

Small mammal taphonomy of three Miocene localities from Damiao, Nei Mongol, China (Post-print)

Authors: Leena SUKSELAINEN, Hannele PELTONEN, Anu KAAKINEN, ZHANG Zhao-Qun, Leena SUKSELAINEN

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Abstract

Predation is the most common cause of death in small mammals and also results in significant modification of prey remains. Postmortem processes such as weathering, trampling, and transportation also alter animal bones and affect the formation of fossil assemblages. This study investigates three Miocene fossil localities from Damiao, Nei Mongol, China, ranging from the early Miocene to the early late Miocene (ca 21–11.6 Ma). By analyzing the sedimentary context and taphonomic features of the small mammal fossil assemblages, we identify the primary agents responsible for fossil accumulation. Results reveal that predation constitutes the fundamental mechanism of accumulation at all three localities; however, the two younger sites exhibit overprinting by fluvial transportation and possible trampling. The three localities may have featured different predators: owls at the oldest site, and diurnal birds of prey or mammalian carnivores at the younger two sites. The study further demonstrates that systematic excavation of small mammals is feasible and can mitigate some of the damage inherent in collection processes.

Full Text

Preamble

Small mammal taphonomy of three Miocene localities from Damiao, Nei Mongol, China

Leena SUKSELAINEN¹, Hannele PELTONEN¹, Anu KAAKINEN¹, ZHANG Zhao-Qun²

(1 Department of Geosciences and Geography, University of Helsinki, Helsinki FI-00014, Finland; leena.sukselainen@gmail.com)

(2 Key Laboratory of Vertebrate Evolution and Human Origins of Chinese

Academy of Sciences, Institute of Vertebrate Paleontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing 100044, China)

Abstract

Predation is the most common cause of death in small mammals. It also causes the greatest modification on their remains. Other postmortem processes, such as weathering, trampling, and transportation all modify bones and contribute to the forming assemblage. Here we examined three Miocene localities from Damiao, Nei Mongol, China with different fluvial subenvironments. The ages span from early Miocene to early late Miocene (ca. 21–11.6 Ma). We describe the sedimentary context and taphonomic features of the small mammal assemblages, and identify the responsible agents for the fossil accumulations. Our study reveals predation as primary means of accumulation for all three localities. However, there is overprinting of other means of accumulation such as fluvial transportation and possibly signs of trampling at the two younger localities. Results indicate possibly different predators for all localities; owls for the oldest one, and diurnal birds of prey or mammalian agents for the younger two. We also show that systematic excavation for small mammals can be done, and in this way it may be possible to reduce some of the damage collecting always produces.

Keywords: Nei Mongol, Neogene, micromammals, digestion, predation, fluvial deposits

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1 Introduction

Taphonomy, the study of preservational processes of organic remains, connects paleontology with biology and geology (Behrensmeyer et al., 2000; Efremov, 1940). Taphonomic processes begin at the moment of death of an organism and continue till its recovery (e.g., Arcos et al., 2010; Lyman, 1994). These processes are sources of bias in the fossil record since they may remove some of the biological information but on the other hand produce information of past environments and fossilization (Arcos et al., 2010; Behrensmeyer and Kidwell, 1985; Fernández López, 1981, 1991). Taphonomic processes affecting fossil assemblages include predation, scavenging, transport, and weathering (e.g., Andrews, 1990; Andrews and Evans, 1983; Behrensmeyer, 1978; Lyman, 1994) and they are portrayed by different taphonomic features such as breakage, intrusive corrosion, rounding, polishing, cracks, staining, scrapes, weathering, pressure damage, and enamel pitting (Table 1).

Due to the limited life range of small mammals they are more sensitive to the local scale environmental changes than large mammals (Demirel et al., 2011;

Redding, 1978; Soligo and Andrews, 2005) and therefore they are useful indicators of past ecologies (e.g., Van Dam, 1997, 2006; Van Dam and Weltje, 1999).

