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# NEW CONTRIBUTION TO THE PALAEOICHNOLOGY AND TAPHONOMY OF THE AHNÍKOV FOSSIL SITE, EARLY MIOCENE, MOST BASIN (THE CZECH REPUBLIC)

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**Abstract:** The material of *Machichnus regularis* and *Machichnus multilineatus* was re-examined with respect to the potential tracemaker. New characters were defined for *M. multilineatus* – scratch profile with flat horizontal bottom and undulated microrelief of scratches. Based on these characters and additional information, both previously suggested tracemakers (beavers and porcupines) are rejected and a new one – a large squirrel is proposed. The squirrel origin of gnawing traces is additionally supported by actuopalaeontologic study on gnawing behaviour of recent red squirrels. On this basis, squirrels are recognized as overlooked but important taphonomic agents in Late Cenozoic assemblages. The tracemaker of *M. regularis* was not unambiguously recognized, but a connection with smaller squirrel or aplodontid species seems probable.

**Key words:** palaeoichnology, taphonomy, biting traces, bone-mammal interaction, Sciuridae, Early Miocene, Most Basin, Czech Republic

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## Introduction

Terrestrial fauna from the Most Basin was first recorded at the beginning of the 20th century in a small Prokop mine, located near the town of Most (Schlosser and Hibsch 1902, Redlich 1902). The next known records are from prospect drilling for brown coal in the western part of the Most Basin, during the 1960s. Samples showed abundant gastropods and mammals (Fejfar 1963, Čtyroký et al. 1964a, b), indicating a promising fossil site. After the coal was excavated in the 1980s and 1990s, a rich community of terrestrial vertebrates was uncovered on the bottom of the opencast, close to the former villages Ahníkov, Kralupy and Spořice (Bužek et al. 1988). Subsequently, fossils were systematically collected by geologists from the Bílina and Tušimice coal mines (today parts of Severočeské doly, a.s., "The North Bohemian Mining joint-stock Company"), and by O. Fejfar from Czech Geological Survey, and later Charles University. In 1993, the fossil site was declared a protected Natural Monument and named "Merkur". However, since 2004 the site has been affected by several slips resulting in site destruction and in 2009, its protected status was officially revoked. In 2010, a new site was discovered about 1 km east-south-east from the first site. Since 2011, intensive research and collecting has been performed by Department of Palaeontology of the National Museum, Prague. Also, all previously discovered specimens from the extinct site were acquired and housed in this institution. This complete collection serves as an excellent base for further palaeontological and taphonomical examinations.

Although both sites are quite similar, and could be regarded as continuation, the variable geologic setting, as well as palaeoenvironmental and other factors make distinguishing between them a more sensible approach. Henceforth, the extinct site, in previous papers named "Merkur", "Merkur-North" or "Ahníkov" (and also sometimes labelled "Sklípek"), is named "Ahníkov I". The new site is named "Ahníkov II". A place sometimes labelled "Kaplička" represents a transitional part, and is included in Ahníkov II.

Both sites, Ahníkov I and II yielded diverse assemblages of terrestrial and aquatic animals, with molluscs and vertebrates showing the greatest diversity. The molluscs



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consist of various terrestrial and aquatic species (Čtyroký et al. 1964b, Kadlecová et al. 2013). Gastropods are very abundant in some facies. Nevertheless, the site is unique primarily for its rich and diverse community of vertebrates. Hitherto, following lower vertebrate groups have been recorded: Teleostei, Anura (Vejvalka 1997, Böhme 2003), Urodela, Allocaudata (Čerňanský 2010a), Crocodylia (Chroust 2016), Testudines, Squamata (Klembara 1979, Fejfar and Schleich 1994, Ivanov 2002, Evans and Klembara 2005, Klembara 2008, 2012, 2015, Čerňanský and Joniak 2009, Čerňanský 2010b, c, 2012, Čerňanský and Bauer 2010, Čerňanský and Venczel 2011). Birds were studied by Mlíkovský (1992, 1996, 1998). The list of mammals was preliminarily summarized by Fejfar (Fejfar and Kvaček 1993, Fejfar et al. 2003, van den Hoek Ostende and Fejfar 2015). The following orders of mammals are recorded: Didelphimorphia, Eulipotyphla (Fejfar and Sabol 2005, van den Hoek Ostende and Fejfar 2006, 2015), Chiroptera (Horáček 2002), Rodentia (Čtyroký et al. 1964b, Fejfar 1990, Fejfar et al. 1998, Kadlecová 2000), Lagomorpha, Carnivora, Perissodactyla (Fejfar et al. 1997, Uhlířová 2001, Heissig and Fejfar 2013, Heissig and Fejfar in prep.), Artiodactyla.

Concerning palaeoichnology, some animal effects on plants and bones are known from the locality. A new ichnogenus and ichnospecies *Lamniporichnus vulgaris* Mikuláš, Dvořák et Pek, 1998, insect larvae boring trace on *Celtis* endocarps, was described by Mikuláš et al. (1998). Several types of biting and gnawing traces on fossil bones have been described as new ichnotaxon (Mikuláš et al. 2006, Mikuláš and Dvořák 2010). Circular holes on cortical bone *Nihilichnus nihilicus* Mikuláš, Kadlecová, Fejfar et Dvořák, 2006 were interpreted as traces of hunting injury, rather than feeding, and irregular chaotically arranged breakings through cortical bone *Brutalichnus brutalis* Mikuláš, Kadlecová, Fejfar et Dvořák, 2006 were interpreted as traces of chewing of bone particles (Mikuláš et al. 2006). Shallow, thin, discrete, parallel to subparallel uniform scratches on cortical bone *Machichnus bohemicus* Mikuláš, Kadlecová, Fejfar et Dvořák, 2006 were interpreted as biting traces, possibly made by crocodylians (Mikuláš et al. 2006, Mikuláš and Dvořák 2010). Interactions between malacofauna and dimylids also seem probable (Hoek Ostende and Fejfar 2015), but the crushing of shells is hard to distinguish from fractioning caused by physical processes. Parallel longitudinal scratches on cortical bone *Machichnus regularis* Mikuláš, Kadlecová, Fejfar et Dvořák, 2006 and *Machichnus multilineatus* Mikuláš, Kadlecová, Fejfar et Dvořák, 2006 were attributed to the gnawing activity of beavers *Steneofiber esseri* (von Meyer, 1846) and *Steneofiber depereti* Mayet, 1908. Re-evaluation of the possible tracemaker of these ichnospecies is the main goal of this paper.

