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MORTALITY PROFILES OF *CASTOR* AND *TROGONTHERIUM* (MAMMALIA: RODENTIA, CASTORIDAE), WITH NOTES ON THE SITE FORMATION OF THE MID-PLEISTOCENE HOMININ LOCALITY BILZINGSLEBEN II (THURINGIA, CENTRAL GERMANY)

WOLF-DIETER HEINRICH[1], LUTZ CHRISTIAN MAUL[2,*]

[1] Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstraße 43, 10115 Berlin, Germany; e-mail: wolf-dieter.heinrich@mfn-berlin.de.
[2] Senckenberg Forschungsstation für Quartärpaläontologie, Am Jakobskirchhof 4, Weimar, Germany; e-mail: lmaul@senckenberg.de.
*corresponding author

Abstract: The Middle Pleistocene site Bilzingsleben II is well-known for its wealth of vertebrate and archaeological remains. Of particular importance is the record of *Homo erectus bilzingslebenensis*. Most palaeontologists consider the find horizon as a primary vertebrate deposit formed during human occupation, while some archaeologists attribute its formation to turbulent gravitational mass flows, inundation or a combination of both. Here we present mortality profiles of the beavers *Castor* and *Trogontherium* to provide further arguments to this controversial discussion. The mortality profiles of *Castor* from Bilzingsleben II, Weimar-Ehringsdorf and Weimar-Taubach are largely identical indicating similar taphonomic filters that were effective in the formation of the find layers. Individuals, which were tentatively classified as suspected ±2–2½ year old beavers dominate by far in all three sites. The structure of these mortality profiles shows similarities to Stiner's (1990) "prime dominated mortality pattern", which is indicative of human hunting. This consideration is supported by the difference of the mortality profile of *Trogontherium* from Bilzingsleben II (dominance of older individuals) in relation to the profiles of non-hominin generated assemblages of Tegelen and Mosbach 2 (dominance of younger individuals). Thus, our data support the interpretation of the Palaeolithic find horizon of Bilzingsleben II as a primary vertebrate deposit, but not the gravitational mass flow and inundation hypotheses.

Key words: Taphonomy, ageing, Castoridae, Pleistocene, Europe

Introduction

In several Pleistocene sites of Central Europe, fossil remains of beavers (Castoridae) are represented in larger numbers and sparkle interest of both palaeontologists and archaeologists. Due to their size, beavers obviously were often prey of carnivorous animals, but also of the prehistoric man. Thus, Castoridae remains recorded in hominin sites must be considered potentially a target of humans' hunting activities. One of these beaver-bearing Pleistocene localities is Bilzingsleben in Central Germany.

The Mid-Pleistocene hominin site Bilzingsleben II is located outside of but close to the northern fringe of the Thuringian Basin, approximately 30 km north of Erfurt and 35 km northwest of Weimar (Text-fig. 1). The locality, an abandoned travertine quarry (called "Steinrinne"), has yielded diverse floral and faunal remains, hominin fossils,

Palaeolithic artifacts and human occupation structures, which were mainly unearthed during extensive excavations between 1969 and 2002 spearheaded by Dietrich Mania (Jena). Highlight of these field works was the discovery of fossil hominin remains that were assigned to *Homo erectus bilzingslebenensis* (see for fuller account, e.g., Vlček 1978, Vlček et al. 2002, Vlček and Mania 2011). The local Palaeolithic find horizon has produced an enormous amount of vertebrate remains, particularly from mammals, including the beavers *Castor fiber* Linnaeus, 1758 and *Trogontherium cuvieri* Fischer, 1809 that form the focus of the present study.

There has been a consensus among most palaeontologists involved in the long-term archaeological and palaeontological investigations at Bilzingsleben II that the bone assemblages from the Palaeolithic find horizon are related to human hunting. They are regarded as a primary concentration of

Text-fig. 1. Geographic position of the beaver-bearing sites discussed in this paper. Red triangles – records of *Castor*, blue dots – records of *Trogontherium*. Bilz II – Bilzingsleben II, Ehr – Weimar-Ehringsdorf, Mosb 2 – Mosbach 2, Taub – Weimar-Taubach, Teg – Tegelen. (This map was created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri).

mainly disarticulated and fractured skeletal remains (primary vertebrate deposit sensu Lyman 1994), accumulated along with artifacts during the time of human occupation (e.g., Guenther 1983, 1991, Mania 1983, Heinrich 1991, Mania and Mania 2002, 2017, Mania and Altermann 2017).

However, this interpretation has recently been challenged by some archaeologists, who argued that the bone assemblages of Bilzingsleben II are not hominin-generated but the result of turbulent gravitational mass flows (Beck et al. 2007, Pasda 2009), inundation (e.g., Steguweit 2003, Müller and Pasda 2011) or a combination of both processes with "possibly other minor geological events" (Pasda 2012). According to Pasda (2012: 40) there are "no indications of any kind of Palaeolithic 'living floor'" in Bilzingsleben II. If these objections were actually true, this would have far-reaching consequences for the scientific significance of the site. Mass flow, for instance, if actually proved, would mean re-working and re-deposition of skeletal remains from the primary embedding place to another spot. Consequently, Bilzingsleben II would only be a secondary vertebrate deposit in the sense of Lyman (1994) with a much-reduced scientific meaningfulness and low value for biostratigraphic correlation and palaeoenvironmental interpretation.

