

Microfauna's Taphonomy comes to age: a tribute to Peter Andrews

Denys C.

Institute of Systematics, Evolution, Biodiversity (ISYEB), National Museum of natural History, CNRS, Sorbonne University, EPHE, University of the Antilles, CP51, 75005 Paris, France. E-mail: christiane.denys@mnhn.fr

Small vertebrates and particularly small mammals despite their small size (less than 2 kilos), are well known to accumulate in large quantities in fossil sites of all ages and all types. Accumulations of small vertebrates have long been neglected due to the fact that their unknown origin and their contemporaneity with the accumulations of large vertebrates and human artefacts was not demonstrated. Moreover, they cannot be collected directly during paleontological excavations and must undergo sieving prior to their sampling, which is not always possible. Andrews' pioneering work (1990): "*Owls, Caves and Fossils*", raises the question of how small mammals can withstand the predation stage, the post-predation modifications, burial and diagenesis during fossilization? Are all small mammal assemblages the result of predation? In such cases, how can predation influence paleoecological interpretations? How can predation and therefore taphonomy processes even influence paleoclimatic interpretations? In this book, he focused on quantifying the taphonomic information playing a role in the accumulation of small mammals and what added value can be drawn from this for the study of fossil paleocommunities? Indeed, microvertebrate taphonomy increases taphonomic information as Sixto Fernández-López has always proposed. Fossils are a *compendium* of information, that is, a physical support of other biotic or abiotic fossils that have been recorded, and its traces must be decoded to identify the past in its maximum detail.

Peter Andrews' interest in the taphonomy of small mammals began in the 1980s under the influence of the work of Mellett (1974) who demonstrated the predation origin of fossil small mammal assemblages and Mayhew (1977) who was one of the first to show the alterations of the enamel of the molars coming from pellets of different raptors, and the stronger attack of the digestive juices of the diurnal raptors compared to the nocturnal ones. Thus, since 1983, Andrews in collaboration with Evans attempted to characterize the bone elements from the excrements of small carnivorous mammals. This will be the beginning of a long series of articles on the taphonomy and paleoecology of small mammals.

Thanks to the use of the scanning electronic microscope (S.E.M.), Andrews (1990) was one of the first to display these alterations of the bone surface linked to digestion on current and fossil bones. To study digestion, Peter Andrews took up the experimental work of Dodson & Wexlar (1975) on the study of the skeletal representation of the bones passed through the digestive tract of an eagle-owl and developed a method of studying fragmentation and digestion of skeletal elements. At the same time, he developed a reference collection of 19 different predators and their corresponding assemblages of pellets and excrements. He first applied his method to the Pleistocene site of Westbury in the UK and Paşalar (Turkey) and interpreted the taphonomic history of fossil assemblages and caves.

The digestion and predation categories established from these assemblages provide information on the type of predator responsible for a fossil accumulation and serve to verify its homogeneity and the quality of the faunal list for subsequent paleoecological interpretations. As with current concentrations, the study of taxonomy, skeletal representation, of fragmentation and of traces of digestion is used to recognize the origin of an accumulation of small fossil vertebrates, in short, to identify the predator for which there are generally no fossils in the site. A criterion used alone is

rarely sufficient to interpret a fossil assemblage, it is often necessary to combine the results.

Subsequently, several authors have used and continued to develop this method for various European and African Plio-Pleistocene micromammal sites (Atapuerca, Olduvai, El Hahroua 2...) and more recently in the Middle East or South America. This method, which has since been slightly improved and adapted to certain regions, is thus still used in taphonomy studies of small vertebrates. In 1999, in collaboration with Anna Pinto, Andrews also provided the first taphonomic study concerning the amphibians of Atapuerca. At the same time, archaeozoological work is developing and includes a taphonomic component in order to distinguish the traces left by human actions from those due to predators and post-predation alterations. In 2016, the taphonomic method was reviewed in collaboration with P. Andrews to provide more reliable criteria for the digestion of rodents, shrews and to facilitate the work for taxonomists (Fernandez-Jalvo et al., 2016). Thus, referentials are gradually being built for Aves, Herpetofauna, Fish, Lagomorphs, etc. and are applied to various archaeological sites (Denys et al., 2018), in particular thanks to a field expedition to Morocco in 2009 (RHOI-Taphonomy project Working Group) (Figure 1).

