiences who may face physical, economic, or social barriers to on-site participation (Marty, 2011; Parry, 2013).

Well-designed web platforms can support inclusive access by integrating features such as multilingual content, assistive technologies, adaptable interfaces, and alternative formats for users with disabilities (Kelly et al., 2009; Drivas & Vraimaki et al., 2025). As a result, digital access is increasingly recognised as a core component of museums’ public mission rather than a supplementary activity. Beyond accessibility, web platforms also play a critical role in reshaping audience engagement. Digital environments allow museums to move from one-way communication models toward more participatory forms of interaction, enabling users to explore, personalise, and even co-create content (Russo et al., 2008; Simon, 2010).

Interactive tools, social media integration, and data-driven personalisation can enhance users’ emotional, cognitive, and social engagement, strengthening the relationship between museums and their publics (Falk & Dierking, 2016). In this sense, web platforms not only replicate on-site experiences but also introduce novel modes of engagement that are not feasible within physical museum spaces.

Given the growing importance of digital presence in the cultural sector, understanding how (and if) web platforms can effectively improve accessibility and public engagement has become a key research topic in museum studies, digital heritage, and human–computer interaction.

5.2 Aims

This chapter addresses the challenge of enhancing the IGF visitor’s engagement through project “Linda.”. “Linda” is a web platform aimed at exploring the potential of a digital, web-based



Figure 5.1: The ex-quarry Cava Liberatori today. Picture taken in spring 2024.

platform to enhance the palaeontological collection resulting from the fossil assemblage of the Early Pleistocene site of Cava Liberatori (Farneta) and centred on the specimen of *Mammuthus meridionalis* (IGF 14838), nicknamed “Linda”. The collection is largely inaccessible to the public and it is stored in two different spaces: the IGF (Firenze) and the Mo.Pa. (Farneta, Cortona, Arezzo). The platform “Linda.” aims also to provide a particular spotlight on the collection potential to support inclusive access and meaningful engagement.

The primary objectives of the project are: 1. To digitally enhance a hidden palaeontological collection by (1) integrating revised taxonomic data, (2) performing three-dimensional models, (3) collecting historical documentation, and (4) making palaeoenvironmental reconstructions, to increase accessibility for on-site and remote audiences.

2. To test a digital platform as a connective tool between museums, linking the IGF and the Mostra Paleontologica di Farneta (Mo.Pa.), and virtually reuniting specimens, archival sources, and contextual information that are physically distributed across different locations.

3. To experiment with new forms of science communication in palaeontology, combining interactive 3D models, palaeoartistic reconstructions, and narrative storytelling to present fossils as components of dynamic ecosystems and research histories, rather than as isolated exhibition objects.

4. To evaluate user engagement and accessibility, assessing how visitors interact with the

platform during museum visits and through remote access, and analysing quantitative and qualitative data to measure effectiveness, usability, and educational impact.

5. To develop a low-cost, scalable, and replicable model for digital enhancement that can be adopted by other institutions, particularly those with limited resources, without requiring substantial modifications to existing museum layouts or infrastructure.

Through these objectives, the project aims to contribute to current discussions on digital museology and palaeontological outreach, providing empirical data and practical insights into the role of digital platforms as complementary tools for heritage interpretation, institutional collaboration, and public engagement.

5.3 Materials and Methods

While examining the fossil material it became clear that taxonomical revision of the Farneta Faunal Unit and a taphonomical analysis of Cava Liberatori were needed. These two topics and their results are discussed in Chapters 3 and 4. For the realisation of the website, we decided to rely on an online website building platform that was free and user-friendly. “Linda.” website focuses on multiple aspects of the Farneta Faunal Unit collection: from its palaeontological value and framework, its fossil faunal assemblage, the specimens related to the Farneta F.U. housed in the IGF and Mo.Pa., to the people who heavily contributed to the scientific and historical value of the collections.

5.3.1 Historical documentation and archival research

The focus of the website is on the site of Cava Liberatori (Fig. 5.1), the former quarry from which IGF 14838 and numerous other specimens were recovered (see Chapter 4). The quarry is now closed and has been completely reshaped into the landscape (Fig. 5.1). To reconstruct the arrangement of fossil bones as they were found and excavated in March 1973 at the quarry, historical documentation was researched in the archives of the IGF. Unfortunately, no useful information about the matter was found. Then, after retrieving the names of those who participated in the recovery of the fossils from Cava Liberatori, Vittorio Borselli, one of the then fossil preparators of the IGF now retired, provided picture slides of the site taken during the

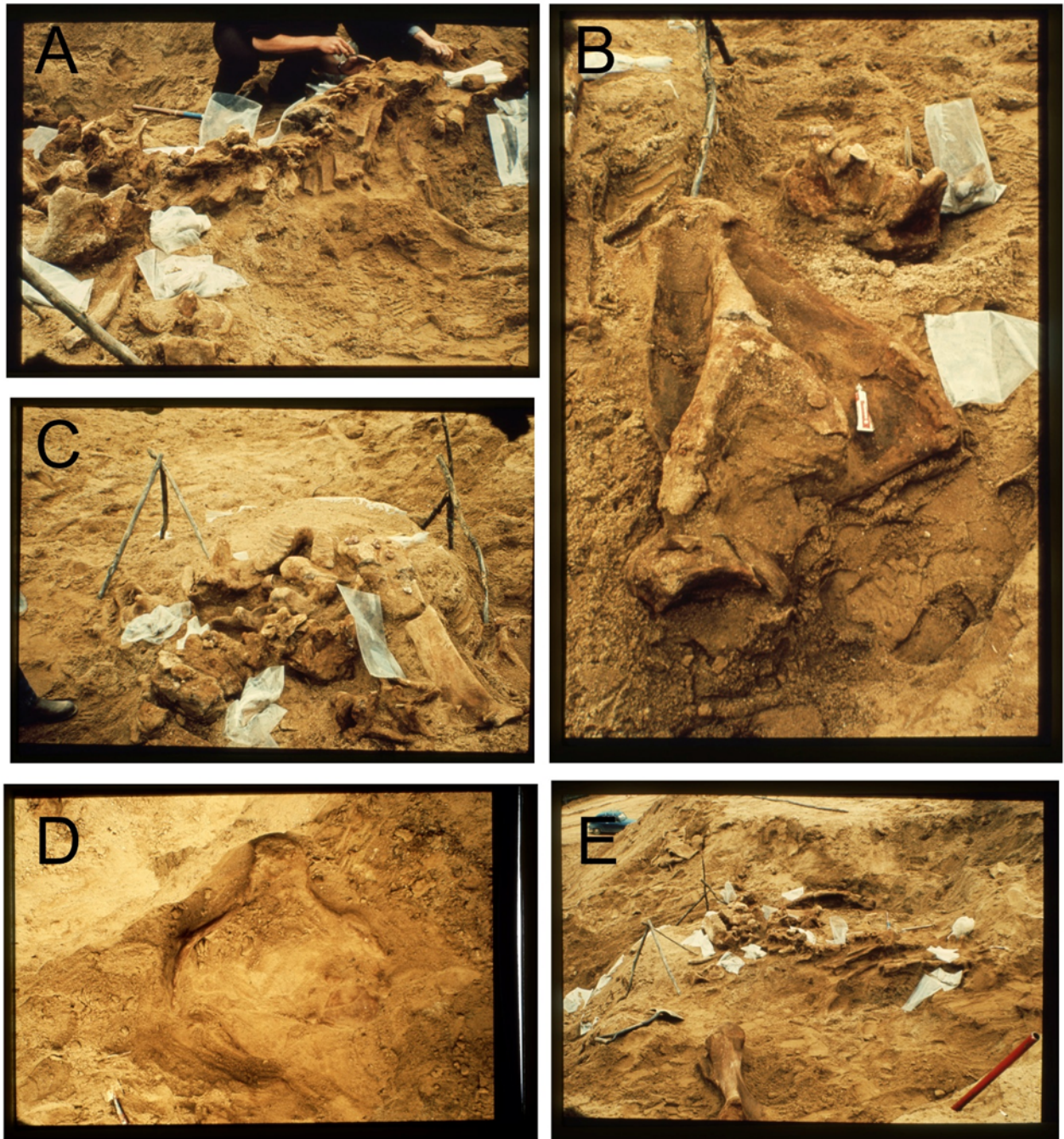


Figure 5.2: Slide pictures taken by Vittorio Borselli at the quarry Cava Liberatori in March 1973, during the recovery of IGF 14838 and associated fossil material. A) IGF 14838 vertebrae in anatomical connection; B) IGF 14838 scapula; C) Lower jaw and cervical vertebrae of IGF 14838; D) Matrix antler-shaped after the removal of IGF 197 V; E) general picture of the quarry.

excavation (Figs. 5.2 – 5.3).

A Canon CanoScan Scanner was used to digitise the pictures and combine them with the information contained in the field labels of specimens from the wooden crate to virtually reconstruct the fossil bones' arrangement. Picture slides can be viewed from both sides, making



Figure 5.3: Slide pictures taken by Vittorio Borselli in March 1973. A) Vittorio Borselli looking at the humerus of IGF 14838; B) general picture of the excavation site; C) Museum personnel and volunteers digging; D) Removal of IGF 197 V; E) Vittorio Borselli and colleague cleaning the tibia of IGF 14838; F) close-up of the lower jaw and first cervical vertebrae of IGF 14838; G) Volunteers cleaning fossil

it hard to understand which view the real perspective of the photographer was, and which side is flipped. To correctly discern left from right, we looked at the wristwatch on the participants in the pictures, assuming most of them were right-handed, therefore keeping the watch on the left wrist.

5.3.2 Digitisation of fossils and online repository

To make the fossil material virtually accessible to the public, most of the fossil specimens were digitised using close-range Structure from Motion, generally referred to as photogrammetry (e.g., Wings & Mallison, 2015), including IGF 14838, which required the use of a ladder and two cameras at once, due to its large size (Fig. 5.4). Image acquisition was performed with a 20 MP Canon EOS R6 equipped with a 24–105 mm Canon lens and a 24 MP Canon EOS R8 with a 24–55 mm Canon lens. Three-dimensional models were processed using Agisoft Metashape Pro (v. 2.1.1) software. The specimens housed at the Mo.Pa. were digitised using the Artec Spider structured-light scanner (Bartolini-Lucenti & Rook, 2023) in addition to close-range photogrammetry. All 3D models were cleaned and repaired to remove artefacts and fill acquisition gaps. Textures were generated when possible. Two versions of each model were exported in .PLY format: a high-resolution, high-polygon model with high-resolution textures for research and conservation purposes, and a lighter low-polygon model with medium-resolution textures optimised for online dissemination and educational use. In total, 44 3D models were published, together with their associated raw/parent data (see Díez Díaz et al., 2026) and complete metadata, including provenance, stratigraphic attribution, specimen identifiers and authorship. MorphoSource was selected as the primary repository due to its good compliance with FAIR data principles (Díez Díaz et al., in press) and its capability to embed 3D models within external platforms (Ioannides et al., 2025). All the IGF material uploaded to MorphoSource is available for viewing and interactive manipulation exclusively through the platform. Under current Italian legislation, digital replicas of objects entrusted to superintendencies are subject to the same regulations governing traditional resin and silicone casts. Consequently, making the 3D models freely accessible could result in potential misuse, including unauthorized commercial exploitation by third parties. Similarly, access to museum collections



Figure 5.4: Photo acquisition of A) IGF 14838 at the IGF and B) an equid metapode at the Mo.Pa. permanent exhibition for the realisation of the 3D model.

for scientific purposes is invariably contingent upon authorization from the relevant curators and the museum director. To avoid undermining ongoing research efforts, to download and view high-quality 3D replicas of the fossils uploaded to MorphoSource, viewers must comply a formal request and submit it to the museum curators.

5.3.3 Palaeoartistic reconstructions for public engagement

To facilitate the understanding of the Farneta Faunal Unit palaeoenvironment information relative to the faunal assemblage and palaeoflora was put together from literature data and from the results obtained in Chapters 3 and 4 of this work. Digital illustrations, infographics, and three-dimensional sculptural reconstructions were produced to synthesise complex palaeobiological information for a non-specialist audience, using a clean, clear language. Distinct colour codes were assigned to each species to facilitate visual identification across the platform.

Reconstructions were based on fossil material housed at the IGF and other specimens published in the literature. Vegetation was reconstructed using pollen assemblages and Calabrian stratigraphic profiles from Tuscany (Bertini, 2010). These assemblages include both extant Mediterranean taxa (e.g., *Quercus*, *Ulmus*, *Salix*, *Poaceae*) and taxa no longer present in Italy but documented in the Early Pleistocene (e.g., *Zelkova*, *Carya*; Bertini & Combourieu-Nebout, 2023). The Farneta Faunal Unit has been correlated to Marine Isotope Stage (MIS) 50, with fossil remains broadly dated between 1.4 and 1.6 Ma (MIS 55–45; Azzaroli, 1998; Cioppi & Napoleone, 2001). Due to chronological uncertainty, the palaeoartistic scene was set during the late phase of an interglacial period, depicting a fluvial plain environment with occasionally arid conditions (Fig.5.5).

5.3.4 Users’ accessibility and visitors’ engagement

User engagement and platform effectiveness were evaluated through anonymous data collection between December 2024 and July 2025, when the IGF closed for renovations (reopening scheduled for spring 2026). Panels containing QR codes redirecting to the website were placed in the IGF and Mo.Pa (Fig. 5.6) in December 2024, so that visitors can use their personal device to visit “Linda.” webpage. In addition, the website is accessible via the official website of the Natural History Museum of the University of Florence (SMA) and is available in Italian and English. Museum staff was asked to introduce the platform to visitors and ensure access to public Wi-Fi.

To test whether the website “Linda.” has successfully improved the visitors’ experience at the IGF museum and Mo.Pa. exhibition, or if it has had a positive impact on visitors’ engagement and accessibility, an anonymous and optional feedback window at the bottom of the website was developed, asking the users to evaluate their satisfaction regarding usability, perceived usefulness and interaction with 3D models. Satisfaction metric is set by giving 1 to 5 “stars” to each question (Table 5.1). The platform (Wix.com) used to develop the website allowed access to different quantitative metrics data: a) total accesses; b) geographic origin; c) device type; d) access pathways; e) visit duration; f) page navigation patterns; and g) temporal distribution of use (Table 5.1).



Figure 5.5: Palaeoartistic representation of the palaeo-environment of Cava Liberatori during the Early Pleistocene (1.6-1.4 Ma). Illustration made by Isacco Alberti.



Figure 5.6: Illustrative panels referring to the Linda. website containing the redirecting QR code.

5.4 Results

5.4.1 The interactive platform Linda.

The website was developed using the Wix.com web environment to ensure ease of use and accessibility. It has been named “Linda.”, after the IGF 14838 nickname that was adopted as the project’s symbolic focal point and served as both the platform’s mascot and narrative anchor. The website is accessible at the following link: <https://labpaleo8.wixsite.com/linda-msnfi>. The platform embeds 3D models hosted on MorphoSource and integrates them with narrative, visual, and educational content.

“Linda.” is designed to function simultaneously as an educational platform, a digital repository interface, and a museum guide accessible via personal devices. The platform consists of two main sections: the “Linda.” Homepage (Fig. 5.7B) focusing on the discovery of fossil bones at Cava Liberatori in 1973, and a second section dedicated to the Mo.Pa. exhibition and its collections (Fig. 5.7C). The homepage is structured into four thematic sections: a) The Discovery (Fig. 5.8), b) The Dig (showing Vittorio Borselli’s pictures; Fig. 5.2-5.3), c)

Question	Response
Did you like our platform?	★ ★ ★ ★ ★
Did you find the Linda platform easy to use?	Yes / No
Did this information help you when you visited the Museum?	Yes / No
Would you also use it at home?	Yes / No
Were you able to interact with the 3D models of the fossils?	Yes / No

Table 5.1: User feedback questionnaire for the Linda platform.

Palaeoenvironment (Fig. 5.5), and d) The Project.

Interactive elements allow users to access dedicated species information pages containing 3D models, illustrations, and contextual data. Sections a) and c) have hyperlinks over each coloured bone or species representation, so that users can be redirected to the species’ information page by directly clicking on it. Species information pages (Fig. 5.9) include the scientific name, palaeoartistic life reconstructions, interactive 3D models with specimen codes, palaeogeographic distribution maps, skeletal scale comparisons, and concise biological summaries. The pages can be reached either by the hyperlinks present in the main section and in the Mo.Pa. section, or accessed through the main menu, placed in the upper right side of the website.

5.4.2 Data collection and users’ feedback

A total of 3610 unique users accessed the “Linda.” platform during the study period (Appendix 12). Users visited the platform from a total of 35 countries, with Italy being the most recurrent country of provenance (87,43%), followed by France (2,57%) and the United States (1,99%). The website “Linda.” was mostly reached from the museum visits (87,8%), followed by access from the SMA official website (3,5%), Instagram (3,3%) and Google search (2,9%). 1391 accesses (38%) were attributed to on-site museum visitors or conference attendees. Average daily access was 15 users, with peak usage occurring during weekends. The highest single-day peak (116 accesses) was recorded on 23 February 2025.

Museum attendance data indicated an average of 50 visitors per day and a monthly average of 1285 visitors. QR-code engagement rates averaged 14%, reaching 19% of total museum visitors during peak months. Platform usage showed distinct weekly patterns, with mobile access peaking on weekends and desktop access dominating weekdays (Fig. 5.10). The average

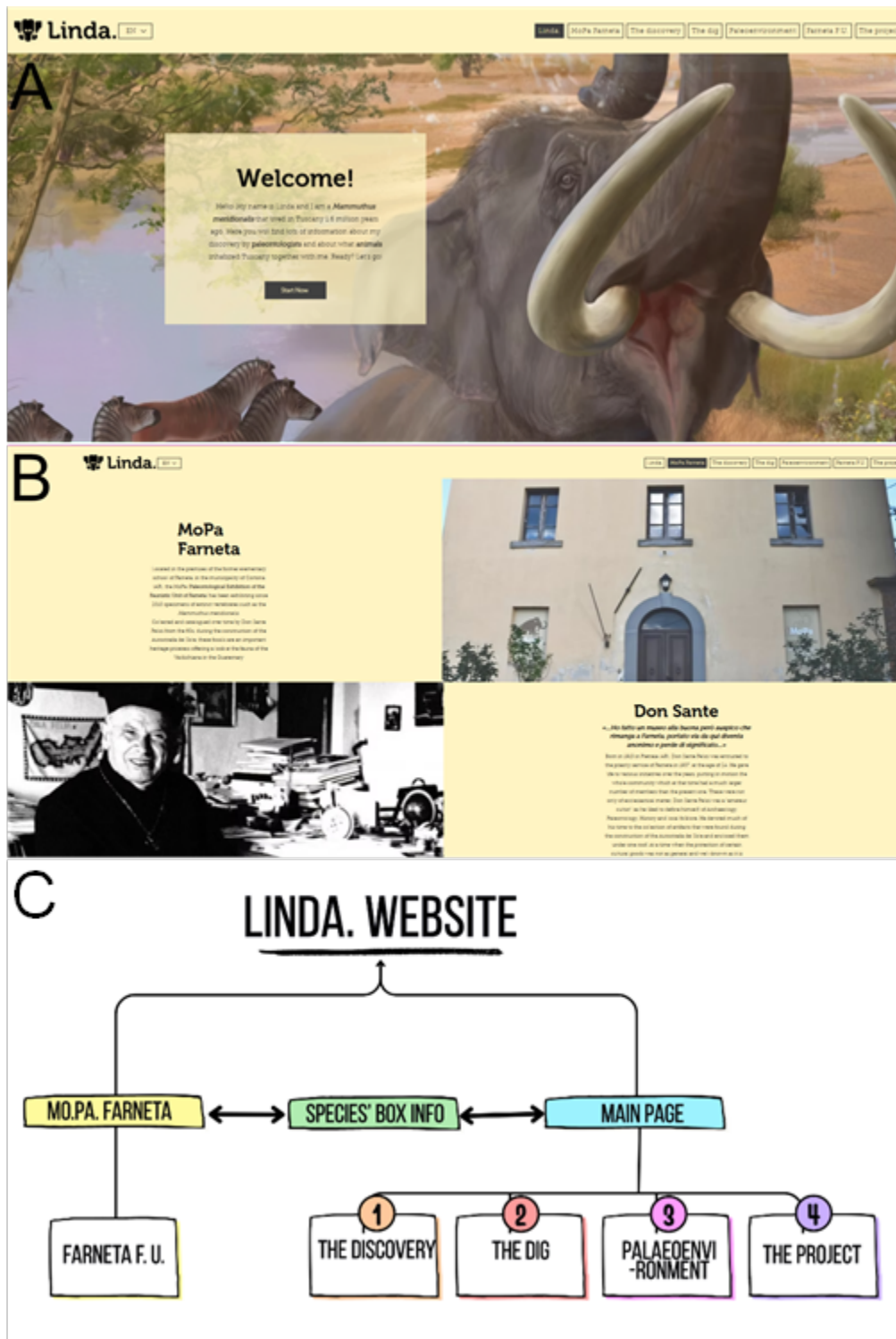


Figure 5.7: A) Section "Linda.", main page of the website; B) Section dedicated to the Mo.Pa. permanent exhibition. C) Scheme of the website's different sections.



Figure 5.8: The discovery section. Each coloured bone is a hyperlink that directly leads the user to the dedicated species page.

session duration was 5.17 minutes, with users viewing an average of 1.6 pages per visit. The homepage accounted for 55% of page views. Of all the accesses to the website, only 23 users (0.6%) answered the feedback form. 65,7% rated the website with 5 stars, 25,7 % with 4 stars and 8,6% with 3 stars. There are no 1- and 2-stars entries.

5.5 Discussion

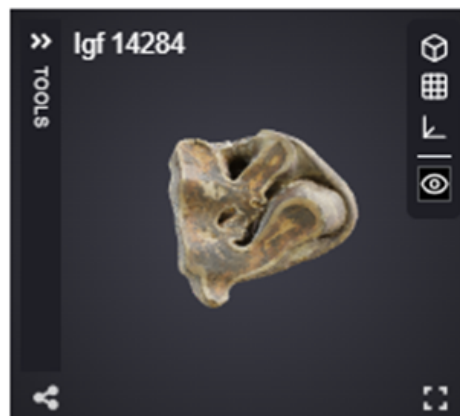
The development of a dedicated website integrating 3D models of fossil specimens has demonstrably enhanced both accessibility and engagement with the Farneta F.U. collection of the IGF, addressing long-standing limitations associated with physical repositories (Macdonald, 2011; Anderson, 2012). The digital platform has attracted people from over 30 countries, providing an effective response to these challenges by enabling open, continuous, and remote

Stephanorhinus etruscus

EN



Upper molar



Temporal distribution

Upper Pliocene-Lower Pleistocene
(3.3 - 0.9 million years ago)

Geographic distribution

Europe, Asia, Africa



Paleoenvironment >

Diet

Grass, leaves, roots, bark

Taxonomy

Family:
Rhinocerotidae

More similar current species

Sumatran rhinoceros
(*Dicerorhinus sumatrensis*)

Trivia

- Two horns on the head
- Perhaps covered by light fur
- Suitable for running

Size

L 3,5 x H 2 m
W 3000 kg

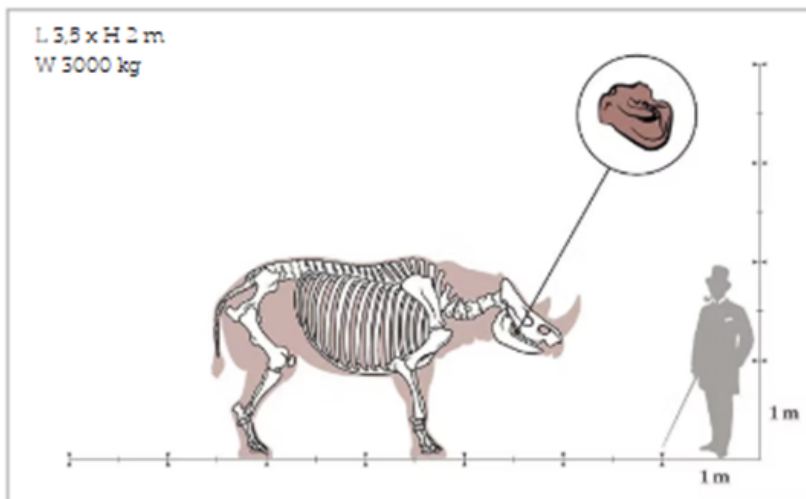


Figure 5.9: One example of the pages dedicated to the fossil species of the Farneta F. U. On the upper left, a palaeoartistic reconstruction of *Stephanorhinus etruscus*, on the upper right, the 3D model of the fossil element of the species. In the middle are presented information about temporal and palaeogeographic distribution. On the lower part, information about diet, size, taxonomy and some generic information about the species' appearance.

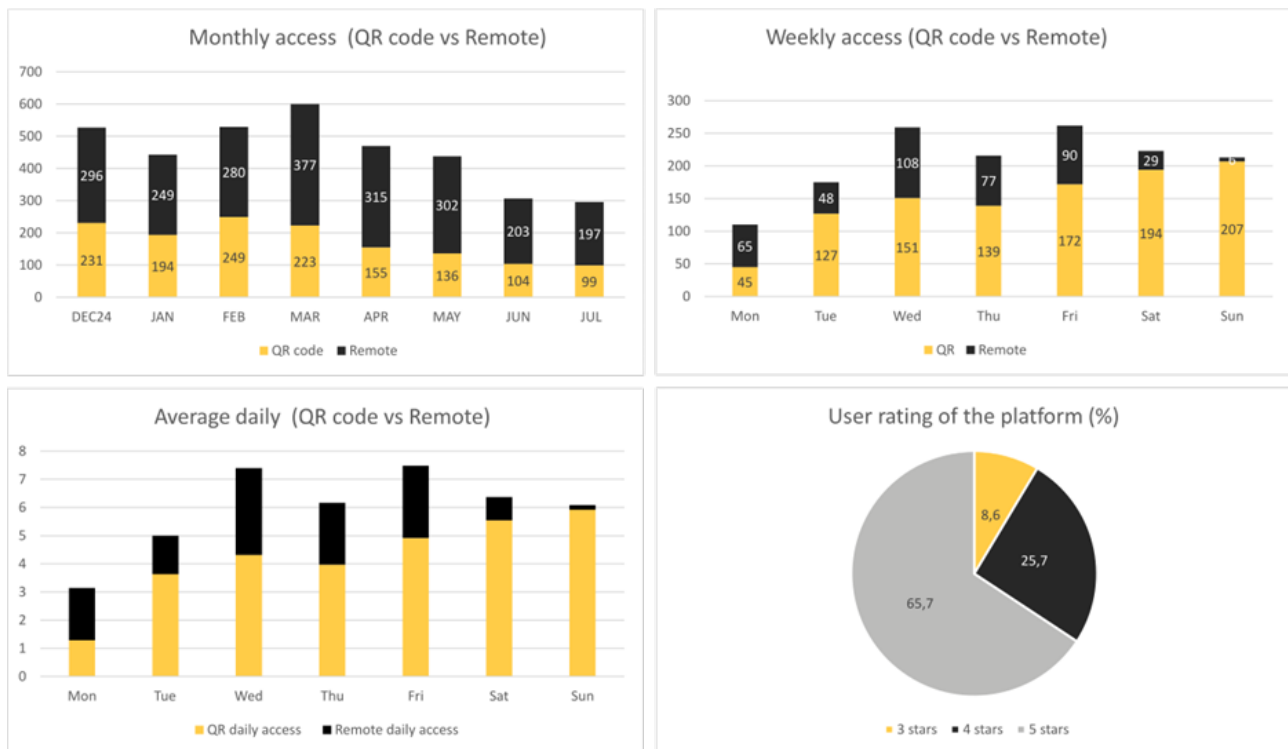


Figure 5.10: Statistics from the website access during the study period.

access to the IGF collection. Interactive manipulation through rotation and zooming provides an experience similar to direct handling while fully preserving the integrity of fragile or unique specimens. The use of MorphoSource as a repository of 3D fossil specimens ensured long-term accessibility for remote researchers and enabled 3D printing for museum-based educational activities. This also improves the collection accessibility by making available for observation fossils not on display in the Museum venues.

