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Taphonomy of Fossil Small Mammals in Eastern Africa: A Methodological Review

Eastern Africa, with its rich and diverse fossil record, provides a unique setting for taphonomy studies. This region's complex geological history and climatic variability have made it a focal point for understanding environmental and climatic shifts over millions of years. Small mammals, ranging from rodents to shrews, are particularly significant in this context, offering insights into past habitats and climatic conditions, which are essential for reconstructing the region's ecological and evolutionary history.

Despite the importance of small mammals in taphonomic studies, their analysis presents unique challenges due to their susceptibility to taphonomic bias and the intricacies involved in their collection and interpretation. Methodological advancements in taphonomy have significantly improved our understanding of these small mammals, highlighting their crucial role in paleoenvironmental reconstructions and studies on human evolution.

Recent advancements in digital technologies, such as 3D digitization, geometric morphometrics, and advanced microscopy, have revolutionized the analysis of small mammal fossils. These tools allow for detailed, non-destructive examinations of bone surface modifications, providing more precise reconstructions of past behaviours and environmental conditions.

This review paper examines various methodologies used in taphonomic analysis of small mammal fossils from eastern Africa. It identifies the strengths and limitations of these methods and proposes ways to enhance their reliability and reproducibility. By addressing these methodological challenges and integrating advanced digital tools, taphonomic research can offer a more comprehensive understanding of eastern Africa's paleoenvironmental history and contribute significantly to our knowledge of ecological and human evolution in this region.

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Pienten nisäkkäiden fossiilien tafonomia: metodologinen katsaus

Itäinen Afrikka on rikkaan ja moninaisen fossiilistonsa ansiosta ainutlaatuinen alue tafonomisille tutkimuksille. Alueen monipuolinen geologinen historia ja ilmastollinen vaihtelevuus ovat tehneet siitä keskeisen alueen miljoonien vuosien aikana tapahtuneiden ympäristöllisten ja ilmastollisten muutosten ymmärtämisessä. Pienet nisäkkäät, jyrsijöistä päästäisiin, ovat tässä yhteydessä erityisen merkittäviä, sillä ne antavat tietoa menneistä elinympäristöistä ja ilmastollisista olosuhteista, jotka ovat oleellisia alueen ekologisen ja evoluutiollisen historian rekonstruoimisessa.

Huolimatta pienten nisäkkäiden merkittävyydestä tafonomisissa tutkimuksissa niiden analyysi asettaa erityisiä haasteita, johtuen niiden alttiudesta tafonomisille vinoumille sekä mutkikkuuksista, jotka liittyvät niiden keräämiseen ja tulkintaan. Metodologiset edistysaskeleet tafonomiassa ovat merkittävästi edistäneet ymmärrystämme näistä pienistä nisäkkäistä ja korostaneet niiden erityisasemaa paleoympäristöllisissä rekonstruoinneissa sekä ihmisen evoluution tutkimuksissa.

Viimeaikaiset innovaatiot, kuten 3D-digitalisaatio, geometrinen morfometria ja kehittynyt mikroskopia, ovat mullistaneet pienten nisäkkäiden fossiilien analysoinnin. Nämä työkalut mahdollistavat yksityiskohtaista ja kajoamatonta tarkastelua luiden pintamodifikaatioista ja mahdollistavat siten tarkempia rekonstruointeja menneistä käytännöistä ja ympäristöolosuhteista.

Tämä artikkeli tarjoaa katsauksen menetelmiin, joita hyödynnetään itäisestä Afrikasta löytyneiden pienten nisäkkäiden fossiilien analyysissä. Artikkelissa arvioidaan eri menetelmien vahvuuksia ja rajoituksia sekä esitetään keinoja parantaa menetelmien luotettavuutta ja toistettavuutta. Ottamalla kantaa näihin metodologisiin haasteisiin ja integroimalla kehittyneitä digitaalisia työkaluja tafonominen tutkimus voi tarjota perusteellisemman käsityksen itäisen Afrikan paleoympäristöllisestä historiasta sekä edistää ymmärrystämme ekologisesta ja ihmisen evoluutiosta tällä alueella.

Introduction

Taphonomy, first described by I. A. Efremov in 1940, as "a study of the transition of animal remains from the biosphere into lithosphere", has evolved to include essential tools with new modified descriptions for paleoanthropological research. The earliest taphonomy definition was made by Johannes Weigelt who was known for his studies on alligators, birds, fishes, and insects, in 1927 (translation into English; Weigelt 1989) which is the full-scale research effort to document processes of vertebrate death, decay, disarticulation, transport, and burial.

Today, the field of taphonomy has expanded to infer past biological, geological, and chemical events or processes that formed the object and its accumulation such as fossils, bones, shells, and pollen (Lyman 1987, 1994; Martin 1999; Shipman 1981) and integrates with disciplines such as paleontology, archaeology, forensic science, conservation biology, and ecology to provide a comprehensive understanding of fossilization and past environments (Behrensmeyer et al. 2000; Cambra-Moo et al. 2024; Haglund & Sorg 2001; Viciano et al. 2022). By collaborating across these fields, researchers can develop more robust models of how organisms decay, become buried, and are preserved over time. This interdisciplinary approach enriches the study of taphonomy, offering broader perspectives and more detailed reconstructions of ancient ecosystems and the conditions that influenced their development.

Contextually using taphonomy enhances the understanding of paleoreconstructions, providing insights into the depositional history and use of archaeological sites. Contextual taphonomy is an archaeological approach that integrates taphonomic variables with stratigraphy and context, often at the intra-site level (Borrini et al. 2012; Meier & Yeshurun 2020; Russell 2011). A majority of zooarchaeological research explores vertebrate taphonomy broadly by entire temporal levels of sites, thus aggregating multiple contexts by period (Lansing et al. 2009; Roberts et al. 2020; Thompson 2020; Thompson et al. 2023). Yet, an increasing number of high-resolution studies go beyond this level to explore taphonomy per context or by other meaningful intra-site divisions (Courtenay et al. 2019; Maté-González et al. 2017; Moretti et al. 2015). This approach presents the rich information offered by the well-established discipline of taphonomy to build depositional histories of site features that contain bones, thereby revealing their formation and use.

Taphonomic studies in paleontology, particularly in eastern Africa, play a pivotal role in understanding paleoecological and paleoenvironmental contexts of mammal fossils (Alin & Cohen 2004; Bedaso et al. 2010; Behrensmeyer 1975; Behrensmeyer et al. 1979; Domínguez-Rodrigo et al. 2015). The region’s complex geological history and climatic variability have created fossiliferous deposits that reveal evolutionary and environmental shifts over millions of years (Behrensmeyer 1988). However, methodological inconsistencies in taphonomic analysis, stemming from excavation techniques, laboratory methods, and interpretative frameworks, have led to varied interpretations of the fossil record (Lyman 1994).

Small mammals (typically referring to rodents, shrews, and other small-sized vertebrates) provide unique insights into past habitats and climatic conditions. Their remains are invaluable for reconstructing eastern Africa's ecological and evolutionary history (Andrews 1990a; Denys 1997; Fernández-Jalvo et al. 1998). Despite their significance, small mammals are particularly vulnerable to taphonomic biases, requiring refined collection and analysis methods to ensure accurate paleoenvironmental reconstructions (Behrensmeyer 1978; Behrensmeyer et al. 1980; Miller et al. 2014). Over time, the importance of small mammals in paleoreconstruction has been increasingly recognized due to their sensitivity to environmental changes and widespread fossil presence (Bedaso et al. 2010; Fernández-Jalvo et al. 1998; Louchart et al. 2009; Reed & Denys 2011; Thompson et al. 2015). However, taphonomic analysis presents significant complexities, particularly for animals with small body sizes and distinct life history dynamics. Although it is known that small mammals are more susceptible to taphonomic bias compared to larger mammals, based on differences in collecting methods, are considered significant indicators in paleoenvironmental reconstructions (Behrensmeyer 1978; Behrensmeyer et al. 1980; Miller et al. 2014). This complexity highlights the need for standardized and refined taphonomic methods to reduce biases and improve the accuracy of paleoenvironmental reconstructions based on small mammal fossils.

This review paper examines the methodologies employed in taphonomic analyses of small mammal fossils from eastern Africa, assessing their strengths and limitations while evaluating the outcomes and approaches of the relatively limited existing studies in this region. It further proposes strategies to enhance methodological reliability and emphasizes the necessity of region-specific research to address the unique climatic and geological contexts of eastern Africa. By refining these approaches, the study aims to support more accurate reconstructions of past environments, ultimately contributing to a deeper understanding of the ecological and geological landscapes in which our ancestors evolved.