## Geological setting

The Ahníkov I + II fossil sites are located in the western part of Most Basin, between the towns of Chomutov and Kadaň (about 2 km south and southwest of the village Zelená). This basin part represents the margin of a large complex of lacustrine and swamp sedimentary deposits. The transitional zone is characterized by a varied stratigraphic and facial environment, which changes abruptly. The layers from the crystalline bedrock up to the base of the main seam coal are strongly influenced by distinctive transport of terrestrial material from the shore, and local, episodic proluvials. The bedrock is biotitic paragneiss, intensively and deeply kaolinized in the distal part (toward the basin). In proximal part (toward shore), the paragneiss is mechanically weathered, and transformed to a heterogeneous mixture of clay and rock debris eluvium. The latter contains occasional bone fragments. Superposing beds of grey and brown aleuritic clays (reworked volcanic material) increase in depth toward the basin centre, and are missing in the proximal parts. They are intercalated with coal seams, root horizons and a discontinuous horizon of limestone and marlstone with plant leaves. In the proximal parts, the clays are poor in carbon and are coloured green, due to $Fe^{2+}$ content. The green clay frequently yields fragments of turtle carapaces, occasionally bone fragments of large and mid-sized mammals. The uppermost beds, positioned just under the base of the main coal seam vary from several tens of centimetres up to a few metres in depth. The beds consist of brown to black aleuritic clays (reworked volcanic material), bountifully interposed with coal slices. The black aleuritic clays are particularly rich in fossil bones and teeth. However, and rather unfortunately, they are also rich in dispersed highly degradable Fe disulphides, which, when combined with carbon, create a galvanic reaction, corroding the fossils. The fossil bones include a mixture of different taxa from fish, amphibians and amniots, to small and large mammals. In some layers and some facies, gastropods occur with varying frequency, in others they are missing completely. In the "Kaplička" section of the Ahníkov II locality, the sequence is especially thick, and composed of gastropod-rich brown clays repeatedly alternating with coal clays (Kadlecová et al. 2013). Bone occurrence in the site is not homogenous. Turtle carapace shells and occasional bone fragments are spread along the entire site, but in some places medium-sized mammalian bones are more abundant. Rich sets of micromammals occur only in a few small places. Gastropods and bones are not co-located to any apparent degree.

The geological development of this locality is quite complex, and a more detailed description is being prepared for publication. The general geological setting of the Most Basin is reviewed in Kvaček et al. (2004) and Mach et al. (2014).

## Material and methods

In this study, we re-examined the original material assigned to *Machichnus regularis* and *Machichnus multilineatus* by Mikuláš et al. (2006), including their holotypes (inv. no. NM-Pv 10120 and NM-Pv 10125, respectively). Additionally, we examined 50 new specimens bearing *Machichnus regularis*- and *Machichnus multilineatus*-type gnawing traces, originating from Ahníkov I and II localities. All the material is housed at the Department of Palaeontology (National Museum, Prague). For comparison, we used also recent bone, antlers and carapace fragments gnawed by red squirrels (*Sciurus vulgaris* Linnaeus, 1758) (see below for details). For general rules of ichnotaxonomic criteria for traces on bones see Pirrone et al. (2014).

The fossil material was collected on the site surface, where it was naturally weathered by cycles of rain erosion, drying and removal of loose material by wind. Smaller fragments were obtained by screenwashing fossiliferous sediment from the most relevant/richest places, done partly on site, partly in National Museum labs. Since the rock and bones contain a significant content of unstable Fe-disulphides, the material was carefully treated to prevent pyrite/marcasite oxidic degradation. During the course of this work, a complex methodology was constructed and published (Sklenář et. al. 2015), and some new treatment techniques were developed (Ekrt et al. 2015).

Both fossil and recent specimens were studied with a Keyence digital microscope, with deep focus composition. Fine details were studied with a Hitachi S-3700N scanning electron microscope, under low vacuum and using a BSE detector. Microreliefs and their cross-sections were constructed with SEM 3D module, using separate imaging from separate segments of BSE detector.

The scratches' morphology, their size and microreliefs were compared with incisor morphology in several rodent groups (both fossil and recent) examined as possible tracemakers. The morphology of scratches of selected lower incisors was experimentally examined on paraffin slice, by simulating the gnawing movement of lower incisors and studying the obtained traces. The following incisor samples were tested and compared: small (NM-Pv 10147) and large (NM-Pv 10148) species of Miocene beaver, large Miocene eomyid rodent *Megapeomys* Fejfar, Rummel et Tomida, 1998 (NM-Pv 10149), Miocene aplodontid *Plesispermophilus* Filhol, 1883 (NM-Pv 10150), large lower sciurid incisor (see Discussion for details) called here large sciurid sp. 1 (NM-Pv 10151), recent porcupine (*Hystrix cristata* Linnaeus, 1758; NM-P6V 090152), red squirrel (*Sciurus vulgaris*; NM-no. 566), and black giant squirrel (*Ratufa bicolor* (Sparrman, 1778); NM-P6V 55461). The mandibles of recent specimens are housed at the Zoological Department (National Museum, Prague), and fossil material is in the collection of Palaeontological Department (National Museum, Prague).