One of the major causes of death of small mammals is predation (e.g., Andrews, 1990; Andrews and Evans, 1983; Fernández-Jalvo, 1995; Reed and Denys, 2011). Predation is also the cause of the greatest modification of small mammal remains (Andrews, 1990). Of different predators, mammals modify the bones of their prey the most due to the usage of their shearing teeth in breaking up the prey before ingestion and due to this damage prey of mammalian predators is less likely to become fossilized (Andrews and Evans, 1983). The least amount of bone breakage is produced by owls, while diurnal birds of prey are intermediate bone breakers (Andrews and Evans, 1983; Andrews, 1990).

Shortly after the death of a small mammal, secondary modifications of the remains takes place. These include decay, and scavenging, which are not easily recognized in fossil samples, for decay leaves little modification, and marks left by scavenging are not readily distinguished from modification by predation. Trampling is another source of modification beginning soon after death resulting in dispersal, breakage, burial or total destruction of the animal remains (Andrews, 1990; Arcos et al., 2010; Williams, 2001). Weathering occurs when bones are lying in the open without protection of some kind (Andrews, 1990; Behrens-meyer, 1978). However, small mammal remains are more likely to be trampled and broken or blown away than to remain exposed to weathering (Andrews, 1990).

Transport of the remains often results in breakage of the bones. However, pellets and scat structures may protect bones for some time (Andrews, 1990; Arcos et al., 2010), but when pellets disintegrate the skeletal material will be exposed to weathering and dispersal (Andrews, 1990; Korth, 1979). Small mammal remains are easily transported by flowing water (Andrews, 1990; Dodson, 1973).

In this study we examine the small mammal taphonomy from three Miocene mammal localities from Damiao in Siziwang Banner, Nei Mongol (Fig. 1 [Figure 1: see original paper]). The site was identified in 2006 and has been excavated in three field seasons since. These excavations have yielded over 30 fossil localities with three main fossil horizons that are magnetostratigraphically dated to range from early Miocene to earliest late Miocene (Kaakinen et al., 2015). Although numerous, the Neogene fossil mammal localities in Central Nei Mongol are scattered, lacking continuous vertical exposures and there are few representatives of early Miocene mammals (Kaakinen et al., 2015; Wang et al., 2009). In Damiao the strata constitute one of the most continuous sequences in Nei Mongol with early, middle, and late Miocene fossil faunas in stratigraphic superposition. Damiao also hosts the latest occurrence of the humid favouring pliopithecoid primate in Central Asia, in the late middle Miocene locality of DM01 (Zhang and Harrison, 2008). Out of the circa 30 localities, three rich localities of different age and sedimentology were chosen for closer inspection. The stratigraphy (Kaakinen et al., 2015) and some mammalian groups have been studied in detail (Wang and Zhang, 2011; Zhang et al., 2011). This however is

the first attempt to study the small mammal taphonomy from the area.

Here we report the results of a taphonomic study of small mammals found from three localities in Damiao. The aims of the study are to characterize the sedimentary context and taphonomic features of the small mammal burials, and to identify the agent(s) responsible for the fossil accumulations. This study also shows that systematic excavation for small mammals can be done and in this way it is possible to reduce some of the damage that always results from the collecting “no matter how careful the technique” (Andrews, 1990).

2 Sedimentological and paleontological framework

The study area is located in central Nei Mongol, ca. 100 km north from Hohhot, near Damiao village in Siziwang Banner (Fig. 1). The area is distinguished by undulating topography ranging between 1250 m and 1350 m a.s.l. The Damiao fossil localities are divided into eastern and western sides that are separated by the Wulanhua-Damiao motorway. All the localities in the area are only a few kilometers from each other. The sedimentary sequence is characterized as a fluvial environment where the bulk of the fine-grained deposits in the sequence represent well-drained floodplains (Kaakinen et al., 2015).

DM16 is stratigraphically the lowest fossil site in Damiao and was paleomagnetically dated at 20–21 Ma (Kaakinen et al., 2015). It occurs within a mudstone interval comprising the basal 16 m of the sequence and extending laterally over hundreds of metres. The sediment succession at DM16 (Fig. 2 [Figure 2: see original paper]) comprises rather monotonous and homogenous redbrown claystone - fine siltstones that commonly exhibit massive weathering appearance. Thin flat lamination and graded beds 1–4 cm thick are recorded in the upper portion of the section. Slickensides, spherical mm-size manganese and calcium carbonate nodules occur throughout and are locally abundant. Some fine-scale alternation of red and green coloration is discernable in the lower portion of this interval.