The analysis follows the framework outlined by Peter Andrews in Owls, Caves, and Fossils (1990a) for categorizing taphonomic agents and incorporates methodologies from The Human Bone Manual by Tim D. White and

Pieter A. Folkens (2005) for structuring the taphonomic analysis on small mammal fossil remains. These works provide the foundation for categorizing taphonomic agents in this paper. Peer-reviewed papers and book chapters selected for this review focus on small mammal fossils from Pleistocene sites in eastern Africa. A topographic map was created using ArcGIS Pro 3.2.0 (Esri 2023) to visually represent these sites, with approximate coordinates determined from data provided in the articles. This enhances the spatial understanding of the research context. Additionally, relevant photographs from the fossil collection at the National Museum of Ethiopia, part of my ongoing research, have been incorporated.

Climatic, ecological, and geological background of East Africa, the cradle of humankind

East Africa, often described as the cradle of humankind, covers approximately 7 million square km; and uniquely encompasses virtually every habitat, including tropical rainforests, deserts in the Horn of Africa and northern Kenya, and various savannah types. The rifting process has created localized habitats, such as montane regions, high escarpments, and lake basins. East Africa's climate ranges from arid to humid, with coastal humidity supporting diverse faunal populations and inland plateaus experiencing cooler, drier conditions (Sepulchre et al. 2006; Trauth et al. 2005). The region has two rainy seasons affecting vegetation, which includes forests at higher altitudes and around lakes, open savannas, and semi-desert in the lowlands. Fertile volcanic soils in rift valleys support agriculture and relic forests with indicator species, reflecting past faunal distributions. These diverse climates and landscapes shape local ecosystems, migratory patterns, and breeding seasons (Kingdon 2014; Yang et al. 2015).

East Africa has hosted the emergence and diversification of humans due to its climatic and ecological changes over the last 6 million years. Climate change has been a major driving force in human evolution, with cycles of cooling and drying over 6 million years. The climatic shifts between 5 and 1.8 million years ago catalyzed periods of speciation and extinction within the hominin lineage. Critical periods around 2.8 million, 1.7 million, and 1 million years ago saw marked evolutionary developments in animals and hominins, notably coinciding with the rise of the genus Homo (Bobe et al.

2007; DeMenocal 1995; DeMenocal 2004; Fortelius et al. 2016; Maslin & Trauth 2009; Potts 2012). These evolutionary milestones align with significant climatic episodes, underscoring the potential influence of environmental changes on evolutionary ways.

During the Pleistocene period (last 2.6 my), there were eleven distinct glacial periods, and the Last Glacial Maximum (LGM) was a phase marked by cooler and predominantly drier conditions in the tropical areas (Gasse et al. 2008). Climate fluctuations have profoundly impacted both the distribution and evolution of fauna and flora. Pollen and spore deposits in marine sediments track the shifting of biomes. This aligns with the dynamic adjustments of savannahs and tropical forests to glacial cycles and sunlight patterns (Trauth et al. 2007). Moreover, in East Africa, these climate changes, particularly periods of intense wetness or drought tied to Earth's orbital eccentricity, appear to have influenced mammalian speciation including hominin evolution. The interplay of rapid climatic shifts, tectonic forces, and volcanic activity in this region not only sculpted its landscape but also offered the environmental diversity that may have been critical for early human evolution (Dupont 2011; Levin 2015). Humid conditions during the Middle Pleistocene (approximately 781,000 to 126,000 years ago) provided environmental stability for early hominins, while abrupt climate oscillations fragmented habitats, driving population isolation and increasing diversity among hominin groups (Foerster et al. 2022).

East Africa's complex habitat mosaics, created by its varied topography and climate, provided a range of ecological niches that likely contributed to the development of diverse human adaptations and innovations. The region's importance is underscored by genetic, fossil, and archaeological evidence, indicating a prolonged and complex process of modern human evolution that was influenced by major climatic oscillations (Mirazón Lahr & Foley 2016; Roberts et al. 2020). These factors combined to make eastern Africa a central area for studying the origins and evolution of *Homo sapiens*, highlighting its critical role in our understanding of human history.

The East African Rift System (EARS) is a prominent geological feature of eastern Africa, characterized by a series of conjunction faults stretching approximately 4,000 km from the Red Sea in the north to the Zambezi River in the south. The rift system, which began forming around 30 million years ago during the Oligocene epoch, is a result of the extension and thinning of the African Plate (McConnell 1972). This geological process has led to significant volcanic activity, particularly in regions like the Ethiopian and Gregory Rifts, which are associated with intense volcanism due to the presence of mantle plumes. In these areas, the interaction between tectonic activity and mantle dynamics has not only shaped the rift structures but also contributed to the formation of volcanic landscapes. These processes have influenced sedimentation patterns and environmental conditions, playing a critical role in shaping the habitats and ecosystems available for early hominins during the Plio-Pleistocene (Nutz et al. 2020; Scoon 2018). These volcanic activities significantly enhance the importance of the area for understanding human evolution, particularly with how environmental changes influenced human habitation and adaptation.

The formation of the EARS created isolated basins with fluctuating moisture and vegetation, shaping early hominin habitats. Periods of increased rainfall formed large lakes, aligning with global climate shifts crucial to human evolution. These cycles of wet and dry climates drove key evolutionary and migratory changes in Africa's mammals and hominins (Maslin & Trauth 2009). This narrative weaves a complex tale of how global climatic patterns and local geological transformations were central to the evolutionary saga of early humans, underscoring the need for more nuanced investigations into this interdependence.

Ecology of East African small mammals

Small mammals, due to their short lifespans, small spatial ranges, response to seasonal behavioural changes, and dispersal upon reaching adulthood, play a crucial role for ecologists (Barrett & Peles 1999). Understanding small mammals' habitat preferences, population dynamics, and behavioural adaptations in their habitats provides insights into the broader paleoecological processes and environmental changes in the past. Rodentia (rodents) is the largest group among all mammals, encompassing over 2,000 species, which account for approximately 44 % of all mammalian species, not just among small mammals. Their size ranges from as small as 10 grams to as large as 66 kilograms (Denys 2011; Winkler et al. 2010; Yalden et al. 1976).

Rodents are distinguished by their single pair of sharp incisors, used for gnawing, tunnelling, and self-defense. They are highly versatile, inhabiting every continent except Antarctica, with many species living in close association with humans. Rodents include five primary families: Muridae (rats and mice), Sciuridae (squirrels), Echimyidae (spiny rats), Heteromyidae (pocket mice and kangaroo rats), and Dipodidae (jerboas and jumping mice) (Winkler et al. 2010). The evolutionary history of rodents dates back to the Paleocene epoch, around 55–60 million years ago, with Paramyidae as the oldest known family. Climatic changes have driven significant faunal turnover, leading to diverse adaptations and the wide distribution of rodents across various ecosystems. These evolutionary processes are not unique to rodents; they share a close evolutionary relationship with Lagomorpha, a group that includes rabbits, hares, and pikas. Together, rodents and lagomorphs form the clade Glires, a connection supported by both morphological and molecular evidence (Blois & Hadly 2009; Hartenberger 1985; Murphy et al. 2001; Reed 2003; Werdelin & Sanders 2010). The taphonomy of small mammal fossils, especially rodents, is crucial for their ecological significance in fossil records.

Fossil species across size categories reflect environmental conditions and habitat diversity. Small mammals like *Mus* and *Gerbillus* indicate open or semi-arid environments, often found in predator-accumulated assemblages. Medium-sized species, including *Otomys* and *Arvicanthis*, are common in diverse habitats and signal wetter, grassland conditions. Large mammals such as *Thryonomys swinderianus* suggest stable, localized environments like riparian zones. Very large species like *Hystrix* provide insights into burrowing behaviours and adaptations to open landscapes (Table 1).