From each species, one lower incisor was used for making 8 scratches. Because the scratch width varies along the entire length of the scratch, 24 measurements were taken for each species, 3 for each scratch. All scratches were approximately the same depth as those in type series of *Machichnus regularis* and *Machichnus multilineatus*. Only the *Machichnus multilineatus* showed adequate detail to characterize the scratches. We measured 8 scratches (24 measurements) on the *M. multilineatus* holotype (Mikuláš et al. 2006: fig. 8C) and on one unpublished specimen (inv. no. MN-Pv 10152; Pl. 1, Fig. 1), morphologically corresponding to *M. multilineatus*. Morphology and sizes of the scratches were characterized, and widths were measured with a Keyence digital microscope, using Keyence measuring software.

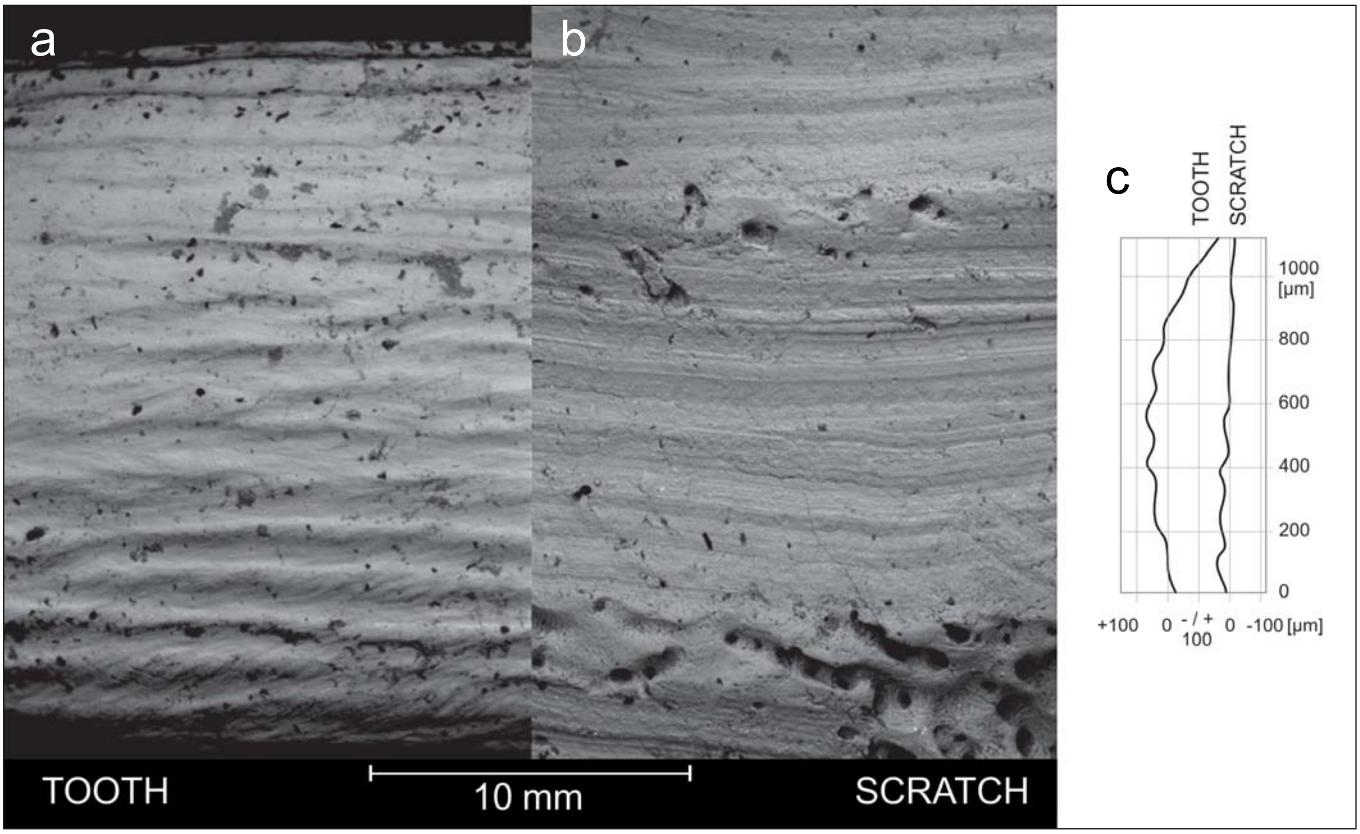
Long-term observations and behavioural experiments were performed on recent wild squirrels. The squirrel-rescue station "Pinky" was utilized for experiments. The station has an excellent spot for monitoring wild squirrels, and much experience with squirrel ethology. Different samples (artiodactyl antlers, bone diaphysis and epiphysis, and turtle carapace fragments) were fixed to a tree trunk near the monitoring point. We studied substrate preferences, style and frequency of scratching or behaviour of males/females/juveniles. The scratches were studied and their morphology, size and pattern were compared with fossil material.

## Results

Fossil gnawing traces from Ahníkov (trace fossil of type 2 sensu Mikuláš et al. 2006) are often shallow and parallelly arranged, usually on large bone surfaces. The maximum length of scratches usually reaches 15 mm, occasionally 20 mm. We recorded single scratches up to 30 mm in length in one case (Pl. 1, Fig. 2). The most common is the typical width of both *Machichnus* ichnospecies (Mikuláš et al. 2006), but much narrower and shallower types are also present. On diaphyses where compacta is thick and good support for opposite (i.e., upper) incisors is present (bone margin or bone cusp), there also occur deep grooves made by repeated in-line scratching (Pl. 1, Fig. 4). Usually the repeated scratching is in one or several parallel grooves, occasionally they are arranged in a fan structure. We recognized typical morphotypes of both *Machichnus regularis* (Pl. 1, Fig. 4) and *Machichnus multilineatus* (Pl. 1, Figs 1, 3), but also transitional types with more or less distinct undulations (see below for details and Mikuláš et al. (2006) for diagnostic morphology for particular ichnotaxa).

