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Study of Putrefactioning Animals: A General Review and Studies in Palaeocene-Eocene Time

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ABSTRACT

Study of putrefactioning animals has multiple roles in paleobiology. Such roles include assessing sample quality pertinent to ecology, biogeographic and evolutionary questions. It investigates the roles of various putrefactioning agents, processes and situations in generating the sedimentary and fossil records and eventually reconstruct the dynamics of organic recycling over time as a part of geologic history. Efremov (1940) first defined study of putrefactioning animals as "the study of the changes (in all its details) of animal remains from the biosphere into the lithosphere". The definition was stated more generally by Behrensmeyer and Kidwell (1985) as "the study of processes of preservation and how they affect evidence in the fossil record". In other words, study of putrefactioning animals focuses on the postmortem, pre- and post- burial histories of faunal remains. Due to the potentially destructive and disruptive nature of burial processes, burial is considered to be a stage intermediate to pre- and post- burial histories (e.g Dixon 1984; Kranz 1974a, 1974b).

INTRODUCTION

Lyman 1994 defines putrefactioning history or putrefactioning pathway as a general chronology of putrefactioning agents and processes affecting animal remains. Gifford-Gonzalez (1992) defines a putrefactioning agent as the source of force applied to hard parts of bone phosphates which are "immediate physical cause" of modification to animal death bodies and skeletal animal fibers. Lyman 1994 defines putrefactioning process as the dynamic action of an agent on animal death bodies and skeletal animal fibers, such as downslope movement, gnawing or fracturing. He also defines a putrefactioning effect or trace as the static result of a putrefactioning process acting on death bodies and skeletal animal fibers, the physical and/ or chemical modification of bone. A putrefactioning analysis essentially involves identifying and/or measuring putrefactioning effects. On basis of such putrefactioning analysis, identifying and measuring the magnitude of effects of putrefactioning processes and agents is the goal of study of putrefactioning animals. Gifford (1981) identifies two basic goals of putrefactioning investigation: (1) "stripping away" the putrefactioning overprint from the fossil record to obtain correct resolution of the prehistoric biotic community and (2) investigating the nature of the putrefactioning processes responsible for a given fossil assemblage and hence enable the writing of putrefactioning histories.

Study of putrefactioning animals has the concentration on a very large time duration or scale, with different putrefactioning drain or filters that puts high-frequency signals or waves by causes of decease or fatality, disintegration, (Briggs 2010; Efremov 1940; Lyman 2010; Martin 1999). The preliminary approach to unravel the study of putrefactioning animals of vertebrates or animals is to reconstruct or rebuild the situation in which burial data are happening (e.g Roksandic 2002). Keeping aside climatic factors (e.g. temperature of surrounding), it is important to the potential of fossilization or diagenesis of organic remains whether the disintegration took place in a subaerial that below the water table or subaquatic surrounding. However, the habitat, the place of decease or fatality, as well as the place of the decease or fatality or disintegration and bedding of animals are rarely same or identical. Therefore, it is very necessary for reconstructing the putrefactioning history of vertebrates or animals to make a documentation of the geological and palaeontological situation. A critical evaluation or assessment of possible context of the cause of dying and the processes of disintegration and bedding, as well as their attendant situations, makes it possible to draw valuable conclusions concerning the surrounding of present and past habitats. Putrefactioning aspects hence have an explosive or volatile nature as far as financial and surrounding politics are concerned, which has already been given importance at the time of the beginning of uniformitarian science or investigation (e.g. Wasmund 1935, 48 p.; Wiman 1914).

A second approach to the remodeling of the putrefactioning fate of fossil animals is their quality and quantity in the fossil history. All the implicit and explicit factors which influenced a decease or fatality body of animals up to its complete and final bedding can be inferred from the totality, the degree of fragmentation. The relative position or disposition as well as from the grade or scale of scattering or dispersal and changes of the animal or vertebrates or animal's skeletal units (e.g. Lyman 1994). Uniformitarian examination on the disintegration of animals which give proof of the time of disintegration and the hardiness of different animal fibers against putrefaction may furnish important hints here. In our view, just in the investigation of the study of putrefactioning animals of fossil vertebrates or animals, too little notice has been given so far to the not simple interactions between the anatomy of soft tissue and skeleton of a death body. Vertebrates or animals have certain putrefactioning predispositions because of their specific bauplan, their useful well-formed or phonological laws and because of their age and sex. These predispositions may result in typical putrefactioning positional association and dislocation, as well as in certain patterns of fragmentation of skeletal units (e.g. Kielan- Jaworowska and Hurum 2006; Schafer 1972). However, the current physical constitution of animals at decease or fatality (e.g. body mass, extent of filling of the intestines, filling condition of the lungs, pathology and cause of decease or fatality) can lead to variations or even eloquent deviations in the positional associations and patterns of fragmentation of skeletal units. In the end, all the modifications of chemical and physical parameters which take place through autolysis and heterolysis in the death body have the potential to cause changes of position up to fragmentation of anatomical unities.