In eastern Africa, small mammals face diverse predators, reflecting the region's rich biodiversity. Predators include birds of prey like owls and eagles, carnivorous mammals such as hyenas and mongooses, reptiles, and even humans. Predation impacts small mammal mortality rates and population sizes, influencing environmental settings. Predators also accumulate small mammal bones, creating assemblages that vary in composition and species representation based on predator niches. These assemblages, often preserved but modified, offer insights into predator activities and environmental interactions. Identifying the predator provides a critical context for understanding biases in bone assemblages and broader ecological hierarchies (Andrews 1990b; Kusmer 1990; Palmqvist & Arribas 2001). Fossil evidence reveals environmental changes over time, with wetter, stable conditions in the Pliocene transitioning to expanding grasslands in the Early Pleistocene. The Middle Pleistocene shows alternating open and closed habitats due to climatic fluctuations, while the Late Pleistocene is marked

Table 1: Most common fossil species by size categories (Data compiled from various sources: Andrews 1990b; Barrett & Peles 1999; Denys 2011; Louchart et al. 2009; Reed 2003; Winkler et al. 2010).

Size Category	**Common Fossil Species**	**Remarks**
Small (< 100 g)	*Mus* (House mouse), *Gerbillus* (Gerbils), *Taterillus* (Gerbils), *Saccostomus* (Pouched mice)	These species are often found in predator-accumulated assemblages, indicating open or semi-arid environments.
Medium (100–500 g)	*Otomys* (Vlei rats), *Arvicanthis* (Grass rats), *Thryonomys gregorianus* (Lesser cane rat), *Acomys* (Spiny mice)	Common in diverse habitats; *Otomys* and *Arvicanthis* are often indicators of wetter, grassland environments.
Large (500 g–2 kg)	*Thryonomys swinderianus* (Greater cane rat), *Tachyoryctes* (Mole rats)	These species are indicators of more stable and localized habitats, such as riparian zones or dense vegetation.
Very Large (> 2 kg)	*Hystrix* (Porcupines)	Rarely found but significant for understanding larger burrowing behaviours and adaptations to open landscapes.

by arid-adapted small mammals and increasing human influence (Table 2). However, interpreting these changes through small mammal fossils is challenging due to taphonomic processes such as bone destruction, transport, predation, rodent gnawing, weathering, and trampling, which can skew fossil assemblages and reduce their representativeness of original communities (Kovarovic et al. 2018).

When analyzing fossil records from the Pliocene of eastern African sites, such as Omo, Aramis in the Afar region, and Olduvai (Figure 1) the challenges increase due to the sites' distinct tectonic and depositional histories, affecting sedimentation rates and fossil preservation. Smaller species, especially those weighing less than 10 kg, are often under-represented at sites like Laetoli due to surface processes that disproportionately affect their preservation (Reed & Denys 2011). As a result, the fossil record may not accurately

Table 2: Most common fossil species by period (Data compiled from various sources (Behrensmeyer & Reed 2013; Belmaker 2018; Bobe 2004; DeMenocal 2004; Denys et al. 2011; Fernández-Jalvo et al. 1998; Louchart et al. 2009; Reed 2003).

Time Period	**Common Fossil Species**	**Remarks**
Pliocene (5.3–2.6 mya)	*Thryonomys gregorianus* (Lesser cane rat), *Arvicanthis* (Grass rats), *Hystrix* (Porcupines)	Fossils reflect wetter and more stable environments, possibly associated with woodland-grassland mosaics.
Early Pleistocene (2.6–0.8 mya)	*Thryonomys swinderianus* (Greater cane rat), *Otomys* (Vlei rats), *Gerbillus* (Gerbils)	Increased representation of open grasslands with intermittent wet phases.
Middle Pleistocene (0.8–0.1 mya)	*Arvicanthis* (Grass rats), *Otomys* (Vlei rats), *Mus* (House mouse).	Reflects climatic fluctuations with alternating open and closed habitats; predator accumulation prominent.
Late Pleistocene (0.1–0.01 mya)	*Mus* (House mouse), *Acomys* (Spiny mice), *Gerbillus* (Gerbils).	Dominated by small mammals adapted to arid or semi-arid environments; influenced by human activities.

reflect the original diversity of these communities. To illustrate, small mammals are notably scarce in the Chiwondo Beds in Malawi, a taphonomic issue that limits their representation (Sandrock et al. 2007). However, despite this scarcity, one new rodent species has been identified in the Chiwondo Beds (Denys et al. 2011). The discovery of this porcupine is significant as it sheds light on the paleoenvironments of the region, suggesting a relatively open landscape around 2.5 to 2.33 million years ago. This finding also highlights taphonomic challenges in the Chiwondo Beds, where small mammals are rare due to sedimentological factors like high-energy systems, hydraulic sorting, and diagenetic processes that likely led to the destruction of smaller mammal bones.

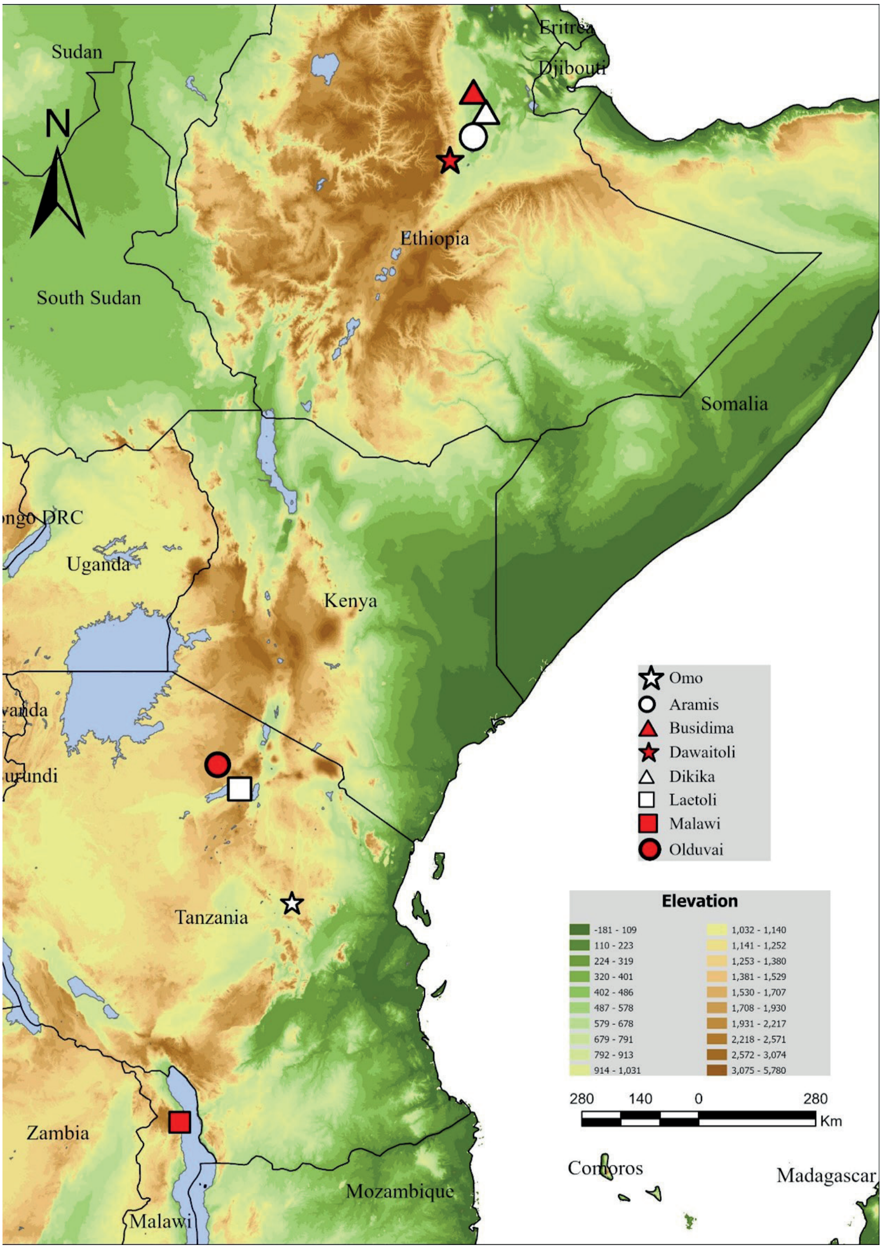

Figure 1. Small mammal fossils sites in eastern Africa.