In order to provide new arguments to this controversial discussion we approach the application of mortality profiles (i.e., age-frequency distributions) to the recorded beaver remains. The time of death of animals provides essential indication about the formation and structure of death assemblages (e.g., Lyman 1987, 1994, Weigelt 1999, Behrensmeyer et al. 2000, Rogers et al. 2007). This holds

also true for beavers, where cheek teeth can provide valuable clues about the age at death of the individuals, the structure of the death assemblages and thus also on the site formation. Therefore, we analyse in the following mortality profiles of *Castor* and *Trogontherium* in order to review the site formation hypotheses that are currently being discussed for Bilzingsleben II. Comparative samples of *C. fiber* originate from the hominin-bearing sites Weimar-Ehringsdorf and Weimar-Taubach, Germany, and samples of *Trogontherium* from the non-hominin sites Tegelen (The Netherlands), and Mosbach 2 (Germany) (for geographic position see Text-fig. 1). This material was chosen because of its regional vicinity to Bilzingsleben (Weimar-Ehringsdorf and Weimar-Taubach), and the sufficient amount of tooth material of Castoridae, respectively (Tegelen, Mosbach).

The genus *Trogontherium* appeared earlier, and stands systematically before *Castor* (e.g., McKenna and Bell 1997: 129–131) and should therefore be discussed first in the text. However, since we have much more information about the latter genus (e.g., more records, more insight in its biology inferred from the two extant species *C. fiber* and *C. canadensis*), in each chapter of this article, we deal with *Castor* first.

The present paper is dedicated to the late Gerhard Storch, whose numerous founding works have improved significantly our knowledge on fossil and extant mammals. In many groups Gerhard was considered to be one of the world-wide leading experts. Also, Castoridae were on his concern, and he described two new beaver taxa (for a list of all taxa described by G. Storch, see Horáček et al. 2019).

Brief characteristics of the sites of the studied samples, and its relation to the life style of beavers

Bilzingsleben II

The geological context of the Bilzingsleben II site, including stratigraphic profiles, numerous excavation maps and extended descriptions, has been summarised in several papers and monographs (e.g., Mania and Mania 2002, Mania and Altermann 2017). The studied beaver remains are from the local Palaeolithic find horizon that mainly consists of (1) a peninsula-like border terrace of loess with human occupation traces ("Uferplatte") and (2) friable travertine sands of an alluvial fan ("Schwemmfächer"), which was used by the fossil humans as a waste damp (e.g., Mania and Mania 2002, Mania et al. 2003, Mania and Altermann 2017). The border terrace and the alluvial fan are overlain by sandy carbonate deposits ("sandiger Seekalk"), which form the upper part of the find horizon (Mania and Altermann 2017), but have not yielded beaver teeth.

The find horizon has produced a rich multi-specific vertebrate bone accumulation (sensu Heinrich 1977). Around 54 species of vertebrates have been identified, including fish, amphibians, reptiles and birds as well as mammals that dominate the vertebrate assemblage. They constitute a temperate *Elephas antiquus-Stephanorhinus kirchbergensis* assemblage, with the stratigraphically/environmentally indicative taxa *Macaca florentinus*, *Homo erectus bilzingslebenensis*, *Ursus deningeri-spelaeus*, *Canis lupus*, *Stephanorhinus hemitoechus*, *Dama clactoniana*, *Sus scrofa*, *Crocidura* ex gr. *russula-leucodon*, *Arvicola mosbachensis*, *Muscardinus avellanarius* and the two beaver species *Trogontherium cuvieri* and *Castor fiber* (Fischer 1991, Fischer and Heinrich 1991, Guenther 1991, Heinrich 1991, 1997b, Musil 1991a, b, van der Made 1998, 2000, Mania et al. 2003, Vlček 2003, Brasser 2017, Mania and Mania 2017).

Already in an earlier investigation, it could be demonstrated that of 1,146 beaver teeth from the local Palaeolithic find horizon (border terrace, alluvial fan) 1.016 (89 %) belong to *Castor*, but only 130 (11 %) to *Trogontherium* (Heinrich 1997a: 123). The same relationship was found in the lower premolar (used in the current study – see section Methods). Finds of the premolars of *Trogontherium* (about 11 %; n = 29) are clearly underrepresented compared to those of *Castor* (almost 89 %; n = 226) (Tabs 2, 4).

Mania (1997) assigned Bilzingsleben II to an interglacial of the Holsteinian Complex. Uranium series and ESR dating yielded age data ranging between 319–350 ka BP and 282–414 ka BP (Mania et al. 2003), indicating Marine Isotope Stage (MIS) 11 (Mania and Mania 2002, Schreve and Bridgland 2002a). The presence of *Arvicola mosbachensis* and the absence of *Drepanosorex* and *Pliomys* place Bilzingsleben II into the early part of the Late Toringian (sensu Fejfar et al. 1998).

Weimar-Ehringsdorf

The travertine sequence of Weimar-Ehringsdorf is located on the left slope of the valley of the Ilm River. Precise locality data with stratigraphic sections and detailed descriptions are given by Behm-Blancke (1960), Steiner and Wiefel (1974), Wagenbreth and Steiner (1974), Schäfer (1991), and Steiner (1993, 2003). The majority of plant, invertebrate and vertebrate fossils comes from travertine deposits divided into the Lower (LT) and Upper Travertine (UT). Fossil vertebrates identified from the LT include amphibians, reptiles, birds, and mammals, of which the latter are most commonly. More than 40 mammalian species have been known so far, among them the indicative species *Ursus tibethanus* (?), *Cyrnaonyx antiqua*, *Canis lupus*, *Lynx lynx*, *Elephas antiquus*, *Stephanorhinus kirchbergensis*, *S. hemitoechus*, *Equus chosaricus*, *Megaloceros giganteus*, *Apodemus maastrichtiensis* etc. (e.g., H.-D. Kahlke (ed.) 1974, 1975, R.-D. Kahlke 2002, Mania et al. 2003).