The productive bed is ca. 1.2 m thick, with one ca. 9 cm thick fossil-rich horizon in the middle of the bed, and is associated with root traces and few desiccation cracks. The bonebed has yielded relatively well preserved but fragmented vertebrate fossil remains, comprising mainly small mammal skeletal elements; dipodid and eomyid rodents are common as well as ochotonid lagomorphs with few insectivores. Large mammals are scarcer and represented by artiodactyls, rhinos and a mustelid. Small mammals at this level are dominated by Oligocene genera, however, by more derived species. In addition to vertebrate remains, the locality contains a dense accumulation of fossil eggshell fragments, a few gastropod shell casts and several bone-bearing pellets in the richest horizon.

Laterally extensive, massive and finely-laminated mudstones that possess a variety of features indicating paleosol development are characteristic of floodplain

deposits (Miall, 1977, 1992, 1996). The sporadic desiccation cracks indicate that the mudstones were probably deposited as ephemeral ponds/lakes at the highest flood stage, and cracks were developed during desiccation (Miall, 1977, 1992).

The richest and only primate-bearing locality, DM01 is associated with latest middle Miocene Tunggur fauna with an age estimate of ca. 12.1 Ma (Kaakinen et al., 2015; Zhang et al., 2011, 2013). The DM01 section is dominated by two clast-supported conglomerate beds that stretch laterally over 60 meters. The well-sorted and densely packed clasts in these beds consist principally of spherical and well-rounded intraformational reworked calcium carbonate nodules up to 8 cm in diameter. The lower unit is up to 60 cm thick and is composed of few-cm-thick beds that often show inverse grading from coarse sand to granules. The upper conglomerate shows variable bed thickness from 1 m to 1.6 m and mainly consists of horizontally stratified pebble-granule conglomerate with subordinate layers of coarse sand and granules. In the sand-dominated parts the internal structures are trough and tabular cross bedding. The lower boundaries are erosive and exhibit discrete scours locally. These reworked pedogenic conglomerates show distinct rust and black colour in the outcrop; concretions have a black manganese staining and manganese and goethite highlights the bedding planes.

The sediments surrounding the conglomerates are mainly composed of well-sorted reddish yellow (7.5 YR 6/6) to light brown (7.5 YR 6/4) fine sands and silts. The primary sedimentary structures, when present, include thin parallel lamination and cross-lamination. These sediments are often calcareous but calcareous nodules are scarce and continuous concretion horizons are absent.

The nodule conglomerates are interpreted as resulting from the avulsive emplacement of channels reworking and concentrating the underlying calcic paleosols (Kaakinen et al., 2015). The abundant occurrence of goethite and manganese indicate an impeded drainage and more humid conditions, although the reworked pedogenic nodules indicate that climate was seasonally dry (cf. Van Itterbeek et al., 2007).

Fossils occur in the sand-granule interbeds throughout the upper nodule conglomerate. In addition to the pliopithecoid, more than 30 species and more than one thousand skeletal elements were found. While large mammals are few and fragmentary, small mammals are abundant and characterized by well-preserved remains. Contrary to DM16 fauna, DM01 fauna is composed of taxa from extant families lacking any Paleogene members.

DM02 locality represents early late Miocene with estimated age of ca. 11.6 Ma (Kaakinen et al., 2015; Zhang et al., 2011, 2013). The DM02 section is predominately fine-grained (Fig. 2). Lithologies are mixtures of reddish brown (5 YR 4/4) to yellowish red (5 YR 4/6) silt and clay with variable amounts of calcium carbonate accumulation as distinct nodules and indurated layers. Most units exhibit no internal bedding structures. DM02 fossils are present in a 0.2-0.4 m thick lens-shaped sandstone body at the lowest portion of the local section.

The fossiliferous unit erosionally overlies the underlying mudstone sequence and passes up with a sharp conformable contact to the overlying coarse siltstone. The sand lens is massive or displays a few centimeters thick horizontal interbeds of silt to poorly sorted coarse -very coarse sand. The constituent grains are mostly angular quartz, embedded in a silt matrix.