In addition to these challenges, there are significant risks involved when working with small mammal fossils in taphonomic studies. Predators often accumulate mammal remains in ways biased by their hunting territories and behaviours, which makes these assemblages less reliable for paleoecological studies. Key issues include the link between territory size, hunting scope, and group size of predators, along with the influence of habitat size and complexity on prey diversity. Territory size is mainly dictated by resource distribution rather than richness and can support a comparable number of predators if productivity is similar. Therefore, in paleoecological studies, small mammal diversity and habitat richness are more critical indicators of prey diversity than the size of predator territories (Andrews 1990a). These risks highlight the potential for misinterpretation when reconstructing past environments based solely on predator-accumulated remains. Predators accumulate small mammal remains in ways biased by their hunting territories and behaviours, which makes these assemblages less useful for paleoecological studies. Key issues include the link between territory size, hunting scope, and group size of predators, along with the influence of habitat size and complexity on prey diversity. Territory size is mainly dictated by resource distribution, not richness, and can support a comparable number of predators if productivity is similar. Therefore, in paleoecological studies, small mammal diversity and habitat richness are more critical indicators of prey diversity than the size of predator territories (Andrews 1990a).

To minimize the effects of taphonomic biases, researchers employ isotaphonomic approaches (Behrensmeyer 1975). This method involves selecting localities that meet specific taphonomic criteria, ensuring that observed faunal changes are not artifacts of differential preservation or accumulation processes. Such an approach helps provide a more accurate representation of the original community structure, leading to more reliable paleoenvironmental reconstructions. Notable examples of studies applying these methodologies include Laetoli in Tanzania, where small mammal remains have been extensively studied to understand their paleoenvironmental implications. The accumulation of these remains is influenced by various factors, including predator activities and sedimentary processes, which are carefully considered in paleoecological studies (Reed & Denys 2011).

The rodent remains from Goda Buticha (43 ka BP to 4 ka BP) reveal that nocturnal bird predation primarily accumulated the assemblages, with

Table 3. Most common fossil species by geography (Data compiled from various sources (Arcos et al. 2010; Bedaso et al. 2010; Denys et al. 2011; Everett 2010; Fernández-Jalvo et al. 1998; Louchart et al. 2009; Reed & Denys 2011; Sandrock et al. 2007).

Region/Geography	**Common Fossil Species**	**Remarks**
Ethiopian Highlands	*Thryonomys gregorianus* (Lesser cane rat), *Otomys* (Vlei rats), *Tachyoryctes* (Mole rats).	Indicators of wet, grassy habitats; reflect montane or highland vegetation.
Afar Region	*Thryonomys swinderianus* (Greater cane rat), *Hystrix* (Porcupines), *Mus* (House mouse).	Suggests mosaic environments, including open grasslands and woodland patches.
Eastern Rift Valley	*Arvicanthis* (Grass rats), *Otomys* (Vlei rats), *Gerbillus* (Gerbils).	Reflects semi-arid to grassland conditions with varying water availability.
Olduvai Gorge (Tanzania)	*Mus* (House mouse), *Thryonomys* (Cane rats), *Arvicanthis* (Grass rats).	Assemblages influenced by predator activity, particularly owls and carnivores.
Laetoli (Tanzania)	*Arvicanthis* (Grass rats), *Gerbillus* (Gerbils), *Acomys* (Spiny mice).	Suggests a mix of dry grasslands and wooded environments with seasonal variability.

minimal post-depositional disturbance. Environmental reconstructions indicate arid Late Pleistocene conditions transitioning to wetter, wooded Holocene habitats, aligning with Middle and Later Stone Age cultural shifts (Stoetzel et al. 2018). In many instances, small mammal fossils are found in conjunction with hominin fossils, providing valuable data for reconstructing past environments. These animals inhabit diverse environments ranging from forests to deserts, and each species has specific requirements that affect their distribution and abundance. In a taphonomic context, the most significant families often include rodents and lagomorphs, which have relatively small territorial ranges (Fernández-Jalvo et al. 1998; Reed et al. 2019). These characteristics make small mammals particularly useful for identifying shifts in past environments over time.

In addition to the sites reviewed in this paper, ongoing taphonomic research as part of the first author's doctoral study is being conducted on small mammal fossils from the Dawaitoli Formation (DW Fm) in the Afar region of Ethiopia (Figure 2). This study contributes to the understanding of the depositional and taphonomic process of the fossil small mammal assemblages stratigraphically associated with hominin findings and their implications for paleoenvironmental reconstructions. The findings of this research, which is currently unpublished, are expected to contribute new insights into the role of small mammals in understanding the paleoenvironmental context of human evolution in eastern Africa.

Sampling methods in taphonomic analyses

Sampling methods are essential in taphonomic analyses, particularly when discerning pre- and post-depositional modifications, a task that gains complexity with smaller animals. In eastern Africa, wet and dry sieving or screening with various mesh sizes is the primary technique used for these

Figure 2. Rodent (*Gerbillinae taterillus*) skull fossil from Afar. Image by S. Yilmaz, 2024, National Museum of Ethiopia.

analyses (Figure 3), as it accommodates the diverse study needs across the region. The choice of appropriate sampling methods significantly impacts paleontological research, as it influences factors such as sampling bias, fossil integrity, representativeness, and practical efficiency.

Wet screening, which involves washing sediments through sieves with water, tends to preserve delicate fossil structures better than dry screening, which might cause more mechanical damage. This method not only helps in recovering smaller, more fragile fossils, potentially overlooked by dry screening, but also in avoiding biases that may alter interpretations of fossil sites. The suitability of each method depends on the specific sediment type, fossil content, and prevailing environmental conditions, aiming to accurately represent the original biotic community or death assemblage (Henderson 1987; Lorenzon 2018). However, the feasibility of these methods is also constrained by practical considerations, such as the availability of resources like water, particularly in arid areas.

Another role of sampling methods by demonstrating noticeable differences in recovered paleocommunities, where surface samples often show enrichment influenced by bias and weathering. In-place bulk collection to obtain more reliable results in taphonomic analyses, minimizing biases associated with surface collections (Forcino & Stafford 2020). Following protocols established by Domínguez-Rodrigo et al. (2009), such methods are commonly used in research on small mammals in eastern Africa.

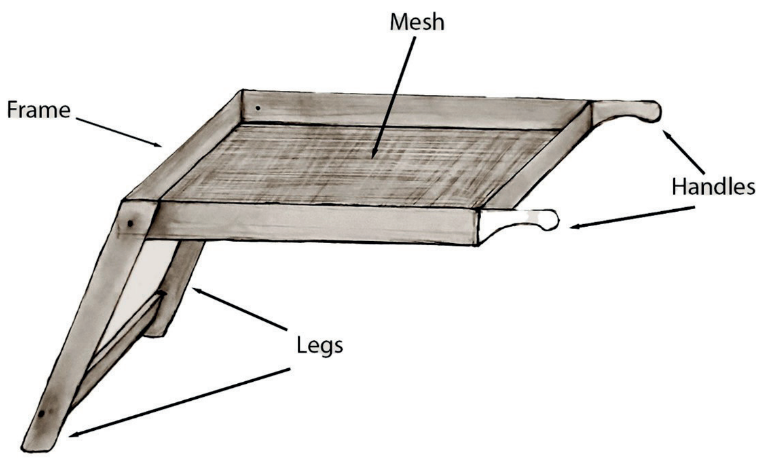

Figure 3. Example of sieving box illustration adapted from Lorenzon 2018. Image by S. Yilmaz.

At sites like Dikika (Thompson et al. 2015), researchers have implemented an additional "circle collections" method to enhance their investigative outcomes. In Laetoli, wet screening has proven particularly effective in earlier collections, significantly improving the diversity and abundance of microvertebrate fossils, and demonstrating its superiority in capturing a broader array of smaller-bodied taxa. In Olduvai, screens used in the field were relatively coarse and it is probable that during sample sorting, crania, and complete postcrania were preferentially selected.

In addition to these studies, the fossil small mammal collection of the first author's doctoral research involves the collection of specimens using a combination of dry sieving/screening, and surface collection methods. These small mammal fossils were collected in association with larger mammal remains, including hominins from the late Pleistocene of the Afar region in Ethiopia. The sampling process was led by the second author, ensuring the recovery of both micro and macrofaunal remains from the site. This method aims to capture a comprehensive representation of the faunal assemblage, providing valuable insights into the paleoenvironmental conditions and potential taphonomic biases inherent in different collection techniques.

Bone modification on small mammals

After the decay of soft tissues, skeletal disarticulation commences, shaped by natural decay processes and interactions with humans or animals. The integrity and type of joints, like sutural ligaments in the skull or synovial capsules in movable joints, are crucial in determining disarticulation patterns. The natural, biological, and physical factors, including microorganism actions, plant growth, predator activities, and human interventions like dismemberment and cannibalism, affect postmortem bone modification as well (Micozzi 1991).