As a third approach to solving putrefactioning problems, it is important not only to include the plentitude of scientific disciplines of human medicine and veterinary medicine, but also those which deal with putrefactioning questions in a practice-oriented manner (e.g. nutrition science, forensic entomology, catastrophe management, chemical and biological engineering; e.g. Andersson et al. 1995; Benecke 2008; Bonhotal et al. 2006; Coghlan 1998; Dittrich and Luttge

2008; Lloyd et al. 2008; Lochner et al. 1980; Ryon et al. 2000; Sledzik and Rodriguez 2002; de Ville de Goyet 2004; Wilhelm et al. 2009). The pioneers of putrefaction investigation already used the store of knowledge of that sort of disciplines (e.g. Wasmund 1935; Weigelt 1927; Wiman 1914, 1942). This is especially true for forensic medicine. For more than a hundred years, this scientific discipline has been striving to gain evidence about disintegration processes in highly different surroundings by observation, dissections and examinations (e.g. Neufeld and Scheck 2010). In the future, this knowledge must be increasingly exploited for study of past animals. In its multidisciplinary approach, the eight articles of the special issue provide disintegration examinations, partly documented by X-ray and high-resolution micro-computed tomography (CT), insights into new approaches to analyse fossil skeletons by using forensic methods and findings, a comparison of the putrefactioning fate of marine lung-breathing fossil reptiles and extant vertebrates or animals and the putrefactioning history of marine and freshwater fishes as well as terrestrial reptiles and vertebrates or animals. Presently, a review of study of putrefactioning animals of Paleocene-Eocene vertebrates or animals has been done. The works are discussed one by one.

Badgley et al. 1995 compares the study of putrefactioning animals of animal's assemblages from two long continental records the early Paleogene of the Bighorn Basin, Wyoming and the Neogene Siwalik sequence of northern Pakistan. Both sequences contain a similar array of fluvial facies, and the abundance of these facies differs among formations. Badgley et al. 1995 documents the surroundings of preservation of animal's localities over time to determine comparability of fossil assemblages within and between sequences. Changes in sample measurement and species richness are noted to reveal potential sampling effects on patterns of faunal turnover. Preservational history determined the surrounding, sample measurement, quality of specimens, taxonomic composition, and spatial and temporal resolution of fossil assemblages and thereby the quality of the fossil record and its suitability for further analyses. In the sequences, changes in prevailing putrefactioning processes reflect changes in lithofacies and habitat distribution. Correlated changes are found in fossil productivity, species richness, and faunal composition. Both sequences contain some episodes of apparent faunal change in which appearances and disappearances of rare taxa can be attributed principally to changes in sample measurement. The Paleogene record has high taxonomic resolution (i.e., to genus or species) for most vertebratian fossil remains. Temporal and spatial averaging of Paleogene fossil assemblages change with lithofacies. The Neogene record has higher taxonomic resolution for remains of small vertebrates or animals (< 2 kg) than of large vertebrates or animals. All formations have same fossiliferous facies, with moderate to high degrees of temporal averaging and low to high degrees of spatial averaging. Different preservational situations impose different constraints on paleoecological and evolutionary analyses. The best opportunities for paleocommunity remodeling are provided by high taxonomic resolution, large samples, and varied surroundings of preservation. These situations are found in limited portions of each record. The best opportunities for documenting evolution within lineages and species replacement patterns are provided by high taxonomic resolution, high temporal resolution, and consistent preservational context. These putrefactioning attributes pertain to the more common Paleogene vertebrates or animals, particularly from the rich paleosol localities of the Willwood Formation, and to the more common Neogene small vertebrates or animals from abandoned-channel fills of the Siwalik record.