The fine-grained deposits that encompass the DM02 section are interpreted as pedogenically modified overbank deposits. Red coloration, carbonate nodules, pedogenic slickensides and overall massive appearance in outcrop are all suggestive of pedogenesis. The fossil find unit, with its erosional base and heterogeneous lithology, indicates sites of episodic injections of coarse sediment on the floodplain surface. Fossil fauna at DM02 contains abundant and diverse fossils of rodents and lagomorphs, together with few specimens of large mammals (Kaakinen et al., 2015). In general the fauna in DM02 is similar to DM01.

3 Material and methods

Materials

Fossil specimens under study were collected from Damiao during three field seasons between 2007-2009. Material from DM01 consists of 185 fossil specimens, both teeth and postcrania. From DM02 158 fossil specimens in total were analyzed, mainly teeth and a few jaw fragments. There was no postcranial material available for our study from DM02. Fossil material from DM16 consists of 360 specimens from the grid of which 255 specimens were taphonomically analyzed. Half of the analyzed specimens are with full grid reference (i.e. coordinate and depth information). Majority of DM16 material is postcrania with few teeth and jaws (Table 2).

Methods

At the pliopithecoid bearing locality of DM01 as well as the adjacent DM02 a restricted area was opened and the sediments screened. A systematic sampling was carried out at the locality DM16, where a grid with 27 squares of 1 m × 1 m in size was set up and collected fossils were given a specific grid reference as well as for most collected specimens a precise location, both horizontal and vertical, within the grid. Dry-sieving of excavated material was done at the site using coarse screen.

The investigated specimens from Damiao showed a wide variety of taphonomic modification. In order to detect, measure, and score the surface alterations on fossil specimens, each element was carefully examined under a stereoscopic light microscope. Taphonomic features analyzed from Damiao material for this study were: breakage, intrusive corrosion, rounding, polishing, cracks, staining, scrapes, weathering, pressure damage, root marks, and surface (enamel) pitting (Fig. 3 [Figure 3: see original paper]).

All the taphonomic features were scored on an ordinal scale of four stages of modification. The scale was developed for the purposes of this study based on Andrews' (1990) work on small mammal taphonomy. Scorings were made depending on the degree of the taphonomic modification on the specimen. The four stages are as follows: 0 = no modification; 1 = light modification; 2 = moderate modification; and 3 = strong modification (Fig. 4 [Figure 4: see original paper]). Additionally in order to detect the microfossil accumulating agent the ratio of major distal elements to proximal elements was calculated as well as the ratio of cranial elements to postcranial elements following Andrews (1990).

Voorhies' Groups are a common way to examine skeletal elements according to their potentiality of being transported fluviially (Behrensmeyer, 1975; Lyman, 1994; Voorhies, 1969). Degree of transport reflects the different settling velocities of different types of bones (Behrensmeyer, 1975; Korth, 1979). Voorhies' Groups have been recalibrated for micromammal studies and the Generalized Sequence of Korth' s settling groups (Korth, 1979) was applied to the present data (Table 3).

Detailed sedimentological logging was done by applying the conventional methods for lithofacies analysis. Vertical heights were measured with Jacob' s staff and Abney level (c.f. Brand, 1995), grain size was determined in the field and for selected fine-grained samples in the laboratory using a Malvern Mastersizer 2000, and sediment colours were defined as Munsell™ codes on fresh samples.

4 Results and interpretation of taphonomic features

Proportions of taphonomic features on specimens at each locality are shown in Fig. 3, bones and dental materials separately. The most prominent feature is the lack of skulls at all localities as well as lack of postcranial material at DM02 (Table 2). The ratio of major distal limb elements to proximal elements for DM16 is higher than for DM01 (Fig. 5 [Figure 5: see original paper]). The ratio of cranial element to postcranial is higher in DM01 than in DM16 (Fig. 6 [Figure 6: see original paper]).

