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INSECT BONE-MODIFICATION AND PALEOECOLOGY OF OLIGOCENE MAMMAL-BEARING SITES IN THE DOUPOV MOUNTAINS, NORTHWESTERN BOHEMIA

Oldrich Fejfar and Thomas M. Kaiser

ABSTRACT

Mammalian assemblages occur at the sites of Detan, Valec, and Dvérce in calcareous and volcanic clay layers at the southern margin of the Doupov Mountains along the Bohemian Rift. The age of the fossiliferous layer at Detan is early Oligocene (Stampian, Suevian), Biozone MP 21, and is K/Ar dated at 37.5 Ma. Mammalian bones and teeth are widely scattered within basal ash layers at Detan and show a high degree of primary fragmentation. Bone and dentine surfaces preserved in these deposits show peculiar trace fossils on predominantly unweathered surfaces. These marks show a high degree of similarity to those seen on bones found in the Pliocene tuffaceous Upper Laetolil beds of Tanzania. They are certainly not the product of rodent gnawing. Rather, isopteran insects, most probably termites, are believed the most likely cause of the marks. The Doupovské Hory volcanics and the Upper Laetolil beds have similar calcareous tuffaceous lithologies. The distribution of plants, molluscs, and insect traces indicate a mosaic of environments during the early Oligocene in northwestern Bohemia.

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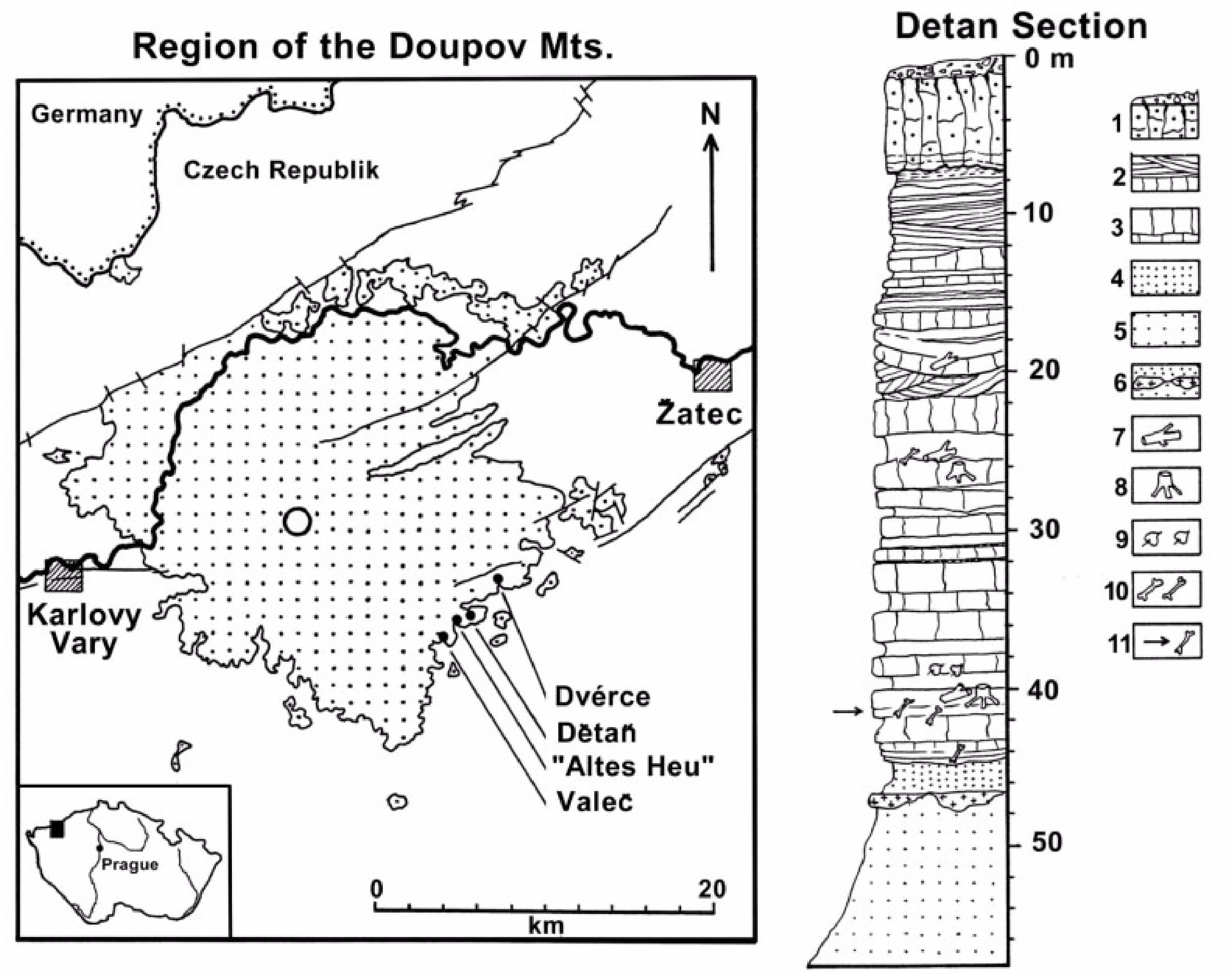

Figure 1. Area of the Doupov Mountains stratovolcano (dotted) between the towns Karlovy Vary and Zatec along the Ohre River rift of northwest Bohemia. The presumed center of the eruption is indicated by a circle. The northern part of the volcanic area is cut by the main tectonic line of the rift. The fossiliferous sites Dvérce, Detan, Altes Heu, and Valec are in the basal level of volcanic ashes on the southeast border of the volcano. Right: Geological section of the clay pit near the village Detan: fine sandy whitish clay (5), lenses of quartzites (6), brownish clay-rich sandy tuffs (4), sequence of heavy-fine bedded occasionally cross-bedded tuffs (2,3,7-11: remains of fossil angiosperm roots and woods (7, 8), record of leaves (9), fragments of bones and teeth (10), fossiliferous layer (11, see arrow in fig. 3.)), strongly weathered two-phased basalt lava flow on the top (1).