Vasileiadou et al. 2007 has undertaken a putrefactioning study on an assemblage of hard parts of bone phosphates and teeth of Isoptychus sp. and Thalerimys fordi (extinct rodent family Theridomyidae) from a single bed in a coastal plain setting, in the Late Eocene (Priabonian) Osborne Member, Headon Hill Formation (Hampshire Basin, UK). The animal's fossils show good preservation and do not bear the marks of obvious long distance transport. The two theridomyid species show similar patterns of mortality, unit representation and surface modifications, which indicate similar processes of accumulation. There is high mortality of juvenile and old creatures indicating accumulation of the assemblage by the action of attritional, not catastrophic agents. The postcranial units show fragmentary states and very low relative abundances. The vast majority of elongate hard parts of bone phosphates (limb hard parts of bone phosphates, phalanges and metapodials) are broken and exhibit a spiral irregular type of fracture with rounded fracture edges indicating that the hard parts of bone phosphates were broken when they were fresh and have subsequently undergone additional modification. The enamel of most of the cheek teeth and incisors shows localized etching to various degrees and most of the hard parts of bone phosphates show etching. By elimination of other modifying agents, the observed etching is attributed to digestive corrosion. Collectively, these data indicate that the majority of the theridomyid creatures were eaten and digested by an animal that could cause high fragmentation during ingestion and with stomach juices of relatively high acidity.

Both these features characterize vertebratian carnivores. The presence of puncture marks on hard parts of bone phosphates of both theridomyid species and comparisons with measurements of bite marks caused by extant vertebratian carnivores suggest predation by a small vertebratian carnivore about the measurement of an arctic fox. The extinct amphicyonid carnivoran Cynodictis cf. lacustris occurs in the same bed and the measurements of some of its teeth match well with the measurements of the puncture marks on the theridomyid hard parts of bone phosphates. A predator–prey interaction is, therefore, deduced for the amphicyonid and the two theridomyid species, thereby reconstructing a small part of the continental Paleogene food chain.

Clyde et al. 1998 have undertaken a study on new stratigraphic and paleontological evidence from the McCullough Peaks, northern Bighorn Basin,Wyoming. The study is incorporated into an iso putrefaction ing faunal database and used to investigate the impact of the latest Paleocene thermal maximum and coincident earliest Wasatchian immigration event on local vertebratian community structure. Surface collections from Willwood Formation over bank deposits provide putrefactioningally consistent and stratigraphically resolved samples of the medium- to large measurement portions of underlying vertebratian communities. Rarefaction shows that the immigration event caused an abrupt and dramatic increase in species richness and evenness. After this initial increase, diversity tapered off to more typical Wasatchian levels that were still higher than those in the preceding Clarkforkian. Wasatchian immigrants were rapidly incorporated into the new community organization, representing ~20% of the taxa and ~50% of the creatures. Immigrant taxa generally had larger body measurements and more herbivorous and frugivorous dietary habits compared to endemic taxa, causing eloquent turnover in body-measurement structure and trophic structure. There was an eloquent short-term body-measurement decrease in many lineages that may have been prompted by the elevated temperatures and/or decreased latitudinal thermal gradients during the latest Paleocene thermal maximum. Rapid short-term climatic change (transient climates) and associated biotic dispersal can have abrupt and long-lasting effects on vertebratian community evolution.

Hellawell et al. 2012 studied the Green River Formation, Wyoming which contains such an abundance of well-preserved flora and fauna that this late early Eocene Lagerstatte is one of the best known from North America. Despite having being studied since the mid-nineteenth century, little is known about the putrefactioning processes that resulted in a diverse suite of organisms, especially abundant fossil fish, being preserved in exquisite detail. Two distinct patterns of completeness and articulation recur among the fossil fish: complete and fully articulated, or extensive fragmentation of the anterior part of the fish only ('half and half' preservation). In this study, in order to decipher the processes involved in the preservation of Fossil Lake fish, specimens of the extant taxon *Carassius auratus* were putrefactioned examination ally over a 6-month period. Various scenarios approximating conditions in the Eocene lake were replicated in the laboratory and each monitored to record the rate of disintegration and how different starting conditions impacted on the study of putrefactioning animals of the fish. Varying salinity or oxygen level did not induce any discernable differences in the pattern of putrefaction; disintegration occurred faster at higher temperatures. Unexpectedly, putrefaction rates varied greatly between replicate samples. Soft animal fibers decomposed rapidly and extensively, and, even in the absence of any disturbance, the skeletal fragmentation that followed was repeatedly much greater than that exhibited by the vast majority of fossil fish from the Green River Formation. The results indicate clearly that putrefaction in a quiet-water surrounding is, on its own, insufficient to explain the consistently high-fidelity preservation of Green River fish: some additional factor is implicated. It has been proposed that microbial mats at the sediment–water interface were key; fish death bodies became adhered to the sediment surface inhibiting floating, fragmentation and loss of hard parts of bone phosphates, with 'half and half' specimens curving laterally and not fully adhering, thus only that part (typically the posterior) in contact with the substrate retained a high degree of skeletal fidelity.