The LT of Weimar-Ehringsdorf has long been known for its hominin fossil remains (see for summary Behm-Blancke 1960, Vlček 1993), artifacts (Behm-Blancke 1960, Schäfer 1991) and other evidences of human occupation such as hearths ("Brandschichten": Behm-Blancke 1960). The Weimar-Ehringsdorf hominin remains are assigned to early neanderthals (e.g., Haidle and Pawlik 2010).

The fossil remains of *C. fiber*, included in the present study, come from the LT, particularly from the so-called "beaver bed" ("Biberschicht"), which was exposed close to the base of the travertine sequence in the quarry Kämpfe in 1917 and the Fischer quarry in 1928 (Behm-Blancke 1960: 20, figs 25, 26).

The age of the LT of Weimar-Ehringsdorf is still controversial. Some authors favour Eemian as age (Behm-Blancke 1960, Schäfer 1991), others do not exclude a pre-Eemian (intra-Saalian) age (e.g., Heinrich 1982, 1987, 2003, Mania 1993, 2006, R.-D. Kahlke et al. 2002, Schreve and Bridgland 2002b). Uranium series and ESR dating of the LT yielded age data between ca. 167 and 244 ka and 127 and 240 ka (e.g., Brunnacker et al. 1983, Blackwell and Schwarcz 1986, see also summarising Mania et al. 2003), correlating with MIS 7. Anyway, the travertine sequence of Weimar-Ehringsdorf is distinctly younger than that of Bilzingsleben II. Also, Weimar-Ehringsdorf is biostratigraphically dated to the early part of the Late Toringian because of the presence of *Arvicola mosbachensis* and the absence of *Drepanosorex* and *Pliomys* (sensu Fejfar et al. 1998).

Weimar-Taubach

The well-known travertine sequence of Weimar-Taubach is located on the right slope of the valley of the Ilm River, about 1.5 km upstream from Weimar-Ehringsdorf. For locality data, history of research and detailed section descriptions see summarising Steiner and Wiefel (1977) and Steiner (1977, 1979). Previously exposed in numerous outcrops (small quarries), the travertine deposits have not been accessible for many years. Nevertheless, the quarries yielded numerous important vertebrate remains in the past, particularly close to the end of the 19th century (Steiner 1977, Steiner and Wiefel 1977, R.-D. Kahlke 2002). Most skeletal remains were collected from friable travertine sands ("Scheuersande": Steiner and Wiefel 1977, "Knochensande": R.-D. Kahlke 2002) near the base of the sequence that also produced beaver cheek teeth (Portis 1878). This find horizon is best to be correlated with the bone-bearing travertine sands ("Travertin-Sande") of the reference profile

established by Steiner (1977). These bone and teeth bearing travertine sands are overlain by a massive travertine bank ("Werkstein-Travertin"). The fossil vertebrate assemblage from Weimar-Taubach includes amphibians, reptiles, birds and mammals. More than 30 mammalian species have been identified, including the following indicative species (H.-D. Kahlke (ed.) 1977, R.-D. Kahlke 2002, Maul 2002): *Canis lupus*, *Crocuta crocuta*, *Elephas antiquus*, *Stephanorhinus kirchbergensis*, *S. hemitoechus*, *Equus taubachensis*, *Dama dama*, *Aces latifrons*, *Megaloceros giganteus germaniae*, *Bison priscus mediator*, *Castor fiber*, *Cricetus major* etc.

The presence of hominins in the period of travertine formation is evidenced by Palaeolithic artifacts and cut marks (Bratlund 1999) as well as by two teeth of *Homo* sp. (Taubach A and B: Behm-Blancke 1960), the precise stratigraphic provenance of which is not known (Steiner and Wiefel 1977).

Weimar-Taubach has generally been considered to be of Eemian (MIS 5e) age (e.g., H.-D. Kahlke (ed.) 1977, von Koenigswald and Heinrich 1999, van Kolfschoten 2002) and is so treated in the present paper. Radiometric dating produced ages of the "Knochensande" between 111–116 ka BP (Brunnacker et al. 1983).

Mosbach 2

At the Mosbach site, located on the eastern edge of the city of Wiesbaden (Hesse), a sequence of fluvial sands and gravels of the Pleistocene Rhine-Main-river system is exposed that has extensively worked in the quarry of the Dyckerhoff Company. It has been traditionally subdivided into three superimposed stratigraphic units: Mosbach 1–3 (e.g., Brüning 1978, von Koenigswald and Tobien 1987, von Koenigswald and Heinrich 1999, Keller and Radtke 2007). The mainly medium- to coarse-grained sands of Mosbach 2 have produced an abundance of disarticulated skeletal remains of both small and large mammals. More than 60 species have been found so far, among them (von Koenigswald and Heinrich 1999, Keller and Radtke 2007): *Macaca* sp., *Canis lupus mosbachensis*, *Ursus deningeri*, *Gulo schlosseri*, *Acionyx pardinensis*, *Elephas antiquus*, *Stephanorhinus etruscus/hundsheimensis*, *S. kirchbergensis*, *Hippopotamus amphibius*, *Alces latifrons*, *Capreolus suessenbornensis*, *Trogontherium cuvieri*, *Castor fiber* etc. The fossil-bearing deposits of Mosbach 2 are normally polarised and attributed to the Brunhes-Epoch (Keller and Radtke 2007). Based on biometrical data obtained from *Arvicola mosbachensis*, Maul et al. (2000) correlated Mosbach 2 tentatively with MIS 15–13, around 600–500 ka BP, covering parts of the late Cromerian, possibly the Cromerian Interglacial IV (van Kolfschoten and Turner 1996: 247, tab. 245). The evolutionary level of *Arvicola mosbachensis* and the presence of *Talpa minor*, *Drepanosorex savini* and *Pliomys episcopalis* assigned the Mosbach 2 assemblage to the earliest part of the Toringian (von Koenigswald and Tobien 1987, von Koenigswald and Heinrich 1999, Maul et al. 2000).