In terms of engagement, the interactive affordances of 3D visualisation foster a more active and inquiry-driven form of learning. Rather than passively consuming interpretative panels or static images, users are encouraged to explore specimens autonomously, compare forms, and develop their own interpretative questions (Falk & Dierking, 2013). This approach aligns with contemporary theories of informal science education, which emphasise participation, exploration, and personal meaning-making as key drivers of engagement and learning (Hein, 1998; Simon, 2010).

Several studies have shown that interactive digital exhibits increase time spent on content and promote deeper cognitive involvement compared to traditional display methods (Economou & Meintani, 2011; Mortara et al., 2014). Though the average time spent on the website indicates

a short visiting period, fossils are contextualised through stratigraphic data, palaeoenvironmental reconstructions and research-oriented explanations, designed to perceive fossils not as static objects but as dynamic evidence within ongoing scientific research (Tallon & Walker, 2008; Kohlstedt, 2015). This contributes to a reconceptualisation of the museum from a space of object preservation to a communicative system in which knowledge is continuously produced, revised, and shared (Mason, 2004; Nielsen, 2017). Finally, digital platforms featuring 3D fossils facilitate new forms of reuse, dissemination, and collaboration. Educators can integrate models into classroom activities and virtual laboratories, researchers can reference and share specimens more efficiently, and the public can engage with palaeontology through familiar digital interfaces (Jeffery et al., 2012; Watkins et al., 2019). In this sense, the website extends the social, educational, and scientific role of the collection well beyond the physical boundaries of the museum.

Overall, the integration of 3D fossil models into a web-based platform represents a powerful strategy for the long-term valorisation of palaeontological collections. By enhancing accessibility, promoting active engagement, and supporting diverse modes of use, the “Linda.” website significantly contributes to the evolving role of museums in the digital age. The integration of the digital platform within the museum context demonstrated a measurable level of visitor engagement, with approximately one-third of platform users accessing it during an in-person visit. Temporal and device-based access patterns suggest complementary use modes, with on-site interaction during weekends and remote exploration during weekdays.

The observed peaks in usage during museum events and conferences highlight the importance of active mediation and promotion by museum staff. Despite a relatively low rate of qualitative feedback submission, user responses indicate high perceived usability and educational value. The platform appears particularly suited for short interaction times, consistent with typical museum visit durations. The website section dedicated to the Mo.Pa. permanent exhibition in Farneta represents a virtual bridge between two separate physical institutions, and the next step would be to monitor whether visitors of the Mo.Pa. in Farneta have visited the exhibition after learning of its existence through our website. The website “Linda.” is designed to have a child-friendly interface, though it is significantly harder for children to reach it: when

visiting the museum, children don't usually have mobile phones, nor do they use the internet as much as adults. For future projects, it would be interesting to provide visitors with tablets at the museum's entrance (to be returned once the visit is finished) so that anyone can visit the website through the QR codes.

5.6 Conclusions

The development of the “Linda.” platform represents an experimental and innovative approach to palaeontological enhancement and science communication within the Italian museum context. By integrating digital tools with traditional collections, the project aimed to generate a productive dialogue between physical and virtual museum experiences. The platform successfully increased accessibility to previously hidden collections, supported inclusive outreach, and demonstrated scalability at minimal cost. Its modular structure allows future expansion, replication, and integration with other institutions. Although still in an early developmental phase, “Linda.” provides a valuable reference model for future digital initiatives in palaeontological museology.

6 A NEW EXHIBITION AT THE URWELTSTEINBRUCH MUSEUM, HOLZMADEN

6.1 Introduction

6.1.1 The Konservat-Lagerstätte deposits of Holzmaden

Located in southwestern Germany (Baden-Württemberg) along the Swabian Alb, Holzmaden is internationally renowned for its exceptionally preserved fossils recovered from the Posidonia Shale (Posidonienschiefer Formation). This sedimentary unit dates to the Lower Toarcian (Early Jurassic), approximately 183 million years ago, and constitutes one of the most extensively studied marine black shale deposits in Europe (Urlichs et al., 1994; Röhl et al., 2001). Fossil assemblages from Holzmaden are dominated by marine vertebrates such as ichthyosaurs (e.g., *Stenopterygius* sp., *Eurhinosaurus* sp.), plesiosaurs (*Plesioneectes* sp.), and thalattosuchian crocodilians (*Steneosaurus* sp.), alongside abundant invertebrates including ammonites, belemnites, crinoids, bivalves, and decapod crustaceans (Hauff, 1921; Urlichs et al., 1994). Particularly noteworthy are specimens preserving soft tissues, stomach contents and embryos, which provide direct evidence for physiology, reproductive biology, trophic interactions, and functional morphology in Jurassic marine organisms (Hauff, 1921; Seilacher et al., 1985). Exceptional fossil preservation at Holzmaden is closely linked to the depositional and geochemical conditions of the Early Jurassic epicontinental sea. The Posidonia Shale was deposited under conditions of fine-grained sedimentation combined with dysoxic to anoxic bottom waters, which significantly reduced scavenging and bioturbation (Röhl et al., 2001). These conditions are commonly associated with the Early Toarcian Oceanic Anoxic Event (T-OAE), a global palaeoenvironmental perturbation marked by widespread oxygen depletion, enhanced organic carbon burial, and major disruptions to the carbon cycle (Jenkyns, 1988; Röhl et al., 2001; Danise et al. 2015). The high-resolution stratigraphic record preserved at Holzmaden provides critical insights into the interactions between environmental change and marine biota during this interval.

6.1.2 The museum Urweltsteinbruch Holzmaden

The Urweltsteinbruch Holzmaden is a museum, quarry and shop located in Holzmaden, Germany (Fig. 6.1). The Urweltsteinbruch building spans two floors: the ground floor and the underground floor. The ground floor hosts the front desk and the museum shop, whereas the underground floor hosts the exhibition area, where large slabs of shale are hung on the wall and display ichthyosaurs, crinoids and crocodilians. The main attraction of the Urweltsteinbruch is the quarry, where visitors, mostly families with children, can dig autonomously to try and find their own fossils. The museum provides all the equipment for fossil extraction: hammer, gloves and goggles. However, there had been no instructions on how to use such tools or on which fossils the visitors were looking for. In general, the museum lacked a space where families and children could be introduced to palaeontology and fossils in general, and to the Holzmaden Jurassic fossil fauna in particular.

6.1.3 Aims of the project

This project was commissioned to Prehistoric Minds s.r.l.s. and Di. Ma. Dino Makers s.r.l.s., with whom I collaborated designing and developing the project. The Urweltsteinbruch Holzmaden asked for a small permanent exhibition located on the underground floor, designed as a preparatory space for visitors. The exhibition aimed to introduce families with children to the world of palaeontology through storytelling and to the exceptional fossil heritage of Holzmaden, providing basic scientific and historical context, key concepts, and interpretative tools necessary to better understand the site. The exhibition was deliberately conceived as a walk-through, concise and accessible introduction, fully aware that the primary focus of the visitor experience is not the indoor display itself, but the active quarry located outside, where fossils are found in situ. The project was realised between December 2023 and March 2024.

6.2 Materials and Methods

The making of the new exhibition followed three different phases: design, production, and setup.



Figure 6.1: Urweltsteinbruch Holzmaden A) ground floor shop and B) fossil gallery, underground floor. Images from the Urweltsteinbruch Holzmaden website.

6.2.1 Exhibition design

The design and development of the permanent exhibition at the Urweltsteinbruch Holzmaden followed a structured, multi-phase methodological approach, combining spatial analysis, curatorial planning, content development, and audience-oriented interpretative design. **Preliminary site inspection and spatial assessment** The project began with the on-site inspection of the museum's exhibition spaces, with particular focus on the underground floor designated to host the new exhibition. This phase aimed to evaluate the architectural layout, visitor circulation, lighting conditions, and existing displays. Measurements were taken to define dimensional constraints for exhibition panels and complementary materials, ensuring compliance with accessibility standards, safety regulations, and fire-escape requirements. Particular attention was paid to preserving sufficient free space for visitor movement, especially considering the high proportion of families with children among the museum's audience. Based on this assessment, a preliminary exhibition pathway was outlined, defining the logical sequence of panels and the overall narrative flow (Fig. 6.2).

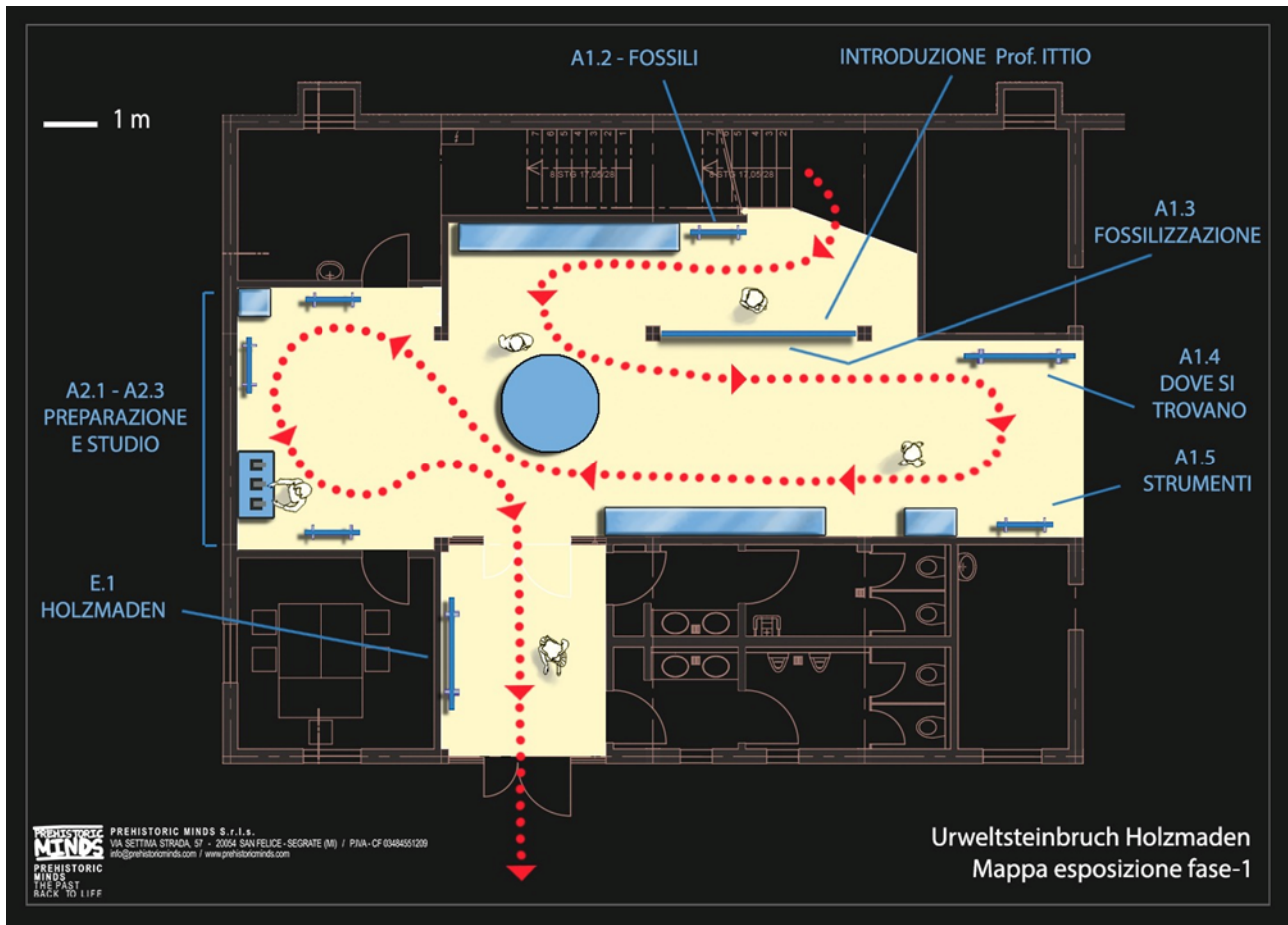


Figure 6.2: Detailed map of the ground floor with exhibition panels and pathways for visitors.

Exhibition planning and content structure Following the spatial assessment, the exhibition was planned conceptually and structurally through a schematic layout developed in spreadsheet format (Microsoft Excel; Fig. 6.3). This tool was used to define the total number of panels, their relative positioning along the exhibition path, and their maximum allowable dimensions. For each panel, the core topic, key messages, and level of scientific depth were specified, ensuring coherence with the overall aims of the project and suitability for a non-specialist audience. The text was first written in Italian and later translated to German using an online translator (DeepL) and checking its accuracy with the Urweltsteinbruch Holzmaden personnel. In parallel, the types of supporting materials to be associated with each panel were identified. These included fossil specimens, replica objects, or illustrative elements intended to reinforce the storytelling approach and facilitate intuitive understanding of palaeontological concepts. This step allowed for an integrated design in which textual, visual, and material components functioned together rather than as independent elements.

Selection of fossil materials To support the scientific and narrative framework of the exhibition, a targeted selection of fossil specimens was carried out. The internal fossil catalogue of the Urweltsteinbruch Holzmaden was reviewed in collaboration with museum staff, with the aim of identifying slabs that were both scientifically representative of the Holzmaden fauna and visually effective for public display. Selection criteria included taxonomic relevance, state of preservation, clarity of anatomical features, and suitability for being interpreted in an educational context. Preference was given to specimens that could be directly linked to the themes introduced in the panels, thereby strengthening the connection between abstract concepts and tangible evidence.

Interpretative tools and visitor guidance In the final design phase, additional interpretative tools were developed to enhance visitor engagement and orientation. A mascot character was conceived as a narrative guide, intended to facilitate identification, maintain the attention of younger visitors, and provide continuity throughout the exhibition. The mascot was integrated consistently across panels and supplementary materials as part of the storytelling strategy. To further support visitor flow and prevent confusion in the exhibition sequence, a printed floor sticker path was designed and installed. This visual guide directed visitors along the intended route, ensuring that panels were encountered in the correct order and reinforcing the narrative progression. Together, these elements were designed to generate a clear, engaging, and accessible preparatory experience, seamlessly connected to the subsequent hands-on fossil-hunting activity in the quarry.

6.2.2 Exhibition production

Once the conceptual structure and contents of the exhibition were defined, and accepted by Urweltsteinbruch Holzmaden, the project moved into the production phase, focused on the realisation of the physical and visual components. The design and production of the exhibition panels were developed in close collaboration with the graphic designer Andrea Morandini, working together with the German graphic design company Super Hero Design. This collaboration was essential to define a coherent visual identity for the exhibition, including the selection of colour palettes that would be visually soothing for visitors while simultaneously evoking the

characteristic tones of Holzmaden fossils (such as dark shales, ochre-brown bones, and metallic highlights) and the broader marine setting of the Early Jurassic. At the same time, a professional cartoonist was involved to develop the visual design of the mascot, producing original illustrations intended to be seamlessly integrated into the panels and to function as a narrative and didactic guide throughout the exhibition. The physical objects associated with the panels, including display elements and interpretative supports, were produced by the personnel of Di. Ma. Dino Makers s.r.l.s., ensuring consistency with both the scientific content and the visual language of the exhibition. One dedicated exhibition station was custom-built by a professional carpenter. Finally, all exhibition panels were printed in large format by a specialised printing service, ensuring high-quality reproduction of texts and graphics suitable for prolonged display in a public museum environment.

Code	Type	Content (summary)	Notes
A1.1	Introductory panel	Guide character (Prof. Ichthyosaur) introducing the exhibition path and the work of the palaeontologist.	Entrance area
A1.2	Informative panel	Geological and palaeontological context of the fossil site, including chronological framework and environment.	Text and graphics
A1.3	Educational panel	Objectives of the exhibition path: fossil observation, 3D models, and interactive activities.	General audience
A2.1	Interactive station	Digital visualisation of fossils and three-dimensional reconstructions.	Touch screen
E1	Outdoor panel	General information about the site and visitor orientation.	Outdoor area

Table 6.1: Structural summary of the contents included in the project spreadsheet.

6.2.3 Shipping

All exhibition panels and three-dimensional components, including the wooden structures, were conceptualised and manufactured in Italy. For the final installation and mounting phase, a dedicated large-capacity transport vehicle was rented by Prehistoric Minds s.r.l.s. to ensure the safe and efficient transfer of all exhibition elements. The complete set of production materials was transported in a single delivery to the Urweltsteinbruch Holzmaden, minimising logistical complexity and reducing the risk of damage during transit.

6.3 Results

6.3.1 Exhibition setup

The permanent exhibition realised on the underground floor of the Urweltsteinbruch Holzmaden consists of a coherent set of interpretative elements designed to guide visitors toward an informed and contextualised experience of the quarry. The exhibition includes a total of 18 wall-mounted panels, one interactive map (wall mounted), one cylindrical wooden exhibition station, one outdoor panel located within the quarry area, and two 3D-printed objects specifically developed to further illustrate the concepts addressed in two of the panels (Fig. 6.4).

All graphic elements share a unified visual identity. The colour palette adopted throughout the exhibition is based on Pantone 726 C and Pantone 719 C, selected to evoke the chromatic range of Holzmaden fossil specimens and their enclosing shales, while maintaining visual comfort and readability. Typography was standardised across all panels: Arial Rounded was used for main titles and section headings, enhancing clarity and approachability, while Garamond was employed for the main body text to ensure readability and a formal, scientific tone consistent with museum communication standards (Fig. 6.5).

A recurring narrative element throughout the exhibition is the mascot “Professor Ichtyo,” whose name explicitly references the iconic Jurassic ichthyosaurs of Holzmaden. The mascot is a reference to the famous 1830 cartoon “Professor *Ichtyosaurus*” of Henry de La Beche. Professor Ichtyo appears on all panels in varying postures and contextual situations, functioning



Figure 6.3: Final exhibition setup. A) Welcome panels, visible once you step down the stairs from the ground floor; B) panels next to the welcome exhibit, about what fossils are and where they are found; C) the anatomy of fossils; D) the preparation of fossils; E) wooden installation about the evolution of the earth through time; F) panel about how old the Earth is.



PANEL LAYOUT
HOLZMADEN MUSEUM
05/03/2024



Figure 6.4: Panel size, colour palette and fonts to be applied in all panels throughout the exhibition.

as a visual guide and narrative mediator, particularly aimed at engaging younger visitors while maintaining coherence for a broader audience. Initially, the mascot was designed as a humanised *Ichtyosaurus* wearing a formal blue coat, with golden trim along the edges, that resembles an 18th-century frock coat, reinforcing the stereotypical “professor” character. The visual design of the mascot was then intentionally revised and simplified. Decorative elements and garment details were reduced to streamline the character’s appearance, making it more suitable for reproduction across different formats. This simplification was primarily motivated by the need to facilitate the production of merchandise based on the mascot and to reduce overall production costs, while preserving the recognisability and narrative function of the character (Fig. 6.6).

6.3.2 Exhibition panels

The exhibition pathway begins with an introductory panel in which visitors are welcomed by Professor Ichtyo and invited to explore the exhibition to discover the world of palaeontology

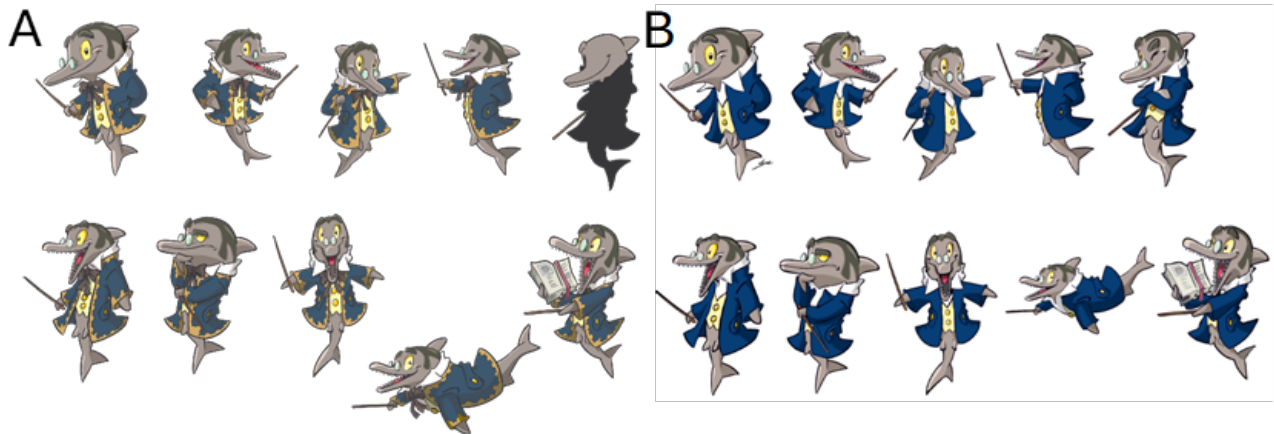


Figure 6.5: Original draft (A) and (B) simplified illustrations of the mascot "Prof. Ichtyo" in different poses.

in general and, in particular, of Holzmaden. Subsequent panels and exhibition stations are organised to progressively introduce and develop the fundamental concepts necessary for understanding the fossil site. These topics include: the definition of fossils; the main types of fossils; the geological and geographical contexts in which fossils are found; an overview of the history of life on Earth; the processes leading to fossilisation; the geological age of the Earth; basic principles of fossil excavation; an introduction to fossil preparation techniques; and an introduction to the study of fossil anatomy. Finally, an outdoor panel installed within the quarry illustrates the different types of fossils that visitors can encounter during excavation activities. This panel directly connects the indoor preparatory exhibition with the hands-on experience in the quarry, reinforcing learning outcomes and supporting informed fossil collecting. The panels contain information written in German; for clarity purposes, the texts reported here are translated into English.

EXHIBIT A.1

Title: Welcome!

Text: Hello! My name is Professor Ichthyosaur, the first specimen of *Ichthyosaurus sapiens*. I am a palaeontologist ichthyosaur, and my job is to search for and study fossils. Palaeontologist, dinosaur, fossils... I'm getting a little ahead of myself, aren't I?

Okay, okay... let's take a moment to understand the meaning of all these words. To do so, I will take you step by step on a fascinating journey to discover the science of ancient living beings, palaeontology, among finds, excavations, museums, and lost worlds. Along the way, I

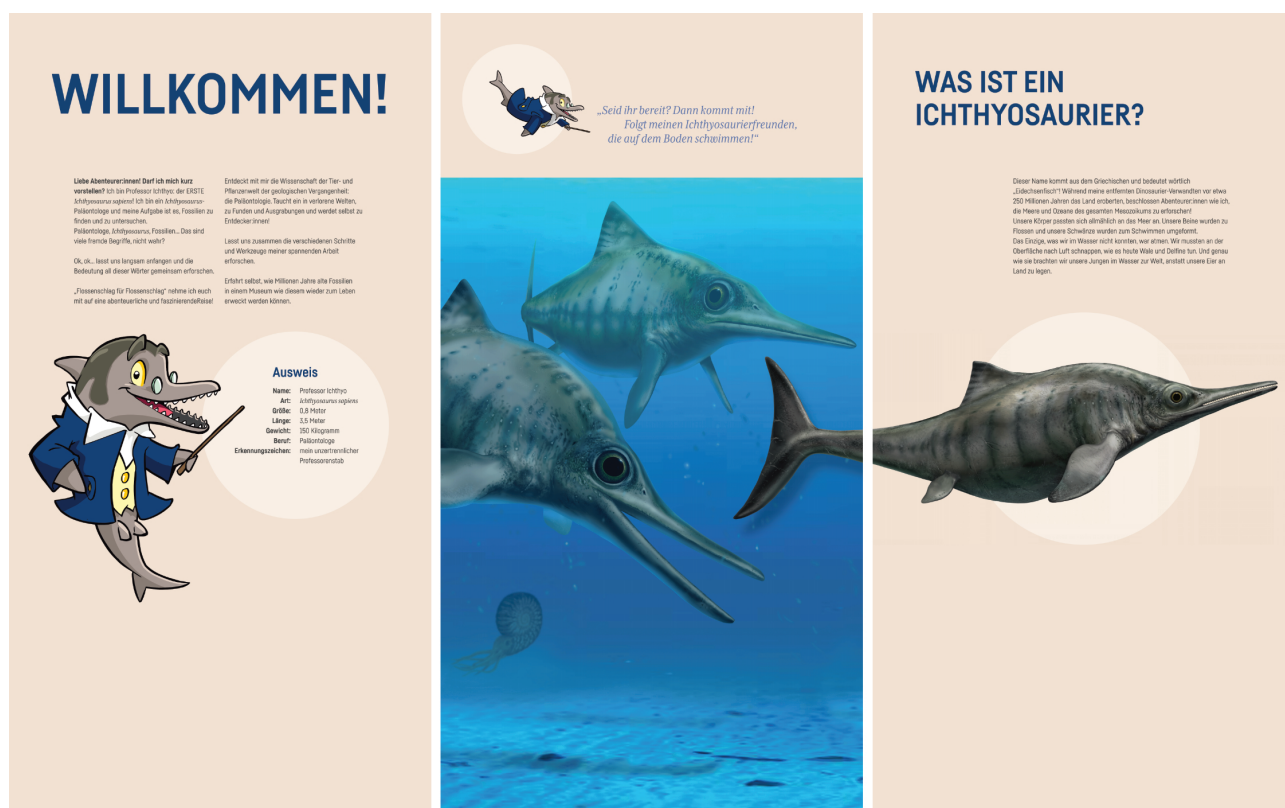


Figure 6.6: Panels A1.1.1, A1.1.2, A1.1.3. placed at the entrance of the exhibition.

will show you the various stages and tools of my work up close. You will learn how a pile of petrified bones, millions of years old, can come back to life in a museum like this...

Are you ready? Then let's go! Follow my fish friends swimming on the floor!

(ID card: internal box on the panel)

Name: Professor Ichthyosaur

Species: *Ichthyosaurus sapiens*

Height: 0.8 meters

Length: 3.5 meters

Weight: 150 kilograms

Occupation: palaeontologist

Distinguishing features: professor's wand

EXHIBIT A1.2

A1.2.1 Title: What are fossils? What science studies fossils? Who studies fossils?

Text: Fossils are the remains of living animals that lived long before us and have been preserved to this day. The word fossil comes from the Latin word fodere, which means “to

WAS SIND FOSSILIEN?



Fossilien sind die Überreste von Lebewesen, die lange vor uns gelebt haben und bis heute erhalten geblieben sind.

Das Wort Fossil stammt von dem lateinischen Wort *fodere*, das „graben“ bedeutet. Tatsächlich werden Fossilien vom Menschen ausgegraben oder von der Natur selbst durch Erosion (Abtragung durch Wind, Wasser oder Eis) aus dem Gestein freigelegt und wieder ans Tageslicht gebracht.

Fossilien entstehen in Sedimentgesteinen.

Auf Meeresböden und auf dem Grund von Seen, wo Flüsse viel Material anschwemmen, schichten sich Sedimente (durch Wasser und Wind transportierte Gesteinskörner), darunter auch Reste von verstorbenen Tieren oder Kalkschalen auf. Diese Anhäufung wird durch steigenden Druck in Jahrmillionen zu festem Gestein.

Im Eruptivgestein, welches durch Erstarren von Magma aus dem Erdkern entsteht, bilden sich hingegen keine Fossilien, da die Hitze und der Druck solcher Gesteine alle Überreste zerstören.

„Fossilien sind versteinerte Überreste von Tieren und Pflanzen, die vor sehr langer Zeit lebten.“

WIE NENNT SICH DIE WISSENSCHAFT, DIE FOSSILIEN UNTERSUCHT?

Die Wissenschaft, die sich mit Fossilien befasst, wird Paläontologie genannt.

Die Geschichte dieses Forschungsgebiets ist sehr alt und beschäftigt schon seit mehreren Jahrhunderten Wissenschaftlerinnen und Philosophinnen.