INTRODUCTION

The study of animal remains preserved in volcanic ashes of the northern Bohemian rift is among the earliest paleontological research on fossil vertebrates in Europe. In this contribution, we review briefly the history of research on the Oligocene mammal-bearing localities of the Doupov Mountains (Figure 1), present the geological setting and the age of the sites, and examine the ecological conditions during that time. We also report the contemporaneous modification of bone and tooth surfaces by insects at the site of Detan.

The first notice of a fossil from the Doupov Mountains was that of Mylius (1718), who described the complete skeleton of a small rodent (*"Wassermaus"* also known as *"Rongeur de Waltsch")* found on a limestone slab from Waltsch in about 1690. Around the same time the rodent was discovered, a number of fish representing several species was collected (Laube 1901). The slab with the rodent was moved to the collection of J.C. Richter, where it was figured and once again called *Wassermaus* in the catalog of the Museum Richterianum (Hebenstreit 1743). Later the slab was moved to the collections of J.H. Linck and then temporarily lost. Nevertheless, the *Wassermaus* from Waltsch was mentioned by Carl Linné (e.g., in the 10th edition, 1758) and by Georges Cuvier (1825) in his *Recherches sur les Ossements* fossiles as *"rat de l eau."* Von Meyer rediscovered the lost slab with its rodent in the Schönburg Castle Kabinett in Waldenburg at Glauchau, Sachsen. In 1856, he (von Meyer 1856) described it in detail for the first time. The last mention before the current episode of research was by Adalbert Liebus (1934).

A second set of important specimens from the Doupov Mountains was noted by Laube (1899) in a short paper on a rhinoceros tooth fragment identified as *Aceratherium minutum* and a pig identified as *Hyotherium*, both from Altes Heu at Valec. The preliminary (and incorrect) determination of the rhino served as evidence for an erroneous Miocene age assignment for the volcanic activity of the Doupovské Hory Mountains. The rhinoceros tooth (a broken brachydont P^1 housed in the Charles University collection) is of *Ronzotherium* sp., a typical lower Oligocene genus (Fejfar 1987).

GEOLOGICAL SETTING

The Doupov Mountains are an important region of Cenozoic volcanic activity in the Bohemian Massif. They are situated in the Ohre River rift, a northeast-southwest trending volcanic zone developed adjacent to crystalline complexes of various ages. The Doupov Mountains composite stratovolcano covers more than 500 km^2. The rocks forming this volcano are mostly basaltic with non-olivine tephrites to foidites prevailing over olivine composition. Trachytoid intrusive bodies occur at several localities, especially at the margin of the volcanic complex. The ratio between massive rocks and volcanic clasts is about 1:4.

Geologic investigation in this region started at the beginning of the last century. Hibsch (1901) first described the stratovolcanic setting. Kopecky wrote his dissertation on the southern part of the area during the late 1940s and compiled regional data during the 1950s and early 1960s for a 1:200 000 scale geologic map. The central part of these mountains became a restricted military area in the post-war period and since 1968 has been strictly closed to access except for marginal areas, restricting geological research until the last few years.

New data indicate a crater vent near the location where the small town of Doupov used to be, in the central part of the mountains. The vent is filled with syenitic rock. Other eruptive vents have been identified in this complex, including a number of parasitic vents whose necks are found scattered throughout the complex. The central area near Doupov has a caldera-like shape modified by erosion. Multiple stages of eruption are indicated by varying genetic composition as is seen in other well-explored volcanic complexes of the Ceské Stredohorí Mountains.

The Doupovsské Hory volcanics have a preserved maximum thickness of about 500 m. The alternation of subaerial lava flows interbedded with volcaniclastic deposits is the main feature of this complex. Reworked pyroclastic rocks are common. Several sedimentary processes have been recognized including lahars, fluvial, and lacustrine deposition, especially in the marginal parts of the complex. Many volcaniclastic deposits show secondary carbonate deposition. Fine-grained reworked tuffs with admixtures of non-volcanic material preserved the fossil flora and fauna.

THE SITE OF DETAN

Plant and vertebrate remains from the sites of Detan, Dvérce, Valec, Vrbice, and others are interbedded in the lowermost layers of the Doupov Mountains stratovolcano, which were originally exposed at Altes Heu (Laube 1899). The locality of Altes Heu, famous as the site near Valec originally considered to be Miocene, is close to a drainage cutting through strata of the same subaerial volcanic tuffs exposed in 1970 at the Detan clay pit, 300 m to the west. At Dvérce-Wärzen (Wenz 1917), mammal fossils (most importantly, the small anthracothere *Elomeryx crispus crispus*) are found in irregular lenses of tuffaceous limestones rich in lacustrine molluscs and with rare freshwater fishes, imprints of leaves, calcified wood, and casts of fruits and rare molds of hickory (*Carya*) nuts (Figure 2).

The most productive site for mammalian remains is situated in a large clay pit south of the village Detan. The layer of white sandy kaoline clay is covered by 45 to 50 m of basaltic tuff (Figure 3). The tuff-clay contact is sharp in most places. The basal beds of the tuff sequence exhibit both subaerial and lacustrine facies along the flat southern slopes of the volcano. All tuff layers are altered and slightly calcareous. Montmorillonite is the most prevalent diagenetic clay mineral. Altered books of biotite and drops of volcanic glass are locally present in the fossiliferous beds.

Aquatic molluscs are missing from the fossiliferous level in the Detan clay pit, although they are abundant in the nearby fine-grained lacustrine facies found at Valec and Dvérce. Leaf imprints are rare, but parts of calcified woody roots, some in situ, are common in some parts of the outcrop. Small pieces of wood charcoal are present but very rarely. Aragonite pseudomorphs, apparently of wood branches and stems (diameter = 100 to 150 mm) are occasionally found.