Concerning the morphology of individual scratches, we defined two levels of morphological differentiation: (a) the general shape of the scratch, and (b) the characters of fine structures in the scratch. In the latter, we were able to distinguish 2 types of structures: (b.1) regular undulation alongside the entire scratch profile (microrelief seen in the cross-section), and (b.2) randomly located, irregular, often sharp and usually much smaller multistriating structures. The irregularly placed striae were found in both ichnotaxa, and we interpret them as traces of accidental small damage/breakage on the incisor's gnawing edge. Such damage can be present in any possible tracemaker, and therefore has no specific value in this respect. On the other hand, the regular undulation (found only in *M. multilineatus*) seemed to be more promising with respect to its possible utility in identifying its maker. From this reason, we restricted the term "striated" in the *M. multilineatus* diagnosis (Mikuláš et al. 2006: 122) to this regular undulation. We subsequently excluded specimen inv. no. NM-Pv 10124 (Mikuláš et al. 2006: fig. 8B) from the type series. Its striation is caused only by multiple irregular striae of type b.2.

The cross-section outline curve of *M. multilineatus* and curve of lower incisor anterior outline (slightly under the gnawing edge) of large sciurid sp. 1 were constructed with 3D option on SEM (the only taxon with undulated incisor edge in present study – see also Tab. 1). The resulting curves show equal undulating pattern (Text-fig. 1). In the scratch profile, the relief is slightly less pronounced than the surface of the actual incisor. It can be explained by partial wearing of the gnawing edge, and also by weathering of the scratch. Distances between the small enamel ridges on the large sciurid sp. 1 incisor and the fine grooves within scratch of




**Text-fig. 1. Comparison of microrelief in large sciurid sp. 1 incisor and *M. multilineatus*, using backscatter electrons of scanning electron microscope. a: Detail of enamel surface from anterior part of large sciurid incisor (NM-Pv 10158). b: Detail of scratch surface in *M. multilineatus* (NM-Pv 10152). c: Comparison of transversal cross-section curves of "a" and "b".**

*M. multilineatus* were measured by a Keyence digital microscope. The average value was 0.199 mm for large sciurid sp. 1 and 0.200 mm for *M. multilineatus*.

To know the exact gnawing trace morphology for particularly rodent taxa, we carried out the following experiment. We chose eight rodent taxa (5 fossil, 3 recent – see Tab. 1) as possible tracemakers (or their morphological equivalents in the cases of recent taxa), and made the artificial gnawing traces (see Material and methods for details). We then studied the morphometrical characteristics of obtained traces, and compared them with *M. multilineatus*. The results are shown in Tab. 1. The scratch profile can be divided into two main groups. Type a: the bottom of the scratch is inclined, and type b: with flat horizontal bottom, which reflect the general morphology of an incisor gnawing edge. Among the studied species, the microrelief is undulated only in large sciurid sp. 1. The width of the scratch (more or less of the same depth) is correlated with incisor width, but does not mirror its absolute size. It strongly depends on scratch depth, more when incisors have an inclined cutting edge and rounded anterior side.

As some previous results indicated squirrels as possible tracemakers, we wanted to know whether such behaviour is known among recent squirrels, and if so, what is the pattern of their gnawing traces. Observation on recent red squirrels (*Sciurus vulgaris*) in the squirrel rescue station proved that bone gnawing is common. Males performed it only once or twice per year, but pregnant females very frequently (see also Carlson 1940). Also juveniles and subadults often practice bone gnawing, especially at the age of two to three months, which covers the range from termination of suckling to reaching adult size. The proposed reason for bone gnawing is to obtain minerals, especially calcium (see also Gobetz and Hattin 2002 – recording squirrel gnawing on carbonate rocks, or Nichols et al. 2016). Typical gnawing behaviour is to hold the bone fragment in forelimbs, fix upper incisors on a bone edge or other support and start gnawing with lower incisors (Text-fig. 2). It is not possible to exclude that in some cases, upper incisors are also used. The above is true for bones and bone fragments, with edges forming an acute to slightly obtuse angles (Pl. 2, Figs 1–6), which allows the squirrel to fix the bone with upper incisors. If a bone with a more open obtuse angle is gnawed, it is gnawed simultaneously by upper and lower incisors, creating roughly equal opposing traces (Pl. 2, Fig. 7a). In transitional cases, the traces made by lower incisors are dominant; traces of the upper ones are in the shapes of points and short scratches (Pl. 2, Fig. 7b).

The bones bearing scratching traces enabled study of gnawing patterns. Predominantly, the scratching is repeated in one line, and slightly turned clockwise and counter clockwise around the fix point (upper incisors). The obtained pattern is more deeply grooved in the middle, with shallower scratches in a fan pattern towards upper incisor support (Pl. 2, Figs 1, 4 – bone margins, 6b). In the central part, and especially in the fan apex, the groove is deepest. Lengths of scratches and resulting grooves are uniform in length, usually about 12 mm, and certainly correspond to a comfortable mouth opening. A few scratches are longer, up to 14 mm.

**Table 1.** ***M. multilineatus*** **and teeth and scratch characteristic of its possible tracemakers. The scratches were simulated into paraffin slice.**