Doch erst in der zweiten Hälfte des 19. Jahrhunderts wurden Fossilien als einzigartige Zeitzeugen erkannt. Es sind Überbleibsel alter Lebewesen, anhand derer sich die Geschichte des Lebens auf unserem Planeten und der lange Prozess der Evolution nachbilden lässt. Dieser hat das Leben von den ersten Mikroorganismen bis zu den komplexen Formen, die wir heute kennen, geprägt.

WER ERFORSCHT FOSSILIEN?

Expert:innen, die sich mit Fossilien beschäftigen, werden Paläontolog:innen genannt.

Der Franzose Georges Cuvier (1769-1832) gilt als Begründer der Paläontologie und der vergleichenden Anatomie (Studium der Gestalt und des Aufbaus von Lebewesen durch den Vergleich ihrer verschiedenen Teile). Er war der erste, der das Phänomen des Aussterbens, d. h. des endgültigen Verschwindens einer Art von der Erde, schlüssig dokumentierte.

WELCHE FOSSILIENARTEN GIBT ES?

Bis heute wurden Fossilien aus Tierknochen und Zähnen, z. B. von Dinosauriern, gefunden. Außerdem gibt es Fußabdrücke, Eier, Nester, Höhlen, Kot (Koprolithen), Schalen, Muscheln, Blätter, Baumstämme, Samen, Pollenkörner, Pflanzenharze (Bernstein) und viele andere Arten von fossilen Überresten. In sehr seltenen Fällen versteinern auch die Weichteile eines Lebewesens, wie z. B. die Haut von Ichthyosauriern.



Figure 6.7: Panels A1.2.1, A1.2.2

dig.” In fact, fossils are dug up by humans or by nature itself through erosion (removal by wind, water, or ice) and brought back to the surface. Fossils form in sedimentary rocks. On the sea floor and at the bottom of lakes, where rivers wash up a lot of material, sediments (rock particles transported by water and wind) accumulate in layers, including the remains of dead animals or limestone shells. Over millions of years, this accumulation becomes solid rock due to increasing pressure. In igneous rock, which is formed by the solidification of magma from the Earth’s core, no fossils are formed because the heat and pressure of such rocks destroy all remains. The science that deals with fossils is called palaeontology. The history of this field of

research is very old and has been occupying scientists and philosophers for several centuries. However, it was not until the second half of the 19th century that fossils were recognised as unique witnesses to history. They are the remains of ancient animals, which can be used to reconstruct the history of life on our planet and the long process of evolution. This process has shaped life from the first microorganisms to the complex forms we know today. Experts who study fossils are called palaeontologists. The Frenchman Georges Cuvier (1769-1832) is considered the founder of palaeontology and comparative anatomy (the study of the form and structure of living organisms by comparing their different parts). He was the first to conclusively document the phenomenon of extinction, i.e., the permanent disappearance of a species from the Earth.

A1.2.2 Title: What can fossilise?

Text: To date, fossils of animal bones and teeth, e.g. from dinosaurs, have been found. There are also footprints, eggs, nests, caves, faeces (coprolites), shells, mussels, leaves, tree trunks, seeds, pollen grains, plant resins (amber) and many other types of fossils remain. In very rare cases, the soft tissues of a living animal, such as the skin of ichthyosaurs, also fossilise.

EXHIBIT A1.3

A1.3.1 Title: How do fossils form?

Text: Fossils are very rare, and for them to form, favourable circumstances must coincide. For this reason, every fossil is a precious treasure that tells us something about our distant past. When an animal or plant dies, its remains can suffer various fates. Consider, for example, a gazelle that dies in the middle of the savanna: What are the chances that its skeleton will remain intact and become a fossil? Very slim, because the skeleton can be eaten by lions or hyenas, nibbled on by insects, dissolved by the sun, rain, and wind, and decomposed by billions of bacteria. And even if the skeleton miraculously remained intact, that wouldn't be enough! Most skeletons that become fossils come from animals that died under special conditions. They may have been washed into lakes and rivers, deposited on the sea floor, buried under mud or debris, or covered by desert sand. Exciting, isn't it?

A1.3.2 Title: Taphonomy

Text: To understand this better, we need to take a step back in time to the Jurassic period



Figure 6.8: Panels A1.3.1, A1.3.2, A1.3.3.

183 million years ago. Let's follow the story of an ichthyosaur whose skeleton was fossilised. The processes we observe from the death of a living animal to its discovery as a fossil are called fossilisation theory or taphonomy: 1. On the shore of a sea, in the middle of a school of fish, swims a hungry ichthyosaur.

2. The ichthyosaur falls ill, dies, and sinks to the sea floor. Scavengers, small fish, and invertebrates feed on the carcass.

3. The skeleton and remains of the ichthyosaur are covered by sediments, and microorganisms attack the soft tissues: skin, muscles, and organs are decomposed.

4. The hardest parts of the skeleton that are still present (bones and teeth) are gradually covered by a thick layer consisting of mud, sand, and mineral grains. This layer prevents decomposition.

5. Over time, further layers are deposited on top of the ichthyosaur. Slowly, the lowest layers compact and solidify; they are gradually transformed into rock.

6. As water seeps in, even tiny mineral grains from the sediment enter the pores and cavities of the bones. These mineral deposits make the bones more stable and heavier. Gradually, these

minerals replace the particles that make up the bones. The ichthyosaur bones fossilise.

7. The movements of the earth's crust lift the rock containing the fossilised ichthyosaur, and a mountain range is formed in place of the ancient sea. Rocks that are not hidden under other rocks or under plants, soil, water, or glaciers are referred to as "exposed."

8. The exposed rock layers are eroded by rain, wind, and ice, worn away and destroyed by tree roots until the layer containing the fossil is exposed. The fossil thus returns to the earth's surface and waits to be discovered!

A1.3.3 Title: The fossils of Holzmaden

Text: When a large number of fossils in excellent condition are found in a limited area, this is referred to as a conservation deposit. Such deposits are famous for the exceptional quality of their fossils. Holzmaden is one of them! Not only have numerous vertebrate fossils been excavated here, but many of the finds were discovered with well-preserved soft tissues, i.e. the parts that very rarely fossilise! How is this possible? To understand this, we need to go back to the Lower Jurassic period 183 million years ago. At that time, Holzmaden and the surrounding area were floodplains with offshore basins of a ancient ocean, the Tethys Sea. At that time, the seabed was characterised by low-oxygen conditions. This favoured the triggering of chemical reactions through which minerals such as apatite, pyrite, gypsum and carbonates settled on the sea floor. They replaced all the bony (and often also the 'soft') parts of animals that had sunk dead to the sea floor. Today, we find fossils in Holzmaden that consist precisely of these minerals.

EXHIBIT A1.4

Title: Where are fossils found?

Text: Fossils are found in sedimentary rocks all over the world. These include not only marine reptiles, but also dinosaurs, pterosaurs, mammals, amphibians, fish and invertebrates that lived on land and in the oceans of the Palaeozoic, Mesozoic and Cenozoic eras. Do you know where the large herbivorous dinosaur *Triceratops* grazed? In which countries did the loud trumpeting of the mighty mammoth echo? Open the windows on the world map and find out for yourself! Did you know that...? Sometimes unexplored fossils are found in museum storage facilities. This is the case with the *Apatosaurus* (formerly known as *Brontosaurus*), which was



Figure 6.9: A) Panel A1.4, B) and C) Interactive map of famous fossils found in each continent.

found in 1879 and whose skull could not be assigned. Almost a century after its discovery, some palaeontologists realised that a skull of this dinosaur species had been excavated together with the skeleton of the first specimen found. It had been lying forgotten in the storage room of a North American museum. The researchers were finally able to identify and classify it. Interactive support: Geographical map of the world, cut into small windows which, if opened, show illustrations of fossil species that have been found in each continent.

EXHIBIT A1.5

A1.5.1 Title: How is a fossil recovered?

Text: Freeing a large ancient reptile from its rocky tomb is no easy task and requires the cooperation of a team of experts and the use of various tools. Here are the tools I always carry with me: backpack; geological map; notepad; pencil; compass; tape measure; magnifying glass; geologist's hammer; chisel; kitchen knife; pickaxe; shovel; awl; toothbrush; trowel.

A1.5.2 Title: Excavation, Documentation, Transport

Text: Excavation: To determine the size of the fossil and to delimit the area in which the skeleton lies, excavation is carried out around the bones. Explosives and mechanical means such as bulldozers, excavators and jackhammers can be used to remove the surrounding hard



Figure 6.10: Panels A1.5.1, A1.5.2.

rock layers. Shovels and picks are used to remove the softer, more brittle rock. The closer you get to the fossil, the more precise and careful you work, first with a hammer, chisel and broom, then with brushes and paintbrushes. Superglue and impregnating agents are always on hand to stabilise the fossil before it is completely exposed and recovered, or to reassemble it if part of the find is accidentally damaged.

Documentation: Throughout the excavation, drawings are made and photographs are taken of the entire site. The position of all bones is carefully measured and noted, and each bone is numbered and listed. Similar to detectives at a crime scene, palaeontologists collect every clue to understand the environment in which the animal lived and how it died. The square that delimits the excavation area is put on paper and divided into sections of equal size. As soon as the finds emerge from the ground, their position is recorded. The geographical coordinates of



Figure 6.11: Panels 2.1.1, 2.1.2.

the find site are recorded using the satellite-based positioning system GPS (Global Positioning System).

Transport: To harden and strengthen the most fragile bones, they are brushed and impregnated with adhesive resins and strengthening impregnating agents. The finest hairline cracks are filled with superglue. When the bones are more than halfway excavated, they are wrapped in aluminium foil and plaster-soaked bandages and reinforced with metal. Once these protective plaster caps have hardened, the bones are recovered. Packaged in this way, they are ready for the often adventurous and bumpy journey to the museum workshops.

EXHIBIT 2.1

2.1.1 Title: Fossil preparation

Text: When a fossil arrives at a museum, it must first be removed from the rock in which it

is embedded and protected from decay. This step is known as preparation. The bones are freed from their hard gypsum shell by moistening the gypsum cap to soften it and then ‘cutting’ it open. The fossil is then freed from the surrounding rock, if possible in its entirety. This work is very delicate and can take months or even years. Some fossils must remain in their surrounding rock, Some fossils must remain in their surrounding rock – such as the skeletons of ichthyosaurs, which, due to their rare preservation with skin impressions in large rock slabs, can only be prepared on one side. ‘Sometimes a fossil even ends up in a hospital, where they examine how it can be freed from the rock or what it looks like inside.’

2.1.2 Title: Types of fossil preparation

Text: MECHANICAL PREPARATION - This method exploits the natural separation between the fossil and the rock and is carried out mechanically by removing small pieces of rock with a whole arsenal of tools such as various hammers and chisels, needles, scrapers and compressed air gravers. Some fossils can also be exposed with the aid of sandblasting equipment. Baking powder, iron powder or even a fine powder made from nut shells is ‘shot’ onto the rock crust covering the fossil through a small compressed air nozzle... very carefully, of course, so as not to damage the surface of the fossil! Sometimes binocular microscopes are also used to work even more precisely, as Dr Slate, our preparator, is doing here.

CHEMICAL PREPARATION - During chemical preparation, the fossil is placed in acid baths that only attack and dissolve the surrounding rock, but not the fossil itself (see the shell on the table). This requires extreme caution and precision! You have to know exactly which acid will not dissolve the valuable fossil into thin air... otherwise you’ll be in trouble with Dr. Slate!

HIGH-TECH FOR ANCIENT BONES -X-ray and computed tomography (CT) examinations make it possible to see and study fossils without having to remove the surrounding rock. These examinations are indispensable when the bones are too small and fragile to be prepared mechanically or chemically. They can serve as a ‘map’ for the preparators to determine the exact position of the bones and remove the rock in the right places.

EXHIBIT 2.2

A2.2.1 Title: How is a fossil studied?



Figure 6.12: Panels 2.2.1, 2.2.2.

Text: To identify fossils, their structure is first examined and compared with related animal forms (living or extinct). If the find, e.g. a dinosaur, is particularly interesting for science, a more detailed examination is carried out. **Procedure:** The first step is to examine the bones, compare them with other bones of similar species that have already been described, measure and describe them, identify each individual bone and recognise any special features (such as protrusions or holes).

Images: Drawings and photographs of the entire bone and its most important features are taken from different angles. **Comparisons:** if the bones resemble those of other dinosaurs or differ from them, it is determined to which group of dinosaurs the animal belongs. **Way of life:** After the appearance of the animal has been sketched, an attempt is made to reconstruct its way of life. The skull, teeth, spine, limbs and signs of muscle attachments provide clues as

to how the animal walked and what it ate. Scientific name: If it turns out that the animal is a species new to science, palaeontologists give it a scientific name. This reflects a visible characteristic, refers to the location where it was found, or is dedicated to scholars, explorers or individuals with special merits. Publication: Finally, all discovered information is summarised in an article and sent to scientific journals with photos and drawings. The article is published after evaluation by experts and the scientific community. THE COMPUTER - The computer is an extremely useful tool for palaeontologists. It enables them to discuss with colleagues from all over the world, exchange photos and drawings, read the latest specialist articles and search for news on the internet. Special programmes can be used to study the anatomy of animals and their family relationships. The computer is an extremely useful tool for palaeontologists.

A2.2.2 Title: Let's examine a dinosaur together!

Text: Here are two perfectly connected bones that we have just uncovered. Follow my reasoning as I try to figure out what bones they are and what animal they belonged to: 1. The two bones are neither vertebrae nor parts of the skull. Among the many bones that make up a skeleton, such elongated elements are found only in the limbs. 2. Among the limb bones, the thigh bone is the one that has a clearly protruding extension (joint head) at its upper end. The massive thigh extension is connected to the pelvic girdle (our pelvis) in the hip joint. The bones connected to the joints are therefore the thigh bone and the shin bone. The body part we are looking for is therefore a leg and not an arm. 3. The leg is positioned vertically beneath the body and therefore cannot belong to a reptile such as a monitor lizard or crocodile. Only mammals and dinosaurs (including birds) have legs like this. 4. The leg dates to the Jurassic period. We know that mammals at that time were rather small and certainly did not have such long, "straight" limbs: so, it can only be a dinosaur leg! 5. Among dinosaurs, the leg is more similar to that of the *Tyrannosaurus* than to that of the *Triceratops* and *Diplodocus*. It is therefore a bipedal dinosaur from the theropod group (lizard-hipped dinosaurs). 6. Among the various theropod dinosaurs from the Jurassic period, only one predatory dinosaur has these special anatomical features on its leg bones: the North American *Ceratosaurus*!

Related material: 3D-printed femur and tibia of *Ceratosaurus* sp., mounted next to the panel A2.2.2.

EXHIBIT 2.3

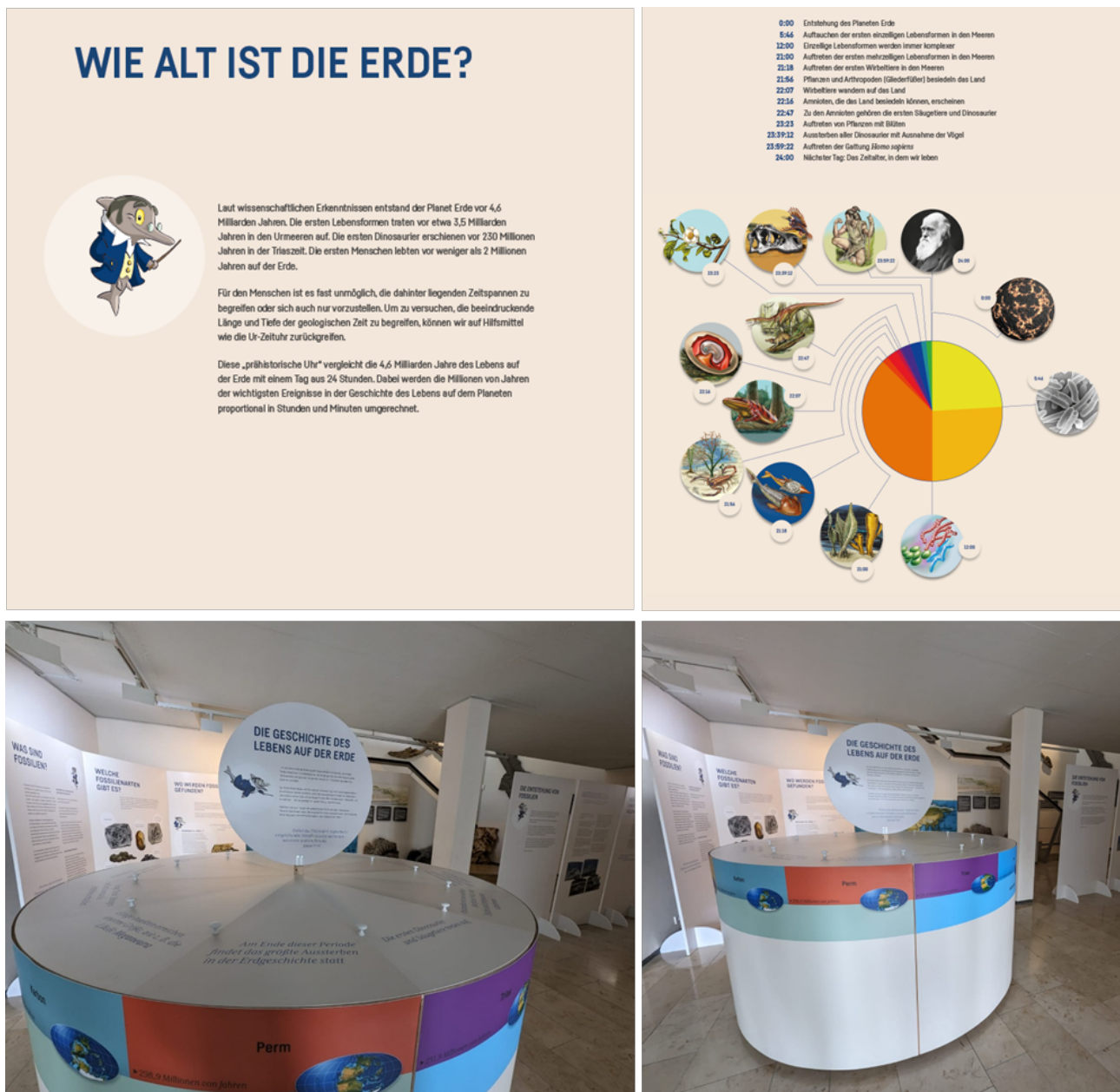


Figure 6.13: Top: Panels 2.3.1, 2.3.2. Below: Installation 2.3, Cylinder with movable and rotatable top.

A2.3.1 Title: How old is the Earth?

Text: According to scientific findings, planet Earth was formed 4.6 billion years ago. The first life forms appeared around 3.5 billion years ago in the primordial oceans. The first dinosaurs appeared 230 million years ago during the Triassic period. The first humans lived on Earth less than 2 million years ago.

It is almost impossible for humans to comprehend or even imagine the time spans involved.

To try to grasp the impressive length and depth of geological time, we can use tools such as the primordial clock. This ‘prehistoric clock’ compares the 4.6 billion years of life on Earth to a 24-hour day. The millions of years of the most important events in the history of life on the planet are converted proportionally into hours and minutes.

A.2.3.2 Title: Geological timeline

Text:

0:00 Formation of planet Earth

5:46 Appearance of the first single-celled life forms in the oceans

12:00 Single-celled life forms become increasingly complex

21:00 Appearance of the first multicellular life forms in the oceans

21:18 Appearance of the first vertebrates in the oceans

21:56 Plants and arthropods (joint-footed animals) colonise the land

22:07 Vertebrates migrate to land

22:16 Amniotes, which can colonise land, appear

22:47 Amniotes include the first mammals and dinosaurs

23:23 Appearance of flowering plants

23:39:12 Extinction of all dinosaurs except birds

23:59:22 Appearance of the species *Homo sapiens*

24:00 The age in which we live

Installation 2.3 Title: History of Life on Earth

Text: To easily retrace a history of immense duration, palaeontologists and geologists conventionally divide the past into main time intervals, called eras, which are in turn subdivided into periods, epochs and ages. This reference allows us to frame the information obtained from the study of fossils more clearly, enabling us to reconstruct the various stages in the history of life on Earth and the long process of change – evolution and extinction – that has characterised it. Fossils also bear witness to the geographical changes that have affected our planet, such as continental drift, the very slow movement of continental masses over millions of years.

EXHIBIT E1

Title: Fossils of Holzmaden

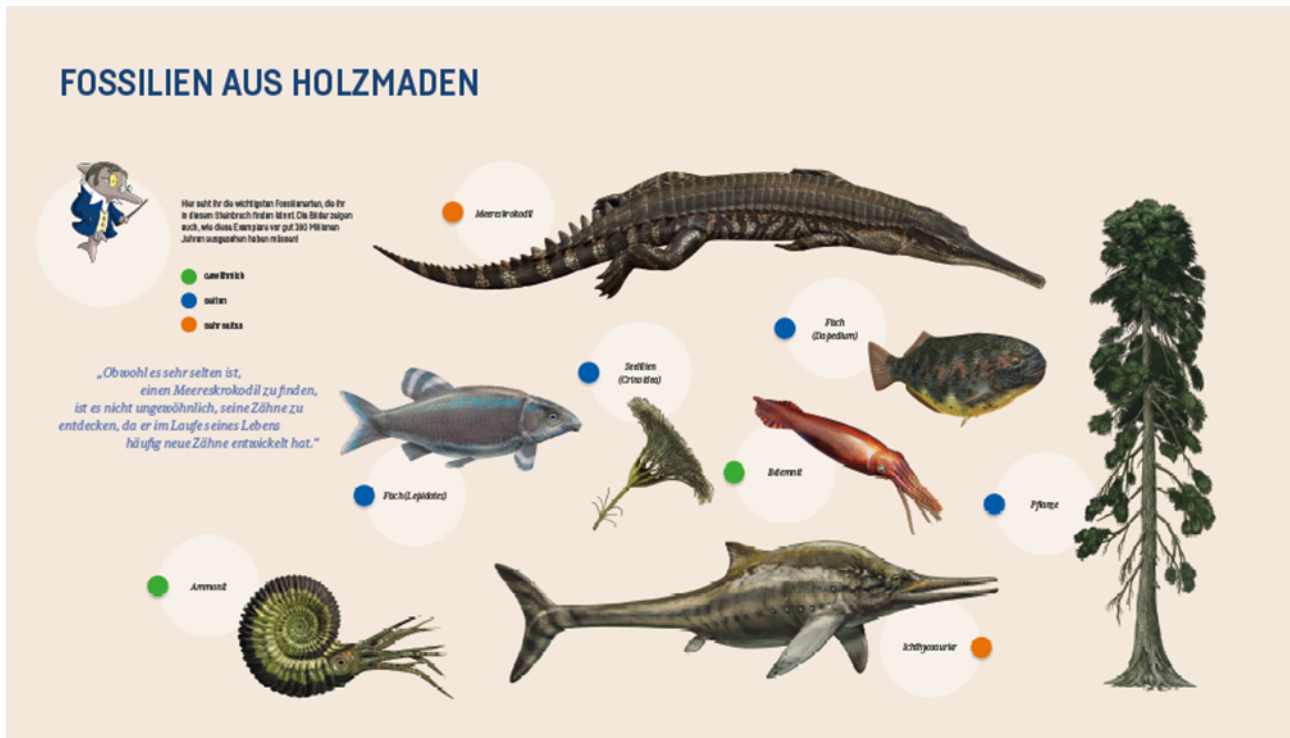


Figure 6.14: Panel E1, placed in the outside quarry.

Text: Here you can see the most important types of fossils that you can find in this quarry. The pictures show you what these specimens must have looked like 180 million years ago!

Green: Common; Blue: Rare; Orange: Very rare

Sea crocodile; Fish (*Lepidotes*); Sea lily (Crinoidea); Fish (*Dapedium*); Belemnite; Plant; *Ichthyosaurus*; Ammonite.

„Although it is very rare to find a marine crocodile, it is not unusual to discover its teeth, as it frequently developed new teeth throughout its life.“

6.4 Discussion

The project demonstrates how a small-scale, permanent exhibition can effectively function as a preparatory interpretative device for an experiential museum context, in line with contemporary museological standards that emphasise meaning-making, accessibility, and visitor-centred design. The overall structure and narrative coherence of the exhibition align with the Contextual Model of Learning proposed by Falk & Dierking (2013), in which personal, sociocultural, and physical contexts jointly shape the visitor experience. By introducing key palaeontological concepts before visitors access the quarry, the exhibition provides cognitive scaffolding that

enhances learning outcomes during the hands-on fossil-hunting activity.

From a museological perspective, the use of concise panels, guided storytelling, and a recurring mascot is consistent with interpretative principles outlined by Tilden (1957) and later expanded in museum education guidelines, where interpretation is most effective when it relates abstract concepts to the visitor's experience and provokes curiosity rather than simply transmitting information. The visual and narrative consistency across panels proved effective in maintaining attention and ensuring continuity, particularly for family groups with children, a core target audience of the Urweltsteinbruch Holzmaden. Several practical and logistical challenges emerged during the implementation phase. The cylindrical wooden exhibition station, while conceptually effective, proved problematic during installation. Although the structure had been professionally fabricated by a carpenter, its assembly on site was carried out by two non-expert personnel. This resulted in unforeseen difficulties, leading to a significant waste of time within an already constrained installation schedule. This highlights the importance of aligning fabrication complexity with the technical expertise available during installing phases (Lord & Lord, 2002).

While the general placement and readability of the panels proved successful, the cylindrical wooden station revealed a significant limitation in terms of accessibility. Its original height prevented younger children from reading the upper portion of the installation, thereby excluding a substantial segment of the intended audience. This shortcoming runs counter to inclusive design guidelines promoted by institutions such as ICOM, which stress the importance of physical and cognitive accessibility for diverse age groups (Garlandini et al., 2018). This issue was addressed through post-installation evaluation: two months after the installation, the structure was modified by reducing its height, making it fully accessible to children aged 4–8 years. This adaptive intervention underscores the value of iterative design and post-opening assessment in exhibition practice. Environmental conditions specific to the site also influenced the exhibition's performance. The constant flow of visitors between the indoor exhibition and the outdoor quarry resulted in the rapid accumulation of dust and dirt within the underground space. This posed a potential risk to the long-term preservation and accessibility/readability of exhibition elements. However, the prior choice of robust and easily cleanable materials mit-

igated these issues, confirming the relevance of preventive conservation principles commonly adopted in hands-on and high-traffic museum environments (Michalski, 1990).

An additional critical aspect that emerged during the project concerns the complexity of coordinating multiple professional figures within a limited timeframe. The exhibition development required the parallel involvement of illustrators, graphic designers, translators, exhibition fabricators, and the museum’s curatorial and managerial direction. Aligning content development, visual production, translation, approval processes, and fabrication proved challenging, particularly when delays or revisions in one sector propagated across subsequent stages. This interdependency resulted in increased organisational stress within an already constrained schedule and required frequent adjustments to the workflow. Similar challenges are widely documented in exhibition planning literature, where multi-disciplinary collaboration is recognised as both a strength and a potential source of inefficiency if not rigorously managed (Dean, 1994; Lord & Lord, 2002). Best-practice guidelines in museology and project management emphasise the importance of clearly articulated production timelines, role definitions, and decision hierarchies, especially in small-scale projects with limited temporal margins (Falk & Dierking, 2013; ICOM, 2017). In retrospect, a more effective scheduling strategy, explicitly detailing deliverables, and dependencies for each professional role, would likely have reduced friction and downtime, ensuring that all contributors could work continuously without bottlenecks. Such an approach would align with iterative and collaborative exhibition models increasingly advocated in contemporary museum practice, where coordination and communication are treated as integral components of interpretative quality rather than as purely logistical concerns.

