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Editorial

Taphonomy and Palaeoecology of Quaternary Vertebrates: Advances in Fossil and Experimental Studies

Emmanuelle Stoetzel [1,*], Janine Ochoa [2] and Juan Rofes [3,4,5]

[1] Histoire Naturelle de l'Homme Préhistorique (HNHP, UMR 7194), CNRS/MNHN/UPVD, Musée de l'Homme-Palais de Chaillot, 17 Place du Trocadéro, 75016 Paris, France
[2] Department of Anthropology, University of the Philippines-Diliman, Palma Hall, Roxas Avenue, Quezon City 1101, Philippines
[3] School of Archaeology, University of the Philippines-Diliman, Albert Hall, Lakandula St., Quezon City 1101, Philippines
[4] Archéozoologie, Archéobotanique: Sociétés, Pratiques et Environnements (AASPE, UMR 7209), CNRS/MNHN, CP56, 55 rue Buffon, 75005 Paris, France
[5] National Museum of the Philippines, P. Burgos Drive, Manila 1000, Philippines
* Correspondence: emmanuelle.stoetzel@mnhn.fr

Since the founding work of Efremov in 1940 [1], the discipline called "taphonomy" has developed considerably, and its importance is now unquestionable in terms of revealing the processes of the formation and preservation of fossil assemblages (and the surrounding sedimentary deposits) and the establishment of reliable palaeoenvironmental reconstructions. Several reference books have been published on this subject [2–6]. Hundreds of articles have subsequently strengthened and complemented these seminal works, particularly from a methodological and experimental point of view and with applications to fossil assemblages, leading to the landmark production of the Atlas of Taphonomic Identifications [7]. The continuing strong interest of the international scientific community in this discipline is still visible, notably through two prominent events simultaneously held in June 2022 in Madrid: the 9th International Meeting on Taphonomy and Fossilization (TAPHOS) coupled with the 6th Meeting of the ICAZ Taphonomy Working Group (TWG-ICAZ), in honour of the 80th anniversary of Efremov's proposal of taphonomy as a new branch of palaeontology.

It has long been established that taphonomy and palaeoecology are inseparable. A taphonomic analysis of a fossil assemblage is an essential prerequisite for palaeoecological studies, particularly for identifying the origin of faunal assemblages and potential biases in species and anatomical representation [6,8–10]. In turn, palaeoecology uses fossil data to examine how organisms and environments change throughout time [11–13]. By studying the patterns of evolution and extinction under environmental change, palaeoecologists can examine the concepts of vulnerability and resilience in species and environments at different scales [14–16]. The Quaternary period is well represented in geographically extensive and high-temporal-resolution records and is particularly important to human evolution. Vertebrate remains, whether accumulated by humans or non-human agents, are frequently well preserved in Quaternary palaeontological and archaeological deposits. Recently, the number and methods of taphonomic and palaeoecological analyses on Quaternary vertebrate assemblages have significantly increased and developed, and this Special Issue aims to highlight the recent works illustrating these advances in palaeontology, zooarchaeology, and paleoenvironmental studies, in light of modern taphonomic referentials and experiments.

We are pleased with the success of this Special Issue, which has resulted in the publication of 16 articles with an extensive global, geographic, and temporal scope, presenting seminal research conducted by internationally recognised specialists from Argentina, Mexico, Brazil, USA, Canada, Australia, Israel, Indonesia, Philippines, Thailand, UK, Spain,

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Portugal, Belgium, and France. We briefly summarise them below arranged by the nature of their contributions into different domains that are not mutually exclusive.

1. Methodological Development/New Fields of Research

Certain processes and taphonomic alterations are less studied than others, although they really require interest and attention. This is notably the case for insect marks on bone remains, for which few studies are available and modern referentials are lacking. Escosteguy et al. [17] explored the aspect and measurement of insect marks observed on bone remains from La Guillerma in Argentina (ca. 1400–600 years BP). They compared them with a variety of marks described in the literature, using a specific classification of insect-produced modifications, and providing high-quality images of a variety of marks, which can be very useful for future studies. The authors also highlighted the utility of studying this type of trace to better understand bioturbation phenomena and to contribute to palaeoecological information based on the ecological requirements of the trace-maker insects.

In addition to providing information on taphonomic and environmental contexts, the study of microvertebrate assemblages can also shed light on the timing and frequency of occupation of sites by humans and non-human predators. In taking the example of La Roche-à-Pierrot in France (Middle-Upper Palaeolithic), Lebreton et al. [18] showed a negative correlation between the proxies for human occupation and micromammal densities. Stratigraphic layers rich in micromammal remains were thus correlated with periods of abandonment or less intense occupation of the site by humans, while other predators were more frequently present.