Tegelen

The renowned fossil site of Tegelen is located near Venlo in the Maas Valley (Province Limburg, The Netherlands).

The sediments that produced skeletal remains are fluvial clays, deposited in channels, oxbow lakes and flood plains of the ancient Maas-(Meuse-) River system (e.g., Westerhoff et al. 1998), which were exposed in several clay pits that now serve as type locality for the Tiglian Interglacial (van den Hoek Ostende 2004). The skeletal material consists mainly of disarticulated fragmentary bones and numerous individual teeth (Guenther 1986). Some bones such as skull and jaw remains of *Trogontherium boisvilletti* (Laugel, 1862) were found in hard concretions. The non-mammalian vertebrate assemblage comprises fish, amphibians, reptiles and birds (for fuller account see van den Hoek Ostende and de Vos 2006: 300, tab. 301, Villa et al. 2018). The mammalian assemblage that has recently been compiled by van den Hoek Ostende and de Vos (2006) comprises ca. 40 species, of which the following are quoted here: *Macaca sylvanus*, *Pliocrocuta perrieri*, *Ursus etruscus*, *Enhydrictis ardea*, *Panthera gombaszogensis*, *Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Sus strozzii*, *Eucladoceros ctenoides*, *Cervus rhenanus*, *Leptobos* cf. *elatus*, *Desmana thermalis*, *Galemys kormosi*, *Petenyia hungarica*, *Beremendia fissidens*, *Hypolagus brachygnathus*, *Trogontherium boisvilletti*, *Castor fiber*, *Hystrix refossa*, *Ungaromys nanus*, *Mimomys pliocaenicus*, *M. tigliensis*, *M. reidi*, *Pitymimomys pitymyoides* etc. The deer and the extinct beaver *Trogontherium boisvilletti* are the most common mammals in the Tegelen fauna (van den Hoek Ostende and de Vos 2006). Van der Meulen (in Freudenthal et al. 1976: 19) noted that "Larger mammal remains have been collected from all levels of the type section and from corresponding deposits in the Tegelen area".

The studied *Trogontherium* remains from Tegelen were collected by P. G. Krause (Berlin) in the years 1907 – 1912, mainly in the clay-pits of the firm "Herfkens & Smulders" and, to lesser extent, in the "Teeuwen's Grube", "Thiessen's Grube" and "Bergers Grube" (Schreuder 1929). Although the exact stratigraphic provenance of these finds is unknown, they are much older than the material of all the other sites discussed in this paper.

The exact age of the Tiglian vertebrate assemblage is still under discussion. Van den Hoek Ostende and de Vos (2006) suggested that the clayey beds in the Tegelen area not all of the same age. Unfortunately, most of the Tiglian fossils are chance finds of clay pit workers without exact stratigraphic provenance data. Exceptions are small mammal assemblages recovered from stream gully deposits of the Russel-Tiglia-Egypte pit (Freudenthal et al. 1976) and from two superimposed levels in clay deposits exposed in the Maalbeek pit (Westerhoff et al. 1998), of which the latter were shown to be slightly older than the former one, even though common species occur in both sites such as *Desmana thermalis*, *Mimomys pliocaenicus*, *M. tigliensis* and *M. reidi* (van Kolfschoten in Westerhoff et al. 1998: 61–62). The stream gully infilling of the Russel-Tiglia-Egypte pit that produced small mammals date from the Tiglian substage TC5, based on pollen spectra (Westerhoff et al. 1998). Records of *Mimomys pliocaenicus*, *M. reidi*, *M. tigliensis*, *Borsodia newtoni*, *Ungaromys dehmi* etc. (van der Meulen in Freudenthal et al. 1976, Tesakov 1998) indicate a late Villanyian age, correlated with MN 17 (sensu Fejfar et al. 1998). However, the exact biostratigraphic relation

of the small mammals from the Russel-Tiglia-Egypte and Maalbeek pits to the large mammal and *Trogontherium* remains collected in the Tegelen area is far from clear.

Palaeoenvironment of beavers

The palaeoenvironments of all studied *Castor*-bearing sites mentioned above included uplands, slopes and valleys as well as wetland areas with dammed pond- or lake-like water bodies fed by spring and brook waters, cascades, and rivulets that flowed down into valleys that were traversed by rivers; flood plains, riparian forests, light deciduous forests and open land stretches were present in the immediate vicinity of the sites (for Weimar-Ehringsdorf see, e.g., Wagenbreth and Steiner 1974: 79, fig. 71, 114, 124; for Weimar-Taubach see Steiner 1977: 84, fig 81; for Bilzingsleben II see Mania and Mania 2002: 82–83, figs 16, 17, Mania et al. 2003).