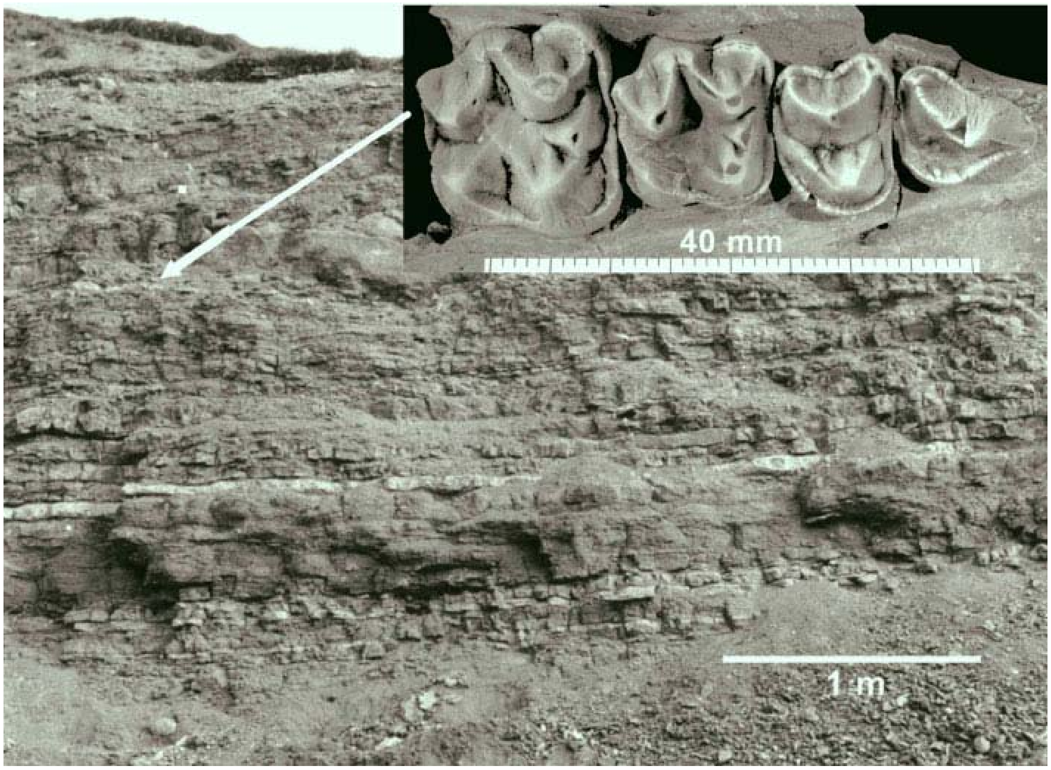

Figure 2. Fine-bedded tuffites and thin freshwater limestones at Dvérce preserved limnic and terrestrial molluscs, leaf and seed flora and, in 1965, two individuals of a small early Oligocene anhracothere *Elomeryx crispus* crispus (in frame: part of the right upper jaw with P3-M2), the arrow indicates its level.

Figure 3. Outcrop of the western slope of the clay pit at Detan. Height -50 m. The fossiliferous layer is marked by an arrow. (Photograph by O. Fejfar 1978.)

Table 1. Oligocene Mammals from the Doupov Mountains, northwest Bohemia.

- Marsupialia
    - *Amphiperatherium* sp.
- Insectivora
    - cf. *Paratalpa* sp.
    - cf. *Neurogymnurus* sp.
    - Quercysorex sp.
- Rodentia
    - Suevosciurus ehingensi
    - *Palaeosciurus nov.* sp.
    - Plesispermophilus cf.P. atavus
    - *Gliravus* sp.
    - Eomys cf. E. zittel
    - cf. *Parasminthus* sp.
    - Paracricetodon cf. P. dehmi
    - Eucricetodon cf. E. murinus
    - Pseudocricetodon montalbanensis
- Artiodactyla
    - Gelocus laubei
    - *Bachitherium* cf. *B. curtum*
    - Lophiomneryx mouchelini
    - *Paroxacron* sp.
    - *Propalaeochoerus* cf. *P. parona*
    - Entelodon antiquum
    - *Anthracotherium* cf. *A. monsvialense*
    - Elomeryx crispus crispu
- Perissodactyla
    - *Ronzotherium* cf. *R. filholi*
- Carnivora
    - *Cephalogale* sp.
    - Pseudocyonopsis cf. P. antiquus
- Creodonta
    - Hyaenodon sp.

Mammal bones at Detan are extremely fragile, fragmented but not abraded, and widely scattered through the basal ash layers. The only example of articulation is a partial vertebral column of a snake in situ. Non-mammalian remains are rare. In the upper part of the ash sequence several large, thick, plastron plates of the giant turtle *Geochelone* were preserved. A small crocodilian is represented by a dermal plate. Bones and dentine of mammals are white, but enamel is light brown with black dendrites.

Age and Correlation

The biochronologic age of the fauna is determined by the presence of significant mammalian taxa (Table 1, Figures 4, 5), especially the rodents *Eucricetodon, Paracricetodon, Pseudocricetodon, Eomys, Plesispermophilus, Palaeosciurus, Suevosciurus,* and the artiodactyls *Gelocus, Entelodon, Lophiomeryx, Anthracotherium,* and *Elomeryx*. This assemblage indicates an age in the mammalian Paleogene zone MP 21. Arguing for placement in the older portion of MP 21 are the index species *Entelodon antiquum* and the general evolutionary level of some rodent species. MP 21 falls within the early Oligocene, in the Stampian (Suevian) stage,

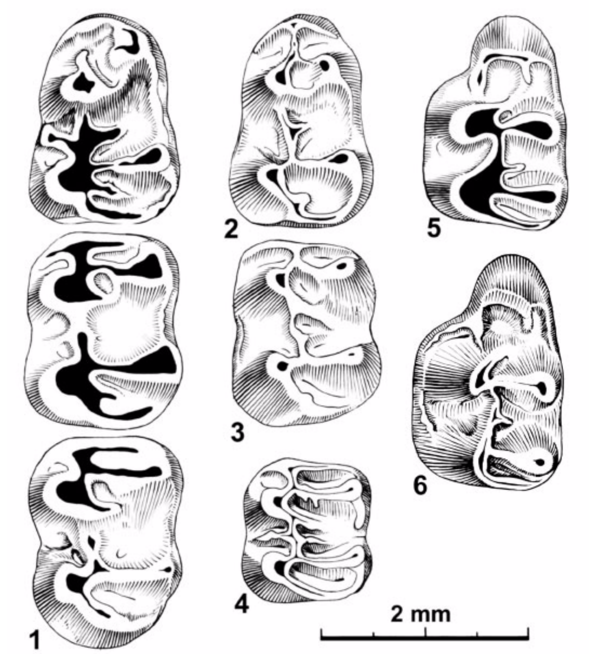

Figure 4. Cricetids of Detan: *Paracricetodon* cf. *P. dehmi,* 1 (left m_1-m_3); *Eucricetodon* cf. *E. murinus*, 2 (left m_1), 3 (left m_2), 5 (left M^1), 6 (left M^1); *Pseudocricetodon montalbanensis,* 4 (left m_2).