Both teeth and bones from DM16 showed high incidence of breakage, intrusive corrosion, rounding, polishing, cracking, enamel pitting and staining (Fig. 3), the taphonomic features that indicate predation (e.g., Andrews, 1990; Andrews and Evans, 1983; Fernández-Jalvo, 1995; Reed and Denys, 2011). The straight and spiral fracture types in broken bone specimens provide further evidence for predation (Shipman et al., 1981) as means of accumulation. Results from DM16 were also inspected with respect to the richest fossil layer. This level showed even more specimens with features associated with digestion (breakage, intrusive corrosion, and scrapes) than layers below or above it. Cracking was detected only from specimens from the richest fossil horizon and below it, and was more common in teeth than bones. Nevertheless, this feature was less

common than other predation features and could result from other taphonomic agents than predation, for example from weathering during subaerial exposure of the remains.

Weathering, in turn, is more common on bones than teeth but is altogether not a very common feature and can be separated from digestion by some unique features on the surface of the specimens. Weathering in small mammal remains can be identified from splitting that occurs along the collagen fiber orientation, flaking or exfoliation of the outer layer of bone (Fig. 4C) as well chipping and splitting of teeth (Andrews, 1990). Of all the localities discoloured dental specimens were found only from DM16.

The ratios of anatomical elements further suggest that predation contributed to the accumulation of the small mammals in DM16. The ratio of distal (tibia + radius) to proximal (femur + humerus) limb elements is low (Fig. 5), indicating predator assemblage, as does the ratio of postcranial to cranial elements (Fig. 6). The absence of more distal parts of limbs is a common feature in predator assemblages as is the deviation from the average skeletal proportions of postcranial to cranial elements, which indicates preferential destruction of a skeletal group - or selection against it (Andrews, 1990) - in this case destruction of, or selection against, cranial elements. The lack of skulls is one main feature of trampled assemblages, although in small mammals evidence of natural trampling is nearly non-existent due to the fragile nature of their bones (Andrews, 1990). Also the low number of isolated teeth at this locality suggests a source of modification of material other than trampling, such as fluvial transportation.

For DM16 bones of all of Korth's settling groups are present (Table 3). However, group I (most easily affected by fluvial transport) is rather poorly represented whilst there is a high representation of least easily transported group III elements (lag deposit). The loss of group I likely results from winnowing of lighter elements during surface runoff.

Less than half of DM16 fossil bones are weathered and when they are, they mostly represent stage 1. This together with even less weathered dental material means that DM16 small mammal remains likely experienced only a short duration of exposure to weathering agents before burial. Taphonomic processes after burial in DM16 are represented by light pressure damage that is present in most specimens, and some rare light root marks. Intrusive corrosion found on specimens is likely digestive in origin as fossils are only partially affected by corrosion (Andrews, 1990).

Both teeth and bone specimens from DM01 showed high incidence of modifications related to predation (breakage, intrusive corrosion, rounding, polishing, enamel pitting and staining; e.g., Andrews, 1990; Andrews and Evans, 1983; Fernández-Jalvo, 1995; Reed and Denys, 2011). Also a high proportion of broken bones together with straight and spiral fracture types indicate predation as means of accumulation (Shipman et al., 1981). Bones from DM01 show highest incidence of stage 3 corrosion and dental material is mostly of stage 2.

High incidence and high level of corrosion both on bone and dental material in DM01 suggest predation. However, the bimodal breakage distribution at DM01 could indicate two different agents forcing the accumulation. Primary means of accumulation would be predation with overprinting of other processes like transportation or trampling. It is said that much of the breakage of bone assemblages is due to transport before or after burial and transportation of small mammal bones produces high levels of breakage (Andrews, 1990). Trampling on the other hand is not well documented in small mammals since their bones are easily destroyed (Andrews, 1990). However, the lack of skulls together with a high number of isolated teeth, proximal femora and distal humeri (Fig. 7 [Figure 7: see original paper]) is in accordance with the few observed trampled small mammal assemblages (Andrews, 1990). The low ratios of distal to proximal limb elements and postcranial to cranial elements in DM01 are characteristic features of many predator assemblages (Andrews, 1990) (Figs. 5, 6).

The members of group I of Korth's settling groups in DM01 are absent (Table 3). This group is the one most easily affected by fluvial transport and might indicate DM01 is a lag assemblage (Behrensmeyer, 1975). However, DM01 has rather low representation of group III (lag assemblage) specimens as well, and this suggests that the assemblage has been affected by fluvial transport.