6.5 Conclusions

The preparatory exhibition developed for the Urweltsteinbruch Holzmaden successfully fulfilled its primary objective: to provide visitors, particularly families with children, with the conceptual tools necessary to understand and appreciate the palaeontological significance of the Holzmaden site before engaging directly with fossil excavation. The integration of scientific accuracy, storytelling, and visual mediation resulted in an effective and coherent interpretative framework that complements the outdoor quarry experience rather than competing with it.

Despite logistical and environmental challenges, the project demonstrates that carefully planned small exhibitions can have a significant educational impact when grounded in established museological theory and responsive to site-specific constraints. The difficulties encountered, particularly regarding installation logistics and child accessibility, proved valuable in refining the exhibition and highlighting the importance of flexibility, evaluation, and adaptability in museum design processes. Overall, this project supports the view that preparatory exhibitions, when thoughtfully designed, represent a powerful tool for enhancing informal science learning and fostering meaningful engagement with palaeontological heritage.

7 A NEW EXHIBITION SPACE IN THE DEN BLÅ PLANET AQUARIUM

7.1 Introduction

7.1.1 The Den Blå Planet Aquarium

Den Blå Planet, the National Aquarium of Denmark, is a major European institution dedicated to marine biodiversity, conservation, and public engagement with ocean science located in the Kastrup district, Copenhagen. Built in 2013 and conceived as a scientific and cultural infrastructure, the aquarium is the largest in northern Europe. Integrating research-driven content with immersive exhibition design, it promotes contemporary debates on environmental awareness and science communication. The mission of Den Blå Planet aquarium is not just to show the complexity and diversity of marine animals, but to promote an integrated understanding of marine ecosystems and their vulnerability in the context of global environmental change (<https://denblaaplanet.dk/en/about-the-blue-planet/science-and-nature-conservancy/>).

The architectural design of Den Blå Planet plays a central role in shaping this framework (Fig. 7.1). The building is organised as a fluid, sculptural structure inspired by marine forms and hydrodynamics, guiding visitors through a sequence of interconnected exhibition halls. These halls are arranged around a central core and are dedicated to different aquatic environments and thematic narratives, reinforcing the concept of the ocean as a continuous and interconnected system. This means that architecture functions not just as a container for exhibitions, but as an active interpretative device that mediates meaning, orientation, and experience (Bennett, 1995; Macdonald, 2011).

Within this spatial configuration, the ocean hall (Fig. 7.1, in orange) holds a key symbolic and functional position. As the primary space of the aquarium, it has hosted large-scale exhibition elements designed to set the tone for visitors' experience. Among these, from December 2019, the ocean hall hosts an exhibition called "Havet For Længe Siden" (in English: The Sea, a long time ago) with in-vivo reproductions of extinct marine animals (Fig. 7.2). These full-scale reconstructions were designed to invoke species that are now extinct but were flourishing in the

oceans of the past, generating a bridge between past and present marine life. Their placement within the hall allowed visitors to get a glimpse of marine animals of the past through tangible, spatially immersive forms, thereby linking evolutionary history to present-day biodiversity and conservation concerns (Alberti, 2005; Falk & Dierking, 2016). Although extinct, their life-size scale, realism, and architectural integration confer a strong sense of presence and corporeality. The exhibition was meant to be temporary and to only last 2, maximum 3 years, yet it quickly became the most visited and appreciated installation of the whole aquarium.

Den Blå Planet is currently planning an extensive redesign of its ocean hall, aimed at introducing an entirely new exhibition concept aligned with updated scientific content and meant to give visitors a new experience. Because of this renewal, the existing configuration can no longer accommodate in-vivo reproductions of fossil animals in their original location.

7.1.2 Aims of the project

The project discussed in this chapter addresses the challenge of exhibition re-adjustment rather than removal. The extinct animal reproductions were the only elements in the aquarium representing concepts such as deep time and extinction, and their popularity among visitors had already made the exhibition last almost twice longer than originally established. Given the interest of this exhibit, the Den Blå Planet committee has decided to retain the in-vivo reproductions within the public experience of the aquarium by relocating them to the restaurant area (Fig. 7.1, yellow star) and redefining their function within this context, emphasising visitors' engagement and learning in aquaria (Hein, 1998; Falk & Dierking, 2013). Rather than being treated as residual or decorative elements, the reproductions are re-conceptualised as exhibition objects embedded within a hybrid space that combines social interaction and informal learning. This approach draws on contemporary museological theories that emphasise the expansion of exhibition practices beyond traditional spaces and the recognition of museums as distributed environments of knowledge production (Clifford, 1997; Simon, 2010). By integrating the reproductions into the restaurant area, the project seeks to activate a setting traditionally associated with pause and consumption as an interpretative space.

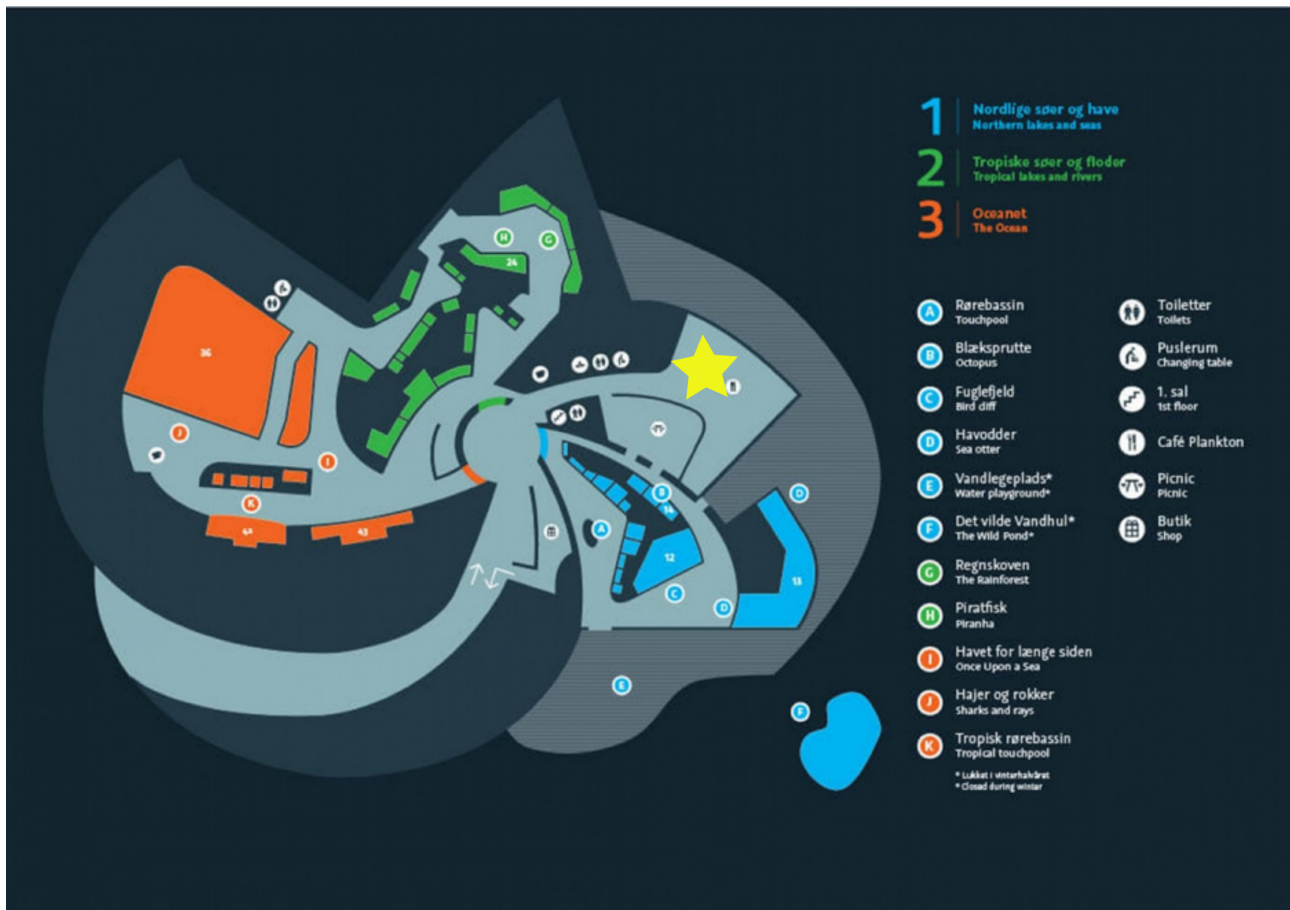


Figure 7.1: Architecture of the Den Blå Planet aquarium. The area highlighted in orange is the main exhibition room; the yellow star indicates the Café Plankton.

7.2 Materials and Methods

The initial project of defining a new exhibition for the ocean hall of the Den Blå Planet started in 2020, during COVID, as a way to further invite audiences to visit the aquarium. Once defined and approved by the aquarium committee, the Italian company Di. Ma. – Dinomakers was employed as the constructor of the new exhibition in 2024. Consequently, Di. Ma. also designed a proposal for relocating the reconstructions, which were made by Italian companies Geomodel, Di.Ma. Dinomakers and the Danish company 10 Tons. Due to the nature of the project and the difficulties of conciliating high-quality exhibition objects and safety regulations, the exhibitions are yet to be realised. For this reason, this chapter will only include the project-proposal presented to the aquarium committee, developed by me and Prehistoric Minds as scientific advisors, Tito&Pio Toso s.r.l. as architectures and TTE- Studio Tecnobrevetti team engineering s.r.l. as engineers.

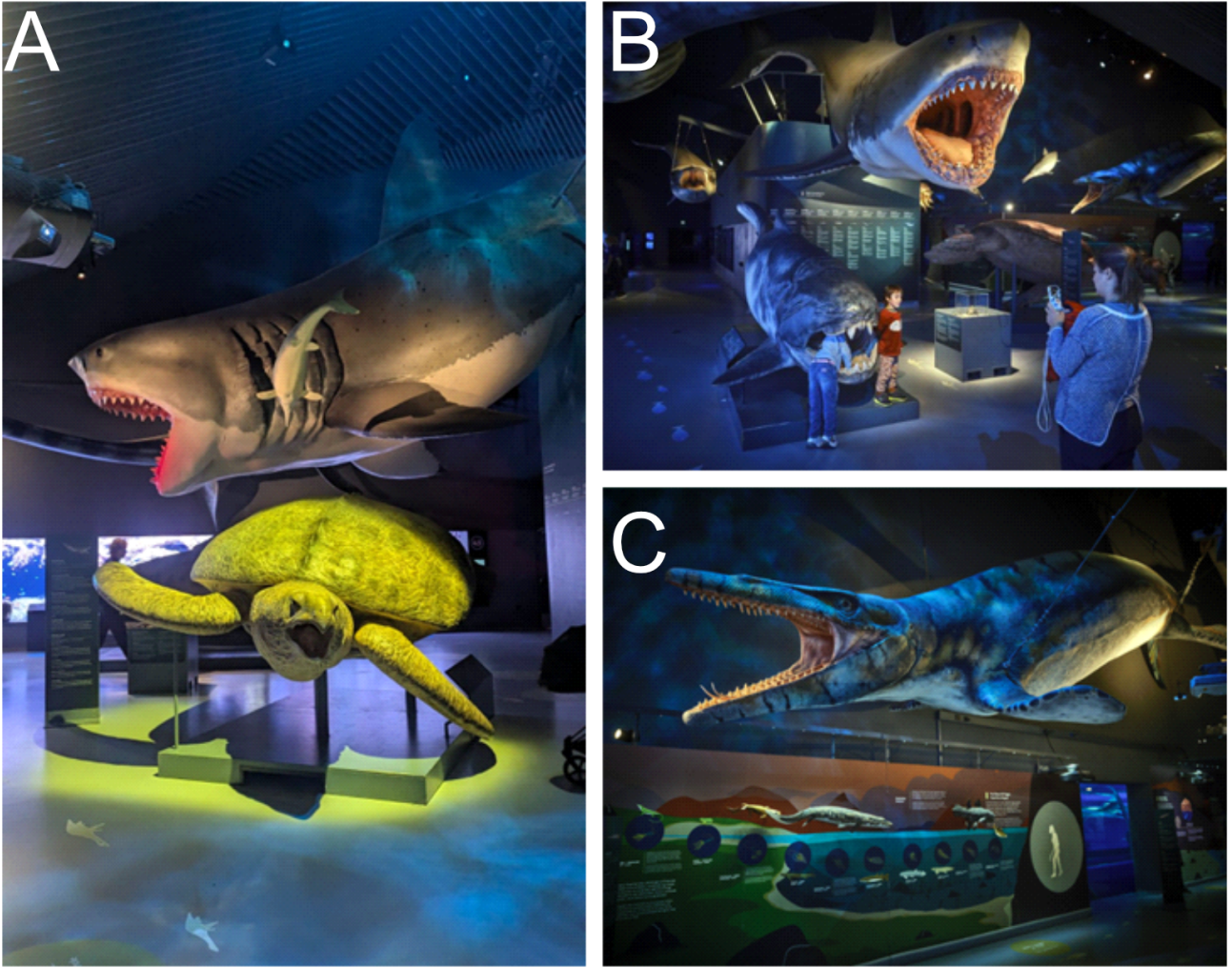


Figure 7.2: In-vivo reconstruction of extinct marine animals exhibited in the Ocean Hall as part of the "Once upon the sea" exhibition. A) *Otodus megalodon*, *Chasmoceras*; B) *Dunkleosteus* (bottom left); C) *Tylosaurus*

The project was structured into two complementary and interdependent components. The first component concerns the architectural, structural, and engineering activities required to safely relocate and physically integrate the in-vivo reproductions within the restaurant area. The second component, in which my work is focused, addresses the museological and exhibition-design strategies developed to ensure visitor engagement while preserving the primary function of the space as an area for eating, rest, and social interaction.

7.2.1 Architectural and engineering design

This phase was curated and implemented by a team of architects and structural engineers. It is reported here for the sake of completeness in the description of the exhibition reorganisation

process. It focused on the technical feasibility, safety, and spatial integration of the relocated reproductions.

A detailed architectural survey of the restaurant area was conducted, including laser-based measurements of floor plans, ceiling heights, structural grids, load-bearing elements, circulation paths, and sightlines. Particular attention was given to visitor flow, seating distribution, emergency exits, and service areas to ensure compliance with building and safety regulations.

The physical characteristics of each reproduction were documented, including mass, centre of gravity, material composition, and attachment points. Structural calculations were performed to determine admissible loads on ceilings, beams, and secondary structures. For suspended elements, static and dynamic load analyses were carried out, incorporating safety factors in accordance with international standards for public spaces. Custom suspension systems were designed using certified materials (e.g. steel cables, anchor plates, load-distribution frames) to ensure stability, redundancy, and ease of maintenance. Fixing solutions were engineered to minimise visual intrusion while guaranteeing long-term structural integrity and reversibility. The design accounted for interactions with existing building systems, including lighting, ventilation, fire suppression, and acoustic treatments. The final layout defined clear spatial zones that maintained the functional hierarchy of the restaurant while incorporating exhibition elements. This zoning strategy ensured that the reproductions were visible from multiple viewpoints without obstructing circulation, seating capacity, or operational efficiency.

7.2.2 Exhibition content and visitors' engagement design

The second methodological component focused on the conceptual and interpretative design of the exhibition, to foster engagement without compromising the restaurant's identity as a place of relaxation and socialisation. The restaurant was treated as a hybrid space rather than a conventional hall. Exhibition formats were therefore designed to be low-threshold, non-intrusive, and optional, allowing visitors to engage at varying levels of attention without imposing a linear or mandatory narrative. Scientific content related to extinct marine animals, deep time, and biodiversity was divided into different units. Priority was given to clarity, accuracy, and relevance, avoiding information overload. Content was framed to stimulate curiosity and reflection

rather than formal learning outcomes. Engagement relied primarily on passive and semi-active formats, such as visual cues, short textual prompts, graphical overlays, and subtle digital interfaces. These tools were designed to be readable at a distance and during brief moments of attention, consistent with the rhythms of eating and conversation.

The exhibition adopted an edutainment approach that merges scientific information with aesthetic and narrative appeal. The reproductions function as focal points that provoke emotional and imaginative responses, while interpretative elements support informal learning through storytelling rather than didactic explanation. Throughout the design process, the primary function of the space as a place for rest, comfort, and social interaction was maintained as a guiding constraint. Acoustic impact, visual density, and cognitive load were carefully controlled to ensure that the exhibition enhanced, rather than disrupted, the dining experience.

7.3 Results

The project proposal for the relocation of the extinct marine animals' reproductions is an exhibition itinerary laid out on paper and submitted to the aquarium committee.

7.3.1 Restaurant with integrated in-vivo reproductions design

The reproductions integrated in the restaurant area are six models in scale 1:1 of the following extinct species: *Dunkleosteus* sp. (weight of the model 200 Kg); *Tylosaurus* sp. (450 Kg); *Elasmosaurus* sp. (250 Kg); *Cameroceras* sp. (150 Kg); *Otodus megalodon*. (800 Kg); *Xiphactinus* sp. (150 Kg). Three models (*Cameroceras* sp.; *Otodus megalodon* and *Elasmosaurus* sp.) are fixed on the wall, while *Dunkleosteus* sp., *Tylosaurus* sp., and *Xiphactinus* sp. are suspended from the ceiling (Fig. 7.3).

A small hallway connects the restaurant with the other aquarium halls. The models were therefore placed in the ceiling so that when entering the restaurant, the visitors are immediately met with the open mouth of the *Otodus* model (Fig. 7.4). The model of *Dunkleosteus* made 10 Tons, and it was realised to be standing on the ground as it is too heavy to be suspended from the ceiling. As an alternative, Di.Ma. Dinomakers proposes an alternative model of the same fossil species, but realised in lighter fiberglass, so that the weight is sustainable by the iron

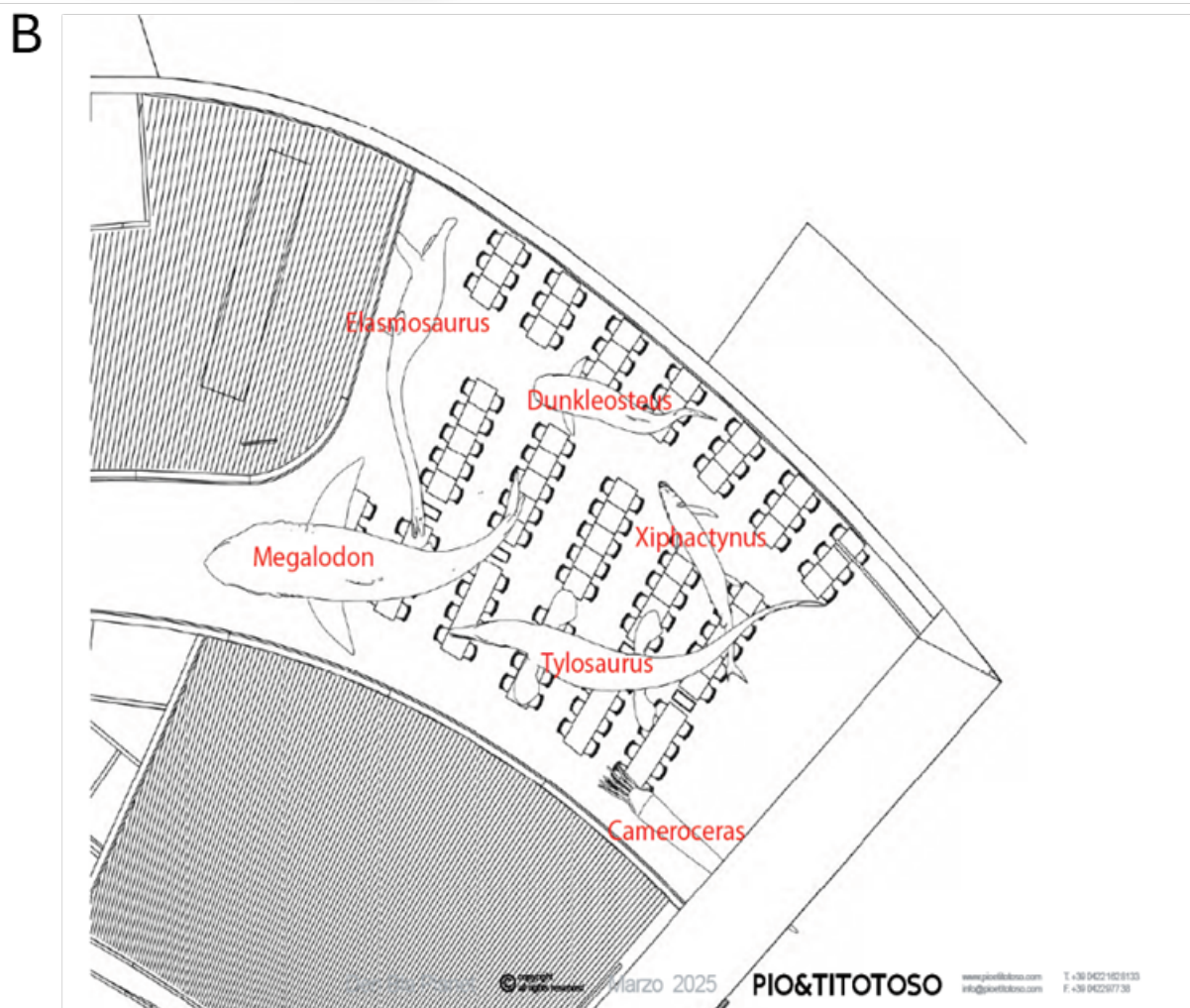
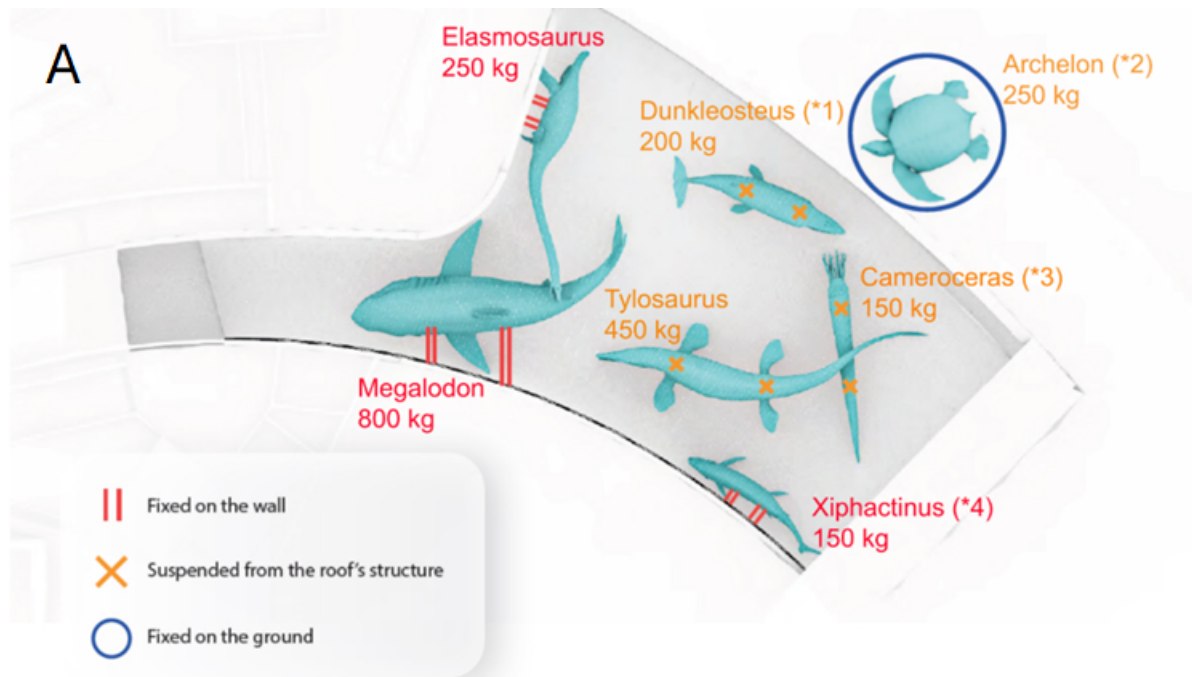


Figure 7.3: First (A) and final (B) draft of the in-vivo reconstructions in the restaurant area made by architecture company Pio & Tito Toso.

cables.

The “Once upon the Sea” exhibit in the Ocean Hall features two more models: *Archelon* sp. (made by 10 Tons) and *Waharoa* sp. (made by Di. Ma. dinomakers). The former was included in the concept design of the new restaurant setup by proposing a lighter, twin model of *Archelon*, so that it could be suspended on the ceiling with the other models and avoid losing any sitting space. Eventually, the Den Bla Planet committee opted to move the *Archelon* model directly to the museum entrance. The *Waharoa* model is not included in the restaurant project.

7.3.2 Edutainment activities proposal

Three main edutainment activities for visitors of the Plankton Café restaurant area were designed and proposed. The first edutainment outcome consists of a disposable paper placemat distributed to visitors seated in the restaurant area. Beyond its functional role, the placemat incorporates a printed QR code that provides access to a dedicated virtual reality (VR) application, compatible with personal mobile devices. This solution allows engagement to remain voluntary and self-paced, avoiding disruption to dining activities (Fig. 7.5). Once the application is launched, visitors are instructed to frame one of the six full-scale reproductions of extinct marine animals suspended from the restaurant ceiling. Image recognition enables the app to identify the selected specimen. Upon successful framing, the static reproduction is transformed into a dynamic digital reconstruction, animated according to swimming patterns and behavioural interpretations derived from current scientific literature. This approach establishes a direct visual and cognitive link between the physical object and its hypothesised living appearance.

Following the animation phase, the application displays structured scientific information, including taxonomic identification, temporal and geographic distribution, palaeoecology, palaeobiology, and selected interpretative facts designed to stimulate curiosity. The species included in the application are listed below:

Cameroceeras Ordovician (470–430 Ma). A giant orthoconic nautiloid cephalopod. Interpreted as an early apex predator of Paleozoic seas, with buoyancy-controlled vertical movement

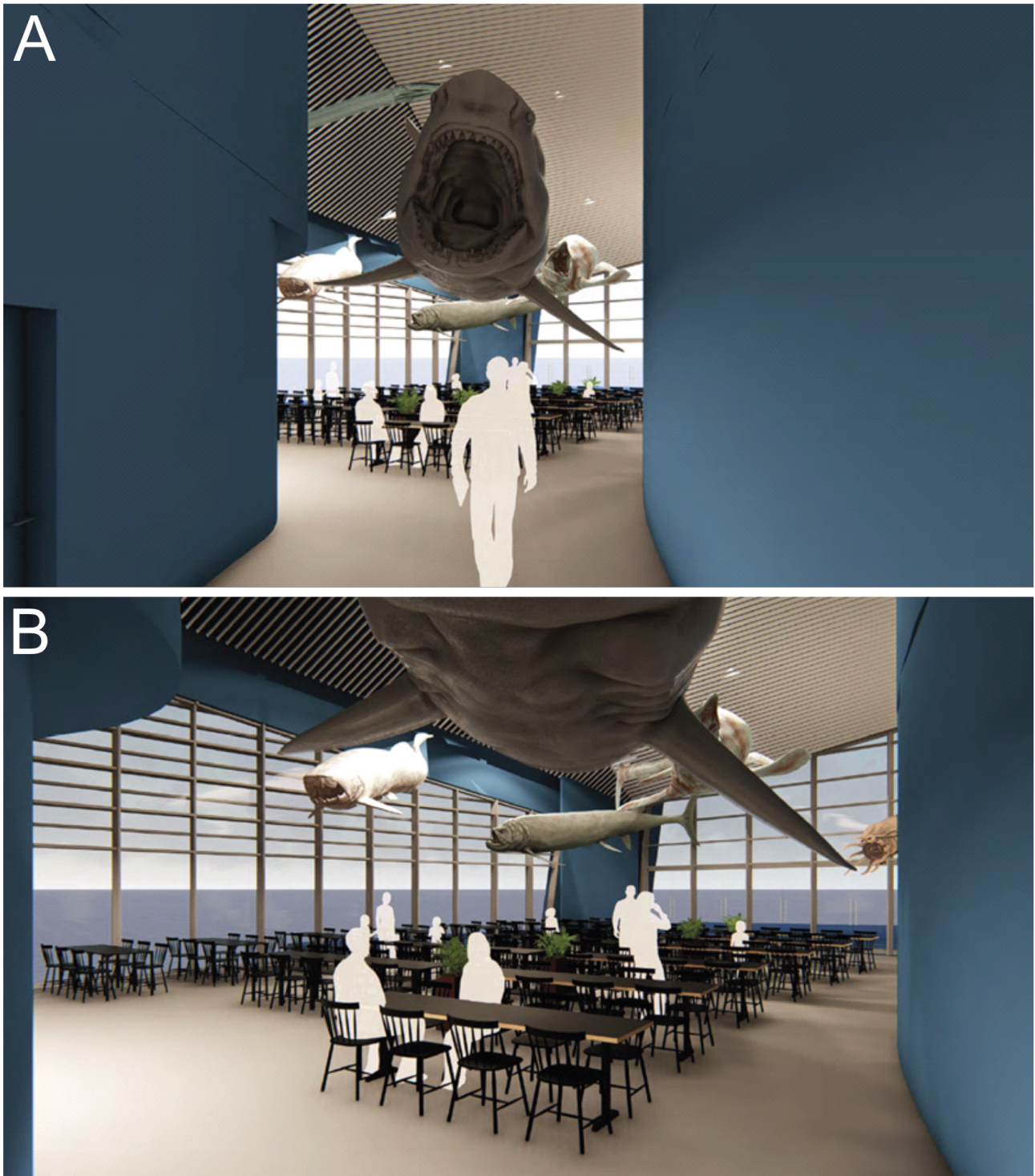


Figure 7.4: Rendering made by architects Pio & Tito Toso of the suspended models. A) Restaurant entrance with open-mouthed *Otodus* model; B) general overview of the restaurant area with integrated seating space.