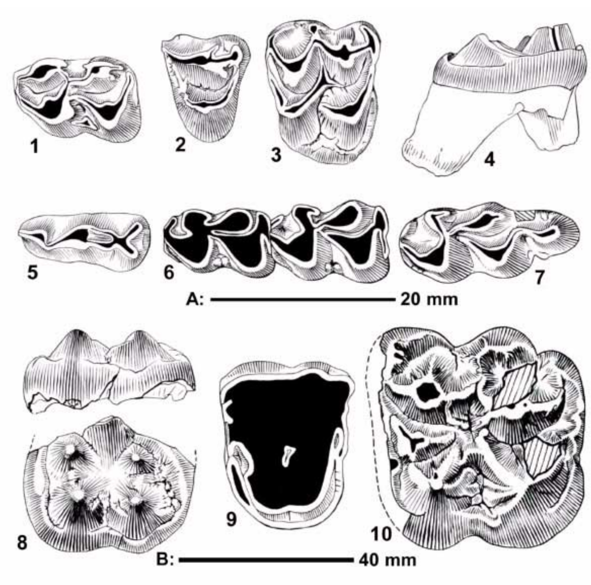

Figure 5. Large mammals of Detan: 1-4 - *Pseudogelocus laubei*, 5 - *Bachitherium* cf. *curtum*, 6, 7 - *Lophiomeryx* cf. *L. pomeli*, 8 - *Entelodon* cf. *E. antiquum*, 9 - *Ronzotherium* sp., 10 - *Anthracotherium* cf. *A. monsvialense*. Occlusal views of the left $m_{1\text{-}2}$ (1), left P^4 (2), left $M^{1\text{-}2}$ (3,4), right M^2 (8), left P^2 (9), left M^3 (10).

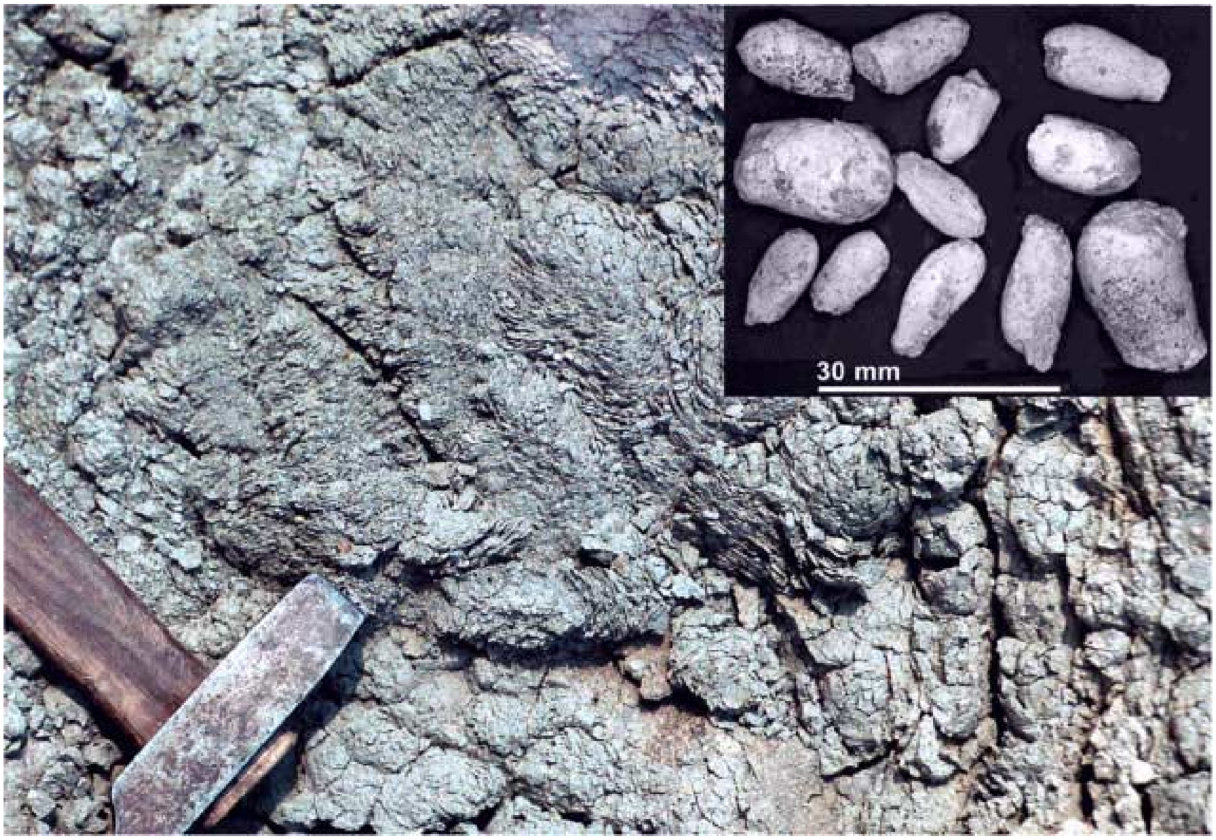

Figure 6. Close-up view of the gray fossiliferous tuff (level 10 in figure 1). In the upper right frame: natural casts of drop-like brood cells or pupal cocoons of solitary burrowing hymenopteran insects scattered in level 10.

and after the *Grand Coupure*. A K/Ar date of 37.5 Ma was determined for Biozone MP 21 from unweathered biotite from the mammal-bearing horizon at Detan (Fejfar 1987, Fejfar and Storch 1994). Correlated European localities include Hoogbutsel (Belgium), Ronzon, Aubrelong 1, Villebramar, and Soumaille (France), and the Bavarian karst fissures of Möhren 13 and 19 (Fejfar 1987).