<table>
<tr><th colspan="2" rowspan="2">TAXON</th><th>TOOTH</th><th colspan="3">SCRATCH</th></tr>
<tr><th>INCISIVE WIDTH (mm)</th><th>PROFILE MORPHOLOGY</th><th>AVERAGE WIDTH (mm)<br>WIDTH RANGE (mm)</th><th>MICRORELIEF</th></tr>
<tr><td rowspan="8">POSSIBLE SCRATCHING AGENT</td><td>aplodontid<br>Plesispermophilus</td><td>1.0</td><td>bottom<br>inclined</td><td>0.6<br>0.4–0.7</td><td>smooth</td></tr>
<tr><td>recent red squirrel<br>Sciurus vulgaris</td><td>0.7</td><td>bottom<br>inclined</td><td>0.5<br>0.4–0.6</td><td>smooth</td></tr>
<tr><td>recent squirrel<br>Ratufa bicolor</td><td>1.5</td><td>bottom<br>horizontal</td><td>1.1<br>0.9–1.2</td><td>smooth</td></tr>
<tr><td>large sciurid sp. 1</td><td>2.3</td><td>bottom<br>horizontal</td><td>1.5<br>1.1–1.8</td><td>undulating</td></tr>
<tr><td>small beaver</td><td>1.6</td><td>bottom<br>inclined</td><td>1.0<br>0.6–1.3</td><td>smooth</td></tr>
<tr><td>large beaver</td><td>4.0</td><td>bottom<br>horizontal</td><td>1.7<br>1.6–2.0</td><td>smooth</td></tr>
<tr><td>large eomyid<br>Megapeomys</td><td>0.7</td><td>bottom<br>inclined</td><td>0.4<br>0.3–0.6</td><td>smooth</td></tr>
<tr><td>recent porcupine<br>Hystrix cristata</td><td>3.0</td><td>bottom<br>horizontal</td><td>2.2<br>1.9–2.4</td><td>smooth</td></tr>
<tr><td>STUDIED ICHNOTAXON</td><td>Machichnus multilineatus</td><td>–</td><td>bottom<br>horizontal</td><td>1.4<br>1.0–1.7</td><td>undulating</td></tr>
</table>

**Text-fig. 2. Red squirrel (*Sciurus vulgaris*) during antler gnawing.**

Occasionally, as a result of non-intensive scratching, the entire scratch fan is shallow, without a deeper grove in the middle (Pl. 2, Fig. 5). Sometimes, the particular scratches are parallelly arranged, when they occur on larger, rounded surface (e.g. larger diaphysis or obtuse angle crests). In this case, the scratching could be performed by both lower and upper incisors, which do not repeat in one line, and result in slender, shallow gnawing traces (Pl. 2, Figs 4 – central part of the specimen, 7a).

## Discussion

Mikuláš et al. (2006) described in detail several ichnofossils from Ahníkov I locality for the first time, and described several new ichnotaxa based on this material. They distinguished 6 main trace-groups, among which group no. 2 includes gnawing (rasping) traces. Two taxa were described – *Machichnus regularis* and *M. multilineatus* – within this group, whose possible tracemaker is re-examined in this paper.

Mikuláš et al. (2006) discuss the possible origin of the two above-mentioned ichnospecies, and concur that the most probable tracemaker can be found among the beaver species, found abundantly at the locality. Contrary to this result, Diedrich (2007) argues that there is no evidence for bone gnawing by beavers (either fossil or recent), and that the gnawing character resembles that of porcupine (Hystricidae

Fischer [de Waldheim], 1817). He therefore assigns these gnawing traces to the porcupine and considers them evidence of porcupine presence at the locality. The absence of porcupine remains in the mammalian assemblage from Ahníkov I is, according to him, only a taphonomical problem. He assumes Late to Middle Miocene age for these fossils. No other possible tracemaker has been discussed until now.

There are two beaver size-groups at the locality – a small and a large one. Except for the fact that we do not know about bone gnawing behaviour in beavers in general, there are also morphometric characters of their gnawing traces in particular, which makes us question these taxa as tracemakers in the case of *M. multilineatus*. In small form the scratch profile is of "type a", with smooth microrelief. In large form the scratch profile is of "type b", similar to *M. multilineatus*, but the microrelief is also smooth (see Tab. 1). From these indications, we exclude beavers as a possible tracemakers of *M. multilineatus*.

The idea of porcupines as possible tracemakers also seems quite doubtful. The age of both sites, i.e. Ahníkov I and II, is Early Miocene, MN 3 (cf. e.g., Fejfar 1990, Heissig and Fejfar 2013), and the earliest European porcupines are known from the Late Miocene localities Csákvar (Hungary) and Kohfidisch (Austria), both from the zone MN 10 (Sen 1999, Sen and Purabrishemi 2010). Such an early appearance of porcupines seems almost impossible. Moreover, there is also morphological evidence excluding *Hystrix* as a possible tracemaker. Although, similarly to *M. multilineatus* or large form of beaver the scratch profile is of "type b" in *Hystrix*, its microrelief is smooth (see Tab. 1). Therefore, porcupines can also be excluded as a possible tracemakers of *M. multilineatus*.

Among the studied rodents, only the scratches made by a large sciurid sp. 1 incisor (NM-Pv 10151) fits in scratch profile, microrelief and size, with those of *M. multilineatus* (see Tab. 1). Moreover, if the microrelief of *M. multilineatus* is compared with the enamel surface morphology of another similar incisor (NM-Pv 10158), both cross-section curves show a similar pattern (Text-fig. 1). We assign these incisors to large sciurid sp. 1, but such a determination is just preliminary.

The above-mentioned incisors fit perfectly with *M. multilineatus* characteristics, but unfortunately, only isolated teeth are available. This fact complicates the final taxonomic determination of the tracemaker. We have several incisors, both lower and upper of this size category, and both of them are slightly striated on their anterior surface. We assume that all these specimens belong to the same species. Based on general morphology, it is possible to deduce that these incisors belong to a large sciurid. Unfortunately, incisors are not usually used for determination in fossil sciurids, and as they are mostly found only as isolated teeth, very little is known about them. Dehm (1950) described a lower incisor of *Palaeosciurus costatus wintershofensis* Dehm, 1950 (assigned to genus *Heteroxerus* by some authors, e.g. Black (1965), Kristkoiz (1992)) from Wintershof-West (MN 3; Germany), and mentioned that it is finely grooved. But this tooth (0.8 × 2.3 mm in cross-section) is much smaller than our incisors (see Tab. 1). Ornamentation of incisors (without additional information) was also mentioned for the Oligocene species of the genus *Palaeosciurus* Pomel, 1853 (de Bruijn et al. 2013). A longitudinal striation of incisors is also broadly mentioned for later taxa of ground squirrels (e.g., Black 1963, Voorhies 1988, Korth 1994, Braun et al. 2011, Kryštufek and Vohralík 2012 etc.). Mein and Ginsburg (2002) mentioned "longitudinal striae on incisor enamel" for *Lagrieva vireti* Mein et Ginsburg, 2002, from La Grive-Saint-Alban (MN 8; France). The squirrel is rather large (incisors size: 1.35 × 4.3, 1.47 × 4.05, 1.6 × 4.4 mm), although smaller than our specimens and much younger. Because the present knowledge does not allow unambiguous determination of discussed incisors, we decided to determine it as large sciurid sp. 1. Concerning the size, the only squirrel of corresponding size recorded at the locality belongs to the genus *Miopetaurista*. But there is no published information about *Miopetaurista* incisors, and an incisor of *Albanensia grimmi* (Black, 1966) from Magersdorf (MN 9; Austria) was characterized as with smooth enamel (Daxner-Höck 1975). Concerning the general form of the teeth, the affinity to ground squirrels seems more probable (e.g. genus *Palaeosciurus*). It is therefore possible that there is a large ground squirrel species in the Ahníkov locality, so far unrecognized on the basis of cheek teeth.