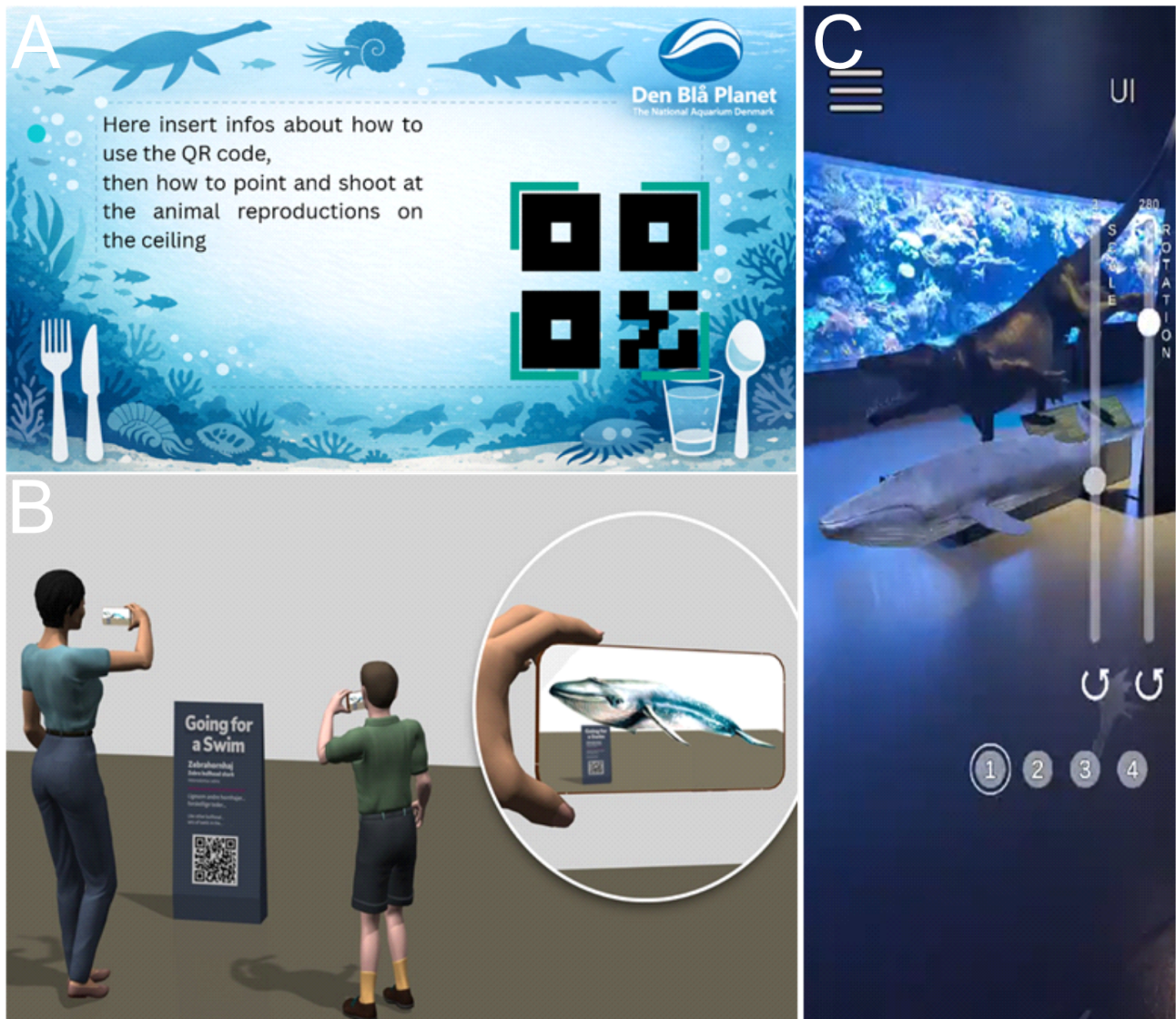


Figure 7.5: Augmented reality activity for visitors of the Café Plankton. A) Paper placemat; preliminary design, with QR code to scan. B) Render of the activity in a panel rather than on a placemat. C) Example of an augment reality smartphone application.

and a predatory lifestyle (Teichert, 1964).

Dunkleosteus Late Devonian (382–358 Ma). A large placoderm fish characterised by dermal armour and powerful jaw mechanics. Interpreted as an apex predator inhabiting shallow epicontinental seas. Palaeoecological reconstructions suggest active predation and possible niche dominance (Anderson and Westneat, 2007; Hlavin et al., 2019).

Xiphactinus Late Cretaceous (100–66 Ma). A large predatory teleost fish known from exceptionally preserved specimens. Palaeoecological data indicate fast swimming and piscivory in offshore marine environments (Stewart, 1999; Friedman, 2012).

Tylosaurus Late Cretaceous (90–80 Ma). A large mosasaur with an elongated snout and

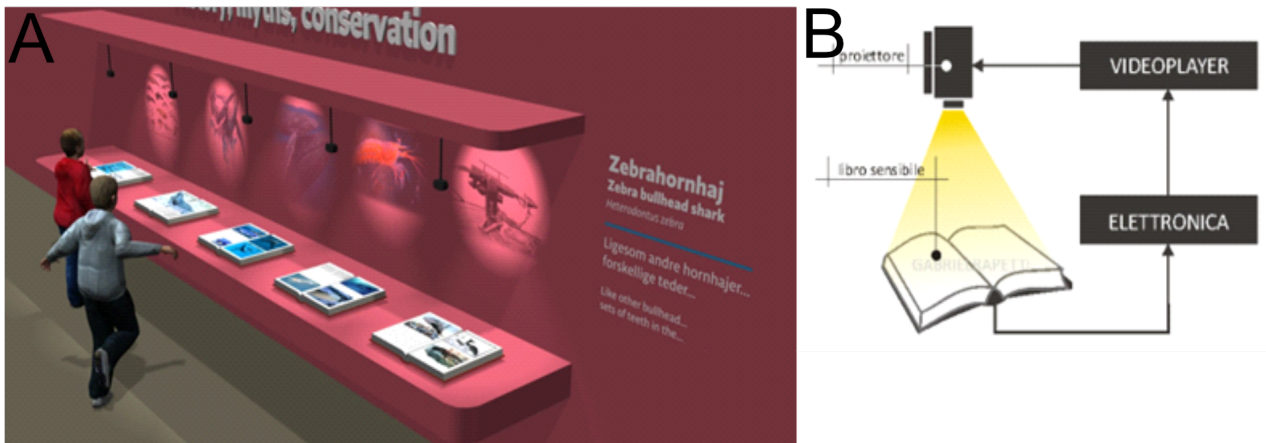


Figure 7.6: A) Working mechanism of the animated book installation. B) Render of how the shelf with the book projection would work.

robust body. Interpreted as an active predator in open marine settings, with evidence of opportunistic feeding behaviour (Russel, 1967; Everhart, 2005).

Elasmosaurus Late Cretaceous (80–65 Ma). A long-necked plesiosaur adapted to pelagic environments. Palaeoecological interpretations suggest a feeding strategy based on small fish and cephalopods, facilitated by stealth and neck flexibility (O’Keefe and Hiller, 2006; Sachs et al., 2016).

Otodus megalodon Miocene–Pliocene (23–3.6 Ma). A giant lamniform shark with a global distribution in warm marine environments. Considered a macropredatory species feeding on marine mammals, with significant implications for trophic structure in ancient oceans (Pimiento and Balk, 2015; Shimada et al., 2016).

The second edutainment activity is located along one side of the restaurant and consists of a shelf displaying two large-format books positioned in an open state. Above the shelf, a concealed projector casts animated sequences directly onto the pages, creating the illusion that the books themselves are animated and that the illustrations are moving autonomously (Fig. 7.6).

The projected content consists of short narrative sequences featuring the same extinct marine species included in the VR application. Animations depict swimming movements, predator–prey interactions, and environmental contexts consistent with palaeoenvironmental reconstructions.

The third edutainment outcome is a small immersive installation designed primarily for

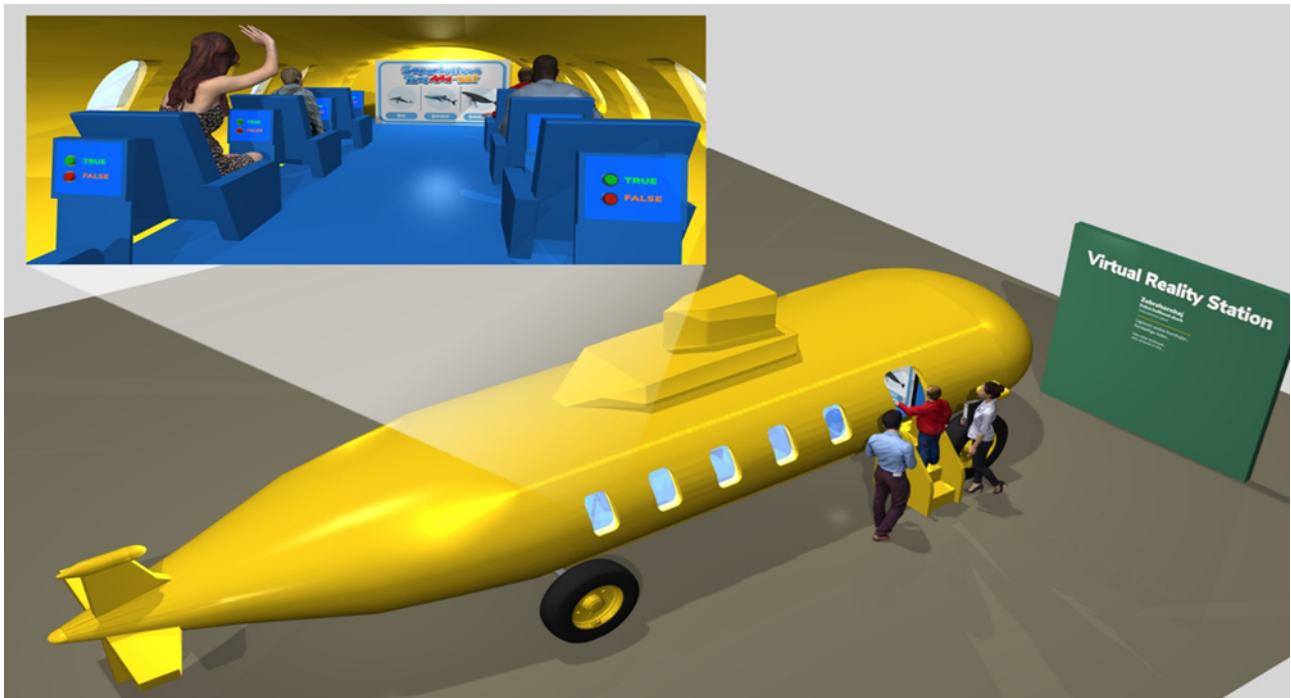


Figure 7.7: Render of the edutainment activity "Skolebus", designed as a virtual reality station reminiscent of a submarine.

children but accessible to mixed-age groups. The structure takes the form of a small school bus reinterpreted as a yellow submarine (hence the name of the installation, a play on the Danish word *skole*, that means school of both fish and students, same as in the English language), accommodating approximately four to six seated participants at a time (Fig. 7.7). Inside the installation, the interior walls are fitted with display panels functioning as simulated windows. These panels present continuous virtual-reality sequences representing ancient seafloors and deep-marine environments corresponding to different geological periods. Visual content includes sedimentary plains, reef-like structures, and open-water scenes populated by reconstructed extinct organisms.

7.4 Discussion

The present project explores the integration of exhibition content within a non-traditional museum exhibition space, the restaurant area of Den Blå Planet, through the adoption of innovative museological and digital techniques. Digital tools such as virtual reality (VR) and augmented reality (AR) were employed to communicate scientifically robust content without compromising the primary social and functional role of the restaurant environment.

The new installation is conceived as an intuitive and low-effort system for visitors. The restaurant context imposes specific cognitive and behavioural constraints: visitors are primarily engaged in eating, resting, and social interaction. Excessive informational density or prolonged attention demands risk generating cognitive overload and disengagement (Falk & Dierking, 2013). For this reason, the exhibition activities were intentionally designed to be optional, self-explanatory, and easy to access, relying on simple and easy-to-use interactions such as QR codes. This approach reflects models of informal learning, in which visitors benefit from short depth and duration of the engagement (Hein, 1998). All activities were designed to function within limited time frames: from a museological perspective, brief interactions support episodic and incidental learning, which has been shown to be particularly effective in hybrid spaces where learning is not the primary motivation (Falk, 2009). It was also important to keep in mind that a short interaction time reduces the risk of prolonged occupancy, crowding, and circulation bottlenecks, thereby preventing spatial congestion and maintaining the restaurant's functionality (Bitgood, 2013).

Another relevant aspect concerns the hybridisation of edutainment and relaxation. The project demonstrates that educational content does not necessarily require explicit instructional framing to be effective. Instead, narrative, atmosphere, and aesthetic coherence can support learning through affective and experiential pathways (Alberti, 2005; Simon, 2010). The animated books and immersive submarine installation, in particular, privilege storytelling and environmental simulation over didactic explanation, allowing scientific content to emerge through visual and emotional resonance rather than formal instruction.

As this work represents a project submission, not yet a realised implementation, practical constraints such as financial costs, technical maintenance and time of realisation were not explicitly addressed. In such a scenario, these factors would inevitably influence the aquarium committee's choice relative to the activities. By its concept design, the Skole-bus installation can be quite expensive. Budgetary limitations or operational constraints might require simplification of digital systems or a reduction in the number of interactive elements. Such adjustments could alter the overall visitor experience and would need to be carefully evaluated during subsequent design and feasibility phases.

The project contributes to broader discussions on the expansion of exhibition practices beyond traditional spaces. By treating the restaurant as a legitimate exhibition hall of the aquarium, the project aligns with contemporary views of museums as distributed environments in which learning can occur across a variety of social and spatial contexts (Clifford, 1997; Macdonald, 2011). Once the project is realised, further evaluation such as visitor studies and behavioural observation would be required to assess long-term effectiveness.

7.5 Conclusions

The re-adjustment of the Ocean Hall *in-vivo* reproductions has become an opportunity to test new exhibition formats and to explore the permeability between educational and non-educational zones within a science institution. The relocated reproductions continue to communicate narratives of extinction and evolution but do so through more informal encounters (Falk & Dierking, 2013). Ultimately, the project positions the relocation of the *in-vivo* reproductions not as a compromise imposed by spatial constraints, but as a deliberate curatorial choice. By preserving these objects and embedding them within a new spatial and social context, Den Blå Planet extends the reach of its exhibition narrative and reinforces its commitment to innovative, adaptive, and visitor-centred museological practice. In conclusion, this project demonstrates the potential of integrating scientifically grounded, technologically mediated edutainment within a leisure setting. By prioritising ease of use, short interaction times, and respect for the primary function of the restaurant space, the design offers a model for future exhibition strategies in aquaria and science centres seeking to maximise engagement while maintaining operational balance.

8 GENERAL CONCLUSIONS

This thesis examined the potential of Virtual Palaeontology and digital museum techniques as tools for the valorisation, communication, and accessibility of geo-palaeontological collections through a holistic approach, based on several case studies. The shift of natural history museums from static repositories of objects towards active mediators between scientific research and society has long been at play, and this research explored how emerging technologies and techniques can contribute to this evolving role (Hooper-Greenhill, 2000; Mason, 2004; Gobbi, 2019). The case studies examined research-driven and design-oriented approaches, highlighting the opportunities and constraints associated with digital and hybrid museum practices.

At the beginning of this work, three main aims were set: 1) to assess the contribution of virtual palaeontological tools to museum exhibits and visitor engagement; 2) to examine their potential to enhance accessibility and inclusivity and 3) to develop a conceptual framework integrating research, conservation, education, and public engagement. Overall, the results suggest that these aims were largely achieved, although with varying degrees of effectiveness across the case studied in previous chapters and subject to some limitations.

The first aim was addressed most directly through the digital and immersive projects developed in chapters 2 and 5. In Chapter 2, the valorisation of the permanent exhibit of Poggio Rosso's block through a 3D printed jigsaw provided an innovative tool for the IGF to explore the value of different aspects of palaeontological heritage through a playful object. The 3D printed jigsaw of Poggio Rosso has also dissemination potential for accessibility, allowing visually impaired visitors to interact with a replica of an actual fossil specimen. The "Linda." platform (Chapter 5) is a good and relatively good example of how 3D models, historical and archival documentation and palaeoenvironmental reconstructions can change the way fossils are perceived, shifting them from static heritage objects to dynamic and fundamental scientific evidence (Falk & Dierking, 2013; Kohlstedt, 2015; Dallas, 2016). Similarly, the exhibition projects (Chapters 6 and 7) showed how immersive and narrative-driven experiences can enhance learning in informal contexts (Hein, 1998; Simon, 2010). At the same time, the results also confirm that technology may be used as a tool for dissemination, and must be tightly

linked to narrative structure, mediation, and contextual framing, to avoid the risk of digital tools being superficial or being interpreted solely as entertainment (Rennie & Williams, 2006; Scopigno et al., 2022).

The second aim (enhancing accessibility and inclusivity) was indirectly fulfilled. Digital platforms enabled remote access to collections that are otherwise inaccessible due to physical, geographical, or institutional constraints, supporting a core dimension of museums' public mission (Parry, 2013; Marty, 2011). The use of 3D models and virtual environments also opened possibilities for tactile engagement, alternative sensory pathways, and adaptable interfaces, aligning with current research on inclusive digital heritage practices (Kelly et al., 2009; Herraiz et al., 2019; Reinhardt et al., 2024). Accessibility emerged as a transversal theme throughout the project. Digital platforms, immersive environments, and 3D models demonstrated flexibility, allowing for future adaptations targeting visitors with diverse needs (Chapter 2). The results suggest that accessibility benefits often emerged as secondary outcomes rather than as explicitly planned objectives, and their success has yet to be fully explored. Future implementations would benefit from a more systematic integration of universal design principles, particularly when addressing visitors with sensory, cognitive, or technological barriers (Sandriester et al., 2025; Plets, 2021).

The third aim (developing a conceptual framework for integrating research and communication) was addressed through Chapters 3, 4 and 5. By linking taphonomic analysis, faunal review, digital platforms, and exhibition design, the research showed how museological innovation ultimately depends on continuity between scientific research and museological practice. This approach is an effective example of how museums work as communicative systems in which knowledge is continuously produced, revised, and shared (Mason, 2004; Nielsen, 2017).

Chapters 3 and 4 successfully fulfilled their research objectives, although the results were only partially addressed to public engagement. Scientific results obtained from research, such as the taxonomic revision of the Farneta Faunal Unit and the taphonomical analyses, are at the core of the website "Linda." However, they have not been (yet) shown or thoroughly explained to the audience. It has been shown that exposing visitors to scientific uncertainty and reasoning processes can enhance scientific literacy and trust (Kohlstedt, 2015; Bucchi & Trench, 2021).

This could be tested in the future by adding a research section to the website, where visitors can learn more about the research carried out before the making of the website. Future implementation of the exposition and of the “Linda.” website will be possibly implemented with this new scientific data. Nonetheless, the “Linda.” platform represents one of the most successful outcomes of the thesis in relation to its stated aims. It effectively addressed the invisibility of stored collections, institutional fragmentation, and limited physical accessibility by generating a shared virtual space connecting multiple museums (Russo et al., 2008; Parry, 2013;). The platform’s layered structure supported different depths of engagement, from casual exploration to research-oriented inquiry, prioritising informal learning and self-directed meaning-making (Falk & Dierking, 2013; Hein, 1998). However, the project also revealed important age-related differences in engagement. Adult visitors demonstrated greater autonomy in navigating digital content, while younger (6-11 years old) audiences required mediation through educators or caregivers, confirming observations reported in previous museum studies (Letourneau et al., 2017). This finding reinforces the idea that digital accessibility must be understood not only as a technical feature but as a socially situated practice shaped by institutional context and visitor behaviour. The exhibition projects developed for the Urweltsteinbruch Museum in Holzmaden (Chapter 6) and the Den Blå Planet aquarium in Copenhagen (Chapter 7) explored the application of classical and digital narrative strategies within experiential and non-traditional museum spaces. These chapters were particularly effective in demonstrating how learning can occur in contexts where education is not the primary motivation, such as leisure or recreational environments (Falk, 2009; Bitgood, 2013).

The Urweltsteinbruch Museum exhibition functioned effectively as a preparatory interpretative device, providing a basic, but fundamental, palaeontological framework before visitors engaged in hands-on fossil hunting. Emphasising relevance and narrative coherence proved fundamental for this project to avoid information overload, and ultimately disinterest in the exhibition (Tilden, 1957; Hooper-Greenhill, 2000). Nonetheless, practical issues related to accessibility and installation logistics highlighted the importance of time-sensitive design from the earliest planning stages and the value of post-opening evaluation (Lord & Lord, 2002).

The Den Blå Planet project further challenged traditional spatial boundaries of museum

learning by embedding educational content within a restaurant environment. The emphasis on short, optional, and intuitive interactions supports episodic learning and minimises learning overload (Falk & Dierking, 2013). While primarily designed for children, the installations also aim to engage with adult audiences through atmosphere and visual storytelling, suggesting strong potential for reinterpretation across age groups.

For the most part, the case studies were finalised during the late stage of the PhD project, which means that their effectiveness as museological innovation is still being implemented in museums and will be assessed only in the future. Long-term visitor studies, behavioural observation, and learning assessments will be necessary to evaluate the project's actual impact (Falk & Dierking, 2013). In this sense, time will ultimately determine the success of the approaches presented here. One of the most significant advantages of working in digital and hybrid environments is their openness to revision and improvement. Virtual platforms and technologically mediated exhibitions are not fixed or final; they can be continuously updated, rearranged, and improved in response to new research, visitor feedback, and institutional priorities (Parry, 2013; Kenderdine, 2021). This open-endedness represents a defining strength of this project and of contemporary museology in general.

In conclusion, this thesis demonstrates that Virtual Palaeontology and digital museological tools can significantly enhance interaction, accessibility, and engagement with geo-palaeontological heritage. The research largely fulfilled the aims outlined in the introduction, while also identifying important limitations and directions for future development. By foregrounding adaptability, interdisciplinarity, and openness to revision, this work contributes to current debates on the evolving role of museums in the digital age (Hooper-Greenhill, 2000; Mason, 2005; Parry, 2013). Ultimately, it suggests that the true value of museology lies not in producing static and definitive solutions, but in creating flexible frameworks capable of evolving alongside science, technology, and society.

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A APPENDIX

1 Appendix 1

Complete measurements database for *Equus stenonis* and *Equus altidens* of the Farneta Faunal Unit. Measurements refer to the international standards for studying fossil horses of Eisenmann et al. (1989) and Bernor et al. (1997).