In DM01 more than half of the analyzed postcranial specimens showed signs of weathering, mainly stage 1. Dental material is less often weathered but more severely, mostly stage 2, indicating short duration of exposure, but longer than in DM16. Postdepositional modification in DM01 is represented by light pressure damage that is detected on most specimens as well as rare and light root marks. Intrusive corrosion in DM01 did not affect whole surfaces and therefore is interpreted to be digestive in origin (Andrews, 1990).

Locality DM02 contains only small mammals and features only isolated teeth (Table 2). The dental material from DM02 presented the same taphonomic features of digestion that strongly indicate predation as for the previous unit DM01 (Fig. 3).

Trampling cannot be fully excluded as a factor affecting the DM02 small mammal fossil assemblage, since the lack of skulls may be associated with trampling (Andrews, 1990). The total absence of postcrania may also be due to trampling, since trampling causes dispersal of bones (Andrews and Cook, 1985) and in addition small mammal bones are fragile and easily broken when not protected by pellets (Andrews, 1990).

The dental material at DM02 is the least weathered of all studied localities, only 4% of teeth at DM02 showing light modification. The near lack of signs of weathering in DM02 indicates short duration of surface exposure prior to burial. After burial DM02 dental material has experienced some pressure damage and root marks, however not severe. Intrusive corrosion is detected from all specimens but affecting only parts of the teeth suggesting digestive origins (Andrews, 1990).

5 Discussion

The large lateral continuity of the DM16 sedimentary beds, their fine-grained lithologies and associated horizontally laminated structures indicate suspension settling in the distal floodplain with periodic input of fine sands. The small mammal remains represent larger grain sizes than the range represented in the sediment matrix and therefore are not likely to have experienced much fluvial transport to the site; the low representation of lighter elements is considered as resulting from winnowing during surface runoff. Sedimentological evidence suggests that conditions were at least periodically oxidizing and conducive for soil formation as evidenced by carbonate nodules, root traces and occasional presence of mottling. The presence of bird eggshells indicates nesting sites and consequently substantiates the subaerial conditions. However, the fairly unweathered bone and teeth surfaces in DM16 do not suggest a prolonged period of subaerial exposure during dry seasons prior to burial.

The sedimentological data indicate that fossil bearing beds at DM01 resulted from reworking of the resistant pedogenic carbonate nodules into an intraformational conglomerate by fluvial avulsion. Some mechanical damage produced by transport is evident in the remains, although in light to moderate stages. It is also easily observed that DM01 shows element sorting by transport processes. The lack of skulls and high proportion of isolated teeth, distal humerus, distal tibia, and proximal ulna as well as fragmentary mandibles (cf. Wolff, 1973; Andrews, 1990) all point to fluvial transportation as a means of accumulation (Fig. 7). Weathered specimens were more common at DM01 than at DM16 although their dominantly light to moderate stages do not indicate extended subaerial exposure. Therefore it is obvious that DM01 contains materials harvested from the floodplain but, based on the relatively well-preserved nature of the remains, they have probably not been transported very long nor far.

The stratified bed of poorly sorted sand that typifies DM02 suggests relatively high-energy injection of sediment to the floodplain. Taphonomical features at DM02 locality are identical to DM01, except that the most prominent feature of DM02 is the total absence of skulls and postcranial elements. This may be due to transportation of all the lighter, more easily moved material away leaving only molars and a few mandibles behind, however, with total absence of postcrania this is uncertain. Another option could be trampling, which could have destroyed the fragile small mammal bones. However, due to the fragile nature of small mammal bones, natural trampling is rarely evidenced in small mammals (Andrews, 1990).

Natural causes of death usually leave animals well preserved, with all parts of the skeleton unbroken and typically one or only a few species present at the bone accumulations (Andrews, 1990). In the three discussed localities from Damiao this seems not to be the case. The fossils are fragmentary, with missing

skeletal elements. While the identifications of specimens are uncertain and in some cases impossible due to the fragmentary nature of material, a variety of species of small mammals were present (Tables 4–6).