Regardless the exact taxonomic determination, the fact itself that the bones were gnawed by squirrel is surprising. In fact, we have not found any paper that would consider squirrels as possible tracemakers in the Late Cenozoic. On the other hand, such behaving is common in recent squirrels (e.g., Coventry 1940, Pokines 2014, Fernández-Jalvo and Andrews 2016); even scratching on human bones has been recorded (Klippel and Synstelien 2007). We therefore studied the gnawing behaviour in recent red squirrels, and compared the obtained patters with that known for the fossil specimens.

Regarding bone preferences, recent squirrels favour artiodactyl antlers, but they also settle for compacta of larger bones (cf. Plate 2). They do not gnaw spongiose bone (as documented by specimen no. NM-d59/2016/8) or cartilage. They usually do not prefer bones of small vertebrates, but in one case gnawing on blackbird skeleton was observed, as a result of lacking of other more suitable substrate. Similar preferences are observed in the fossil material (cf. Plate 1). The traces are most frequent on turtle carapace fragments, and sometimes on bone diaphyses or antlers. Scratching of articular surfaces and epiphysis is only occasional (e.g., Pl. 1, Fig. 6). The same preferences are recorded by Fernández-Jalvo and Andrews (2016) for recent and fossil rodents in general. The similarity is also in the preferred location of the gnawing traces, which affect primarily substrate edges (one of the diagnostic characters of the ichnogenus *Machichnus* – see Mikuláš et al. 2006; see also Pl. 1, Fig. 6). The differences are in the shape and microrelief of scratches (caused by incisor morphology), and partly also in scratch orientation and size. In *M. multilineatus*, the repeated scratchings are usually not arranged into fan, as they are in recent squirrels. The fan pattern is more frequently present in *M. regularis*, in this cases its average angle is ca. 22° (Pl. 1, Fig. 4). In the recent sample, the fan average angle is ca. 34° (Pl. 2, Figs 1, 4, 5, 6b). The length of scratches is rather larger in *M. multilineatus* as compared to recent squirrels (but shorter in type series of *M. regularis*). The obtained data confirm gnawing behaviour in squirrels, and legitimize them as possible tracemakers. Based on the fine morphology of *M. multilineatus*, we see the squirrel we call large sciurid sp. 1 as the most suitable possible tracemaker. In the case of *M. regularis*, it seems almost certain that it is caused by different tracemaker. The general pattern, slender width and smooth microrelief of *Machichnus regularis* is different, and indicates a smaller tracemaker, with different fine incisor morphology. Compared with recent squirrel scratching, similar structures are produced by squirrels, and therefore a tracemaker related to Sciuromorpha is also probable. The proportions of the scratches indicate a smaller tracemaker than the tracemaker of *M. multilineatus*.

## Ichnological consequences

The ichnogenus *Machichnus* was erected ten years ago (Mikuláš et al. 2006), together with its three ichnospecies, i.e., *Machichnus regularis*, *M. multilineatus* and *M. bohemicus*. In the same paper, further bioerosion trace fossils from the locality Ahníkov were described: *Nihilichnus nihilicus* n. igen. et isp. and *Brutalichnus brutalis* n. igen. et isp. The paper by Mikuláš et al. (2006) got several new authors interested in the ichnotaxonomic approach to biting traces. Biting traces are frequently studied outside ichnology, and so papers on biting traces sometimes do not comply with standard ichnologic terminology, or deep-rooted aims of ichnologic studies.

Between 2006 and 2016, a surprisingly heterogeneous material was classified as *Machichnus*: biting traces on bones from terrestrial to fresh-water settings (e.g., crocodilian bites; Milàn et al. 2010, 2011, Schwimmer 2010), bites on whale bones (Jacobsen and Bromley 2009), or biting traces on lithic (phosphatic) substrate (Chumakov et al. 2009). Regardless this diversity, *Machichnus* appeared in the field of interest of S. G. Lucas (2016), who proposed a new terrestrial, substrate-based ichnofacies for traces on/in bone accumulations in terrestrial settings: the Cubiculum Ichnofacies. Lucas (2016) placed indirectly all biting traces on bones to his new ichnofacies, namely *Machichnus*.

The above-quoted papers and the present study enable inferring the following starting points for future studies:

1. The biting/gnawing behaviour itself is a widespread phenomenon throughout the entire Phanerozoic biosphere. It is usually joined with feeding behaviour, or with interactions among variable organisms. The resulting record (i.e., biting trace) often has good fossilization potential; therefore, closely undetermined biting traces will represent facies-crossing traces.
2. In favourable conditions on a studied locality (e.g., limited transport, diversity of finds, long time for fieldwork), a precise morphometric study can result in reliable conclusions on the tracemaker.
3. Most of finds of the ichnogenus *Machichnus* obviously belong to the newly erected Cubiculum Ichnofacies (Lucas 2016); finds of *Machichnus* therefore represent a provisional criterion for determination of this ichnofacies.
4. Attention to detail, necessary for morphometric study of *Machichnus* and its tracemaker, will not automatically enable erection of a new ichnotaxon. For ichnotaxa, Bertling et al. (2006) excluded a simple dimension (e.g., width) from acceptable ichnotaxobases. However, combination/ratio of dimensions is a valid ichnotaxobase.