Specimen	Species	Bone	Side	Locality	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	
IGF14171	<i>E. stenonis</i>	Selvella	1ph3		Selvella (Gioiella)	86.5	76.5	34.2	52.1	40.4	47	43.1	27.1	53					
IGF14185	<i>E. stenonis</i>	Selvella	mt3	sx	Selvella (Gioiella)	296	287.1	35.3	31.8	55.2	47.1	48.6	13.6	7.8	51	47.2	40.1	31.4	34
IGF14186	<i>E. stenonis</i>	Selvella	mt3	sx	Selvella (Gioiella)	282	274.9	35.5	33.7	54.8	44.6	47.7	12	8.2	52.4	47.7	39.3	29.5	34
IGF14190	<i>E. stenonis</i>	Selvella	mt3	dx	Selvella (Gioiella)	295.7	288.7	35.7	32.7	52.8	45.5	48.2		7.2	49.6	51.2	39.3	29.3	33.8
IGF14324	<i>E. stenonis</i>	Selvella	1ph3		Selvella (Gioiella)	85	74	34	57.3	40	47.7	41.2	26.7	48.5					
IGF14325	<i>E. stenonis</i>	Selvella	1ph3		Selvella (Gioiella)	85.6	74.5	35.7	59	40	47.7	44.7	28.3	51.6					
IGF14337	<i>E. stenonis</i>	Selvella	txP4-P3	dx	Selvella (Gioiella)	31.1	26.3	31		60.2					11.6	5.2			
IGF14338	<i>E. stenonis</i>	Selvella	txP3-P4	dx	Selvella (Gioiella)	30.6	28.2	29.2		64.2					9.3	5.5			
IGF14339	<i>E. stenonis</i>	Selvella	txM2-M1	dx	Selvella (Gioiella)	26.1	23	29.2		41.9					9.6	4.4			
IGF14340	<i>E. stenonis</i>	Selvella	txM2-M1	dx	Selvella (Gioiella)	27.3	25	27.8		66.8					10.8	4.3			
IGF14341	<i>E. stenonis</i>	Selvella	txM3	dx	Selvella (Gioiella)	28.7	30.4	27.5		52.9					11	5.5			
IGF14343	<i>E. stenonis</i>	Selvella	txP3-P4	sx	Selvella (Gioiella)	29.6		26.2		62.2					9.9	5.8			
IGF1015313	<i>E. altidens</i>	Farneta	tmp2	sx	Farneta zona	30.9	24.4	13.2	9.1	12.8	12.9		11.6	13.4	48.6				
IGF105314	<i>E. altidens</i>	Farneta	tmp3-p4	dx	Farneta zona	28.7		12.5	11.1	11.5	13.8		10.9	11.4					
IGF105315	<i>E. altidens</i>	Farneta	txM2-M1	dx	Farneta zona	26.3	23.6	27.4		52					7.6	4.1			
IGF105316	<i>E. altidens</i>	Farneta	tmp3-p4	dx	Farneta zona	29.4	25.2	17.8	11.3	12.9	14.5		16.6	15.7	51.8				

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Specimen	Species	Bone	Side	Locality	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
IGF105129	<i>E. altidens</i> Farneta	tmp3-p4	dx	Cava Liberatori (Farneta)	28.9	25.9	13.9	11.1	16	14.7		13.5	12.9					
IGF14281	<i>E. altidens</i> Farneta	txM2-M1	dx	Cava la Rotta (Farneta)	24.7		25.5							10.2	4.9			
IGF14282	<i>E. altidens</i> Farneta	tmm2-m1	sx	Cava Liberatori (Farneta)	23.7	20.7	12.3	9.5	11.5	16.1		14.2	13.5	53.7				
IGF2842V	<i>E. altidens</i> Farneta	tmm2-m1	sx	Case Palazzi (Farneta)	24.4	21.2	12.9	11.3	12	13.1		13.3	13.1	51.3				
IGF2842V	<i>E. altidens</i> Farneta	txM2-M1	dx	Case Palazzi (Farneta)	30.6	25	26.9		67.3					11.9	5.2			
IGF4022V	<i>E. altidens</i> Farneta	txM1	sx	Presso Farneta (Farneta)	23.3		28.6							9.7	6.7			
IGF4022V	<i>E. altidens</i> Farneta	txM1	dx	Presso Farneta (Farneta)	22.4		27.5							9.1	7.4			
IGF4022V	<i>E. altidens</i> Farneta	txM2	sx	Presso Farneta (Farneta)	25.3		23.3							10.5	6.6			
IGF4022V	<i>E. altidens</i> Farneta	txM2	dx	Presso Farneta (Farneta)	25.5		27.5							10.4	7			
IGF4022V	<i>E. altidens</i> Farneta	txM3	sx	Presso Farneta (Farneta)	30.2		22.8							10.9	6.2			
IGF4022V	<i>E. altidens</i> Farneta	txM3	dx	Presso Farneta (Farneta)	30		24							11.1	6.6			
IGF4022V	<i>E. altidens</i> Farneta	txP2	sx	Presso Farneta (Farneta)	35.1		22.6							6.7	6.7			
IGF4022V	<i>E. altidens</i> Farneta	txP2	dx	Presso Farneta (Farneta)	35.9		22.6							6.6	6.8			
IGF4022V	<i>E. altidens</i> Farneta	txP3	sx	Presso Farneta (Farneta)	25.6		27.8							7.9	7			
IGF4022V	<i>E. altidens</i> Farneta	txP3	dx	Presso Farneta (Farneta)	26		27.3							8.7	8			
IGF4022V	<i>E. altidens</i> Farneta	txP4	sx	Presso Farneta (Farneta)	26.4		29.6							9.9	7.7			
IGF4022V	<i>E. altidens</i> Farneta	txP4	dx	Presso Farneta (Farneta)	26.9		29.5							10.7	8.1			
IGF785v	<i>E. altidens</i> Farneta	Mt3	dx?	Cava Oppiello ? (Farneta)	249	247	30.6	29.9	49.7	38.2	40	10.2	8.8	46.2	45.9	34.4	27.3	28.7
IGF9108v	<i>E. altidens</i> Farneta	Mt3		Farneta zona	255	253	30.5	29.2	51.5	39.2	37.7	5.9	10.2	44.6	44.4	34.5	25.3	27.3
IGF9109v	<i>E. altidens</i> Farneta	Mt3		Farneta zona	265	263	30.4	30.7	48	38	34.5	8.6	9.8	44.7	44.6	35.2	24.8	28.6
IGF9114v	<i>E. altidens</i> Farneta	mc3		Farneta zona	224	216	29.6	22.6	42.2	29.5	39	8.9	7.8	45.8	45.5	34.8	26.5	29.3
IGF14171	<i>E. altidens</i> Selvella	mc3	dx	Selvella (Gioiella)	248.7	239.8	35.4	28.4	51.6	33	39.6	15.9	11.4	47.6	48.3	37.2	29.2	31.3
IGF14172	<i>E. altidens</i> Selvella	mc3	sx	Selvella (Gioiella)	243	227.2	33.6	27.1	48.3	32.5	36.6	15.2	7.8	45.4	45.2	37.3	29.1	30.8
IGF14173	<i>E. altidens</i> Selvella	mc3	sx	Selvella (Gioiella)	237.5	220.8	30.8	23.8	47.2	30.1	36.8	16.3		43.3	44.6	34.3	26.7	29

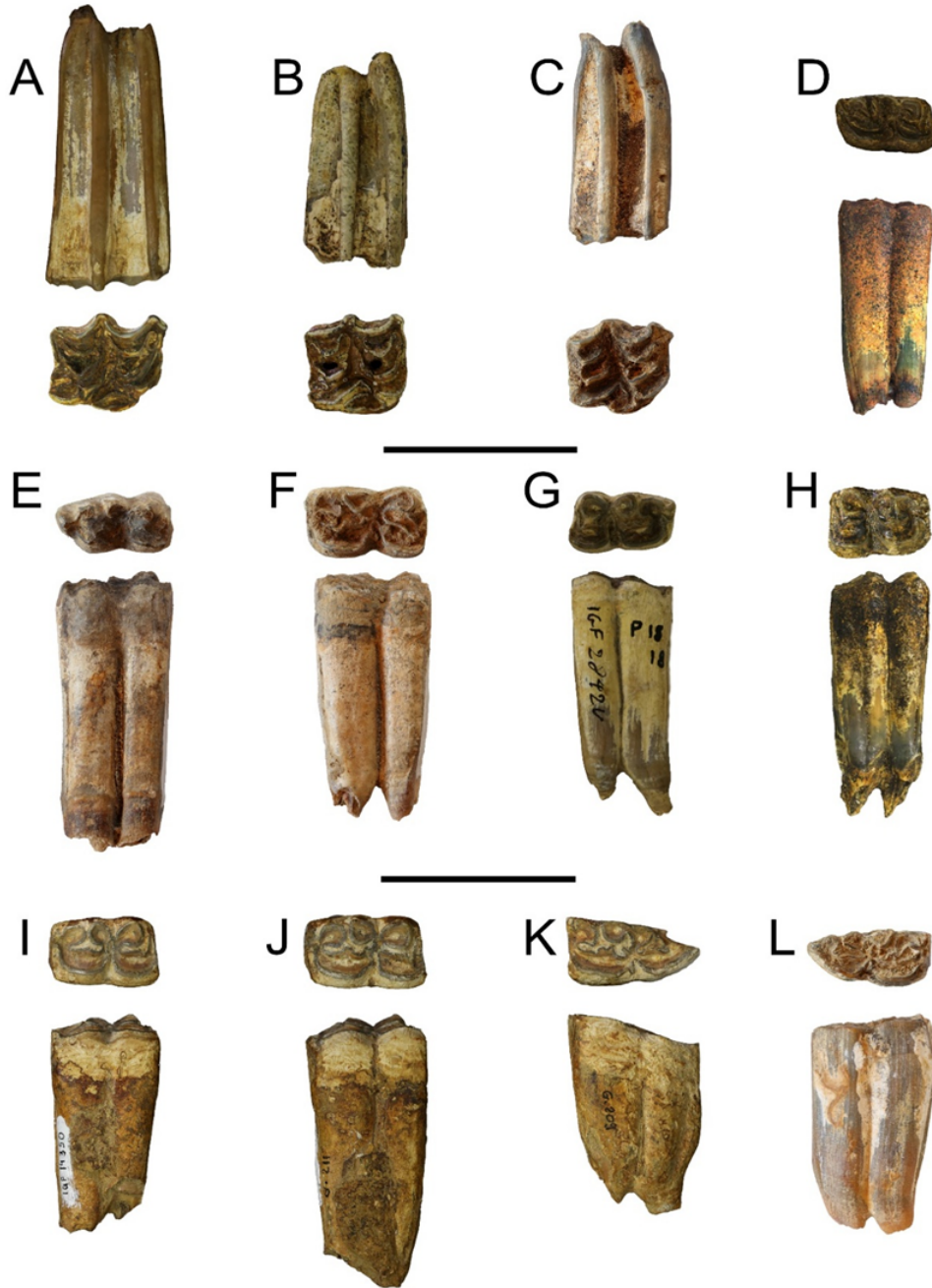
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Specimen	Species	Bone	Side	Locality	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	
IGF14174	<i>E. altidens</i>	Selvella	mc3	sx	Selvella (Gioiella)	248	233	34	26.3	52.2	33.1	43.2	15.5	9.4	45.6	46.8	36.1	23.4	26.7
IGF14176	<i>E. altidens</i>	Selvella	mc3	sx	Selvella (Gioiella)	245	235.5	35.2	27.6	46.9	33.7	34.4	15.3	7.6	47.5	47.2	35.6	27.6	29.6
IGF14177	<i>E. altidens</i>	Selvella	mc3	sx	Selvella (Gioiella)	238.4	229.4	34.5	25.3	46.3	33.3	36.9	14.3		44.8	45.3	34.9	27.3	29.2
IGF14180	<i>E. altidens</i>	Selvella	mc3	sx	Selvella (Gioiella)	241.6	224.8	33.6	27.4		31.2		9.6	8.6	47.1	46.8	35.9	28.4	27.2
IGF14181	<i>E. altidens</i>	Selvella	mc3	sdx	Selvella (Gioiella)	245.3	237.1	35.9	27.8	49.6	31.9	39	15.3	8	47.5	47.5	35.9	27.5	29.3
IGF14182	<i>E. altidens</i>	Selvella	mc3	dx	Selvella (Gioiella)	252.4	240.3	35.7	28.5	50.3	35	39.2	15.6	9.5	47.8	50.3	37.5	29.5	31.8
IGF14183	<i>E. altidens</i>	Selvella	mc3	dx	Selvella (Gioiella)	255	242.2	35.5	28.5	51	33.2	38	15.9	8.5	45.5	46.6	35.2	27.8	30.5
IGF14184	<i>E. altidens</i>	Selvella	mt3	sx	Selvella (Gioiella)	277	267	31.8	31.5	49.2	39.4								
IGF14187	<i>E. altidens</i>	Selvella	mt3	sx	Selvella (Gioiella)	269.9	265	31.7	31.2	51.6	42.8	44.5	10.7	11.3	46.3	45.9	34.7	25.2	27.9
IGF14312	<i>E. altidens</i>	Selvella	Mandibola		Selvella (Gioiella)		129.2	84.7	92.7			66.5			62.4	79.4	39.7		

A.2 Appendix 2

Equus altidens isolated upper (A-C) and lower (D-L) teeth in labial and occlusal view. A) IGF 2842v; B) IGF 14281; C) IGF 105315; D) IGF 105129; E) IGF 105314; F) IGF 105316; G) IGF 2842v; H) IGF 14282; I) IGF 14350; J) IGF 14349; K) IGF 14348, L) IGF 105313. Scale bar 5 cm.



A.3 Appendix 3

Principal components and loading distribution of the principal component analyses described in Chapter 3.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
PCA mc3 — Importance of components									
Standard deviation	2.7327	0.68321	0.54308	0.46080	0.40635	0.38500	0.34100	0.29763	0.20065
Proportion of Variance	0.82970	0.05186	0.03277	0.02360	0.01835	0.01647	0.01292	0.00984	0.00447
Cumulative Proportion	0.82970	0.88158	0.91435	0.93790	0.95629	0.97276	0.98568	0.99553	1.00000
PCA mc3 — Loadings									
M1	0.29912	0.77462	0.12128	-0.21791	0.29443	-0.37111	0.14161	0.05554	-0.02744
M3	0.33648	-0.33018	0.19367	-0.09226	0.29405	-0.36459	-0.65128	-0.28452	0.08499
M4	0.32079	0.02453	0.81579	0.10188	-0.12331	0.44760	0.06868	0.01046	-0.01513
M5	0.34151	-0.05467	-0.04027	0.10839	-0.68277	-0.41321	0.27478	-0.39224	0.02719
M6	0.32832	-0.19573	-0.19732	-0.84169	-0.06354	0.28817	0.13863	0.00589	0.01377
M10	0.34960	-0.26730	-0.06951	0.15726	0.06543	-0.17719	0.09814	0.48494	-0.70448
M11	0.34857	-0.23982	-0.09555	0.23182	0.21814	-0.08859	0.30780	0.38693	0.67692
M12	0.34007	0.05159	-0.33992	0.32636	0.38758	0.38514	0.18133	-0.55041	-0.15892
M14	0.33257	0.34267	-0.33498	0.16870	-0.37329	0.29604	-0.56488	0.27229	0.10534
PCA mt3 — Importance of components									
Standard deviation	2.6960	0.69086	0.62896	0.51000	0.41495	0.39980	0.34305	0.30150	0.24025
Proportion of Variance	0.80760	0.05303	0.04395	0.02890	0.01913	0.01776	0.01308	0.01010	0.00641
Cumulative Proportion	0.80760	0.86066	0.90461	0.93350	0.95265	0.97041	0.98349	0.99360	1.00000
PCA mt3 — Loadings									

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	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
M1	0.30188	0.76470	0.12264	0.11289	-0.46319	-0.25624	0.11111	0.06124	-0.00325
M3	0.32935	-0.27128	-0.47908	-0.09247	-0.53953	0.14346	-0.45728	0.24307	0.00039
M4	0.32174	0.23851	-0.35910	-0.74243	0.36750	-0.03042	0.13591	-0.07060	0.00273
M5	0.34191	-0.18465	0.12019	0.15369	0.35145	-0.72324	-0.29953	0.26953	-0.04451
M6	0.30995	-0.40434	0.62153	-0.40718	-0.32856	-0.01393	0.27327	-0.00824	0.07383
M10	0.35206	-0.17450	-0.17388	0.25756	-0.02934	-0.02514	0.24906	-0.49720	-0.66204
M11	0.35120	-0.12955	-0.22159	0.32667	0.05785	-0.00839	0.26252	-0.30686	0.73318
M12	0.34927	0.02931	0.03618	0.25061	0.25890	0.45584	0.32602	0.64527	-0.12473
M14	0.33857	0.19765	0.38091	0.04716	0.23790	0.42553	-0.59870	-0.31894	0.03385
PCA 1ph3 — Importance of components									
Standard deviation	2.0870	0.53980	0.44194	0.29487	0.26627				
Proportion of Variance	0.87110	0.05828	0.03906	0.01739	0.01418				
Cumulative Proportion	0.87110	0.92937	0.96843	0.98582	1.00000				
PCA 1ph3 — Loadings									
M1	0.41905	-0.89189	0.09124	0.13648	-0.04442				
M3	0.44973	0.36114	0.48546	0.52697	-0.39237				
M4	0.46245	0.11809	-0.08480	-0.74212	-0.46288				
M5	0.44263	0.17036	-0.80948	0.32969	0.10539				
M6	0.46083	0.17645	0.30588	-0.21032	0.78658				

A.4 Appendix 4

Complete MANOVA results performed on the pc values of the third metacarpals and third metatarsals discussed in Chapter 3.

	pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted
1	E. altidens Dmanisi vs E. altidens PN	1	2,193332109	7,451049925	0,244689426	0,0069993	1
2	E. altidens Dmanisi vs E. altidens Venta Micena	1	25,20790439	40,91671975	0,440359064	9,999E-05	0,03679632
3	E. altidens Dmanisi vs E. apolloniensis	1	97,74811118	195,0034722	0,847828384	9,999E-05	0,03679632
4	E. altidens Dmanisi vs E. cf. major	1	88,72003501	334,0113247	0,940846957	9,999E-05	0,03679632
5	E. altidens Dmanisi vs E. grevyi	1	19,34804094	27,13568656	0,347289283	9,999E-05	0,03679632
6	E. altidens Dmanisi vs E. livenzovensisi ER	1	100,4863374	313,221903	0,939979936	9,999E-05	0,03679632
7	E. altidens Dmanisi vs E. livenzovensisi Liv	1	132,8960151	112,1809212	0,800258125	9,999E-05	0,03679632
8	E. altidens Dmanisi vs E. major Liv	1	397,732366	741,0627541	0,969897761	9,999E-05	0,03679632
9	E. altidens Dmanisi vs E. major Seneze	1	123,9858829	409,635253	0,962409129	0,054594541	1
10	E. altidens Dmanisi vs E. senezensis	1	15,91320371	47,62499643	0,605723353	9,999E-05	0,03679632
11	E. altidens Dmanisi vs E. senezensis Vigna Nuova	1	0,453966202	1,49985269	0,085706589	0,225777422	1
12	E. altidens Dmanisi vs E. simplicidens	1	26,4106704	31,51661305	0,329959491	9,999E-05	0,03679632
13	E. altidens Dmanisi vs E. stehlini	1	34,20890337	37,90135734	0,506016963	9,999E-05	0,03679632
14	E. altidens Dmanisi vs E. stenonis Dmanisi	1	8,830969534	28,63507361	0,614024411	0,00229977	0,846315368
15	E. altidens Dmanisi vs E. stenonis mygdoniensis	1	2,745758203	4,414926627	0,196963689	0,055694431	1
16	E. altidens Dmanisi vs E. stenonis Olivola	1	54,11583395	130,7738424	0,861636237	9,999E-05	0,03679632
17	E. altidens Dmanisi vs E. stenonis Pantalla	1	18,40875067	60,82041812	0,79172204	0,059894011	1
18	E. altidens Dmanisi vs E. stenonis SV	1	159,2869589	267,9338722	0,856199651	9,999E-05	0,03679632
19	E. altidens Dmanisi vs E. stenonis UV	1	132,9954147	201,9857425	0,878253323	9,999E-05	0,03679632
20	E. altidens Dmanisi vs E. suessenbornensis Akha	1	671,8503954	908,8778433	0,959868107	9,999E-05	0,03679632

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21	E. altidens Dmanisi vs E. suessenbornensis PN Alb & Pal	1	9,814451627	14,97109773	0,384158995	0,00059994	0,220777922
22	E. altidens Dmanisi vs E. suessenbornensis Suess	1	59,65459258	197,0919878	0,924915056	0,055494451	1
23	E. altidens Dmanisi vs Z.altidens Farneta	1	0,212124292	0,775203724	0,041288698	0,430256974	1
24	E. altidens Dmanisi vs Z.E. altidens Selvella Gioiella	1	3,615614169	12,38551597	0,407612495	0,00079992	0,294370563
25	E. altidens Dmanisi vs Z.E. stenonis Selvella Gioiella	1	43,7009844	161,3616168	0,89964408	0,00069993	0,257574243
26	E. altidens Dmanisi vs Z_suss	1	5,332436652	17,6177641	0,52406115	0,052694731	1
27	E. altidens PN vs E. altidens Venta Micena	1	25,72000603	37,97820933	0,468992951	9,999E-05	0,03679632
28	E. altidens PN vs E. apolloniensis	1	83,16002351	147,7989753	0,85040188	9,999E-05	0,03679632
29	E. altidens PN vs E. cf. major	1	87,61617246	394,8364212	0,970504116	0,00059994	0,220777922
30	E. altidens PN vs E. grevyi	1	24,16937024	30,34864268	0,419477706	9,999E-05	0,03679632
31	E. altidens PN vs E. livenzovensis ER	1	100,1170348	314,5504924	0,966211079	0,00089991	0,331166883
32	E. altidens PN vs E. livenzovensis Liv	1	115,5884681	72,58838837	0,792550122	9,999E-05	0,03679632
33	E. altidens PN vs E. major Liv	1	334,6162554	496,8283297	0,972593533	0,00019998	0,073592641
34	E. altidens PN vs E. major Seneze	1	129,1560183	469,0186835	0,985294695	0,108589141	1
35	E. altidens PN vs E. senezensis	1	21,33253923	63,05428396	0,741341659	9,999E-05	0,03679632
36	E. altidens PN vs E. senezensis Vigna Nuova	1	0,796247298	2,891501802	0,292321819	0,217178282	1
37	E. altidens PN vs E. simplicidens	1	28,6233037	31,04092143	0,360769282	9,999E-05	0,03679632
38	E. altidens PN vs E. stehlini	1	13,39780274	12,30761126	0,305342115	0,00059994	0,220777922
39	E. altidens PN vs E. stenonis Dmanisi	1	13,56579412	46,31740622	0,837302567	0,00619938	1
40	E. altidens PN vs E. stenonis mygdoniensis	1	0,385695385	0,41925875	0,044510801	0,577842216	1
41	E. altidens PN vs E. stenonis Olivola	1	58,30955908	121,1647543	0,909886065	0,00039996	0,147185281
42	E. altidens PN vs E. stenonis Pantalla	1	22,63728475	82,20530204	0,921529328	0,112388761	1
43	E. altidens PN vs E. stenonis SV	1	125,9714193	190,2461346	0,840881259	9,999E-05	0,03679632
44	E. altidens PN vs E. stenonis UV	1	118,0710712	144,5350373	0,883816946	9,999E-05	0,03679632
45	E. altidens PN vs E. suessenbornensis Akha	1	468,6667144	539,8791313	0,949022563	9,999E-05	0,03679632

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46	E. altidens PN vs E. suessenbornensis PN Alb & Pal	1	14,36576841	16,81087512	0,528463145	0,00089991	0,331166883
47	E. altidens PN vs E. suessenbornensis Suess	1	64,63337406	234,7103946	0,971039723	0,117988201	1
48	E. altidens PN vs Z.altidens Farneta	1	1,257467354	5,629593155	0,384808593	0,03749625	1
49	E. altidens PN vs Z.E. altidens Selvella Gioiella	1	7,052159449	27,13003044	0,750899739	0,00719928	1
50	E. altidens PN vs Z.E. stenonis Selvella Gioiella	1	49,18196209	225,8680062	0,961680605	0,00589941	1
51	E. altidens PN vs Z.suss	1	7,670539933	27,85488891	0,799167342	0,110988901	1
52	E. altidens Venta Micena vs E. apolloniensis	1	44,3583969	61,15373699	0,526489621	9,999E-05	0,03679632
53	E. altidens Venta Micena vs E. cf. major	1	50,21804263	73,72174679	0,642613531	9,999E-05	0,03679632
54	E. altidens Venta Micena vs E. grevyi	1	11,8272789	14,30213997	0,167664492	9,999E-05	0,03679632
55	E. altidens Venta Micena vs E. livenzovensisi ER	1	64,25510275	89,34615405	0,690752305	9,999E-05	0,03679632
56	E. altidens Venta Micena vs E. livenzovensisi Liv	1	80,86932189	69,91466784	0,592925962	9,999E-05	0,03679632
57	E. altidens Venta Micena vs E. major Liv	1	342,8933013	424,9755082	0,90811485	9,999E-05	0,03679632
58	E. altidens Venta Micena vs E. major Seneze	1	99,81274722	132,1376968	0,785889776	0,02619738	1
59	E. altidens Venta Micena vs E. senezensis	1	25,20824035	39,3051333	0,435248051	9,999E-05	0,03679632
60	E. altidens Venta Micena vs E. senezensis Vigna Nuova	1	3,936553979	5,211430311	0,126455944	0,02549745	1
61	E. altidens Venta Micena vs E. simplicidens	1	4,976374869	5,501506842	0,061468315	0,01469853	1
62	E. altidens Venta Micena vs E. stehlini	1	155,7214142	159,2247257	0,736385375	9,999E-05	0,03679632
63	E. altidens Venta Micena vs E. stenonis Dmanisi	1	3,68895172	5,024080682	0,116773691	0,0169983	1
64	E. altidens Venta Micena vs E. stenonis mygdoniensis	1	14,14110941	16,01905725	0,296544554	0,00149985	0,551944806
65	E. altidens Venta Micena vs E. stenonis Olivola	1	31,70848613	41,88221905	0,505322125	9,999E-05	0,03679632
66	E. altidens Venta Micena vs E. stenonis Pantalla	1	13,02552329	17,24391619	0,323866414	0,02369763	1
67	E. altidens Venta Micena vs E. stenonis SV	1	140,5607227	186,0667714	0,741104728	9,999E-05	0,03679632
68	E. altidens Venta Micena vs E. stenonis UV	1	102,7788374	120,9553557	0,715901282	9,999E-05	0,03679632
69	E. altidens Venta Micena vs E. suessenbornensis Akha	1	687,0565639	790,0264338	0,931605906	9,999E-05	0,03679632
70	E. altidens Venta Micena vs E. suessenbornensis PN Alb & Pal	1	0,481382353	0,556161448	0,012482257	0,489251075	1

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80	E. altidens Venta Micena vs E. suessenbornensis Suess	1	42,08432306	55,71358045	0,607473617	0,02539746	1
81	E. altidens Venta Micena vs Z_altidens Farneta	1	7,407487678	10,31987145	0,213574067	9,999E-05	0,03679632
82	E. altidens Venta Micena vs Z_E. altidens Selvella Gioiella	1	0,989920944	1,362681865	0,034618624	0,256674333	1
83	E. altidens Venta Micena vs Z_E. stenonis Selvella Gioiella	1	23,20433863	32,3875999	0,460132182	9,999E-05	0,03679632
84	E. altidens Venta Micena vs Z_suss	1	0,966917953	1,280060062	0,03433632	0,326267373	1
85	E. apolloniensis vs E. cf. major	1	7,762238129	13,86457105	0,366162105	0,00059994	0,220777922
86	E. apolloniensis vs E. grevyi	1	56,97562133	69,5732591	0,563012254	9,999E-05	0,03679632
87	E. apolloniensis vs E. livenzovensensis ER	1	16,97119019	27,34420045	0,543144994	0,00019998	0,073592641
88	E. apolloniensis vs E. livenzovensensis Liv	1	9,380936701	7,087876462	0,186092718	0,00989901	1
89	E. apolloniensis vs E. major Liv	1	165,7232877	213,2767879	0,89133923	9,999E-05	0,03679632
90	E. apolloniensis vs E. major Seneze	1	65,37778024	97,79819912	0,837326259	0,0469953	1
91	E. apolloniensis vs E. senezensis	1	61,27398802	114,3619572	0,77083074	9,999E-05	0,03679632
92	E. apolloniensis vs E. senezensis Vigna Nuova	1	12,82125188	19,17922786	0,502347191	0,050194981	1
93	E. apolloniensis vs E. simplicidens	1	47,81145203	52,09561968	0,437426832	9,999E-05	0,03679632
94	E. apolloniensis vs E. stehlini	1	274,4072711	266,0659982	0,869309233	9,999E-05	0,03679632
95	E. apolloniensis vs E. stenonis Dmanisi	1	8,379475205	13,12241434	0,384568753	0,00059994	0,220777922
96	E. apolloniensis vs E. stenonis mygdoniensis	1	43,97763414	48,47081625	0,697714794	0,00089991	0,331166883
97	E. apolloniensis vs E. stenonis Olivola	1	9,945226997	14,42319983	0,375377373	9,999E-05	0,03679632
98	E. apolloniensis vs E. stenonis Pantalla	1	7,189052901	10,75405779	0,361431636	0,04739526	1
99	E. apolloniensis vs E. stenonis SV	1	44,31427778	61,45655676	0,561469852	9,999E-05	0,03679632
100	E. apolloniensis vs E. stenonis UV	1	33,70497674	39,73590511	0,561750147	9,999E-05	0,03679632
101	E. apolloniensis vs E. suessenbornensis Akha	1	281,072627	320,5683087	0,886605106	9,999E-05	0,03679632
102	E. apolloniensis vs E. suessenbornensis PN Alb & Pal	1	24,24012017	27,74163319	0,506773941	9,999E-05	0,03679632
103	E. apolloniensis vs E. suessenbornensis Suess	1	21,27933242	31,83161591	0,62621688	0,04479552	1
104	E. apolloniensis vs Z_altidens Farneta	1	29,46523888	48,40145603	0,697412688	0,00019998	0,073592641