In all cases where a detailed taphonomic study of the remains of microvertebrates has been carried out, it is found on the one hand that it is generally different predators that have contributed to the origin of the bone assemblages, and on the other hand that the small fossil vertebrates record, in addition to digestion, traces of numerous post-predation modifications accompanied by significant geochemical modifications. In fact, small vertebrate faunas are very good models for the study of the paleoenvironments and ecosystems of the past. Thanks to the dynamics created by the work of Peter Andrews, these analyses show that the taxonomic identification of prey and the taphonomic identification of predators and events during fossilization allow us to obtain a precise and reliable knowledge of the origin and taphonomic history of a fossiliferous deposit and its implications for paleoenvironmental, paleoecological and paleoclimatic interpretation.

In parallel with the development of taphonomic methods applied to sites with small mammals and in order to better interpret post-predation modifications according to climato-edaphic conditions, observed during his previous work on the Miocene sites of the East African Rift or then in the 1980s. on the sites of Westbury, Paşalar or Atapuerca, Peter Andrews, whose main motivation was to obtain the most precise and quantified paleoecological interpretations of hominin sites possible, developed an experimental approach concerning the study and monitoring both degradation and the dispersal of small mammal bones exposed to the open-air in temperate environments or buried in bog in the Rhulen region of Wales for more than 30 years (Armour-Chelu and Andrews 1996; Andrews and Armour-Chelu 1998, Andrews & Fernandez-Jalvo 2019), monitored the degradation of a camel carcass in the Arab Emirates (Andrews 1995, Andrews & Whybrow 2005) and participated in the Overton Down experiment, UK, initiated by archaeologists in 1961 to determine fungal attacks, insect damage, surface alterations and the degradation of buried cooked bones. The bones were exhumed in 1993 and analysed by Armour Chelu & Andrews (1994) but the experiment is still ongoing. The site of Draycott cave, Somerset, UK, served as a place of experimentation in 1977, and the trampling, the dispersion of carcasses, the weathering of bones of large mammals but also of amphibians were observed, described and figured by Andrews & Cook (1985), Andrews (1995). Soil bioturbation has also been described by Armour-Chelu & Andrews (1994). The effects of water transport on the bones of small mammals have also been analysed using various experiments (Fernandez-Jalvo & Andrews 2003) always improved and described in the Atlas of Taphonomy published in 2016.

The publication of the 1990 work also prompted numerous neo-taphonomic studies to adapt the taphonomic method to other continents (Fernández et al., 2017), to other than small mammal taxa and to other lesser-known predators. Thus, references on birds, herpetofauna, fish, lagomorphs have thus multiplied in the literature and the taphonomic method has been adapted to these taxa and their

particular skeletal characteristics. In addition, experimental work on digestion processes and post-predation modifications has given rise to numerous research and methodological developments involving teams of archaeologists, paleogeneticist, palynologists (Figure 3).

Peter Andrews was thus the first taphonomist of small vertebrates and demonstrated that the digestion and predation categories established from present-day predator accumulations can be used on fossil assemblages. These categories provide information on the type of predator responsible for a fossil accumulation and are used to check its homogeneity and the quality of the faunal list for subsequent paleoecological interpretations. As with present-day assemblages, the study of faunal taxonomy, skeletal, fragmentation and digestion patterns is used to recognize the origin of an accumulation of small fossil vertebrates. Moreover, Peter Andrews showed that the post-predation alterations observed on the bones of small vertebrates bear the same signature as those of the bones of large mammals.

Since 1990 and the publication of the book *Owls, Caves and Fossils*, there are still gaps in terms of modern taphonomic references for certain regions of the globe. Thus, there is still a lack of references concerning the predators of the Middle East and the eastern regions of Europe or even of certain rare European raptors and carnivorous mammals likely to have had more widespread distributions in the Quaternary (snowy owl, arctic fox, dhole etc...). Similarly, few experiments are underway to understand the climato-edaphic effects in steppe and desert environments as well as those concerning algae, lichens, roots, etc. for small mammals. Finally, despite some attempts, few works concern the mechanisms of sedimentation, formation of sites in caves or their modelling.

In line with Efremov, Peter Andrews paved the way for taphonomy and paleoecology work for a whole generation of archaeozoologists and paleontologists, many of whom he trained. It also rehabilitated the importance of small vertebrates in the formation of sites when they had remained neglected. His "taxon-free" approach developed in the methods called: "Taxonomic Habitat Indices" (THI, Evans et al., 1981) and "Habitat Weighting" applied to extant and fossil species brought innovative quantitative methods. Involved as a member of the scientific committee of the "Journal of Taphonomy" since its creation, he was present at the start of the TAPHEN network in 2011 (<https://taphonomy-network.blogspot.com>), which he encouraged and supported. This network, which has become European, makes it possible to structure the community of researchers working on the topic.