Insect Activity at Detan

In the main fossiliferous layer of Detan, in the lower part of the ash sequence, local concentrations of peculiar drop-like natural casts (diameter = 5 to 8 mm) are found. These trace fossils are apparently brood cells or pupal cocoons of solitary burrowing hymenopteran insects (cf. Sphecoidea or Halictini; Figure 6). Similar trace fossils were recognized at Laetoli, Tanzania (Ritchie 1987).

A unique black lens (about 1.5 m wide, 0.6 m high) was discovered in the lower part of the ash sequence during fieldwork in 2000. The shape of the lens is oval, with a distinct reddish zone on its surface (Figure 7). The lens matrix is composed of hard, calcareous, black Mn-Fe oxides, with less resistant pockets of sediment. The lens contains shiny black shells of terrestrial molluscs, which are otherwise completely unknown in the Detan site, along with a concentration of crushed small bones and rare rodent molars, both light gray in color. Within the black lens, the most prevalent mammal is the small dormouse *Gliravus* and *Bransatoglis*. *Paracricetodon, Pseudocricetodon, Eomys*, and indeterminate insectivore molars are rare and partly crushed. The lens is interpreted as the remnant of an insect colony, possibly that of termites, because within the hard matrix of the lens, passages reminiscent of those in termitaries occur.

Bone and dentine surfaces from Detan show peculiar traces on unweathered surfaces (Figures 8-11). These traces are unlike rodent gnawing or corrosion from plant roots. They appear most similar to marks seen on bones found in the Pliocene tuffaceous Upper Laetolil beds (3.46 Ma) of Tanzania (Sands 1987, Watson and Abbey 1986). For comparison, Figure 12 shows a specimen in the Natural History Museum (Berlin) collected by the 1934-1936 Kohl-Larsen expedition from the Pliocene tuffaceous beds in the southern Serengeti.

Figure 7. The black lens (- 1.5 m wide, 0.6 m high) in the fossiliferous level at Detan is interpreted as a remnant of an insect colony, possibly termites. (Photograph by R. Mikulas 2000.)

DISCUSSION AND CONCLUSIONS

Data from sediments, plants, and animals allow inferences to be made about the environment surrounding Detan during the Oligocene. As volcanic activity began, a system of shallow lakes extended through the lowlands of this area. The lakes were surrounded by riparian forest with alder, elm and other broad-leaved trees. Ferns (*Rumohra*) and lianas (*Smilax*) grew at forest edges. Laurel-oak evergreen forests with cypress and mahonia undergrowth grew along standing water. On the slopes of the rising volcano, pine forests grew, as seen in some tuffaceous layers with abundant pine needles, twigs, and cones. Rare molds of hickory nuts (Carya) demonstrate that a species of this mostly North American genus was present. The early Oligocene was characterized by climatic deterioration, recognized mainly by the influx of *Alnus, Ulmus,* and *Zelkova* in the vegetation, and by the extinction of some Eocene thermophilous plant taxa (Fejfar and Kvacek 1993).

The geologic context of the Doupovské Hory volcanics is not unlike that of the Upper Laetolil Beds. Both were derived primarily from volcaniclastic sources in a rift setting. They exhibit a similar secondarily calcareous and tuffaceous lithology. Both also preserve insect trace fossils and have bones and teeth modified by the actions of insects. By comparison with Laetoli, the presence of of termites, termite mounds, drop-like brood cells and pupal cocoons of solitary burrowing hymenopterans suggests that, at least in the area where they are preserved, the southern slopes of the Doupov volcano were not densely vegetated. Together with this association, the absence of aquatic molluscs, otherwise abundant in the nearby fine-bedded lacustrine tuffites suggests a rather dry, well-drained environment. Such a pattern, and the vegetation of the region, indicates a patchy environmental mosaic.

Watson and Abbey (1986) postulated that osteophagous behavior in termites is targeted at bone collagen to alleviate nitrogen deficiency, which is a characteristic problem in subtropical carbonatitic soils. Similar to Laetoli, insect modification of bones and teeth at Detan predominantly affects unweathered bone surfaces, which presumably at the time of modification had not suffered collagen decomposition. If this relationship is true,