Bai et al. 2011 studied the vertebratian fauna of the chalicothere pit, lower Eocene basal Arshanto Formation, Erlian Basin, Inner Mongolia, comprises at least eight species, of which *Litolophus gobiensis* is the most abundant large mammal, presented by at least 24 creatures and 1252 specimens of skulls, mandibles, and postcranial units. The Litolophus assemblage is dominated by young adult creatures, while juveniles are under presented, an age profile that conforms to the theoretical model of a catastrophic assemblage. The assemblage is characterized by skeletal units with limited weathering and moderate fragmentation, and a paucity of isolated teeth, suggesting that the death bodies were probably exposed to the surrounding after decease or fatality for only a brief period. Fluvial activity was prominent and had sufficient energy to align most long hard parts of bone phosphates of Litolophus (153.1 kg in mean value) in a NNE-SSW direction. Most units in the assemblage belong to Voorhies Groups II and/or III, while units of

Group I are rare. In addition, the Litolophus death bodies were evidently disturbed by predators and/or scavengers before burial. Damage to the ends of long hard parts of bone phosphates is unevenly distributed, probably reflecting both preferential feeding behavior by predators or scavengers and the timing of epiphyseal fusion in Litolophus. The scarcity of juvenile creatures can also partially be attributed to predation or scavenging; however, it seems unlikely that the chalicothere pit was a scavenger den.

Astibia et al. 2005 studied the sirenian vertebrae and ribs which have been have been discovered from two Middle Eocene localities of the Pamplona Basin, Navarre (western Pyrenees). These outcrops correspond to different lower Bartonian lithostratigraphic units: the lower part of the Pamplona Marl Formation (Uztarrotz site) and the upper part of the Ardanatz Sandstone (Ardanatz site). The former represents a deep and low-energy sea floor far away from a deltaic slope; the Ardanatz surrounding probably corresponds to a semi-closed deltaic bay periodically affected by catastrophic floods (i.e., fluvial hyperpycnal flows). The presence of epibiotic activity suggests that the hard parts of bone phosphates were exposed for a while prior to the burial. The histological structures are well preserved except in the peripheral region, where tubular-like microstructures filled by pyrite and iron oxides probably correspond to microbial bioerosion. The major mineral portion of the fossil hard parts of bone phosphates is francolite (carbonate fluorapatite). In the

Ardanatz samples there is evidence of secondary francolite due to the late replacement of original carbonate fluorapatite through internal fractures. The Ardanatz and Uztarrotz sirenian fossils do not show any evidence of re-elaboration. They have similar sum of rare earth units (REE) concentrations relative to the host rock, but comparatively lower than in other animals fossil hard parts of bone phosphates. This feature may be due to the dense compact structure of pachyosteosclerotic sirenian hard parts of bone phosphates.

Dyke et al. 2009 studied the pattern, pace and extent of the evolutionary radiation of modern birds (Neornithes) by the end-Cretaceous (65 Ma) which has long been debated. Well-dated putrefactioningally understood and phylogenetically constrained fossil birds from both sides of the Cretaceous–Paleogene (K–Pg) boundary are required to quantify the shape of this radiation, but have largely been lacking. Dyke et al. 2009 reports on a large collection of fossil birds from the Lower Eocene of Denmark (ca. 54 Ma) that includes three-dimensionally preserved, articulated specimens from carbonate concretions as well as skeletal imprints and feathers. These birds are from a marine diatomite sequence (the Fur Formation), a low-energy deep-water preservational surrounding unique to the Cretaceous and Paleogene avian fossil record. Dyke et al 2009 presents putrefactioning and palaeoecological evidence gleaned from these birds that in amalgamation with phylogenetic data have implications for unravelling avian survivorship across the K–Pg boundary as well as for the pattern of the neornithine evolutionary radiation.