Physical agents

Bone surface modifications are critical in understanding the interactions between skeletal remains and their environment. Various types of modifications provide different insights.

Weathering

Bone weathering analysis stands as a critical method in both paleoecology and archaeology, providing deep insights into the timing, environmental settings, and ecological interactions linked with fossil finds. This technique enriches our grasp of ancient life and its surroundings by playing a key role in taphonomic studies and the reconstruction of past landscapes. Through the classification of bones into specific weathering stages, researchers can reveal the time elapsed since an organism's death. This process reveals whether bone collections stem from slow, ongoing natural processes or sudden, catastrophic events. Moreover, it underscores the impact of local environmental factors on the rate of bone weathering, offering valuable information about the ancient depositional settings and the ecological frameworks they supported. Bone weathering analysis thus facilitates a comprehensive understanding of past ecosystems, the evolution and habits of extinct species, and the detection of biases and patterns of preservation in the fossil record. As such, it proves to be an invaluable resource for the accurate interpretation of archaeological and paleontological sites, significantly advancing our knowledge of prehistoric life and habitats (Behrensmeyer 1978).

For mammals larger than 5 kg, the six weathering stages apply, but no classification exists for smaller animals. The bones of smaller mammals like the African hare (*Lepus capensis*) show different weathering characteristics, with more cracking and splintering than flaking. Similarly, the bones of birds, reptiles, and fish differ from those of mammals and each group will require separate studies for weathering characteristics (Behrensmeyer 1978). As a result, these bones can be more challenging to study within the same framework used for larger mammals. The lack of a formal classification system for the weathering stages of small mammal bones highlights the need for further research to develop criteria that account for the unique taphonomic processes affecting these smaller specimens.

However, in Olduvai, the weathering analysis of small mammals in Bed-I reveals several key findings. In particular, the fossils from the FLK-Zinj level show evidence of weathering stages 3–4, indicating prolonged exposure on the ground for approximately 10 to 15 years based on comparative modern studies. This level also displays signs of desquamation (surface peeling), which aligns with the high alkalinity of the sediment. In contrast, other levels such as FLKN6 exhibit less or no weathering, suggesting more rapid burial or non-exposure to open-air agents (Fernández-Jalvo et al. 1998). These findings imply different post-mortem processes and exposure durations between levels, impacting the condition of the fossil assemblages and potentially the environmental interpretations.

Trampling

Experimental studies on trampling effects have shown that trampling-induced damage can be misinterpreted as tool marks or carnivore gnawing (Courtenay et al. 2019; Domínguez-Rodrigo et al. 2009; Olsen & Shipman 1988). In Aramis, the high preservation and completeness of the bone assemblages suggest a low degree of trampling, consistent with environments where ground cover (e.g., vegetation) or softer sediment protects bones. The data also reveal predator bias, likely from barn owl predation, with most small mammal bones originating from small forested or savanna-like patches within a larger woodland setting. This bias provides valuable insights into the openness of the environment and predator-prey dynamics (Louchart et al. 2009). Further research across a broader range of environmental conditions and soil substrates is necessary to enhance our understanding of trampling impacts (Fernández-Jalvo et al. 2022). A comprehensive understanding of trampling effects is essential for accurately reconstructing past environments and distinguishing between natural and anthropogenic modifications in fossil assemblages.

Abrasion

Abrasion depends on sediment size, and bones previously altered by digestion or weathering were more susceptible to surface loss and rounding. It is important to consider these factors when interpreting fossil assemblages to avoid confusion between abrasion and other taphonomic processes like digestion (García-Morato et al. 2019). Abrasion patterns from small mammals in Olduvai, often referred to as polishing, were particularly evident on bones, indicating interaction with abrasive surfaces. This was attributed to factors such as sediment movement or trampling after burial. The degree of abrasion varied across different levels, with more pronounced polishing in certain layers like FLK-Zinj, where bones exhibited signs of extended exposure to mechanical processes (Arcos et al. 2010). These findings suggest that abrasion, along with other taphonomic factors, contributed to the alteration of the small mammal assemblages, impacting the completeness and preservation of skeletal elements.

In the Laetoli small mammal specimens, moderate levels of abrasion were frequently noted, especially in those from the Upper Ndolanya Beds (Reed & Denys 2011). This suggests that these specimens experienced more intense wear. Abrasion is commonly associated with diagenetic processes, likely due to the extended exposure of fossils to sedimentary environments.

In the Chiwondo Beds, the minimal abrasion of fossils indicates that the assemblages at these sites experienced relatively limited transport after deposition. The evidence suggests a mixture of autochthonous and allochthonous deposition, meaning that some remains were likely buried near the place of death, while others were transported over short distances (Sandrock et al. 2007). The lack of significant abrasion supports the idea that these fossils were deposited in a relatively low-energy environment such as a delta plain, where hydraulic sorting and minor transport occurred without heavily wearing down the bones.

Nonhuman biological agents

Digestion

The identification of digestion marks left by predators is crucial for understanding predator-prey dynamics in paleoenvironments (Figure 4). Digestion, in this context, refers to the chemical and mechanical alteration of bones as they pass through a predator's digestive system, resulting in features such as etching, pitting, or rounding on bone surfaces. These modifications are key parameters in taphonomic analyses, offering insights into the role of predators in small mammal ecology and the processes that influence fossil preservation (Dodson & Wexlar 1979; Korth 1979; Mayhew 1977; Mellett 1974).

The taphonomic data from Laetoli, particularly regarding digestion and breakage levels of small mammal fossils, provide insights into the environmental context during the Pliocene. The digestion marks observed on many small mammal bones suggest high predatory pressure, particularly from avian predators, such as owls and raptors. These marks indicate that such predators were significant in the ecosystem, contributing to the high digestion levels observed. This suggests an open landscape, where avian predators could easily spot and capture prey, aligning with the mosaic of grassland, shrubland, and open woodland habitats reconstructed from the site (Reed & Denys 2011). Thus, the digestion and breakage analyses help confirm a dynamic landscape with a mix of open and more densely vegetated areas, which would have affected both the behaviours of predators and the preservation of small mammal fossils at the site.

Taphonomic studies of small mammals from Olduvai Bed-I have demonstrated how environmental interpretations can be significantly altered through detailed analyses of small mammal taphonomy, particularly with digestion. Digestion processes have been shown to modify the composition of fossil assemblages, thereby complicating the reconstruction of past environments. This highlights the intricate interplay between environmental conditions and fossilization processes, suggesting that interpretations based solely on faunal composition may overlook key taphonomic factors that can obscure the true nature of ancient ecosystems (Fernández-Jalvo et al. 1998).

According to the taphonomic analysis of the small mammal fossils from FLK NW in Olduvai Gorge, the low presence of digestion marks indicates that the bones were primarily accumulated by predatory birds, most likely *Tyto alba* (barn owl). The lack of severe digestion damage on the bones suggests that these predators tend to swallow their prey whole and that they hunt small mammals from the surrounding environment. This information reveals that these predators were common in the area and collected their prey from nearby open spaces. The barn owl's hunting habits and the accumulation of pellets suggest that the environment during that period likely consisted of open landscapes (Arcos et al. 2010). These findings contribute to the reconstruction of the paleoenvironment, indicating that open habitats played a significant role in shaping the small mammal community at FLK NW during that time.

At the Boolihinan locality, situated in the upper Busidima Formation, small rodent fossils reveal distinctive taphonomic modifications. Evidence of gastric-acid etching on bone surfaces suggests that many of these remains were likely consumed and regurgitated by raptors, highlighting the role of avian predators in the accumulation and preservation of small mammal assemblages. The presence of whole raptor pellets alongside these remains further supports the conclusion that the assemblage results from raptor predation. The acid etching on the bones is a clear indicator of digestion by raptors, providing taphonomic insights into the ecological interactions between predators and prey during this period (Everett 2010). These taphonomic indicators suggest that raptors played a key role in shaping the small mammal assemblage at Boolihinan, offering valuable clues about predator-prey dynamics and the ecological conditions of the upper Busidima Formation.

In Aramis, the absence of extensive digestive damage (only 0.9 % on molars and 10.7 % on incisors) suggests that the micromammal remains were primarily accumulated by a predator like the barn owl (*Tyto*). Barn owls produce low levels of digestion and modification on bones compared to other predators, which indicates a relatively low degree of bone breakage (Louchart et al. 2009). These findings imply that barn owls were likely the main accumulators of micromammal remains at Aramis, offering valuable insights into predator activity and the relatively low degree of bone alteration in the assemblage.