Small mammal (fossil) assemblages most often result from predation (e.g., Andrews, 1990; Arcos et al., 2010; Fernández-Jalvo, 1995; Fernández-Jalvo et al., 2016). Owls are commonly cited as a source for accumulations of small vertebrate fossils (Andrews, 1990; Andrews and Evans, 1983; Dodson and Wexlar, 1979), but there is rich evidence of various other predators like diurnal raptors and mammalian carnivores involved in the accumulation of small mammal vertebrate remains as well (Andrews and Evans, 1983 and references therein). Predation seems to be a likely agent of accumulation for all localities in Damiao, however, there are differences in the intensities of digestion-associated features between localities (Fig. 3), which might point to different predator species as dominant accumulation agents. Mammalian carnivores have a complete digestion and high levels of gastric acidity and therefore digestive corrosion (Andrews, 1990). Nocturnal owls, in turn, have relatively low levels of acidity of gastric juices and corrosion whilst diurnal birds of prey feature intermediate acidity and corrosion of bone and dental remains. Signs of intrusive corrosion in Damiao specimens are very great for both bone and dental material in all three localities, being most severe in DM01 (Fig. 3) and least pronounced but abundant in DM16. DM02 molars exhibits similar distribution of corrosion stages as dental material in both DM01 and DM16. However, incisors and molars are known to have different response to digestion (Andrews, 1990; Fernández-Jalvo et al., 2016) and when excluding incisors, it is evident that DM02 and DM01 are more alike. The high incidence of intrusive corrosion could also be of pedogenic rather than digestive origin. However, the former should affect all parts of the bone rather than just small parts of it (Andrews, 1990). Considering that the fossils from Damiao are partially affected by corrosion and show other abundant predation-related taphonomic features, corrosion seems more likely to be the result of digestion for these localities.

In addition to corrosion, indications of predation in Damiao localities is evidenced by several other taphonomic features. Nearly all of the dental material from the three localities showed signs of pitting. Breaking, rounding and staining of dental material were common features in DM01 or DM02 but less abundant in DM16. These taphonomic features on both dental specimens and bones indicate predation as an accumulating agent for all localities and possibly similar, more destructive predation for DM01 and DM02 than for DM16.

Relative proportions of skeletal elements may reveal the identity of the bone accumulator since all predators produce bone loss (Andrews, 1990; Andrews and Evans, 1983; Lyman, 1994). Mammalian predators produce the largest relative loss of distal limb parts, while the opposite occurs for owls. Diurnal raptors are set in between the two groups (Andrews, 1990; Lyman, 1994). The relatively high proportion of distal limb elements and low ratio of cranial to postcranial material together with lightly digested elements suggest the involvement of owls

in DM16. Several fossilized predator pellets at or right above the richest fossil layer further support this interpretation. Additionally, a few discoloured teeth indicate that diurnal raptors may have contributed to the formation of the assemblage (cf. Andrews, 1990; Mayhew, 1977).

For DM01, the relatively low proportion of distal limb elements and high ratio of cranial to postcranial material point to diurnal raptor or mammalian predator as possible producers of the assemblage even without the discoloration which may be concealed by strong manganese coloration. Significant alteration by digestive processes in nearly all elements could favour a mammalian predator origin. For DM02 the teeth exhibit similar evidence of digestion as in DM01, perhaps suggesting the same predator implicated in the deposit formation.

At all localities some transportation of material is indicated, transportation of different duration for all localities and this results in selective loss and/or destruction of elements (e.g., Andrews, 1990; Behrensmeyer, 1975; Behrensmeyer et al., 2000; Korth, 1979). However, the fluvial transportation has not been extensive for any of the localities as the taphonomy and preservational state of specimens suggest.

All field collecting methods may play an important role in bone modification and some damage is always done (Andrews, 1990). In our study we conducted systematic excavation at DM16, and this material shows less severe stages of breakage compared to DM01 or DM02, both for bone and dental specimens. It seems likely that this method is slightly less destructive, but the differences are not statistically significant, preventing a definitive conclusion concerning the reason for breakage. The systematic sampling in DM16 did result in a clearly more representative set of specimens than DM01 (not to mention DM02) with more comprehensive representation of different skeletal elements (Table 2). However, it did not produce higher species diversity than at the two younger localities (Tables 4-6).