Peter Andrews ecosystemic approach and his experience in the field, his global vision of the phenomena of site formation and fossilization have enabled great advances in taphonomy and paleoecology, as well as a more precise characterization of paleoclimatic events and their implications.

Finally, if Efremov founded Taphonomy, Peter Andrews is the founder of microvertebrate taphonomy, without his important contribution we would not have been able to obtain so much and so diverse information that we know today is essential for the study of the past.

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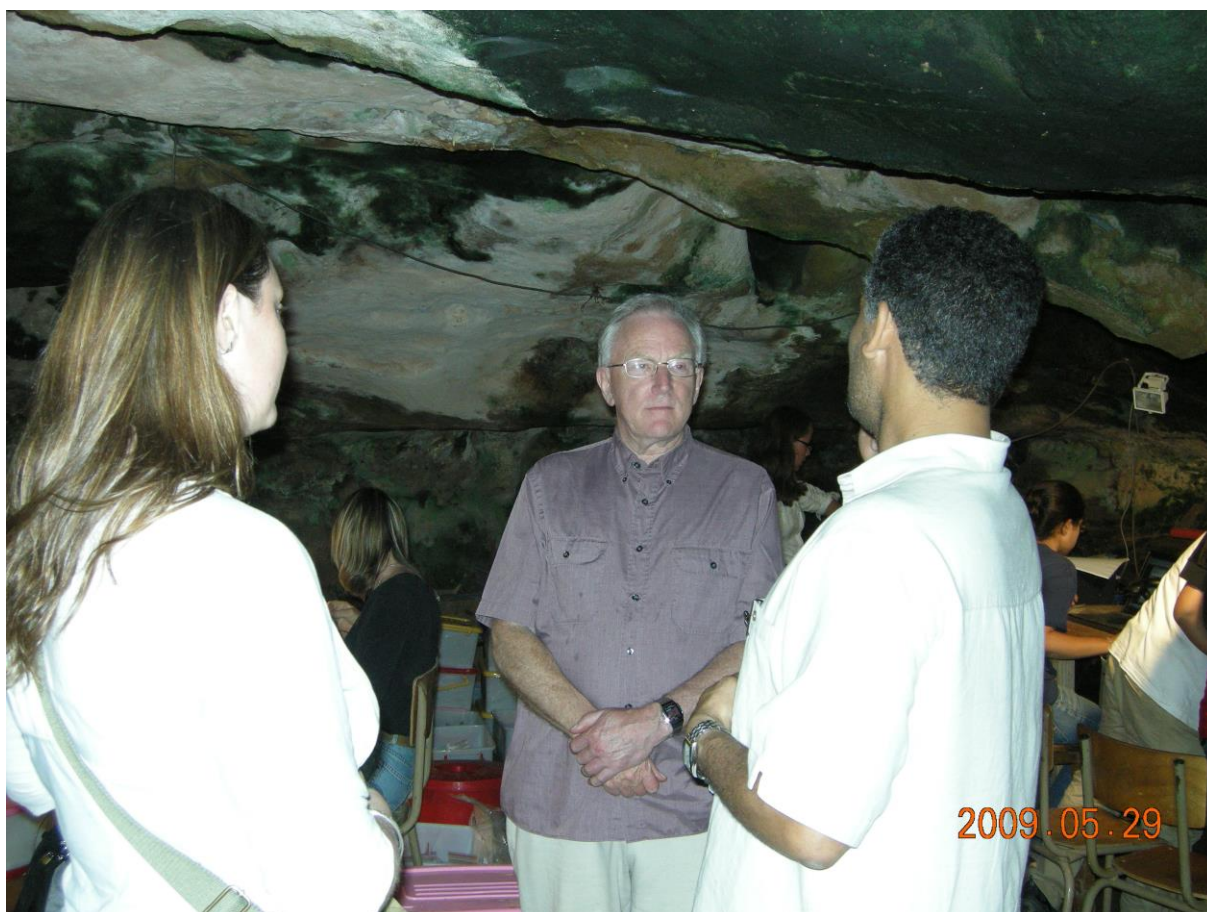


Figure 1: Peter Andrews, Denee Reed, Emmanuelle Stoetzel in the “Contrebandiers” Cave (Morocco) on 05/29/2009 (RHOI – Taphonomy Working Group)



Figure 2: "TaphoProcess" Project team members in Riofrio Natural Park in Spain, May 2011. From left to right: Louis Scott, Yolanda Fernandez-Jalvo, Eva Maria Geigl, Lyne Bell, Peter Andrews, Emmanuelle Stoetzel.