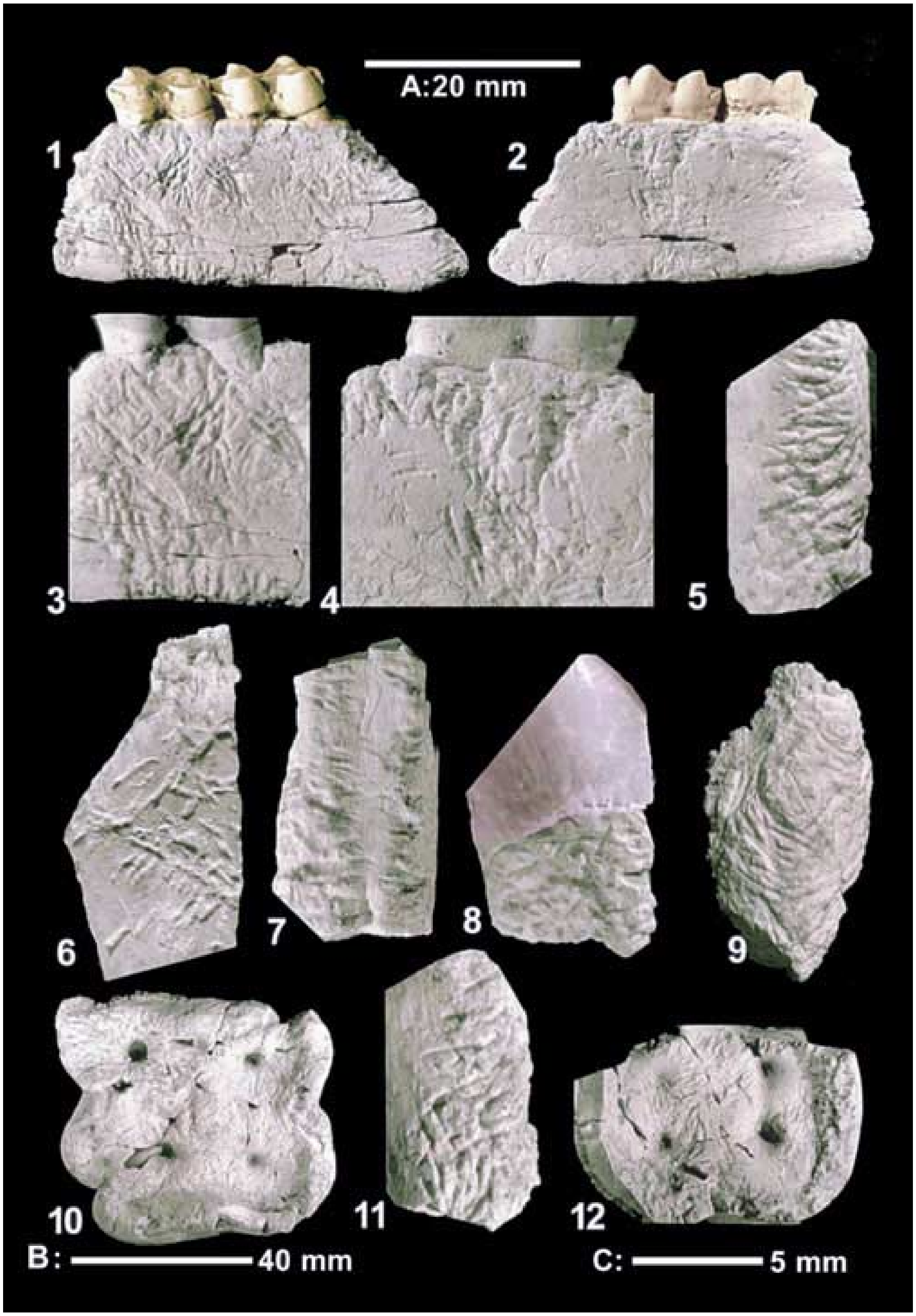

Figure 8. Samples of insect traces on mammalian remains from Detan. 1-4, left lower jaw of *Lophiomeryx* cf. *pomeli.* 5, 6, 7, 11, samples of fragmented bones. 8, 10, 12, samples of teeth with gnawed dentine. Scale bar is 20 mm for 1-9, 11.

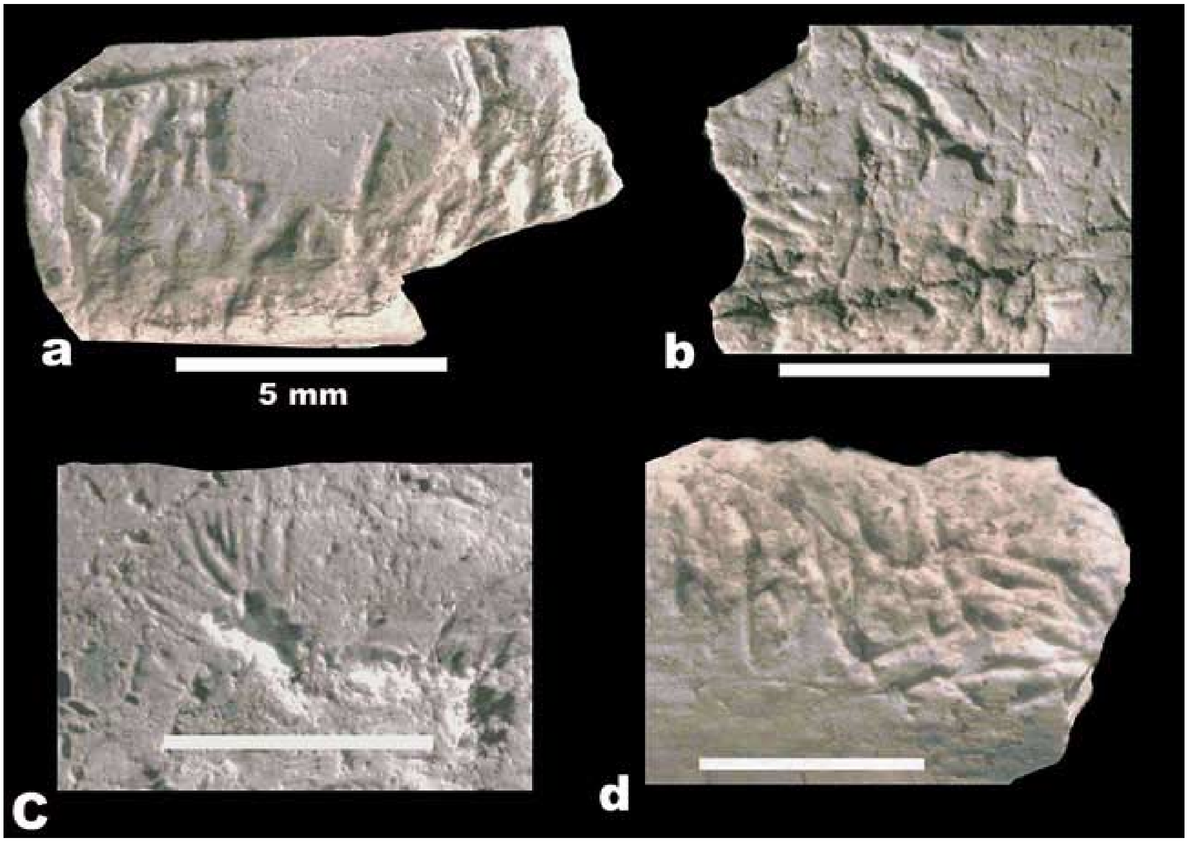

Figure 9. Examples of insect traces on mammalian bone fragments from Detan. Scale bar is 5 mm for a-d.