Plant marks

Root marks on mammal bones are post-depositional modifications caused by plant roots interacting with buried bones. Roots leave imprints or

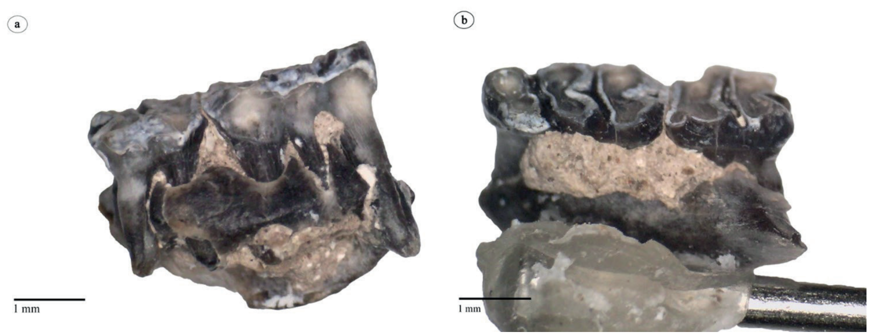

Figure 4. Photo of an *Arvicanthis* left mandible fragment with molar 1 and molar 2. a) Lingual view of the mandible displaying moderate digestion on the molars. b) Buccal view of the same mandible fragment. Images by S. Yilmaz, 2024, National Museum of Ethiopia.

grooves, and their organic acids can corrode bone surfaces where direct contact occurs. These marks, distinguished by branching patterns and localized etching, provide clues about post-burial environmental conditions and are distinct from processes like digestion or weathering (Fernandez-Jalvo & Andrews 1992).

The study on the taphonomy of the small mammal fossils from Aramis reveals that root etching on the bones is extremely rare. This is significant because root etching is often indicative of prolonged exposure to soil conditions where plant roots can grow over and leave marks on bones (Louchart et al. 2009). The lack of such marks suggests that the fossils were likely buried rapidly, reducing the time they were exposed to environmental factors like plant root growth.

Analysis of small mammal fossils from Olduvai revealed root marks concentrated in specific stratigraphic levels. These marks, alongside other taphonomic features like polishing and rounding, indicate post-depositional processes that altered the bone surfaces (Fernández-Jalvo et al. 1998). Root marks are important indicators of interaction between plant growth and the fossils, often reflecting the conditions of the soil and the environment in which the bones were buried.

In the Busidima region, small mammal fossils, particularly those from the Boolihinan locality show significant evidence of root or plant marks. These marks are observed as root etchings on the surface of bones, a common indicator of post-burial interaction with plant material. Such etching often occurs when roots grow around or through buried fossils, leaving distinct patterns on the bones (Everett 2010). These marks are essential in taphonomic studies as they provide insight into the post-depositional environment, such as soil composition and moisture levels, which influenced fossil preservation

In the taphonomic study of small mammal fossils from FLK NW level 20 in Olduvai Gorge, the researchers found evidence of postdepositional surface damage caused by plant roots. Root marks were identified as superficial alterations on the bones, typically resulting in slight surface etching (Arcos et al. 2010). These root marks, along with other forms of corrosion, were part of the natural post-burial processes that occurred after the bones were buried, interacting with soil properties such as alkalinity and moisture, which can further damage fossil surfaces.

Modifications by human: Cut mark analysis on small mammals in the context of human-animal interactions

Cut marks are linear grooves or incisions found on the surfaces of animal bones, which are typically produced by sharp-edged tools, such as stone flakes, used by ancient hominins. The morphology of these cut marks, including their width, depth, and cross-sectional shape, can vary significantly depending on several factors. These factors include the mechanical properties of the bones, such as hardness and elasticity, and the type and condition of the stone tool edge, which may change due to use and attrition. Complexity of accurately diagnosing cut marks due to the overlapping characteristics that can be produced by different actors (e.g., hominins, carnivores) and processes (e.g., butchery, abrasion) should be emphasized (Braun et al. 2016). Thus, a comprehensive understanding of cut marks involves considering the physical properties of both the bone surfaces and the tools that created them, highlighting the need for detailed and controlled experimental analysis to accurately interpret these traces of ancient behaviour.

To investigate the proposed cut marks on Olduvai material (Fernández-Jalvo et al. 1998), it is essential to note that small mammal fossils from East Africa remain underrepresented in the research. While numerous studies worldwide have analyzed cut marks on small mammals, such analyses are lacking in East Africa. This gap is likely due to the challenges posed by open environmental conditions in the region, which complicate the preservation and analysis of such marks.

From eastern Africa, there is one specific study on cut marks found on small mammals from Olduvai Gorge, which provides unique insights into early hominin behaviour (Fernández-Jalvo et al. 1999). This study, conducted at Bed-I of the site, reveals the earliest evidence of human predation on small mammals dating back to 1.76 million years ago. The presence of cut marks on hedgehog mandibles suggests that these marks were made during skinning activities, emphasizing the opportunistic and generalist dietary strategies of early hominins in this region. This finding enriches our understanding of how small mammals were integrated into the diet and subsistence practices of ancient human ancestors in eastern Africa.

Advance data analysis in taphonomy

Statistical modelling

Statistical modelling plays a critical role in understanding the complexities of taphonomy, employing a range of techniques including regression models, survival analysis, factor and principal component analysis, cluster analysis, Monte Carlo simulations, Bayesian models, and time-series analysis. These methodologies are integral to the multivariate taphonomic approaches (Behrensmeyer et al. 2000; Milideo 2015; Yrarrazaval et al. 2024). Additionally, indices such as the dominance index, Simpson's index of diversity, and Shannon diversity index are utilized to measure various ecological metrics like taxonomic representation, diversity, richness, and evenness. The Omo Mursi Formation provides a significant window into the eastern African Pliocene, offering insights into past biodiversity and ecological conditions.

Skeletal element representation and breakage level

Analysis of assemblage composition, including the comparison of minimum number of elements to the dominance and evenness indices, along with considerations of bone surface modifications and skeletal completeness, deepens our understanding of ancient life forms. Furthermore, distinctions between proximal and distal limb bones are examined to interpret survivorship values and assess the comparative rates of preservation within fossil assemblages.

The calculation of the Number of Identified Specimens (NISP), Minimum Number of Elements (MNE), and Minimum Number of Individuals (MNI) followed the methodology outlined by Lyman (1994). In determining the MNE, factors such as age, side, and the alignment of anatomical markers were considered. The skeletal completeness of the individuals represented at the fossil site and the Relative Abundance (Ri) of specific skeletal elements per taxon were computed using the formula provided by Andrews (1990a). Additionally, Kolmogorov-Smirnov tests were conducted to compare the observed skeletal representation with the expected skeletal representation based on the estimated MNI for each taxon. These tests aimed to identify any significant biases in the skeletal representation among different taxa.

In taphonomic research, several statistical methods may employ to analyze the data effectively include such as the Kruskal-Wallis and Mann-Whitney U tests, which were used to compare the carbon isotope composition of fauna from the Mursi Formation with that from other Pliocene sites. These non-parametric tests are particularly useful for comparing data sets that do not necessarily follow a normal distribution, which is common in geological and paleontological studies. Additionally, the Median test to further assess differences in central tendency among groups, which complements the findings from the other tests by providing insights into the median values across different samples. These statistical tools helped to draw significant conclusions about dietary patterns and environmental conditions reflected in the isotopic data, enhancing our understanding of the ecological dynamics during the Pliocene era in the region (Drapeau et al. 2014).

Taphonomy's interdisciplinary nature is crucial in addressing complex paleobiological questions and devising strategies to reduce the effects of sample incompleteness and biases in paleontological research. Analysis of assemblage composition, including the comparison of minimum number of elements (MNE) to the dominance and evenness indices, along with considerations of bone surface modifications and skeletal completeness, deepens our understanding of ancient life forms. Furthermore, distinctions between proximal and distal limb bones are examined to interpret survivorship values and assess the comparative rates of preservation within fossil assemblages. By integrating these methodological insights, taphonomic research significantly advances our understanding of past ecological and environmental conditions, providing a comprehensive framework for paleoreconstruction in eastern Africa.