These conditions fully meet the habitat preferences of extant beavers that are semi-aquatic and strictly herbivore rodents. Both, the Eurasian beaver (*C. fiber*) and the North American beaver (*C. canadensis*) show similarities in their behaviour and habitat requirements (Müller-Schwarze and Sun 2003: 6, tab. 1.1), even though the latter seems to have a greater ecological adaptability (Rosell and Sun 1999). Preferred habitats include primarily slowly-flowing or stagnant water bodies, such as lakes, ponds, oxbow lakes, rivers, streams, creeks and their marshy outlets that are surrounded by thickly overgrown banks and riparian forests (Djoshkin and Safanow 1972, Freye 1978). The extent of stagnant water must be at least 40 m to be inhabited by beavers; the minimum water depth should be 1.5–2.0 m (Freye 1978) to provide protection from predators and ice-free access to underwater food storage during winter (Baker and Hill 2003). Beavers built lodges and burrow dens in banks with underwater entrances. To secure the underwater access to the lodges, beaver set up dams of trunks, branches, twigs, reeds, mud and stones in order to keep the water at a constant height.

The food spectrum of the Eurasian beaver includes approximately 300 plant species (Djoshkin and Safanow 1972). The most important components are deciduous woody plants. In spring and summer, the food consists mainly of aquatics, shrubs, herbs, grasses, sedges and, to a lesser extent, of softwood (twigs, buds, leaves, fruits) such as from willows (*Salix*) and poplars (*Populus*) (Heidecke 1989, Rosell and Czech 2000, Schröpfer 2009), as the bark of the softwoods is thicker and more nutritious than that of other species of wood (Heidecke 1998). In late autumn and winter, beavers eat mainly woody food of deciduous trees and shrubs, in particular barks; conifers are often avoided.

A look at the list of plants identified in the Thuringian travertine sites reveals that many of these species doubtless belong to the food spectrum of beavers. In Bilzingsleben II, plants eaten by beavers are preserved as imprints (D. H. Mai 1983, 1989, 2000, Mania et al. 2003), pollen (Erd 1993, 1997) and wood (Mania and Schoch 2017, Schoch 2017) such as deciduous trees (e.g., *Populus tremula*, *Salix cinerea*, *Betula pubescens*, *Acer campestre*, *Rhamnus alnus*, *Fraxinus excelsior*, *Ulmus* sp.), coniferous trees (e.g., *Abies* sp., *Picea abies*, *Pinus* sp.), and shrubs (e.g., *Corylus avellana*, *Viburnum latana*). In addition, herbs (e.g., *Filipendula*) and grasses (*Carex* sp.) as well as various aquatics (*Alisma*,

Sparganium plantago-aquatica, *Nymphaea* sp., *Salvinia* sp.) have been identified (Erd 1997).

The plant macrofossils recovered from the Lower Travertine of Weimar-Ehringsdorf include leaf imprints and incrustations of fructifications (D. H. Mai 1974, Vent 1974, Stebich and Schneider 2002). There are also numerous deciduous plant species that belong to the beaver's diet, including, for instance, *Populus tremula*, *Salix cinerea*, *Corylus avellana* and *Tilia cordat*a. This holds likely also true for the Eemian travertine of Weimar-Taubach, where, unfortunately, the fossil plant record is extremely meagre. Fossil reed stalks indicate *Phragmites* (Steiner 1977) that is eaten by the beaver (Hinze 1950). Overall, the fossil record of plants at the studied Thuringian travertine sites indicates habitats with rich supply of food that fulfilled the beaver's nutritional requirements.

The assessment of the life style of *Trogontherium* is problematic, as it became already extinct in Europe during the Middle Pleistocene. Its biology has been partly reconstructed from dental and skeletal features, whereby the associated faunas and floras, the sedimentary context, etc. provided further useful data. Habit reconstructions are given, for instance, by Schreuder (1951: 416, fig. 414) for *Trogontherium boisvilletti* and more recently by Fostowicz-Frelik (2008: 775, fig. 777) for *T. cuvieri*.

Trogontherium is generally considered being a semi-aquatic rodent as well (Rybczynski 2007). Proportions of the limb bones (e.g., foreshortening of humerus and femur, prolongation of radio-ulnar and tibio-fibular bones) and the un-flattened tail etc. indicate that it was likely more cursorial than *Castor* (e.g., Guenther 1965, Motuzko 1972, Mayhew 1978b, Fostowicz-Frelik 2008), although it had webbed skins (Schreuder 1929, 1951, Mayhew 1978b). In addition, the large diastema and the more anteriorly protruded incisors in *Trogontherium* could indicate better adaptations for digging. Like *Castor*, *Trogontherium* was able to gnaw deciduous trees and shrubs to consume barks (Fostowicz-Frelik 2008). However, Mayhew (1978b) considered it unlikely that *Trogontherium* could cut down trees, as suggested by Schreuder (1929).

For the camp site Bilzingsleben II, it is therefore likely that beavers initially dammed spring and creek waters (Guenther 1991, Heinrich 1991) that led to the formation of a 200 × 300 m large lake, which was drained by a cascade (Mania and Altermann 2017). It is therefore conceivable that part of the numerous wood remains of Bilzingsleben II (Schoch 2017) originate from lodges and dams of *C. fiber*. While fossil wood remains with gnawing marks indicate that *Castor* built lodges and dams during the Pleistocene (e.g., Aalto et al. 1989), it is unclear whether *Trogontherium* even did so, because fossil records are missing so far.

Finds from *Castor* and *Trogontherium* are often found together in Early and Middle Pleistocene aquatic deposits. However, remains of *Trogontherium* are usually more abundant in fine-grained sediments deposited in slow-running and stagnant waters (Mayhew 1978b) such as sluggish rivers and oxbow lakes. In Bilzingsleben II, it remains unclear, whether *Castor* and *Trogontherium* lived side by side (sympatric) in one common habitat or separated (allopatric) in different habitats. Because of the better digging abilities, it would be conceivable that *Trogontherium* lived primarily

in and at the ancient Wipper River, where dens were dug in the loose bank deposits, whereas *Castor* inhabited the wet travertine landscape, where lodges and dams were built.