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105	E. apolloniensis vs Z.E. altidens Selvella Gioiella	1	11,55411958	18,50313235	0,468396587	0,00069993	0,257574243
106	E. apolloniensis vs Z.E. stenonis Selvella Gioiella	1	4,114908797	6,786262069	0,244230838	0,00939906	1
107	E. apolloniensis vs Z_suss	1	0,747791008	1,118615738	0,055601029	0,384161584	1
108	E. cf. major vs E. grevyi	1	53,73824521	66,63966778	0,624905058	9,999E-05	0,03679632
109	E. cf. major vs E. livenzovensis ER	1	1,783175472	6,951178723	0,435778374	0,02949705	1
110	E. cf. major vs E. livenzovensis Liv	1	0,209999691	0,122836946	0,007173866	0,817418258	1
111	E. cf. major vs E. major Liv	1	57,6702034	84,01961751	0,875025538	0,00059994	0,220777922
112	E. cf. major vs E. major Seneze	1	42,08129829	286,1758695	0,982828247	0,142857143	1
113	E. cf. major vs E. senezensis	1	56,89225646	182,0361495	0,901007814	9,999E-05	0,03679632
114	E. cf. major vs E. senezensis Vigna Nuova	1	19,74458847	134,2740125	0,964099548	0,142857143	1
115	E. cf. major vs E. simplicidens	1	48,95269661	52,38865838	0,497099585	9,999E-05	0,03679632
116	E. cf. major vs E. stehlini	1	185,8467041	164,9837933	0,863862794	9,999E-05	0,03679632
117	E. cf. major vs E. stenonis Dmanisi	1	15,51074619	75,21151671	0,914853779	0,01029897	1
118	E. cf. major vs E. stenonis mygdoniensis	1	57,6306371	56,92217244	0,890491832	0,01049895	1
119	E. cf. major vs E. stenonis Olivola	1	7,3879779	16,12211011	0,617182534	0,00179982	0,662333767
120	E. cf. major vs E. stenonis Pantalla	1	4,963359974	33,75356545	0,870979613	0,142857143	1
121	E. cf. major vs E. stenonis SV	1	15,83933719	23,78173956	0,411578809	9,999E-05	0,03679632
122	E. cf. major vs E. stenonis UV	1	10,86682436	12,89267061	0,431298721	0,00019998	0,073592641
123	E. cf. major vs E. suessenbornensis Akha	1	70,21165637	79,04613592	0,745393835	9,999E-05	0,03679632
124	E. cf. major vs E. suessenbornensis PN Alb & Pal	1	37,24152945	41,64324891	0,762093209	9,999E-05	0,03679632
125	E. cf. major vs E. suessenbornensis Suess	1	10,34939656	70,38156332	0,933670784	0,142857143	1
126	E. cf. major vs Z.altidens Farneta	1	41,14662201	352,1465453	0,980509349	0,01079892	1
127	E. cf. major vs Z.E. altidens Selvella Gioiella	1	21,59453717	131,7815575	0,949561021	0,00989901	1
128	E. cf. major vs Z.E. stenonis Selvella Gioiella	1	0,786430654	7,174263212	0,50614717	0,0109989	1
129	E. cf. major vs Z_suss	1	3,874096787	26,34597937	0,84048991	0,142857143	1

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130	E. grevyi vs E. livenzovensis ER	1	64,13126608	75,57554038	0,659613214	9,999E-05	0,03679632
131	E. grevyi vs E. livenzovensis Liv	1	86,32435643	67,79201681	0,590563862	9,999E-05	0,03679632
132	E. grevyi vs E. major Liv	1	346,8366762	373,3037587	0,898869203	9,999E-05	0,03679632
133	E. grevyi vs E. major Seneze	1	100,9087296	112,0469118	0,76198072	0,0259974	1
134	E. grevyi vs E. senezensis	1	5,512401276	7,441910868	0,12955542	0,00179982	0,662333767
135	E. grevyi vs E. senezensis Vigna Nuova	1	2,40717881	2,672880264	0,070949719	0,075992401	1
136	E. grevyi vs E. simplicidens	1	2,763860654	2,856455117	0,033270126	0,076792321	1
137	E. grevyi vs E. stehlini	1	126,7231555	118,1305259	0,678402166	9,999E-05	0,03679632
138	E. grevyi vs E. stenonis Dmanisi	1	0,943896715	1,083621212	0,028453734	0,312868713	1
139	E. grevyi vs E. stenonis mygdoniensis	1	14,63385049	14,29665657	0,278705427	0,00239976	0,883111689
140	E. grevyi vs E. stenonis Olivola	1	24,9647276	28,23421159	0,413783803	9,999E-05	0,03679632
141	E. grevyi vs E. stenonis Pantalla	1	9,979650591	11,08119222	0,24047104	0,02419758	1
142	E. grevyi vs E. stenonis SV	1	107,3442101	128,5787031	0,66766834	9,999E-05	0,03679632
143	E. grevyi vs E. stenonis UV	1	84,20873419	87,72850862	0,651150299	9,999E-05	0,03679632
144	E. grevyi vs E. suessenbornensis Akha	1	691,5265365	719,7098221	0,92661352	9,999E-05	0,03679632
145	E. grevyi vs E. suessenbornensis PN Alb & Pal	1	2,322530788	2,35476191	0,051918736	0,102789721	1
146	E. grevyi vs E. suessenbornensis Suess	1	43,66633625	48,48617305	0,580768902	0,02689731	1
147	E. grevyi vs Z.altidens Farneta	1	4,753372464	5,56504889	0,130742218	0,01189881	1
148	E. grevyi vs Z.E. altidens Selvella Gioiella	1	0,161702116	0,187362683	0,005038343	0,795120488	1
149	E. grevyi vs Z.E. stenonis Selvella Gioiella	1	22,64003715	26,54850131	0,417767544	0,00019998	0,073592641
150	E. grevyi vs Z.suss	1	1,508943564	1,675498909	0,04568442	0,224677532	1
151	E. livenzovensis ER vs E. livenzovensis Liv	1	3,446650976	1,844290101	0,103354636	0,185181482	1
152	E. livenzovensis ER vs E. major Liv	1	36,81432406	44,62360223	0,802242222	0,00059994	0,220777922
153	E. livenzovensis ER vs E. major Seneze	1	33,7286983	85,7406675	0,95542712	0,166666667	1
154	E. livenzovensis ER vs E. senezensis	1	63,9802306	171,481791	0,900252933	9,999E-05	0,03679632

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155	E. livenzovensis ER vs E. senezensis Vigna Nuova	1	23,90900533	60,77833356	0,938250959	0,166666667	1
156	E. livenzovensis ER vs E. simplicidens	1	60,91686783	62,89787327	0,547424173	9,999E-05	0,03679632
157	E. livenzovensis ER vs E. stehlini	1	190,7940978	158,3295769	0,86363357	0,00019998	0,073592641
158	E. livenzovensis ER vs E. stenonis Dmanisi	1	20,60334964	54,17455044	0,900290074	0,019998	1
159	E. livenzovensis ER vs E. stenonis mygdoniensis	1	68,39387811	51,77817479	0,89615456	0,01889811	1
160	E. livenzovensis ER vs E. stenonis Olivola	1	9,064234328	15,04909123	0,625765485	0,00189981	0,699130087
170	E. livenzovensis ER vs E. stenonis Pantalla	1	3,98532915	10,1309804	0,716934007	0,166666667	1
171	E. livenzovensis ER vs E. stenonis SV	1	14,2214519	19,98476373	0,377179444	9,999E-05	0,03679632
172	E. livenzovensis ER vs E. stenonis UV	1	8,071584897	8,514863862	0,34733474	0,00159984	0,588741126
173	E. livenzovensis ER vs E. suessenbornensis Akha	1	42,05233462	44,0504106	0,628838721	9,999E-05	0,03679632
174	E. livenzovensis ER vs E. suessenbornensis PN Alb & Pal	1	48,56382041	46,75525717	0,795762957	0,00039996	0,147185281
175	E. livenzovensis ER vs E. suessenbornensis Suess	1	7,140889011	18,15263029	0,819434534	0,166666667	1
176	E. livenzovensis ER vs Z.altidens Farneta	1	49,37330031	178,8668575	0,967544209	0,01909809	1
177	E. livenzovensis ER vs Z.E. altidens Selvella Gioiella	1	28,66755229	86,63728445	0,935231262	0,01729827	1
178	E. livenzovensis ER vs Z.E. stenonis Selvella Gioiella	1	1,739164427	6,499059337	0,519963876	0,122987701	1
179	E. livenzovensis ER vs Z.suss	1	6,647138991	16,89748383	0,808589396	0,166666667	1
180	E. livenzovensis Liv vs E. major Liv	1	92,50084438	49,05277968	0,720804939	9,999E-05	0,03679632
181	E. livenzovensis Liv vs E. major Seneze	1	48,51512422	20,55171201	0,631355795	0,071092891	1
182	E. livenzovensis Liv vs E. senezensis	1	82,37607784	65,71965235	0,708799598	9,999E-05	0,03679632
183	E. livenzovensis Liv vs E. senezensis Vigna Nuova	1	19,42406646	8,228316972	0,406772199	0,068793121	1
184	E. livenzovensis Liv vs E. simplicidens	1	80,59617528	62,70746315	0,511032186	9,999E-05	0,03679632
185	E. livenzovensis Liv vs E. stehlini	1	299,3503266	173,6730514	0,840327514	9,999E-05	0,03679632
186	E. livenzovensis Liv vs E. stenonis Dmanisi	1	15,98824348	7,708891902	0,355102966	0,00969903	1
187	E. livenzovensis Liv vs E. stenonis mygdoniensis	1	64,54858402	26,05802982	0,650507025	0,00149985	0,551944806
188	E. livenzovensis Liv vs E. stenonis Olivola	1	8,033685655	4,244693261	0,199800167	0,03469653	1

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189	E. livenzovensis Liv vs E. stenonis Pantalla	1	5,050541286	2,139482722	0,151312659	0,145585441	1
190	E. livenzovensis Liv vs E. stenonis SV	1	24,80900449	20,24724834	0,330582171	9,999E-05	0,03679632
191	E. livenzovensis Liv vs E. stenonis UV	1	15,66126787	8,966125112	0,271979952	0,00109989	0,404759524
192	E. livenzovensis Liv vs E. suessenbornensis Akha	1	137,0130596	90,32405596	0,726521149	9,999E-05	0,03679632
193	E. livenzovensis Liv vs E. suessenbornensis PN Alb & Pal	1	47,65001497	24,29989058	0,548531616	0,00019998	0,073592641
194	E. livenzovensis Liv vs E. suessenbornensis Suess	1	12,71389777	5,385791952	0,309781226	0,074092591	1
195	E. livenzovensis Liv vs Z.altidens Farneta	1	45,27195751	22,30905483	0,614421249	0,00239976	0,883111689
196	E. livenzovensis Liv vs Z.E. altidens Selvella Gioiella	1	22,82580238	11,11924674	0,442658447	0,0059994	1
197	E. livenzovensis Liv vs Z.E. stenonis Selvella Gioiella	1	0,636619143	0,31427193	0,021955146	0,637236276	1
198	E. livenzovensis Liv vs Z.suss	1	3,369720712	1,427462688	0,10630919	0,286171383	1
199	E. major Liv vs E. major Seneze	1	7,515859466	7,013453752	0,50048003	0,112488751	1
200	E. major Liv vs E. senezensis	1	303,4717502	512,9023101	0,958870995	9,999E-05	0,03679632
201	E. major Liv vs E. senezensis Vigna Nuova	1	69,05737422	64,44115972	0,902017268	0,110688931	1
202	E. major Liv vs E. simplicidens	1	347,4679848	339,5041445	0,860584481	9,999E-05	0,03679632
203	E. major Liv vs E. stehlini	1	622,5199469	483,4567414	0,945254412	9,999E-05	0,03679632
204	E. major Liv vs E. stenonis Dmanisi	1	100,0761993	109,7085433	0,924184058	0,00529947	1
205	E. major Liv vs E. stenonis mygdoniensis	1	195,5567172	127,0460171	0,933845913	0,00659934	1
206	E. major Liv vs E. stenonis Olivola	1	93,59291607	98,96402321	0,891856841	0,00039996	0,147185281
207	E. major Liv vs E. stenonis Pantalla	1	22,70631488	21,18848683	0,751671665	0,111888811	1
208	E. major Liv vs E. stenonis SV	1	163,3899814	199,9931373	0,847453191	9,999E-05	0,03679632
209	E. major Liv vs E. stenonis UV	1	107,8158002	97,1084698	0,836359914	9,999E-05	0,03679632
210	E. major Liv vs E. suessenbornensis Akha	1	0,402248379	0,379373587	0,012912923	0,601939806	1
211	E. major Liv vs E. suessenbornensis PN Alb & Pal	1	226,5218076	184,7438536	0,924903822	9,999E-05	0,03679632
212	E. major Liv vs E. suessenbornensis Suess	1	0,62250735	0,580895176	0,076626198	0,774722528	1
213	E. major Liv vs Z.altidens Farneta	1	160,968247	191,0193416	0,955004351	0,00579942	1

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214	E. major Liv vs Z.E. altidens Selvella Gioiella	1	118,1830425	134,413127	0,937244238	0,00769923	1
215	E. major Liv vs Z.E. stenonis Selvella Gioiella	1	42,6629163	50,96760465	0,849918968	0,00659934	1
216	E. major Liv vs Z_suss	1	34,46422982	32,16043128	0,821248138	0,108089191	1
217	E. major Seneze vs E. senezensis	1	102,370704	278,4122689	0,948877393	0,059794021	1
218	E. major Seneze vs E. senezensis Vigna Nuova	1	68,57689229	#N/D	1	#N/D	#N/D
219	E. major Seneze vs E. simplicidens	1	98,30891764	96,71967659	0,6683243	0,02019798	1
220	E. major Seneze vs E. stehlini	1	166,5974516	122,5299729	0,853689097	0,04289571	1
221	E. major Seneze vs E. stenonis Dmanisi	1	70,1430852	198,0426412	0,990002132	0,25	1
222	E. major Seneze vs E. stenonis mygdoniensis	1	114,8405468	36,15949723	0,947588408	0,25	1
223	E. major Seneze vs E. stenonis Olivola	1	56,24509536	73,09725773	0,935977265	0,142857143	1
224	E. major Seneze vs E. stenonis Pantalla	1	30,30865185	#N/D	1	#N/D	#N/D
225	E. major Seneze vs E. stenonis SV	1	60,77680184	80,44483094	0,735026316	0,03229677	1
226	E. major Seneze vs E. stenonis UV	1	52,14968709	46,03633936	0,793232996	0,070792921	1
227	E. major Seneze vs E. suessenbornensis Akha	1	9,618757708	9,102736689	0,292666744	0,04159584	1
228	E. major Seneze vs E. suessenbornensis PN Alb & Pal	1	94,0148645	69,06093567	0,896186052	0,102689731	1
229	E. major Seneze vs E. suessenbornensis Suess	1	6,428802282	#N/D	1	#N/D	#N/D
230	E. major Seneze vs Z.altidens Farneta	1	99,07466548	2396,544788	0,999166161	0,25	1
231	E. major Seneze vs Z.E. altidens Selvella Gioiella	1	79,05846792	383,9390965	0,994817835	0,25	1
232	E. major Seneze vs Z.E. stenonis Selvella Gioiella	1	40,24077944	2507,737281	0,999203104	0,25	1
233	E. major Seneze vs Z_suss	1	41,7033217	#N/D	1	#N/D	#N/D
234	E. senezensis vs E. senezensis Vigna Nuova	1	1,648881145	4,484376123	0,23015241	0,056494351	1
235	E. senezensis vs E. simplicidens	1	13,72749046	15,925712	0,201781037	0,00029997	0,110388961
236	E. senezensis vs E. stehlini	1	71,81925251	75,89213717	0,678261575	9,999E-05	0,03679632
237	E. senezensis vs E. stenonis Dmanisi	1	1,78568873	4,877532973	0,22294712	0,01759824	1
238	E. senezensis vs E. stenonis mygdoniensis	1	14,75604074	21,13812883	0,55425186	0,00239976	0,883111689

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239	E. senezensis vs E. stenonis Olivola	1	23,74287466	50,71801911	0,717186648	9,999E-05	0,03679632
240	E. senezensis vs E. stenonis Pantalla	1	8,905184097	24,21896512	0,617531978	0,060893911	1
241	E. senezensis vs E. stenonis SV	1	69,70251173	111,8282576	0,717637862	9,999E-05	0,03679632
242	E. senezensis vs E. stenonis UV	1	65,36743486	92,36096092	0,773795387	9,999E-05	0,03679632
243	E. senezensis vs E. suessenbornensis Akha	1	500,9439409	644,4113653	0,945700935	9,999E-05	0,03679632
244	E. senezensis vs E. suessenbornensis PN Alb & Pal	1	9,044518699	12,67968816	0,355375532	9,999E-05	0,03679632
245	E. senezensis vs E. suessenbornensis Suess	1	46,37800617	126,1318465	0,893716405	0,059294071	1
246	E. senezensis vs Z.altidens Farneta	1	3,971266806	12,05972064	0,414997817	0,00159984	0,588741126
247	E. senezensis vs Z.E. altidens Selvella Gioiella	1	2,083638482	5,976104585	0,260100861	0,00559944	1
248	E. senezensis vs Z.E. stenonis Selvella Gioiella	1	25,02378782	76,68380048	0,818538532	0,00119988	0,441555844
249	E. senezensis vs Z.suss	1	3,175989189	8,637572288	0,365417065	0,057994201	1
250	E. senezensis Vigna Nuova vs E. simplicidens	1	3,325123707	3,271370464	0,063805013	0,098290171	1
251	E. senezensis Vigna Nuova vs E. stehlini	1	2,114915816	1,555489445	0,068962788	0,262873713	1
252	E. senezensis Vigna Nuova vs E. stenonis Dmanisi	1	3,126088035	8,826226125	0,815263419	0,25	1
253	E. senezensis Vigna Nuova vs E. stenonis mygdoniensis	1	1,342737102	0,422783589	0,174503241	0,75	1
254	E. senezensis Vigna Nuova vs E. stenonis Olivola	1	11,33602045	14,73252029	0,746611182	0,142857143	1
255	E. senezensis Vigna Nuova vs E. stenonis Pantalla	1	9,605695142	#N/D	1	#N/D	#N/D
256	E. senezensis Vigna Nuova vs E. stenonis SV	1	14,77271282	19,55332214	0,402718522	0,03129687	1
257	E. senezensis Vigna Nuova vs E. stenonis UV	1	17,49363739	15,44291198	0,56272862	0,073392661	1
258	E. senezensis Vigna Nuova vs E. suessenbornensis Akha	1	70,1465512	66,38337346	0,751084405	0,04409559	1
259	E. senezensis Vigna Nuova vs E. suessenbornensis PN Alb & Pal	1	2,871219126	2,109124769	0,208635744	0,206079392	1
260	E. senezensis Vigna Nuova vs E. suessenbornensis Suess	1	34,08489829	#N/D	1	#N/D	#N/D
261	E. senezensis Vigna Nuova vs Z.altidens Farneta	1	0,131166246	3,172817015	0,613363474	0,25	1
262	E. senezensis Vigna Nuova vs Z.E. altidens Selvella Gioiella	1	1,853234924	9,000039606	0,818182473	0,25	1
263	E. senezensis Vigna Nuova vs Z.E. stenonis Selvella Gioiella	1	14,4860871	902,7484356	0,997789441	0,25	1

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264	E. senezensis Vigna Nuova vs Z_suss	1	3,898589125	#N/D	1	#N/D	#N/D
265	E. simplicidens vs E. stehlini	1	163,6869971	146,0332967	0,679119462	9,999E-05	0,03679632
266	E. simplicidens vs E. stenonis Dmanisi	1	1,326346262	1,339822969	0,026097148	0,247175282	1
267	E. simplicidens vs E. stenonis mygdoniensis	1	16,04165628	14,54613963	0,225360335	0,00149985	0,551944806
268	E. simplicidens vs E. stenonis Olivola	1	24,94729936	25,1198271	0,321555078	9,999E-05	0,03679632
269	E. simplicidens vs E. stenonis Pantalla	1	10,45248785	10,28351515	0,176439515	0,01759824	1
270	E. simplicidens vs E. stenonis SV	1	122,2074613	133,1001121	0,633508049	9,999E-05	0,03679632
271	E. simplicidens vs E. stenonis UV	1	89,19923459	85,79291915	0,588457379	9,999E-05	0,03679632
272	E. simplicidens vs E. suessenbornensis Akha	1	733,9994718	713,2553949	0,910629406	9,999E-05	0,03679632
273	E. simplicidens vs E. suessenbornensis PN Alb & Pal	1	0,748531523	0,702382906	0,012387185	0,425257474	1
274	E. simplicidens vs E. suessenbornensis Suess	1	41,41765855	40,74810949	0,459143408	0,01709829	1
275	E. simplicidens vs Z.altidens Farneta	1	6,587801046	6,739936355	0,118786463	0,00909909	1
276	E. simplicidens vs Z.E. altidens Selvella Gioiella	1	0,206835016	0,210195897	0,004186319	0,751524848	1
277	E. simplicidens vs Z.E. stenonis Selvella Gioiella	1	20,75202872	21,25326523	0,298277772	9,999E-05	0,03679632
278	E. simplicidens vs Z_suss	1	0,888058016	0,873701859	0,017876728	0,359264074	1
279	E. stehlini vs E. stenonis Dmanisi	1	32,86954319	25,83647285	0,529040517	0,00029997	0,110388961
280	E. stehlini vs E. stenonis mygdoniensis	1	6,156186801	4,056566819	0,149929104	0,0439956	1
281	E. stehlini vs E. stenonis Olivola	1	123,2879079	98,93518351	0,791892089	9,999E-05	0,03679632
282	E. stehlini vs E. stenonis Pantalla	1	31,94776895	23,4971137	0,528059277	0,04589541	1
283	E. stehlini vs E. stenonis SV	1	365,0470899	361,7024928	0,878553079	9,999E-05	0,03679632
284	E. stehlini vs E. stenonis UV	1	274,7931199	215,1604061	0,867021494	9,999E-05	0,03679632
285	E. stehlini vs E. suessenbornensis Akha	1	1134,000579	941,3568246	0,956316654	9,999E-05	0,03679632
286	E. stehlini vs E. suessenbornensis PN Alb & Pal	1	64,21450776	47,2126793	0,619485888	9,999E-05	0,03679632
287	E. stehlini vs E. suessenbornensis Suess	1	90,76335413	66,75511067	0,760697698	0,0449955	1
288	E. stehlini vs Z.altidens Farneta	1	8,151653554	6,547453847	0,221591135	0,01109889	1

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289	E. stehlini vs Z_E. altidens Selvella Gioiella	1	23,98731842	19,04780439	0,453003544	0,00069993	0,257574243
290	E. stehlini vs Z_E. stenonis Selvella Gioiella	1	91,33006668	73,48664556	0,761625043	0,00069993	0,257574243
291	E. stehlini vs Z_suss	1	17,14050535	12,60658933	0,375122545	0,04159584	1
292	E. stenonis Dmanisi vs E. stenonis mygdoniensis	1	12,42347689	7,038545937	0,637633433	0,1	1
293	E. stenonis Dmanisi vs E. stenonis Olivola	1	5,33682814	8,200337257	0,539483902	0,03689631	1
294	E. stenonis Dmanisi vs E. stenonis Pantalla	1	5,167148684	14,5889758	0,879438006	0,25	1
295	E. stenonis Dmanisi vs E. stenonis SV	1	10,67674189	14,63335109	0,320672288	0,00089991	0,331166883
296	E. stenonis Dmanisi vs E. stenonis UV	1	13,92407639	13,63016051	0,493307323	0,00259974	0,95670433
297	E. stenonis Dmanisi vs E. suessenbornensis Akha	1	112,6050246	112,8141457	0,824579543	0,00029997	0,110388961
298	E. stenonis Dmanisi vs E. suessenbornensis PN Alb & Pal	1	2,234552119	1,926500825	0,161531102	0,158684132	1
299	E. stenonis Dmanisi vs E. suessenbornensis Suess	1	29,02660711	81,95399334	0,976177429	0,25	1
300	E. stenonis Dmanisi vs Z_altidens Farneta	1	5,082691025	25,70115662	0,86532511	0,1	1
301	E. stenonis Dmanisi vs Z_E. altidens Selvella Gioiella	1	0,909292799	3,246918741	0,448041279	0,1	1
302	E. stenonis Dmanisi vs Z_E. stenonis Selvella Gioiella	1	8,311697094	44,90037814	0,918201042	0,1	1
303	E. stenonis Dmanisi vs Z_suss	1	0,844009144	2,382983293	0,543689796	0,25	1
304	E. stenonis mygdoniensis vs E. stenonis Olivola	1	40,51431815	27,80621591	0,798886497	0,01449855	1
305	E. stenonis mygdoniensis vs E. stenonis Pantalla	1	22,29323296	7,019403143	0,778255837	0,25	1
306	E. stenonis mygdoniensis vs E. stenonis SV	1	64,29750745	70,52746612	0,694663905	0,00019998	0,073592641
307	E. stenonis mygdoniensis vs E. stenonis UV	1	67,63262768	47,47240112	0,77225552	0,00159984	0,588741126
308	E. stenonis mygdoniensis vs E. suessenbornensis Akha	1	224,965067	182,4100444	0,883726589	0,00029997	0,110388961
309	E. stenonis mygdoniensis vs E. suessenbornensis PN Alb & Pal	1	10,44776619	6,059294792	0,377307651	0,02469753	1
310	E. stenonis mygdoniensis vs E. suessenbornensis Suess	1	58,48872915	18,41617006	0,902038434	0,25	1
311	E. stenonis mygdoniensis vs Z_altidens Farneta	1	2,087248565	1,297521763	0,244929954	0,4	1
312	E. stenonis mygdoniensis vs Z_E. altidens Selvella Gioiella	1	6,965079189	4,119083963	0,507333584	0,1	1
313	E. stenonis mygdoniensis vs Z_E. stenonis Selvella Gioiella	1	38,85436049	24,34490692	0,858881174	0,1	1

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314	E. stenonis mygdoniensis vs Z_suss	1	7,884601531	2,482600746	0,553830441	0,5	1
315	E. stenonis Olivola vs E. stenonis Pantalla	1	1,46578553	1,904964371	0,275883302	0,285714286	1
316	E. stenonis Olivola vs E. stenonis SV	1	1,142303634	1,507872045	0,042465852	0,213878612	1
317	E. stenonis Olivola vs E. stenonis UV	1	2,566692284	2,501820725	0,128286521	0,119088091	1
318	E. stenonis Olivola vs E. suessenbornensis Akha	1	117,5287739	117,1191762	0,812655049	9,999E-05	0,03679632
319	E. stenonis Olivola vs E. suessenbornensis PN Alb & Pal	1	21,56554554	19,02248201	0,594035216	0,00039996	0,147185281
320	E. stenonis Olivola vs E. suessenbornensis Suess	1	19,29004587	25,06973178	0,833719834	0,142857143	1
321	E. stenonis Olivola vs Z_altidens Farneta	1	24,07921231	42,88962611	0,859690269	0,01189881	1
322	E. stenonis Olivola vs Z.E. altidens Selvella Gioiella	1	11,08711318	18,22208413	0,722465441	0,01339866	1
323	E. stenonis Olivola vs Z.E. stenonis Selvella Gioiella	1	1,853842246	3,345102721	0,32335133	0,056694331	1
324	E. stenonis Olivola vs Z_suss	1	2,30351444	2,99369372	0,374506933	0,142857143	1
325	E. stenonis Pantalla vs E. stenonis SV	1	0,670279352	0,887188986	0,029684591	0,393860614	1
326	E. stenonis Pantalla vs E. stenonis UV	1	0,566197921	0,499824277	0,039986504	0,713728627	1
327	E. stenonis Pantalla vs E. suessenbornensis Akha	1	22,27447668	21,07950967	0,489316379	0,04479552	1
328	E. stenonis Pantalla vs E. suessenbornensis PN Alb & Pal	1	11,50282667	8,449684813	0,513668493	0,099290071	1
329	E. stenonis Pantalla vs E. suessenbornensis Suess	1	11,37377851	#N/D	1	#N/D	#N/D
330	E. stenonis Pantalla vs Z_altidens Farneta	1	14,00960533	338,882261	0,994132872	0,25	1
331	E. stenonis Pantalla vs Z.E. altidens Selvella Gioiella	1	8,682732912	42,16677501	0,954717092	0,25	1
332	E. stenonis Pantalla vs Z.E. stenonis Selvella Gioiella	1	2,491580245	155,2710648	0,987283103	0,25	1
333	E. stenonis Pantalla vs Z_suss	1	4,257631163	#N/D	1	#N/D	#N/D
334	E. stenonis SV vs E. stenonis UV	1	1,732832199	2,001113625	0,046536321	0,146885311	1
335	E. stenonis SV vs E. suessenbornensis Akha	1	304,6040325	344,018333	0,870892068	9,999E-05	0,03679632
336	E. stenonis SV vs E. suessenbornensis PN Alb & Pal	1	56,67148049	63,92737542	0,633399761	9,999E-05	0,03679632
337	E. stenonis SV vs E. suessenbornensis Suess	1	21,12684843	27,96372463	0,490904076	0,03149685	1
338	E. stenonis SV vs Z_altidens Farneta	1	38,97652363	54,94033172	0,639284613	0,00029997	0,110388961