The Afar region shows varying completeness in small mammal bones across species and localities. For example, the bones from the from the families Muridae and Thryonomyidae different degrees of preservation, with larger species such as Thryonomys generally having more complete skeletal elements. In the smaller rodents, bone completeness was often compromised due to the digestive processes of raptors, resulting in more fragmentary remains. The large size of the Thryonomys species may explain why their bones were often found more intact compared to smaller rodents subjected to predation. In the ongoing research of the first author at the DW sites, the most common taxa include cane rats (*Thryonomys*), mole rats (*Tachyoryctes*), blind mole rats (*Heterocephalus*), porcupines (*Hystrix*), gerbils (*Taterillus* and *Gerbillus*), and murines such as *Otomys*, *Arvicanthis*, *Thallomys*, and *Mus*. These taxa are being examined to understand patterns of bone preservation and the factors influencing their completeness across different localities.

Fossil preservation at Olduvai Gorge varies significantly between levels. At FLKNN2, 23–31 % of complete femora and humeri indicate relatively low degradation and good preservation. In contrast, FLK-Zinj shows higher fragmentation, with evidence of weathering and digestion suggesting prolonged exposure before burial. (Fernández-Jalvo et al. 1998). Overall, preservation ranges from moderate to poor, influenced by factors like predation, weathering, and environmental exposure. Similarly, the taphonomic analysis of FLK NW small mammal fossils reveals extensive breakage across both cranial and postcranial elements (Arcos et al. 2010). Fragile cranial bones, like the maxilla, show high breakage rates, likely due to trampling, with no complete maxillae preserved. Mandibular fractures were frequent, indicating intensive damage. While robust postcranial elements, such as the femur and humerus, remained partially intact, many long bones display breakage marks, some caused during excavation and sieving. The patterns suggest trampling, particularly in predator dens or nests, as a primary factor, with most breakage occurring before burial.

In Aramis, the preservation of abundant postcranial elements and mostly intact jaws suggests high bone completeness, with minimal fragmentation or transport. The vertical alignment of bones in silty clay indicates rapid burial after death, preventing scattering and reflecting stable depositional conditions (Louchart et al. 2009). This preservation pattern highlights the site's potential for detailed paleoenvironmental and taphonomic analyses. While Aramis demonstrates exceptional bone preservation under stable depositional conditions, the preservation patterns at Laetoli present a stark contrast. The fragmented fossils at Laetoli reflect the influence of predation and post-depositional processes in an open, dynamic environment (Reed & Denys 2011). This dry, seasonal landscape with patches of woody vegetation likely supported diverse species and shaped predator-prey dynamics. Descriptive and frequency analyses of fragmented versus complete bones help interpret these relationships and align with environmental reconstructions based on faunal and botanical evidence. These patterns provide valuable insights into species interactions and the processes influencing fossil preservation at Laetoli.

The small rodent fossils in the Upper Busidima formation show significant fragmentation, likely caused by postmortem processes such as trampling or fluvial transport. In contrast, larger rodents like Thryonomys and Hystrix exhibit minimal breakage, with no evidence of raptor predation, suggesting their size contributed to better preservation (Everett 2010). These differences in breakage patterns offer insights into postmortem processes and species-specific preservation within the formation.

The classification of breakage levels in the taphonomic perspective of small mammals was originally based on Andrews's (1990) work focusing on cave samples with less fragmentation. Incorporating both quantification and breakage pattern analysis enhances the reconstruction of the taphonomic history of small mammal fossil assemblages, providing valuable insights into their abundance, composition, preservation, and deposition patterns, thereby improving our understanding of past ecological and environmental conditions. Taphonomy's interdisciplinary nature is crucial in addressing complex paleobiological questions and devising strategies to reduce the effects of sample incompleteness and biases in paleontological research. Notably, a new breakage category was identified in Olduvai (Arcos et al. 2010), involving mandibles broken at the diastema, considered a higher degree of breakage than previously described by Andrews due to factors like predation and possibly trampling.

Spatial analysis

Spatial analysis in taphonomy involves the examination of the spatial distribution and patterns of fossil remains to infer past environmental conditions, ecological interactions, and site formation processes. Understanding the spatial relationships among fossilized remains can provide insights into the behaviour of ancient organisms, post-depositional processes, and the integrity of the fossil record (Behrensmeyer et al. 2000). Although it may seem related to taxonomy, spatial analysis primarily focuses on the positions and distributions of fossils, addressing questions about how, where, and why fossil remains are found. Through these analyses, the formation of fossil accumulations, the processes involved, and the environmental factors that played a role can be understood. This analysis helps to identify the original living conditions and habitats of extinct species, understand post-mortem transport and deposition processes, detect patterns of predator and scavenger activity, assessing the effects of environmental factors on the preservation of remains. Some of the techniques that can be used in taphonomy are listed below:

Geospatial mapping involves the use of Geographic Information Systems (GIS) to create detailed maps of fossil distribution. This technique allows researchers to visualize spatial relationships and identify patterns that might not be evident from raw data alone. GIS can be used to map the locations of small mammal fossils across various sites in eastern Africa, helping to correlate fossil distributions with geological features and past environmental conditions. Additionally, used for small mammals' habitat preferences and the influence of climatic changes on their populations.

Spatial statistical methods are used to analyze the distribution of fossils quantitatively. These methods help to determine whether the distribution is random, clustered, or uniform (Bailey & Gatrell 1995). K-function Analysis, Ripley's K-function, and Nearest Neighbour Analysis techniques can be used to analyze the spatial distribution of small mammal fossils within a specific site, to infer the processes that led to their accumulation.

Density analysis involves calculating the density of fossil remains within a given area. Kernel density estimation (KDE) is a common method used to create a continuous surface representing fossil concentration. KDE can be applied to small mammal fossil assemblages to identify high-density areas that might represent predator dens or natural traps. Applying KDE to map the density of shrew fossils in a cave site, revealed areas of concentrated predation activity (Ingicco et al. 2020).

Spatial autocorrelation measures the degree to which fossils that are close to each other are more similar than those further apart. Moran's I and Geary's C are common indices used for this purpose (Bevan & Lake 2016; Dale & Fortin 2014). These indices help in identifying spatial patterns and understanding the factors influencing the distribution of small mammal fossils, helping to distinguish between natural and anthropogenic accumulation patterns.

Point pattern analysis examines the spatial arrangement of individual fossil points within a study area. Techniques like the Quadrat Method and the G-function are often employed (Boots & Getls 2020). It can be used to study the distribution of small mammal bones within a stratigraphic layer, identifying areas of high fossil concentration and potential taphonomic processes.

Integrating spatial analysis with other taphonomic data, such as bone surface modifications and breakage patterns, provides a comprehensive understanding of site formation processes. Advanced techniques like GIS and 3D modelling can enhance this integration. Combining spatial analysis with SEM data on bone surface modifications to correlate fossil distribution with specific taphonomic processes like trampling or carnivore activity.

Research on small mammal taphonomy in East Africa tends to rely on more traditional statistical modeling and spatial analysis approaches rather than advanced statistical methods. In Olduvai Gorge Bed-I, the taphonomic and paleoecological analysis focuses on reconstructing environmental and faunal changes using methods such as the taxonomic habitat index (THI), taphonomic modifications, and predator behaviours (Fernández-Jalvo et al. 1998). These techniques help infer environmental changes and identify biases in the fossil record. The analysis emphasizes conventional taphonomic methods like examining surface modifications, bone breakage patterns, and weathering, with linear trend analysis being the only statistical method mentioned to explore the relationship between taphonomic variables and stratigraphy (Reed & Denys 2011). Similarly, at Aramis, the focus is on environmental reconstruction and bone accumulation patterns through faunal assemblages, without using advanced spatial statistical techniques (Louchart et al. 2009). At Dikika, the study employs traditional methods like surface modification analysis with microscopes and statistical tests on mark types and distributions. Although multivariate analysis is used to differentiate trampling marks from cut marks, spatial analysis techniques are notably absent from the study (Thompson et al. 2015).

3D Digitization techniques

3D digitization techniques have revolutionized the field of taphonomy by enabling detailed, non-destructive analysis of fossil remains. These techniques include methods such as photogrammetry, CT scanning, and laser scanning, which create highly accurate three-dimensional models of fossils. These models allow researchers to examine surface modifications, morphological details, and structural integrity with unprecedented precision. The application of 3D digitization in taphonomy not only enhances the accuracy of paleoenvironmental reconstructions but also facilitates the sharing and preservation of digital fossil records for future studies.