It is important to mention that, like other rodents, beavers are exposed to a considerable predator risk. This also applies to *Castor* and *Trogontherium* from Bilzingsleben II. Carnivores hunting *C. fiber* include wolves (*Canis lupus*), wolverines (*Gulo gulo*), bears (*Ursus arctos*) and lynxes (*Lynx lynx*) (e.g., Djoshkin and Safanow 1972, Rosell and Czech 2000, Gable and Windels 2018). The red fox (*Vulpes vulpes*) is reported to occasionally predate beaver kits (e.g., Djoshkin and Safanow 1972, Kile et al. 1996, Rosell and Czech 2000, Graf et al. 2016). Other predators known to prey on juvenile beavers are some birds of prey, among them the White-tailed Eagle (*Haliaeetus albicilla*) and the Eagle Owl (*Bubo bubo*) as well as predatory fish such as the pike (*Esox lucius*) and the wels catfish (*Silurus glanis*), one the largest freshwater fish in Eurasia (e.g., Djoshkin and Safanow 1972). Probably, *Trogontherium* had to do with the same predators as *Castor*. However, the most dangerous enemy of beavers was man for millennia, and there are many indications that this also applies to the fossil beavers from the Thuringian travertine sites.

Material and methods

Material

Morphology, preservation, sample size and storage

The present study is based on lower milk (dp4) and deciduous (p4) premolars of *Castor* and *Trogontherium*, because in the dentition of beavers these teeth can be identified most certainly. The p4 is larger and higher crowned than the remaining cheek teeth. The premolar basic pattern consists of three notches (striids) on the lingual (para-, meso-, metastriid) and one on the labial (hypostriid) side (e.g., Stirton 1935, Hugueney 1999), which are cementless in *Trogontherium*, and filled with cement in *Castor*. Each notch corresponds to an enamel loop (flexid) on the grinding surface. With progressive wear, four flexids appear on the grinding surface ("3+1" fold pattern: Mayhew 1979), designated as para-, meso-, meta- and hypoflexid (Stirton 1935). Actually, flexids and striids are visible parts of enamel "invaginations". However, this basic pattern can be modified by fusion of flexids and formation of enamel islets (e.g., Hünermann 1966, Mayhew 1979, Stefen 2009), owing to a specific mode of mastication (Stefen et al. 2011). In advanced stages of wear, the flexids lose the contact to the external wall of the tooth and form enamel islets (fossettids). In addition, the length of the occlusal surface increases with advancing age in *C. fiber* (Heinrich 1991, Stefen 2009). An elongation of the grinding surface with increasing age is observed also in *Trogontherium*. Moreover, in p4 of this genus the basic dental pattern is extended successively in the course of evolution by an antero-lingual striid and flexid up from the Middle Pleistocene (see for fuller account Heinrich 1998).

In Bilzingsleben II, the preservation of the premolars of *Castor* and *Trogontherium* varies sizeably. Only portions of the samples are completely preserved. The majority of cheek teeth are damaged, particularly at the tooth base, owing to dry sieving of the sediments (Guenther 1983). On the jaw fragments and teeth, there are no sanding marks due to transport in running waters. The dentin and the roots of teeth are usually light-brown, the enamel is light-grey to grey coloured. The cement deposits in the notches of the enamel walls in *Castor* are also light brown in colour. Dendrites occur occasionally. There is neither significant differences in their state of preservation of teeth between *Castor* and *Trogontherium*, as previously suggested by Guenther (1983), nor between the beaver teeth recovered from the alluvial fan and border terrace.

Also, in Weimar-Ehringsdorf and Weimar-Taubach, a mixture of fairly complete and fragmentary cheek teeth of *Castor* has been found, which are usually grey to light brown in the colour.

The studied premolars of *Trogontherium* from Mosbach 2 are usually slightly damaged. The colour of the enamel walls is mainly grey-black, occasionally yellow-brown, that of the dentin light brown, whereas the enamel loops on the grinding surface have grey to dark grey colourations. In addition, manganese stains and dendrites are seen some time.

The cheek teeth of *Trogontherium* from the clay pits in the Tegelen area are pretty well preserved, as already noted by Schreuder (1929). The colour of dentin varies mainly between light brown and strong dark brown, the enamel is predominantly dark with a slightly bluish tinge.

A total of 416 lower premolars (dp4 and p4), 278 of *Castor*, and 138 of *Trogontherium* has been investigated (Tabs 2, 4), which are stored in the following institutions: Bilzingsleben – collection of the Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt, Halle; Weimar-Ehringsdorf and Weimar-Taubach – collection of the Senckenberg Forschungsstation für Quartärpaläontologie Weimar; Mosbach 2 – Naturhistorisches Museum Mainz; Tegelen – Museum für Naturkunde Berlin.

Methods

Mortality profiles

In the following we first use mortality profiles. These are histograms (line or bar charts) in which the percentage frequencies of defined age groups (see below) are shown. This type of mortality profile is often used in archaeozoology and palaeontology (Lyman 1987, Stiner 1990, Lyman 1994, Reitz and Wing 2009). Subsequently, we generated a ternary diagram (using the relative abundance of only three age groups in an assemblage: juveniles, prime and old adults) introduced by Stiner (1990) and modified by Discamps and Costamagno (2015) (see section: Mortality profiles of fossil *Castor* samples).