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339	E. stenonis SV vs Z.E. altidens Selvella Gioiella	1	20,39418188	28,32323233	0,477439128	0,00019998	0,073592641
340	E. stenonis SV vs Z.E. stenonis Selvella Gioiella	1	3,634409589	5,134783998	0,142100863	0,0169983	1
341	E. stenonis SV vs Z_suss	1	4,30800013	5,702115472	0,164316077	0,065593441	1
342	E. stenonis UV vs E. suessenbornensis Akha	1	162,166548	149,6623641	0,814877696	9,999E-05	0,03679632
343	E. stenonis UV vs E. suessenbornensis PN Alb & Pal	1	55,71687324	45,51254282	0,694714949	9,999E-05	0,03679632
344	E. stenonis UV vs E. suessenbornensis Suess	1	16,97795975	14,98768564	0,555352758	0,072092791	1
345	E. stenonis UV vs Z.altidens Farneta	1	43,12233963	44,1432831	0,759215523	0,00169983	0,625537446
346	E. stenonis UV vs Z.E. altidens Selvella Gioiella	1	23,91521809	23,90607288	0,63066604	0,00249975	0,919908009
347	E. stenonis UV vs Z.E. stenonis Selvella Gioiella	1	2,657562566	2,730582076	0,16320903	0,100589941	1
348	E. stenonis UV vs Z_suss	1	5,374824052	4,744749928	0,283357467	0,070092991	1
349	E. suessenbornensis Akha vs E. suessenbornensis PN Alb & Pal	1	321,7851859	282,7819682	0,904086543	9,999E-05	0,03679632
350	E. suessenbornensis Akha vs E. suessenbornensis Suess	1	0,415252515	0,392975311	0,017549044	0,752024798	1
351	E. suessenbornensis Akha vs Z.altidens Farneta	1	184,1341497	189,4235698	0,887547565	0,00039996	0,147185281
352	E. suessenbornensis Akha vs Z.E. altidens Selvella Gioiella	1	133,7688996	135,6970618	0,849715457	0,00029997	0,110388961
353	E. suessenbornensis Akha vs Z.E. stenonis Selvella Gioiella	1	45,9855446	47,40932245	0,663909428	0,00069993	0,257574243
354	E. suessenbornensis Akha vs Z_suss	1	34,11628444	32,28603563	0,594739241	0,04249575	1
355	E. suessenbornensis PN Alb & Pal vs E. suessenbornensis Suess	1	40,23345762	29,55447783	0,786976135	0,100389961	1
356	E. suessenbornensis PN Alb & Pal vs Z.altidens Farneta	1	4,571198612	4,165732237	0,294071084	0,0459954	1
357	E. suessenbornensis PN Alb & Pal vs Z.E. altidens Selvella Gioiella	1	0,267723346	0,236871235	0,023139026	0,721927807	1
358	E. suessenbornensis PN Alb & Pal vs Z.E. stenonis Selvella Gioiella	1	19,48197045	17,83614119	0,640754804	0,00509949	1
359	E. suessenbornensis PN Alb & Pal vs Z_suss	1	1,080908334	0,794007855	0,090289646	0,392160784	1
360	E. suessenbornensis Suess vs Z.altidens Farneta	1	48,07959828	1163,010847	0,998283278	0,25	1
361	E. suessenbornensis Suess vs Z.E. altidens Selvella Gioiella	1	34,27474026	166,4516548	0,988127157	0,25	1
362	E. suessenbornensis Suess vs Z.E. stenonis Selvella Gioiella	1	11,24821731	700,9698689	0,997154928	0,25	1
363	E. suessenbornensis Suess vs Z_suss	1	15,63134188	#N/D	1	#N/D	#N/D

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364 Z_altidens Farneta vs Z_E. altidens Selvella Gioiella	1	2,374353013	19,20572501	0,827628743	0,1	1
365 Z_altidens Farneta vs Z_E. stenonis Selvella Gioiella	1	26,06532141	908,4007143	0,995615961	0,1	1
366 Z_altidens Farneta vs Z_suss	1	4,597870147	111,2191667	0,982335146	0,25	1
367 Z_E. altidens Selvella Gioiella vs Z_E. stenonis Selvella Gioiella	1	13,06658222	117,7377816	0,967142493	0,1	1
368 Z_E. altidens Selvella Gioiella vs Z_suss	1	1,12067252	5,442427689	0,731270483	0,25	1
369 Z_E. stenonis Selvella Gioiella vs Z_suss	1	2,726886988	169,9349828	0,988367696	0,25	1

A.5 Appendix 5

List of elements recovered from Cava Liberatori.

Envelope	Field note	Date	Element number	Taxon	Skeletal element
1	Linda - under the scapula	-	1A	?Cervid	Jaw fragment
			1B	Artiodactyla	Metapode distal end
			1C	Cervid	Antler fragment
2	5 m West from Linda		2A	Cervid	Femur
			2B	<i>Pachycrocuta brevirostris</i>	Coprolite
			2C	?cervid	Third phalanx
3	Linda - 50 cm above Dama - Cava Liberatori, Farneta		3A	Artiodactyla	Ulna proximal epiphysis
4	5 m West from Linda	05/03/1973	4A	Bovid	Astragalus
5	2 m East from Linda	27/03/1973	5A	Indet.	Long bone fragment
			5B	Indet.	Rib
6	Cava Liberatori, between the antlers of the Dama	-	6A	?Cervid	Scapula
7	Cava Liberatori (rubble) in the unloading area. Berzi, Borselli	05/04/1973	7A	Cervid	Metapode
			7B	Cervid	Antler fragment
8	Cava Liberatori - unloading area	28/09/1973	8A	Indet.	Axis vertebra
			8B	Cervid	Antler fragment
9	Cava Liberatori	23/03/1973	9A	Indet.	Rib fragment
10	Cava Liberatori, quarry pit East from Linda		10A	Large artiodactyl	Rib fragments
11	Cava Liberatori 30 m from Linda's dig - Borselli, Menotti, Mazz-	31/10/1974	11A	Large artiodactyl	Rib

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Envelope	Field note	Date	Element number	Taxon	Skeletal element
12	From the unloading area - Borselli, De Giuli, Migliorini	21/03/1973	12A	<i>Pecten jacobaeus</i>	Shell fragment
			12B	Cervid	Antler fragment
			12C	Cervid	Tibia (diaphysis)
			12D	Cervid	Antler fragment
			12E	Indet.	Rib
13	Cava Liberatori 50 m from Linda, B - see A	26/03/1973	13A	Large artiodactyl	Two fragments of a rib
14	Cava Liberatori, rubble	22/03/1973	14A	Bovid	Humerus
15	Dicerorhinus etruscus, pm sup sx, Cava Liberatori (rubble)	27/03/1973	15A	<i>Stephanorhinus</i> sp.	Molar
16	Cava Liberatori, Farneta. Recovered by Borselli under the Elephas "Linda" humerus, Panthera cf. toscana, tibia dx. IGF 14285	25/03/1973	16A	<i>Panthera cf. toscana</i>	Tibia
17	Cava Liberatori, Farneta. Retrieved by Borselli - Mazzini close to the elephant "Linda"'s dig, 2 m East from its scapula; Cervus radius		17A	? <i>Pseudodama</i> sp.	Radius
18	5m O West from Linda	28/03/1973	18A	Indet.	Skull fragment
19	Cava Liberatori, from the quarry pit	26/03/1973	19A	Cervid	Antler fragment
			19B	Indet.	Acetabulous fragment
			19C	<i>Equus</i> sp.	Lower p3-p4
			19D	Indet.	Rib fragment
20	Cava Liberatori, Farneta	-	20A	Indet.	Epiphysis
21	50m O West from Linda	-	21A	<i>Equus</i> sp.	Lower m1-m2
22	Cava Libeatori, underneath Linda's vertebra	27/03/1973	22A	<i>Equus</i> sp.	Lower p3-4
23		03/04/1973	23A	Indet.	Broken metapode

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Envelope	Field note	Date	Element number	Taxon	Skeletal element
24	Cava Liberatori (Rubble) in the quarry pit. Borselli, Berzi	05/04/1973	24A	Indet.	Pelvic bone fragment
			24B	large artiodactyl limb bone	Limb bone fragment
25	Linda fragment underneath the jaw.		25A	Indet.	Two bone fragments
26	Cava Liberatori, isolated	25/03/1973	26A	Indet.	Vertebra fragment
			26B	Indet.	Bone fragment
			26C	Indet.	Bone fragment
Exhibited	Cava Liberatori		IGF14838	<i>Mammuthus meridionalis</i>	<i>Mammuthus meridionalis</i> “Linda”
				“Linda”	
Exhibited	Cava Liberatori		IGF194 V	<i>Pseudodama farnetensis</i>	Antlers and upper skull
				holotype	

A.6 Appendix 6

Taphonomic and preservation features of the analysed specimens

Element number	Distance	Bone completeness	Weathering stage	Element size (cm)	Class size	Predation marks	Bioturbation marks
1A	1	medium	3	14,0	2	P	A
1B	1	low	2	5,0	1	A	A
1C	1	medium	3	12,5	2	A	P
2A	2	high	1	30,0	3	A	A
2B	2	high	2	4,0	1	A	A
2C	2	high	1	4,0	1	A	A
3A	1	low	3	13,0	2	A	P
4A	2	high	1	7,5	1	A	A
5A	1	low	5	7,5	1	A	A
5B	1	high	4	8,0	1	A	P
6A	1	high	2	15,4	2	P	P
7A	3	medium	1	28,0	2	A	A
7B	3	medium	4	7,0	1	A	A
8A	3	medium	3	6,0	1	A	A
8B	3	medium	4	8,0	1	A	P
9A	3	medium	3	14,0	2	A	A
10A	3	medium	3	65,0	3	A	P
11A	3	medium	4	40,0	3	A	A
12A	3	medium	2	2,5	1	P	A

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Element number	Distance	Bone completeness	Weathering stage	Element size (cm)	Class size	Predation marks	Bioturbation marks
12B	3	high	2	16,0	2	A	A
12C	3	medium	4	16,0	2	P	P
12D	3	medium	3	24,0	2	A	A
12E	3	medium	3	16,0	2	A	A
13A	3	medium	3	35,0	3	A	P
14A	3	high	2	23,0	2	A	A
15A	3	high	1	5,0	1	A	A
16A	1	high	1	23,0	2	P	P
17A	1	low	2	21,0	2	A	P
18A	2	medium	4	8,0	1	A	A
19A	3	low	3	14,0	2	A	P
19B	3	low	3	9,0	1	A	A
19C	3	high	2	5,0	1	A	A
19D	3	low	4	10,5	2	A	A
20A	3	high	4	8,0	1	A	A
21A	3	high	1	4,0	1	A	A
22A	1	low	1	5,5	1	A	A
23A	1	low	3	12,0	2	A	A
24A	3	medium	4	17,0	2	A	P
24B	3	low	2	30,0	3	A	P
25A	1	medium	5	3,0	1	A	A

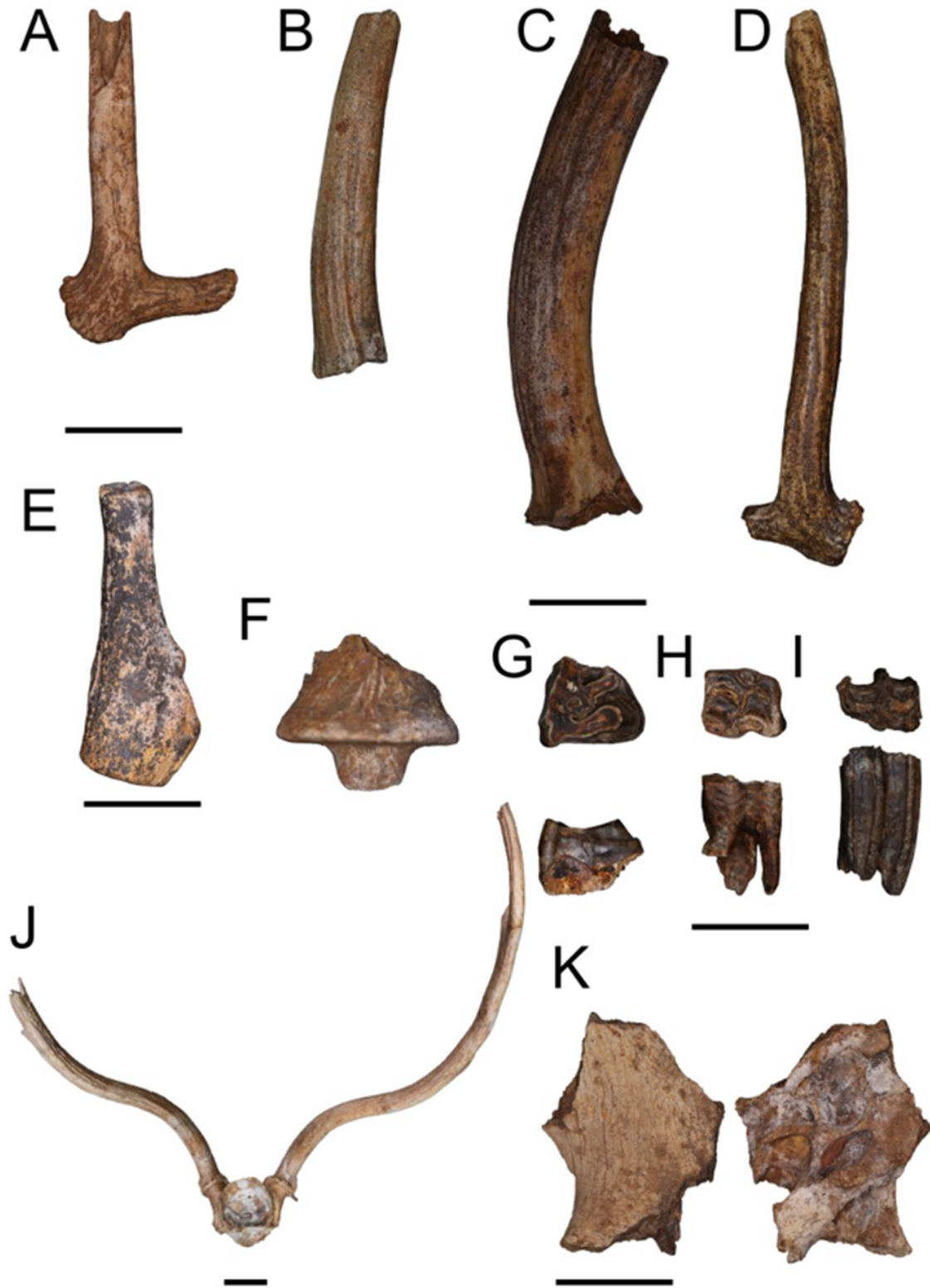
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Element number	Distance	Bone completeness	Weathering stage	Element size (cm)	Class size	Predation marks	Bioturbation marks
26A	3	low	3	26,0	2	A	P
26B	3	low	5	12,0	2	A	A
26C	3	low	5	10,0	1	A	A
IGF194 V	1	medium	2	40,0	3	A	A

A.7 Appendix 7

Cranial elements from the faunal assemblage of Cava Liberatori. A) 19A; B) 12B; C) 8B; D) 12D; E) 7B; F) 8A; G) 15A; H) 21A; I) 19C; J) IGF 197V; K) 18A. Scale bar 5 cm.



A.8 Appendix 8

Rib fragments from the faunal assemblage of Cava Liberatori. A) 19D; B) 5B; C) 10A, proximal fragment; D) 12E; E) 9A; F) 10A, distal fragment; G) 13A, proximal fragment; H) 13A, distal fragment; I) 11A. Scale bar 5 cm.



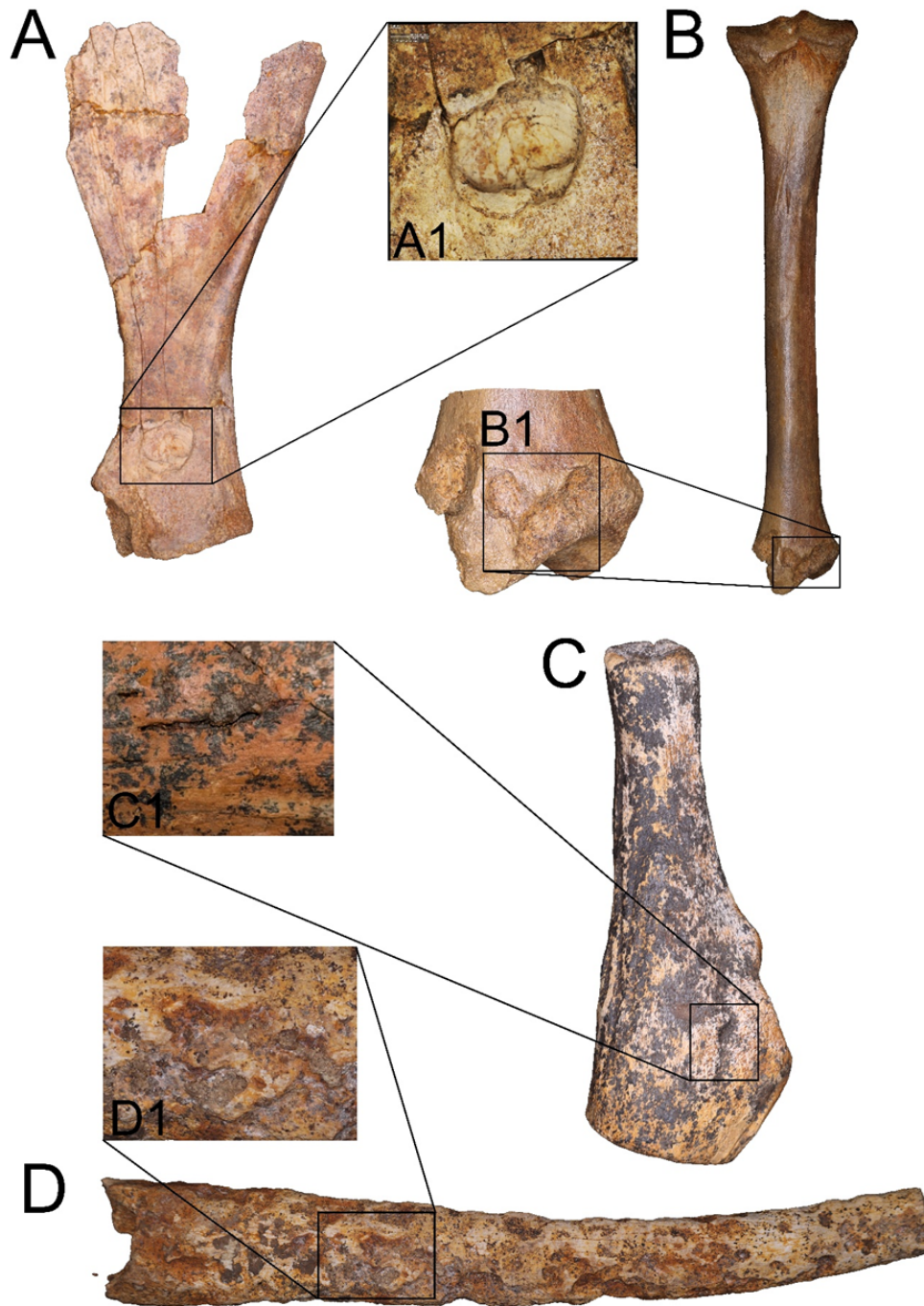
A.9 Appendix 9

Post cranial elements from the faunal assemblage of Cava Liberatori. A) 24A; B) 19B; C) 2C; D) 2B; E) 4A; F) 14A; G) 12C; H) 2A; I) 7A. Scale bar 5 cm.



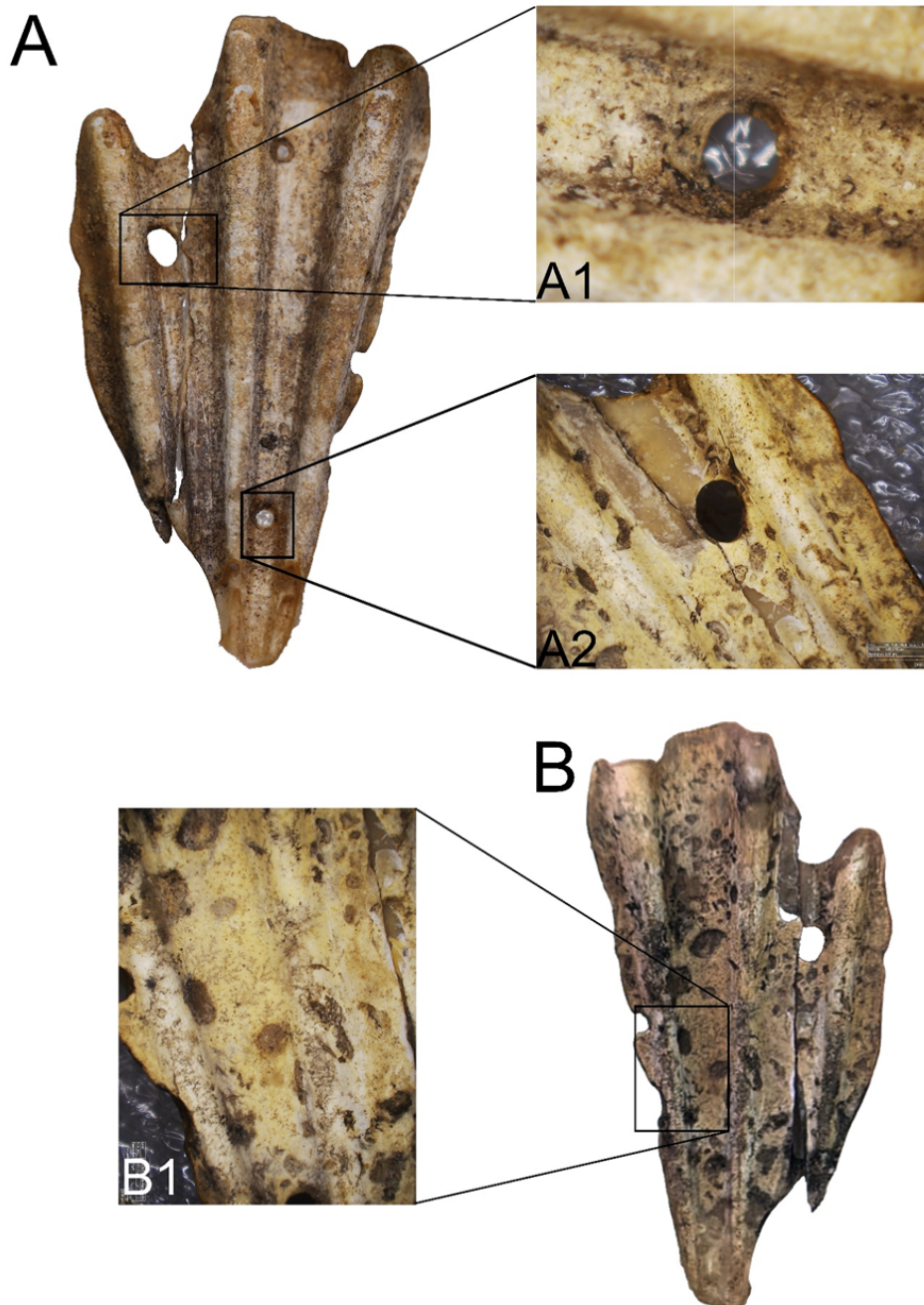
A.10 Appendix 10

Bioturbation and predation marks, examples. A) 6A; A1) Detail of deep large pit consistent with large predator bite; B) 16A; B1) Detail of three small pits consistent with cuspid marks of a predator tooth; C) 7B; C1) Root mark; D) 5B; D1) Heavy pitting caused by insect larvae. Specimens not to scale.



A.11 Appendix 11

Specimen 12A, *Pecten jacobea*, with surface details. Images not to scale. A) Dorsal surface; A1) Predation hole; A2) Inorganic-made hole; B) ventral surface; B1) detail on manganese oxidation and bioerosion of the surface.



A.12 Appendix 12

List of individual accesses to the website Linda. from Dicembre 2024 to July 2025. The list is a preview; to access the full list of entrances please click on the following link: <https://figshare.com/s/15c1a7bf53ce17526940>

URL path	Date	Session day	Browser		Device	City	Country	Region
/schede- animali/stephanorhinus- etruscus	01/12/2024	Sunday	Chrome		Mobile	Unknown	Italy	Unknown
/schede- animali/stephanorhinus- etruscus	01/12/2024	Sunday	Mobile	Samsung	Mobile	Florence	Italy	FI
/schede- animali/stephanorhinus- etruscus	01/12/2024	Sunday	Mobile	Samsung	Mobile	Florence	Italy	FI
/	01/12/2024	Sunday	Safari		Mobile	Unknown	Italy	Unknown
/schede- animali/stephanorhinus- etruscus	01/12/2024	Sunday	Chrome		Mobile	Unknown	Italy	72
/	01/12/2024	Sunday	Chrome		Mobile	Unknown	Italy	Unknown
/	01/12/2024	Sunday	Safari		Mobile	Unknown	Italy	Unknown
/	01/12/2024	Sunday	Chrome		Mobile	Florence	Italy	FI
/	01/12/2024	Sunday	Safari		Mobile	Unknown	Italy	Unknown

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URL path	Date	Session day	Browser		Device	City	Country	Region
/	01/12/2024	Sunday	Mobile	Samsung	Mobile	Florence	Italy	FI
			Browser					
/schede-animali/mammuthus-meridionalis-mandibola	01/12/2024	Sunday	Chrome		Mobile	Lucca	Italy	LU
/schede-animali/stephanorhinus-etruscus	01/12/2024	Sunday	Chrome		Mobile	Milan	Italy	MI
/	01/12/2024	Sunday	Chrome		Mobile	Florence	Italy	FI
/schede-animali/mammuthus-meridionalis-difesa	01/12/2024	Sunday	Safari		Mobile	Unknown	Italy	Unknown
/	02/12/2024	Monday	Chrome		Mobile	Unknown	Italy	25
/schede-animali/stephanorhinus-etruscus	02/12/2024	Monday	Safari		Mobile	Collesalveti	Italy	LI
/	02/12/2024	Monday	Chrome		Mobile	Unknown	Italy	25
/schede-animali/mammuthus-meridionalis-difesa	02/12/2024	Monday	Chrome		Mobile	Unknown	Italy	25

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URL path	Date	Session day	Browser	Device	City	Country	Region
/schede- animali/stephanorhinus- etruscus	03/12/2024	Tuesday	Mobile Browser	Samsung	Mobile	Milan	Italy MI
/	03/12/2024	Tuesday	Chrome	Mobile	Florence	Italy	FI
/	03/12/2024	Tuesday	Chrome	Mobile	Parma	Italy	PR
/	03/12/2024	Tuesday	Chrome	Mobile	Perugia	Italy	PG
/schede- animali/stephanorhinus- etruscus	03/12/2024	Tuesday	Chrome	Mobile	Perugia	Italy	PG
/en/schede- animali/pseudodama- farnetensis-palchi	04/12/2024	Wednesday	Safari	Mobile	Madrid	Spain	M
/schede- animali/mammuthus- meridionalis-difesa	04/12/2024	Wednesday	Mobile Browser	Samsung	Mobile	Florence	Italy FI
/schede- animali/pachycrocuta- brevirostris	04/12/2024	Wednesday	Chrome	Mobile	Florence	Italy	FI
/	04/12/2024	Wednesday	Safari	Mobile	Madrid	Spain	M

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URL path	Date	Session day	Browser	Device	City	Country	Region
/schede- animali/stephanorhinus- etruscus	04/12/2024	Wednesday	Chrome	Mobile	Pelago	Italy	FI