Brand et al. 2000 in the study seeks to document and account for the distribution, abundance, and putrefactioning condition of fossil turtles in a fossiliferous section of the Bridger Formation, Unit B (Early Middle Eocene of Wyoming). The following patterns were documented: (1) Fossils were non-randomly distributed stratigraphically and sedimentologically with most specimens concentrated in mudstones within a few meters above two of three widespread limestone beds. These concentrations were not artifacts of accumulations of eroded fossils on low angle slopes. (2) Fossil concentrations above limestones were widespread in the study area—tens of kilometers in at least one case. The well-exposed Black Mountain turtle layer shows a gradient in fossil density, highest to the south and lowest to the north. (3) Most specimens from fossil accumulations exhibited a similar putrefactioning condition, with many shells mostly intact and unweathered, and with no skulls and few limb units. Few units bore predator tooth marks. Some hard parts of bone phosphates in channel deposits were abraded, but most hard parts of bone phosphates in fine-grained sediment were not. The largest concentrations of turtles were associated with specific layers of fine-grained sediment. These features suggest mass mortalities of turtles, and burial before many shells disarticulated. A model is presented to account for these data. In this model, a limestone forms in a shallow, basin-wide lacustrine surrounding. Then, a series of fluvial/lacustrine sedimentary units resulting from a large-scale episode of volcanism accumulated in the lake and buried the turtles. The volcanic event may have been the cause of decease or fatality, from breathing ash-choked air, for large turtle populations in the lake/marsh surrounding, which were then buried early in the volcanic episode. Turtle populations evidently did not recover eloquently until another shallow lake filled the basin.

Srivastava 2002 studied the vertebrae belonging to the teleost fishes from the Lower Eocene gypseous shales of the Naredi Formation (Nareda locality), Kachchh are described. All the vertebrae represent the trunk portion of the fish; they are short, amphicoelous and imperforate. Only the centrum portion of the vertebrae is preserved with base of neural arch. The measurement of the vertebrae is variable, possibly representing different aged creatures who died in some unusual situations (trapped in shallow region of lagoon). The preservational features of the vertebrae suggest complete fragmentation due to the long post-mortem exposure. The vertebrae were initially sorted in the marine system (Voorhies Group I) and were deposited in oxidizing condition and low energy surrounding.

CONCLUSION

In conclusion, there have been nine studies on vertebratian study of putrefactioning animals in Paleocene-Eocene time. Badgley et al. 1995 studies the putrefactioning attributes pertaining to the more common Paleogene vertebrates or animals, particularly from the rich paleosol localities of the Willwood Formation, and also to the more common Neogene small vertebrates or animals from the abandoned channel fills of the Siwalik record. Vasileiadou et al. 2007 deduces a prey-predator interaction from the amphicyonid and the two theridomyid species, thereby reconstructing a small part of the continental Paleogene food chain. Clyde et al. 1998 studies a new stratigraphic and palaeontological evidence from the McCullough Peaks, northern Bighorn Basin, Wyoming. Hellawell et al. 2012 studied the Green River Formation, Wyoming, and proposes that the microbial mats at the sediment-water interface were key. The fish death bodies became adhered to the sediment surface inhibiting floating, fragmentation and loss of hard parts of bone phosphates, with ‘half and half’ specimens curving laterally and not fully adhering, thus only that part (typically the posterior) in contact with the substrate retained a high degree of skeletal fidelity. Bai et al. 2011 studied the vertebratian fauna of the chalicothere pit, lower Eocene basal Arshanto Formation, Erlian Basin, Inner Mongolia. Astibia et al. 2005 studied the sirenian vertebrae and ribs which have been discovered from the two Middle Eocene localities of the Pamplona Basin, Navarre (western Pyrenees).Dyke et al. 2009 studied the evolutionary radiation of modern birds (Neornithes) in the Cretaceous-Paleogene boundary. Brand et al. 2000 documents and accounts for the distribution, abundance, and putrefactioning condition of fossil turtles in a fossiliferous section of the Bridger Formation. Srivastava 2002 studied the vertebrae belonging to the teleost fishes from the Lower Eocene gypseous shales of the Naredi Formation, Kachch.

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