Age groups of Castor

Compare the following notes with Text-fig. 2. Although various approaches of age determination of *Castor* individuals based on dental characters have been already published (e.g., van Nostrand and Stephenson 1964, Larson and van Nostrand 1968, Hatting 1969, Piechocki and Stiefel 1977, Mayhew 1978a, 1979, Piechocki 1986, Heinrich 1991, Baker and Hill 2003, Müller-Schwarze 2011), no one of these methods is consistently applicable throughout

our fossil material of isolated teeth. Some of the methods refer to consecutive relative age groups only (relative age classes), others to age groups given in years (year classes).

Freye (1978: 954, fig. 927) figured six successive stages of basal cavity closure (from wide open base to early root formation) in cheek teeth of *C. fiber*, but did not refer them to ages in years. Based on known-age material, van Nostrand and Stephenson (1964) used three dental criteria of mandibular cheek teeth in *Castor canadensis* for distinguishing year classes: eruption of permanent premolar (p4), gradual closure of the basal cavity of molars, and the basal cement-layer deposition. Special attention was given to the mandibular molars, since counting of the basal cement-layer of m1 and m2 "provide the clearest indication of age" (van Nostrand and Stephenson 1964). Hartmann (1992) used X-ray photographs to determine the age of Eurasian beavers from Sweden. Criteria were also here the gradual tooth root closure and the annual deposition of cement and dentin layers, especially on the second lower molar. In addition, the body weight was considered. Klevezal's (2007: 140, fig. 112.146) age classification of *C. fiber* is based on basal cement-layer counting in longitudinal sections of the first lower molar. However, the use of isolated m1 and m2 causes difficulties, since these molars cannot be safely separated from each other.

Here we apply a relative age classification for *C. fiber* based on dp4 occurrence, and on p4 eruption and consecutive stages of basal cavity closure. The defined age groups do not represent equal long segments of the potential life span. However, we discuss to what extent these individual age groups can be linked to ages in years of extant beavers considering the following difficulties:

First, the cement-layer counting could not be applied here, since it would cause considerable interventions on rare, completely preserved fossil premolars of mainly elder individuals.

Second, the dental criteria, introduced by van Nostrand and Stephenson (1964), are based on individuals of *C. canadensis*. It is not yet clear, if these data may also be applied with certainty to *C. fiber*.

Third, deviations from the normal temporal presence of the dp4 and p4 in the oral cavity exist, as observed by Hinze (1950), however, in a vanishingly small number of beavers of the middle Elbe River in Central Germany.

- *Castor* Age group 0: The dp4 is small, brachyodont and with two roots; still in use. Suspected life year: The dp4 is said to usually erupt as early as at the age of about one month (Hinze 1950, Hatting 1969, Mayhew 1978a), and it is shed out with 8–10 months (Djoshkin and Safanow 1972) or 13–14 months (e.g., Stiefel and Piechocki 1986). According to van Nostrand and Stephenson (1964: 432, fig. 431), the dp4 is present in ca. 6–12 months old Canadian beavers. However, in the Eurasian beaver in very rare cases it can appear later and remain longer in the oral cavity. Hinze (1950: 73–74) reported from the middle Elbe River region (Central Germany) two 1¾ year old beavers with dp4 and dP4 and concluded that the premolar exchange is completed in most beavers during the first half of the 3rd year of life. Freye (1978) wrote that the premolar exchange starts in

C. fiber with 1½ years old beavers and is finished in 2½ years old individuals. These data are to be regarded as rare extreme exceptions. Therefore, here we tentatively assign the deciduous molar to age group 0, ranging from about 1 month to about 14 months.

- *Castor* Age group 1: Pulp cavity wide open; abrasion traces on the tooth crown missing or weakly developed.
- *Castor* Age group 2: Pulp cavity wide open, tooth crown worn. Suspected life year: The p4 erupts at the age of 5–7 months, but is still covered by the dp4 at this stage of life (e.g., Djoshkin and Safanow 1972). Other authors reported p4 usually comes into wear around the end of the first year of life or slightly later (e.g., Reichenau 1912, Piechocki and Stiefel 1977: 13–14 month; Mayhew 1978a: 10–12 months, 1979; Stiefel and Piechocki 1986: 9–11 months). The large basal cavity is still widely open. According to van Nostrand and Stephenson (1964: 432–433, fig. 431B), the p4 of *C. canadensis* is fully erupted at about 12 months. As with the dp4, the eruption of the p4 may be delayed in very rare exceptions. Hinze (1950: 73) noted from the middle Elbe River region a 1¾ year old beaver with un-erupted lower p4 as well as two allegedly 2¼ and 3 years old beavers with just faintly grinded lower premolars. Unfortunately, van Nostrand and Stephenson (1964: 432, fig. 431) did not figure any specimen of age groups 1 and 2 with a widely open, unrestricted basal cavity, enclosing the lower ends of the enamel loops. However, it is worth to note that the lower premolars of these age groups are clearly lesser advanced and thus somewhat younger than representatives of group 3, which are older than 1½ years (see below). Therefore, we tentatively assign premolars of group 1 and 2 to ca. 1–1½ year old individuals, of which the unworn specimens (age group 1) are slightly younger than the just worn ones (age group 2).
- *Castor* Age group 3: Pulp cavity open, filled with dentin beads, tooth crown worn. Suspected life year: A p4 of an 1½ to 2 year old Canadian beaver (van Nostrand and Stephenson 1964: 432, fig. 431B) is similar to specimens of our age group 3. As in the North American specimen, the large, non-constricted basal opening is filled with "beadlike" dentin deposits. Consequently, we tentatively add the specimens of age group 3 to ±1½–2 years old beavers.
- *Castor* Age group 4: Cavity clearly constricted, filled with dentin beads, tooth crown worn. Suspected life year: Specimens are more advanced and thus older than those of group 3, since they have a partially constricted basal cavity with enclosed "beadlike" dentin deposits. Therefore, we assign these lower premolars tentatively to ±2–2½ year old beavers.
- *Castor* Age group 5: Base of the tooth closed, except for slit- or pore-shaped residual openings, tooth crown worn. Suspected life year: According to van Nostrand and Stephenson (1964: 433–434, fig. 431C), in the Canadian beaver the basal opening of the p4 of this age group is typically closed, except for two openings. This condition is seen in some specimens from the Thuringian travertine sites recorded here in age group 5. In addition, there are lower premolars with two smaller openings, connected by a very narrow longitudinal slot. Other p4