The pattern of the fragmentation of micromammal bones is often used to characterise the taphonomic impact of predators on prey remains in modern referentials (owl pellets, faeces) but is rarely applied in fossil contexts. Durocher et al. [19] proposed a new methodology based on geometric morphometric analyses on rodent mandibles, allowing the characterisation of fragmentation patterns in modern and fossil assemblages in a "continuous" and adaptable way, without restriction/resorting to a priori categories based on subjective criteria.

2. Modern Referentials and Experiments

Modern referentials are essential to better understand and disentangle taphonomic processes, characterise the specific marks produced by biotic and non-biotic agents, and generate transpositions to fossil assemblages in reliable and reproducible ways. Several papers in this collection have made methodological contributions by initiating experimental studies and successfully applying these to archaeological contexts.

Fernández-Jalvo et al. [20] designed a trampling experiment using equipment that allows the control of different parameters. They explored and characterised the effects of trampling on modern small mammal bones, raising interesting issues related to site formation processes. The different patterns of breakage observed on modern bones were then applied to the fossil site of Wonderwerk Cave in South Africa. Their comparative analysis showed that trampling was an important factor responsible for the high degree of breakage observed in the assemblage, together with other factors such as predator digestion and excavation procedures.

Significant strides have also been made in the field of traceology in recent years. Okaluk and Greenfield [21] specifically explored chop marks, which were produced on sheep, cattle, pig, and deer bones through an experiment using a variety of implements (chipped stone, ground stone, copper, and bronze axe heads). The macroscopic observations made by the authors, supported by high-quality images, allow the effective discrimination of traces left by various tools and also open the way for future microscopic studies. Here, again, the patterns observed on modern material were applied to an archaeological faunal assemblage (Göltepe in Turkey), and the taphonomic evidence suggests the use of metal tools in the butchery process.

Few studies on modern assemblages produced by avian and mammalian predators opt for a multi-taxa approach, and even fewer are interested in inter-observer variability. Stoetzel et al. [22] applied this integrative approach to the analysis of barn owl pellets from Dominica Island in the French Antilles, in which two observers were used for each considered taxon (rodents, bats, birds, squamates). The authors found high similarities in the taphonomic results obtained for the considered faunal groups, but some differences emerged at several levels: between observers, between taxa, between elements, and even between different parts of the same element. This methodological contribution raises important considerations relating to the reliability and reproducibility of neo- and palaeo-taphonomic analyses.

3. Analysis of Fossil and Sub-Fossil Assemblages

Most studies presented in this Special Issue focus on the new analyses of fossil and sub-fossil faunal assemblages that incorporate taphonomic methods, including investigations on the origin of the assemblages and post-depositional processes and consideration of their cultural and archaeological contexts.

Powley et al. [23] provided a taphonomic analysis of *Stegodon* remains from Mata Menge in Indonesia, a Middle Pleistocene site that has yielded the earliest fossil evidence for *Homo floresiensis*. The authors observed several surface alterations (weathering, fragmentation, trampling, fluvial abrasion), notably highlighting the effects of fluvial transport and long exposure of bones before burial. Although incontrovertible evidence for human modification could not be clearly established, the evidence regarding the formation of the *Stegodon* bonebed provides important additional context for this hominin-bearing layer.

Wattanapituksakul et al. [24] performed a zooarchaeological analysis of the faunal assemblage of Ban Rai Rockshelter in Thailand (Terminal Pleistocene to Middle Holocene). They highlighted the human exploitation of the diversity of species among large and small mammals, birds, reptiles, fish, and arthropods, with differences between the archaeological layers. Although the relative abundance of taxa is influenced by site preservation processes, these differences may be due to an adaptation of human populations to a changing environment during the Pleistocene–Holocene transition and beyond, becoming more focused on arboreal taxa during the Early and Middle Holocene.

Competition between human groups and large carnivores for shelter and prey is also the subject of multiple studies, which span an extensive geographical and time range. Daura et al. [25] delved into this question through the analysis of faunal and human remains, lithic assemblages, and the chronostratigraphic context of Cova del Gegant in Spain (Middle Palaeolithic). The detailed analysis of the large mammals, birds, and microvertebrates revealed a high level of faunal diversity at the site, as well as the intervention of both human and non-human predators in the accumulations. The site was mainly used by carnivores such as hyenas, but also by Neanderthals as a brief stopping place, within the context of high human mobility during the Middle Palaeolithic.