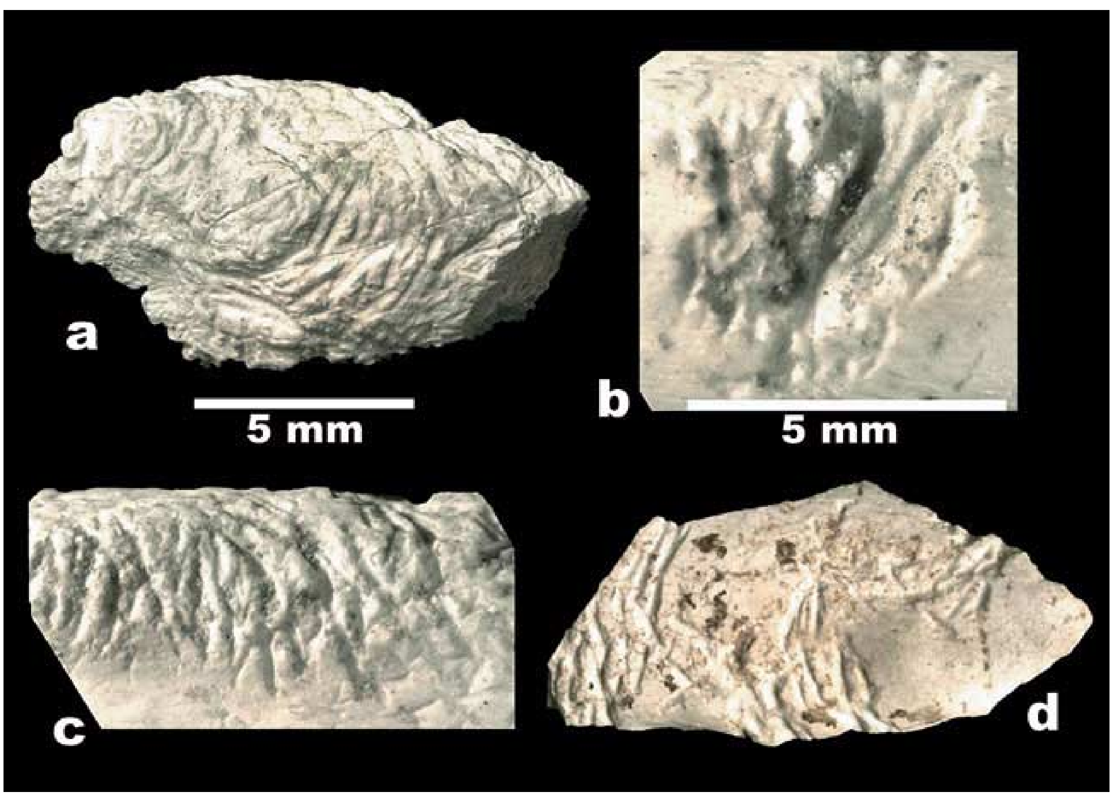

Figure 10. Examples of insect traces on mammalian bone fragments from Detan. Scale bar is 5 mm for a-d.

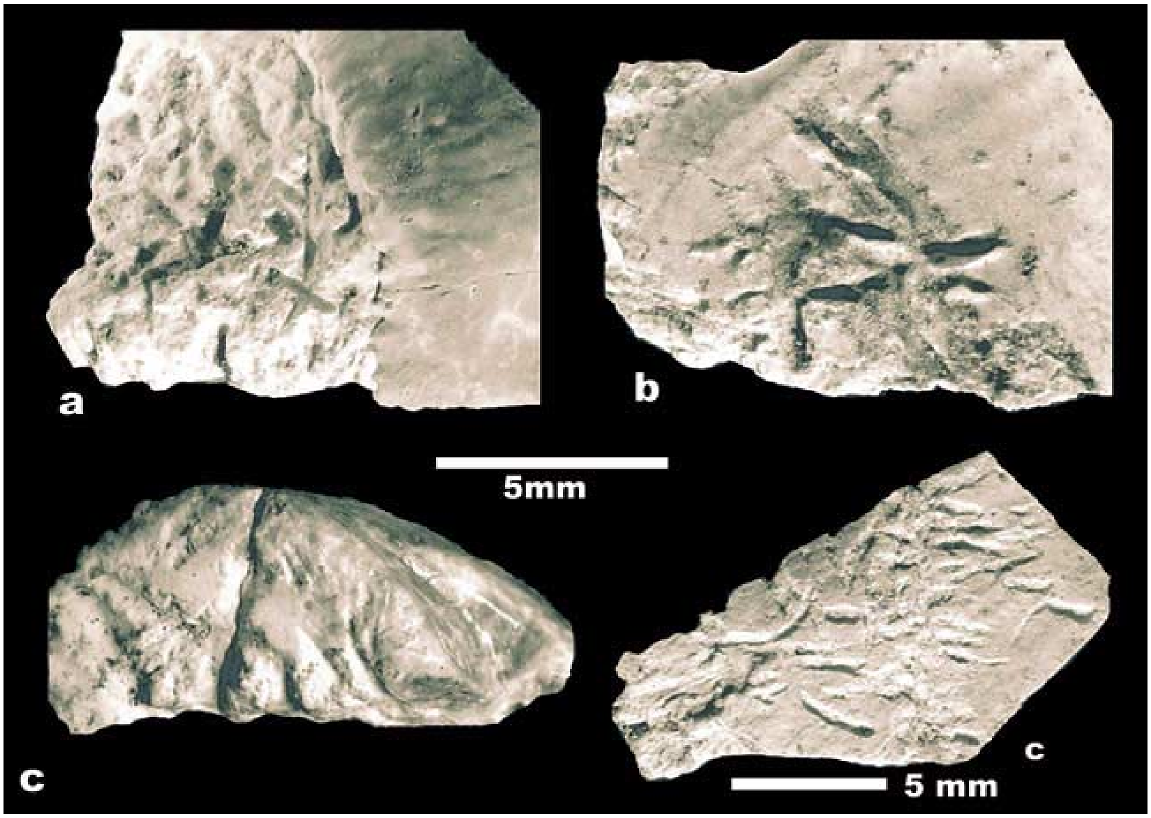

Figure 11. Examples of insect traces on mammalian bone fragments from Detan. Scale bar is 5 mm for a-c.