Large mammal fauna from Damiao has relatively stable pattern through time with cervoids as ruling group excluding the dominance of widespread open environment for the sequence (Kaakinen et al., 2015). Indication of closed and humid environment for DM01 comes from the presence of the humid favouring pliopithecoid primate (Zhang and Harrison, 2008) as well as anchitheriine horse and the cervid *Euprox alticus* (Kaakinen et al., 2015; Wang and Zhang, 2011). Sedimentological evidence also supports this with abundant goethite and manganese occurrence indicating more humid climate for DM01. However, the small mammal fauna in the entire sequence is dominated by rodents with only relatively few insectivores, which might indicate more dry and open environment (Klietmann et al., 2015; Van den Hoek Ostende, 2001) than that inferred from the large mammals. Taphonomy and preservational state of the specimens suggest that small mammals were collected within the fluvial system, however, the primary accumulators were predators. Predators, however, often prey outside their living habitats affecting the faunal composition of the fossil accumulation and further paleoecological interpretations based on the exposed fauna (e.g.,

Fernández-Jalvo et al., 2016) and therefore small mammals from Damiao may represent habitats of some distance away.

Yet many small mammal predators, even if hunting outside their living/nesting habitats, are rarely foraging far but within few kilometers distance depending on the stage of the breeding cycle and season (e.g., Hardey et al., 2009 and references therein). It can be hypothesized that all three localities were predator accumulations that encountered fluvial transportation to the final burial sites. Based on taphonomy, sedimentology and fauna the environment was likely predominantly closed with more open surrounding areas as a gallery forest with surrounding grassland. The youngest locality, DM01, was likely the most humid.

6 Conclusions

The bone material in Damiao was mainly accumulated by predators and deposited in a fluvial setting. Some reworking by fluvial process took place in DM01 and DM02. DM16 represents distal part of the flood plain whereas DM01 portrays a channel-fill, and DM02 is a result of an episodic flood discharge to the floodplain.

Accumulating predators were likely owls for DM16, and diurnal birds of prey for DM01 and DM02. However, mammals are not fully excluded for contributing to DM01 fossil assemblage.

Systematic sampling of DM16 resulted in a wider range of skeletal material, however, it did not produce taxonomically richer sample than the more traditional excavation methods used at DM01 and DM02. Breakage was less pronounced in the systematic sample, but the difference was not statistically significant.

Environmental conditions for Damiao were rather stable throughout. It represents fluvial system, with mosaic grassland-forest environment (perhaps gallery forest with surrounding grassland). DM01, the only primate bearing locality, seems to have been the most humid, although seasonally dry.

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Chinese Abstract Translation

Title: Taphonomic Study of Miocene Small Mammals from Damiao, Inner Mongolia

Authors: Leena SUKSELAINEN¹, Hannele PELTONEN¹, Anu KAAKINEN¹, ZHANG Zhao-Qun²

(1 Department of Geosciences and Geography, University of Helsinki, Helsinki FI-00014, Finland)

(2 Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing 100044, China)

Abstract: Predation is the most common cause of death in small mammals, and also causes significant modification to the remains of prey. Postmortem processes such as weathering, trampling, and transportation also alter animal bones and affect the formation of fossil assemblages. This study examined three Miocene fossil localities in Damiao, Inner Mongolia, ranging in age from early Miocene to early late Miocene (approximately 21–11.6 Ma). By analyzing the sedimentary background and taphonomic characteristics of each small mammal fossil assemblage, the primary causes of fossil accumulation were identified. The results show that predation was the fundamental cause of small mammal fossil accumulation at all three localities, with superimposed fluvial transportation and possible trampling factors at the two younger localities. The three localities may have had different predators: the early Miocene locality was dominated by owl predation, while the middle and late Miocene localities were dominated by diurnal birds or mammals. The study also demonstrates that systematic excavation of small mammals is feasible and can reduce damage produced during the sampling process to some extent.

Keywords: Nei Mongol, Neogene, small mammals, digestion, predation, fluvial deposits

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Note: Figure translations are in progress. See original paper for figures.

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