## Conclusions

The scratches on bone surface representing ichnotaxa *Machichnus multilineatus* were not caused by beavers (Mikuláš et al. 2006) or porcupines (Diedrich 2007). We regard as the probable tracemaker a large squirrel. Some smaller scratches including ichnospecies *Machichnus regularis* might be caused by smaller sciuromorphs (Sciuridae or Aplodontidae).

Bone gnawing is very common in recent squirrels, and identical structures also occur on Late Cenozoic (especially Pleistocene) bones. Therefore, not only porcupines can be regarded as bone gnawers during the Late Cenozoic. The scratches have to be evaluated in context of accompanying fauna.

Based on observation, recent squirrels are able to consume almost entire antler or other suitable bone (Pl. 2, Figs 2, 3, 6a). Such a fact should be projected to the evaluation of collected fossil association. Squirrels should be regarded as a significant taphonomic factor in palaeontology (cf. Pl. 1, Fig. 5).

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## Explanations to the plates

## PLATE 1

*Machichnus multilineatus* from the locality Ahníkov II. (Most Basin, the Czech Republic)

1. Turtle carapace fragment covered by parallel scratches (NM-Pv 10152).

Gnawing trace most probably produced by the same tracemaker as *M. multilineatus* (Ahníkov II.)

2. Artiodactyl metapodial bone with isolated, especially long scratches (NM-Pv 10153).

*Machichnus multilineatus* from the locality Ahníkov I. (Most Basin, the Czech Republic)

3. Fragment of large bone covered with parallel and semi-parallel scratches (NM-Pv 10154).

*Machichnus* cf. *regularis* from the locality Ahníkov II. (Most Basin, the Czech Republic)

4. Turtle carapace fragment with scratches on the bone margin, partly forming a fan pattern (NM-Pv 10155). There are apparent scratches of individual as well as multiple scratching in the same place.

*Machichnus* sp. from the locality Ahníkov I. (Most Basin, the Czech Republic)

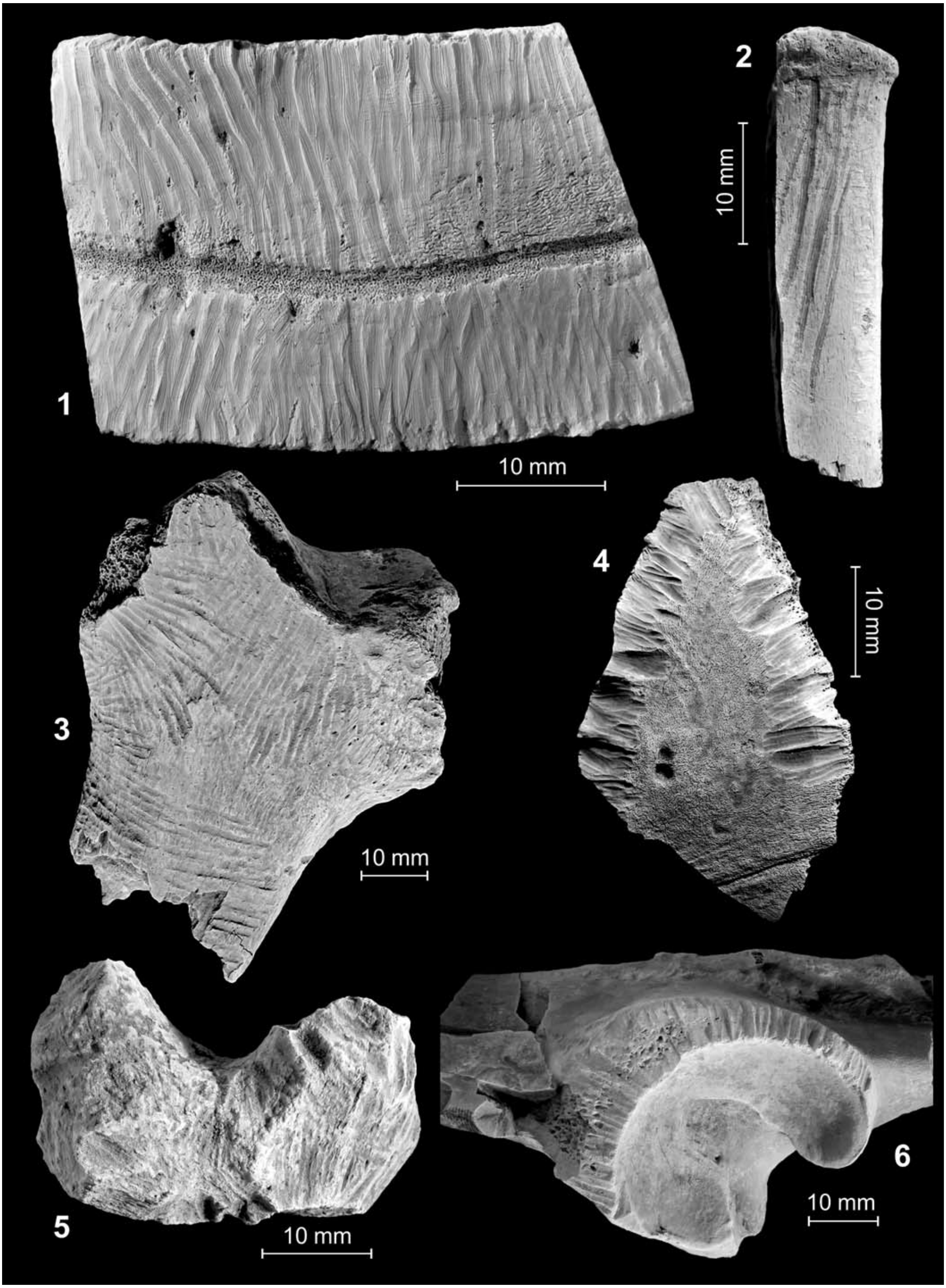
5. Almost completely gnawed antler (NM-Pv 10157). The rest represents the part where the antler branched.
6. Pelvis fragment with gnawing traces around the acetabulum margin (NM-Pv 10156). Part of the margin is removed by gnawing. There are also present marks caused by upper incisors used as support during gnawing.