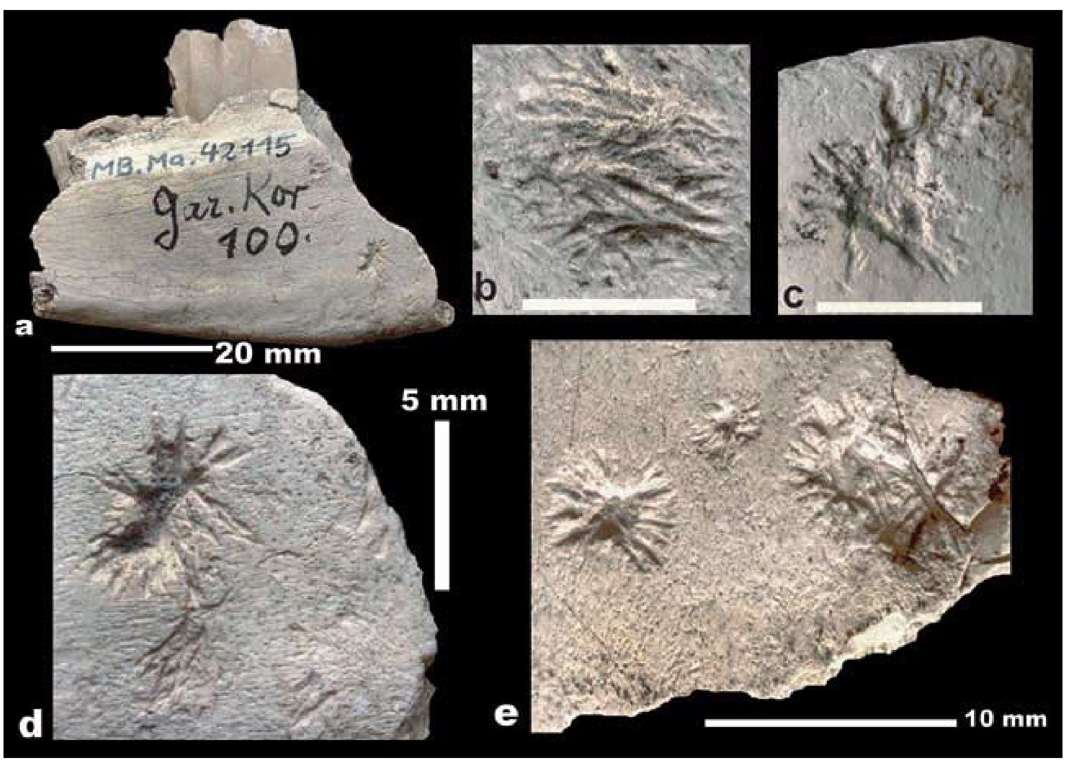

Figure 12. Examples of insect traces on mammalian remains from the Pliocene tuffaceous beds in southern Serengeti (Tanzania) collected by the 1934-1936 Kohl-Larsen Expedition. Currently housed in the collections of the Museum of Natural History, Berlin. A-E: mandible of a small bovid (MB. Ba. 42115, Gar.Kor.100), traces on the lingual and buccal side of the lower jaw. Scale bar is 5 mm for b-d. (Photograph by O. Fejfar 2004.)

the observed marks could have been produced in response to similar dietary requirements among insects, exacerbated by their distribution in nitrogen-poor soils often characteristic of semi-arid regions.

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REFERENCES

Cuvier, G. 1825. *Recherches sur les Ossements Fossiles*. Paris.

Fejfar, O. 1987. A Lower Oligocene mammalian fauna from Detan and Dvérce NW Bohemia, Czechoslovakia. *Münchner Geowissenschaftliche Abhandlungen*, A, 10:253-264.

Fejfar, O. and Kvacek, Z. 1993. Excursion Nr. 3. Tertiary basins in Northwest Bohemia. *63. Tagung der Paläontologischen Gesellschaft Prag*, 1-35.

Fejfar, O. and Storch, G. 1994. Das Nagetier von Valec-Waltsch in Böhmen - ein historischer fossiler Säugetierfund - (Rodentia: Myoxidae). *Münchner Geowissenschaftliche Abhandlungen*, A, 26:5-53.

Hebenstreit, J.E. 1743. *Museum Richterianum continens fossilia animalia vegetabilia marina illustrata iconibus et comentariis; accedit de gemmis sculptis antiquis liber singularis*. Lipsiae.

Hibsch, J.E. 1901. Über die geologische Spezialaufnahme des Duppauer Gebirges im nordwestlichen Böhmen. *Verhandlungen der Geologischen Reichsanstalt*, Wien.

Laube, G. 1899. Säugetierzähne aus dem Basalttuff von Waltsch. *Lotos*, 1:1-8.

Laube, G. C. 1901. Synopsis der Wirbelthierfauna der böhmischen Braunkohlenformation und Beschreibung neuer, oder bisher unvollständig bekannter Arten. *Beiträge zur Kenntnis der Wirbelthierfauna der böhmischen Braunkohlenformation,* 2: 1-76.

Liebus, A. 1934. Das Nagetier von Waltsch. *Lotos*, 82:47-50.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteristibus, differentiis, sinonimis, locis* (edition decima). Holmiae.

Meyer, H. von. 1856. Ueber den Nager von Waltsch in Böhmen. *Palaeontographica*, 4:75-79.

Mylius, G.F. 1718. *Memorabilia Saxoniae Subterraneae Pars II., i.e. Unterirdischen Sachsens Seltsamer Wunder der Natur* (Anderer Theil), Friedrich Groschussen, Leipzig.

Ritchie, J.M. 1987. Trace fossils of burrowing Hymenoptera from Laetoli, p. 433-438. In Leakey, M.D. and Harris, J.M. (eds.), *Laetoli: A Pliocene Site in Northern Tanzania*. Clarendon Press, Oxford.

Sands, W.A. 1987. Ichnocoenoses of probable termite origin from Laetoli, p. 409-433. In Leakey, M.D. and Harris, J.M. (eds.), *Laetoli: A Pliocene Site in Northern Tanzania*. Clarendon Press, Oxford.

Watson, J.A.L. and Abbey, H.M. 1986. The effects of termites (Isoptera) on bone: Some archaeological implications. *Sociobiology,* 11:245-254.

Wenz, W. 1917. Zur Altersfrage der böhmischen Süsswasserkalke. *Jahrbuch des Nassauischen Vereins für Naturkunde, Wiesbaden*, 70:1-83.