Techniques such as metallographic microscopy, CT scanning, μCT scanning, photogrammetry, and digital microscopy were employed to create detailed 3D models (Barreau et al. 2022). These methods revealed numerous cut marks, some not visible to the naked eye, suggesting post-mortem processing. Recent advancements in 3D imaging techniques have significantly enhanced the analysis of cut marks on animal fossils, providing deeper insights into prehistoric human behaviours and tool use. For instance, 3D digital microscopy has revealed that different tools, such as un-retouched flint flakes and burins, create distinct groove morphologies, emphasizing the need to understand tool mark morphology for accurate archaeological interpretation (Moretti et al. 2015). Similarly, studies on projectile impact marks have refined diagnostic criteria, confirming drag marks as reliable indicators of prehistoric hunting strategies, applicable even in complex zooarchaeological (Duches et al. 2020). Quantitative micromorphological analyses using high-resolution imaging have distinguished between ancient and experimentally produced cut marks, underscoring the robusticity of early hominins' butchery techniques (Boschin et al. 2021). Additionally, low-cost methodologies, like macro-photogrammetry combined with computer vision, have offered accessible and detailed characterizations of cut marks, enabling broader application and more comprehensive analysis of prehistoric butchery practices (Maté-González et al. 2017).

In the study of *Paranthropus boisei* skeletons from Olduvai Gorge, researchers applied geometric morphometrics to analyze surface bone modifications, differentiating between marks made by carnivores and hominins. Their findings suggest that most marks were made by carnivores, likely felids, providing valuable insights into hominin-predator interactions in the Lower Pleistocene (Aramendi et al. 2019). This integration of geometric morphometrics and advanced imaging techniques not only refines our understanding of predator-prey dynamics but also highlights their growing role in experimental archaeology, where tool mark identification and classification benefit from both methodological precision and computational advancements. Research by Maté-González (2015) demonstrated that different tools leave distinguishable marks on bones, confirming the effectiveness of 3D imaging in experimental cut mark analysis using micro-photogrammetric methods. Additionally, there is a potential for combining geometric morphometrics with machine learning algorithms to classify cut marks with high accuracy, illustrating the benefits of integrating computational methods with 3D imaging (Courtenay et al. 2019).

Portable methods like micro-photogrammetry (M-PG) and structured light scanner (SLS) techniques. These methods produce statistically similar results, with SLS offering faster data collection and processing. The validation of these techniques enhances the ability to conduct detailed morphological studies of cut marks in situ, providing high-resolution 3D models crucial for analysing prehistoric butchering practices (Maté-González et al. 2017). Digitalization methods such as geometric morphometrics, 3D digitization, and advanced microscopy have profoundly impacted the study of small mammal remains in taphonomy. These technologies provide detailed, non-destructive analyses of BSMs, facilitating more accurate reconstructions of past human behaviours and environmental conditions. As digital tools continue to evolve, their integration into taphonomic research will undoubtedly enhance our ability to interpret the archaeological record with greater precision and clarity.

Taphonomic analysis in eastern Africa has provided critical insights into fossilization processes and the environmental conditions influencing fossil preservation. At sites such as Dikika and Olduvai Gorge, scanning electron microscopy (SEM) has been extensively employed to study the morphological characteristics and anatomical positions of marks on fossils. In the Dikika research, SEM combined with secondary electron imaging (SEI) and energy dispersive X-ray (EDX) analysis revealed a long cut on a fossil that contained a rock fragment, shedding light on early tool use. Similarly, at Olduvai Gorge, light and scanning electron microscopes were utilized for analysis to examine taphonomic modifications in detail, with SEM specimens prepared using conductive carbon cement and gold sputtering for precise imaging.

Technological advancements in the field have expanded beyond traditional microscopy, with methods like photogrammetry and CT scanning offering new avenues for analyzing fossil remains. Recent studies demonstrate that photogrammetry can produce 3D reconstructions whose resolution equals or even exceeds that of certain laser scanners (Falkingham

2012; Petti et al. 2008; Remondino et al. 2010). When integrated with statistical analyses, these techniques fall under the umbrella of "virtual paleontology", significantly advancing the ability to study fossils without physical manipulation (Courtenay et al. 2019; Cunningham et al. 2014; Maté-González et al. 2019). However, these innovations come with ethical considerations, particularly regarding data sharing and the protection of copyrights. An analysis of the 200 most-cited paleontology papers from 2017–2018 revealed that while 122 of these papers described 3D objects, only 31 % made their data publicly available online (Lewis, 2019), highlighting the need for more transparent and accessible research practices in this emerging field.

By using 3D microscopy and geometric morphometrics, researchers were able to analyze how different cutting tools impact the morphology of cut marks. The depth of the cut significantly affects the shape of the cut-mark cross-sections, providing crucial insights into the tools and techniques used by hominins. This relationship aids in interpreting archaeological BSMs, offering a window into past human behaviours and technological capabilities (Boschin et al. 2021). Building on these advancements, the integration of 3D imaging, geometric morphometrics, and microscopy has revolutionized taphonomic studies, enabling precise analysis of bone surface modifications. These methods refine our understanding of natural and anthropogenic processes, predator-prey dynamics, and early hominin behaviours. As technological innovations progress, ensuring open access to data will be crucial for fostering collaboration and enhancing interpretations of the archaeological record.

Conclusion

The field of taphonomy has evolved significantly since its inception, incorporating advanced methodologies and interdisciplinary approaches to enhance our understanding of fossilization processes and paleoenvironmental reconstructions. Modern advancements such as 3D digitization techniques, geometric morphometrics, micro-photogrammetry, and advanced microscopy have revolutionized the study of fossil remains. These innovations allow for more precise, non-destructive analyses, providing deeper insights into the taphonomic processes that shape the fossil record. The integration of these techniques has particularly benefitted the study of small mammal fossils, which are crucial for reconstructing past environments and understanding depositional, ecological, and evolutionary dynamics.

Small mammals, with their rapid responses to environmental changes and their widespread presence in the fossil record, serve as vital indicators of past climatic and ecological conditions. Their susceptibility to taphonomic biases and the challenges involved in their collection and analysis make them a unique focus for methodological advancements in taphonomy. By addressing these challenges and leveraging new technologies, researchers can gain a more accurate and comprehensive understanding of the paleoenvironmental history of regions like eastern Africa. This, in turn, provides valuable context for human evolutionary studies, highlighting the interconnectedness of ecological and evolutionary processes. The ongoing evolution of taphonomic methods thus underscores the importance of small mammal fossils in advancing our knowledge of the past, contributing significantly to the broader fields of paleontology, archaeology, and ecology.

The accumulation of taphonomic studies on small mammals from eastern Africa over the past several decades has provided invaluable insights into the processes affecting fossil preservation and environmental reconstruction. While there are numerous challenges, such as differential destruction, predator bias, and sampling methods, researchers have made significant advances in understanding how these biases influence the fossil record. This growing body of work emphasizes the importance of small mammals as key indicators in paleoenvironmental studies.

The number of taphonomic analyses focusing on small mammals from sites like Omo, Hadar, and Olduvai Gorge reflects the increasing recognition of their significance in reconstructing ancient ecosystems (Arcos et al. 2010; Everett 2010; Louchart et al. 2009; Wesselman 1984). Despite the underrepresentation of small mammal remains due to their fragile nature, recent methodological advancements, such as isotaphonomic approaches and advanced statistical modelling, have enabled more accurate interpretations. These efforts have demonstrated that small mammals offer critical data regarding habitat changes, predator-prey dynamics, and environmental fluctuations, often reflecting ecological shifts more accurately than larger species.

Additionally, these studies highlight the nuanced impact of taphonomic processes, from predator accumulation to weathering and trampling, on the preservation of small mammal fossils. For instance, the high completeness of postcranial elements at sites like Aramis or the digestive marks found in Laetoli indicate predator-specific accumulation patterns that shape our understanding of the Pliocene and Pleistocene ecosystems. The taphonomic markers, including bone surface modifications and breakage patterns, provide detailed evidence of how these assemblages were formed and preserved.

Despite the complexities of interpreting these records, small mammals remain a crucial part of paleoenvironmental studies in eastern Africa. Their presence in fossil assemblages offers a lens through which researchers can reconstruct past habitats with greater precision. Ongoing work in refining techniques and addressing the biases inherent in small mammal taphonomy will continue to expand our knowledge, enabling more accurate reconstructions of ancient environments and their evolutionary contexts.

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