## PLATE 2

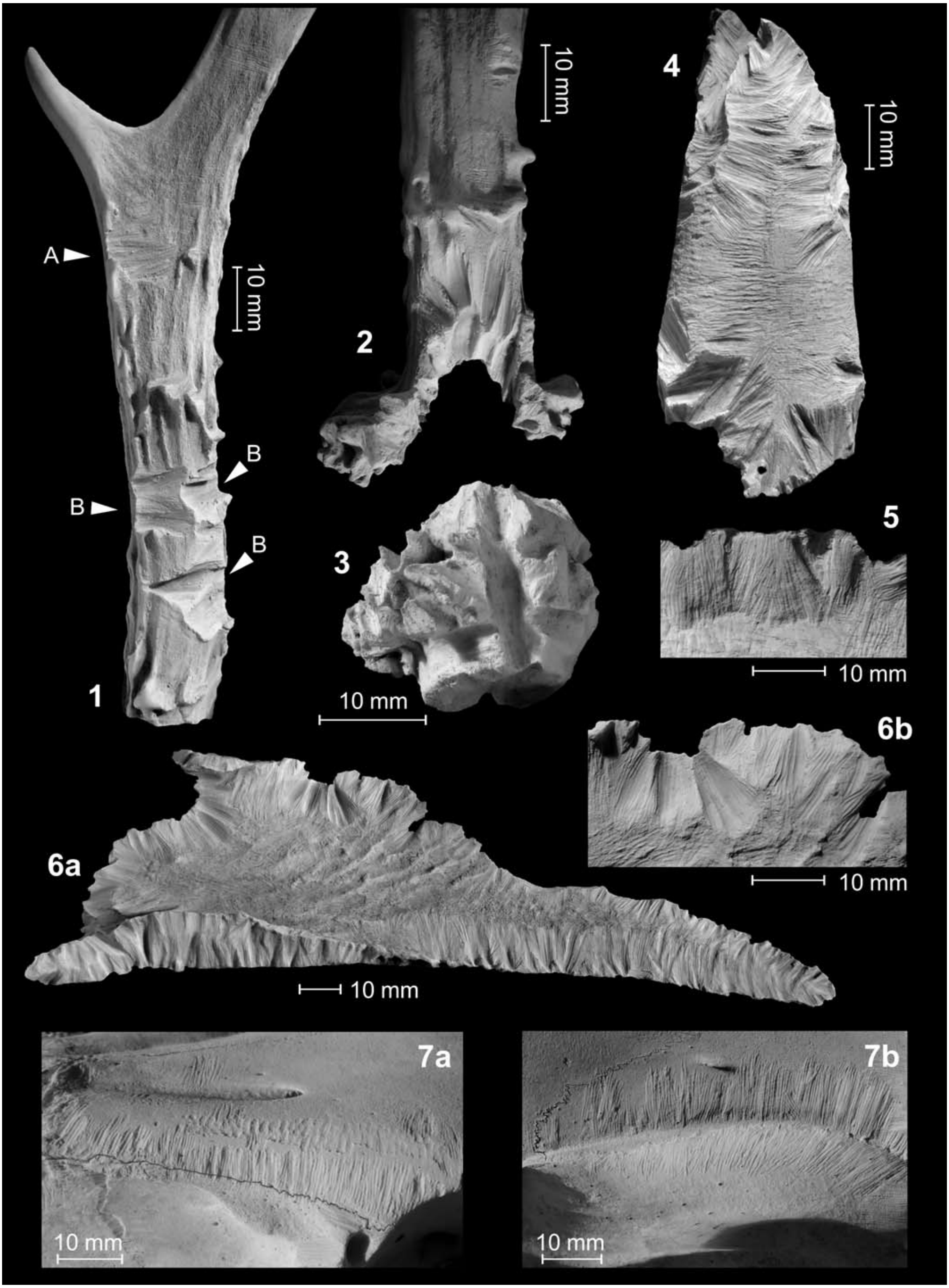
Gnawing traces made by recent red squirrels (*Sciurus vulgaris*)

1. Roe deer antler with two scratching types (NM-d59/2016/1).
   a: individual superficial scratching;
   b: deep multiple, fan-shaped scratching.
2. Roe deer antler with the base removed by intensive gnawing (NM-d59/2016/2).
3. Rest of antler base (NM-d59/2016/3). This specimen is the remnant of a complete antler given to red squirrels during our experiments.
4. Artiodactyl metapodium (NM-d59/2016/4) covered with both, individual parallel scratchings (in central part of bone; made by both, upper and lower incisors), and multiple scratching on the edges, mostly arranged into fan-pattern (made dominantly by lower incisors). Both of these gnawing traces characters are caused by the same tracemaker, and the differences in trace morphology and arrangements are caused by the substrate morphology.
5. Fragment of large cortical bone with shallow fan-pattern (NM-d59/2016/5).
6. Scapula fragment (NM-d59/2016/6).
   a: General view with apparent gnawing traces on the edges;
   b: detail of multiple scratches forming fan-pattern.
7. Skull of wild boar (*Sus scrofa*) (NM-d59/2016/7).
   a: Detail of gnawing traces on the edge with obtuse angle on parietal bone; scratches of equal size caused by both upper and lower incisors are apparent; b: Detail of gnawing traces on the edge with obtuse angle on frontal bone; the gnawing traces caused by upper incisors are represented only by rather short lines and dots; this morphology is a result of upper incisors not firmly dug into the material, but moving slightly during the gnawing action of the lower jaw.

**PLATE 1**



## PLATE 2



1
A
B
B
B
10 mm
2
10 mm
3
10 mm
4
10 mm
5
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6a
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7a
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7b
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