Rofes et al. [26] explored the potential of micromammals to reconstruct human activities, biostratigraphy, and palaeoenvironments at El Portalón de Cueva Mayor in Spain (Early Late Chalcolithic). The authors demonstrated the differences in the small-mammal spectrum among different areas and phases of human activity (e.g., burials, prepared floors, activity floors, and fumiers) and provided the first Holocene sub-fossil record of multiple rodent, shrew, and bat species in the Sierra de Atapuerca. They also showed the presence of the specimens of Late Pleistocene age into the Late Chalcolithic prepared floors, arguing for pollution from allochthonous sediment and advising caution regarding paleoenvironmental conclusions for this unit.

Royer et al. [27] focused on the question of the origin of the small mammal assemblage from Ittenheim in France (Late Saalian–Late Weichselian). They compared the fossil assemblage of Ittenheim with two modern accumulations produced by a red fox and a badger, alongside data from the literature. In light of the data on anatomical representation, the presence of tooth marks, and the intensity of digestion, the authors concluded that

a small mammalian carnivore was the main accumulator of the Ittenheim assemblage. They also pointed out that the taphonomic impact of small carnivores is still too little known compared with that of owls, and that differences are observable according to the considered prey, i.e., medium-sized prey such as European hamster vs. small prey such as small microtines.

Tilby et al. [28] provided a preliminary taphonomic analysis of the micromammal assemblage from Shanidar Cave in Iraqi Kurdistan (Middle Palaeolithic levels). They especially considered the fragmentation of bones and teeth, and surface alterations such as digestion, black staining, and root etching. The authors concluded that, in most respects, the taphonomic processes remained constant throughout the sequence and micromammals were accumulated by category 1 or 2 predators. They discussed the potential predators that could have been involved and linked the slight increase in Manganese staining and root etching in the lower layers to the relatively wet and warm conditions at this time.

Compared with large and small mammals, other taxa such as amphibians, reptiles *s.l.*, and birds have received less attention in taphonomic studies. Two works published in the present Special Issue focus on these poorly known taxa.

Rufà and Laroulandie [29] presented the taphonomic history of the bird assemblage of Grotte Vaufrey in France (Middle Pleistocene). The faunal spectrum, as well as anatomical representation, digestion traces, and tooth/beak/claw marks, pointed to a non-human accumulation for most of the assemblage. Moreover, the origin may differ considering the species, and some of them may have frequented and died in the site naturally. Some examples, however, displayed clear anthropic action (such as burning and cutting marks), arguing for the occasional consumption and exploitation of some birds by Neandertals.

Finally, Rubinatto Serrano et al. [30] provided an interesting archaeological and ethnographic overview of sub-fossil assemblages dominated by anuran remains in the Tiwanaku sites of Peru (700–1100 CE), exploring the respective roles of humans and other predators in these accumulations, and showing the need for further taphonomic analysis for such peculiar assemblages. The authors discussed the environmental, cultural, and taphonomic explanations related to the anomalously high quantity of anuran remains found in the Tiwanaku sites in comparison to other sites in the area.

4. Palaeoenvironmental Inferences

Two studies published in this Special Issue are especially focused on the palaeoecological implications and palaeoenvironmental models deduced from faunal analyses.

Arroyo-Cabrales et al. [31] considered the entire faunal spectrum (molluscs, amphibians, reptiles, birds, and mammals) of San Josecito Cave in Mexico (45,000–11,000 BP). A revision of the faunal assemblage and site taphonomy, stratigraphy, and geochronology showed the presence of numerous extinct species at the site and the succession of several local faunas throughout the sequence, with high potential for Late Quaternary climatic reconstructions.

Traditionally, paleoenvironmental reconstructions are based on the faunal spectra and ecology of present-day species. However, in recent years, new methods have emerged that can provide valuable information on landscape and climatic changes through time. Uzunidis [32] used morphometric and use-wear analyses on archaeological *Equus* remains from European sites in an attempt to observe changes under climatic pressure and vegetation changes during the Middle Pleistocene, also exploring geographic and seasonal variability.

In conclusion, owing to all these multidisciplinary contributions, this Special Issue provides both new data and new avenues to explore the importance of taphonomic studies and multi-taxa approaches for understanding depositional processes and palaeoenvironmental reconstructions based on faunal remains in archaeological and palaeontological contexts. We are also attentive to the development of new methods, such as biomolecular approaches, which have not necessarily been mentioned here but can provide new proxies and ways to ascertain taphonomic contexts and taxonomic designations. This diverse array

of methods ensures the integrity of the assemblages and surrounding deposits and thus helps in understanding biases in palaeoenvironmental reconstructions.

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