have only one or two pore-like residual openings that are about to close the dental base completely, as known by even older individuals. The basal opening of the p4 (and that of the three molars) is usually completely closed over by 4 years in *C. fiber* (Mayhew 1979) and *C. canadensis* (van Nostrand and Stephenson 1964: 432). Therefore, the specimens of age group 5 are here tentatively assigned to about 2½–4 year old beavers. More precise age information could be achieved from completely preserved fossil specimens by basal cement-layer-counting or X-ray examinations.

- *Castor* Age group 6: Base of the tooth with roots, tooth crown deeply worn.
- *Castor* Age group 7: Base of the tooth crown with roots, tooth crown heavily worn. Suspected life year: Lower premolars, considered tentatively as being ca. 4 years old and older, are rooted and deeply worn (age group 6) or heavily worn (age group 7). In addition, important parts of the tooth crown are worn away. Exact age information could only be obtained by basal cement-layer counting or possibly also by X-ray examinations.

Demographic data of extant Castor

General knowledge of reproductive and demographic data of extant *C. fiber* is important for the interpretation of the fossil mortality profiles. Extant beavers live in families (colonies), including normally the monogamous parents, youngs of the current year (kits, < 12 months old), youngs of the previous year (yearlings, 12-months-old), two-years-olds and sometimes older young (subadults, > 24 months old) that have not been driven away from the territory where they were born (Baker and Hill 2003). Campbell-Palmer et al. (2016: 12) reported that "most 2-year-old will begin to search for territories of their own in the spring", but also this

dispersal may be delayed occasional (Mayer et al. 2017). On average, an extant beaver family in Central Europe consists of three to six animals (Schröpfer 2009).

The life expectancy of extant beavers is decisively influenced by factors as diet change from milk to vegetable food, infections of wounds, accidents by tree felling, harsh winters, drowning in floods due to snowmelt in spring, starvation, viral, bacterial, parasitic diseases and other violent and non-violent causes of death (Hinze 1950, Piechocki 1962, Djoshkin and Safanow 1972). The mean adult life expectancy of *C. fiber* in the wild was reported to be 12–14 years (Nolet et al. 1997, Campbell-Palmer et al. 2016). However, in particular the juvenile beavers in the first two years of life are affected by high mortality rates (Campbell-Palmer et al. 2016). In Central and Northern Germany (Lower Saxony, Saxony-Anhalt), the pup mortality in *C. fiber* was estimated up to 54 % or more in the first year (e.g., Stiefel and Piechocki 1986, MUNR 1999, NLWKN 2011). For Germany in general, the survival rate before reaching sexual maturity is about 2 % (Heidecke 1991, NLWKN 2011).

The density of beaver populations varies considerably in space and time, depending on habitat quality, climatic conditions, terrestrial behaviour, predators, diseases etc. (Campbell-Palmer et al. 2016). However, the average age structure seems to be rather constant. An overview of some extant populations from Eurasia (Tab. 1) reveals that juvenile (kits, yearlings) and adult beavers achieved almost exclusively the highest proportions in the examined extant beaver populations.

C. fiber reaches sexual maturity between 1¾ and 2 years, but it can be delayed beyond the age of 3 years (Campbell-Palmer et al. 2016). Busher (2016: 160) reported that "sexual maturity most often occurs in two years old beavers of both sexes". Schröpfer (2009) specifies that in Central Europe

Table 1. Age structure of some extant populations of the Eurasian beaver (*Castor fiber*) from Eastern Europe and the Far East (from Djoshkin and Safanow 1972, Safonov and Saveljev 1992, Campbell 2009).

Localities	< 1 year	1 year	2 years	≥ 3 years
Usman River, Russia	19.20 %	10.60 %	14.90 %	55.30 %
Usman River, Russia	28.00 %	18.00 %	8.00 %	46.00 %
Average	**23.60 %**	**14.30 %**	**11.45 %**	**50.65 %**
Voronezh River, Russia	30.70 %	17.50 %	12.80 %	39.00 %
Khopjor River, Russia	32.20 %	16.40 %	12.70 %	38.70 %
Khopjor River, Russia	35.00 %	19.80 %	10.20 %	35.00 %
Moksha River, Russia	30.30 %	17.00 %	12.30 %	40.40 %
Average	**32.10 %**	**17.70 %**	**12.00 %**	**38.20 %**
Kershenez River, Russia	37.20 %	18.60 %	9.30 %	34.70 %
Belaja Kholunica River, Russia	21.80 %	9.30 %	7.80 %	60.80 %
Average	**29.50 %**	**13.90 %**	**8.60 %**	**47.78 %**
Bjarehzina River, Belarus	28.00 %	11.70 %	19.50 %	40.80 %
Nemta/Amur River, Russia	37.00 %	16.90 %	8.90 %	37.20 %
Telemark, south Norway	13.00 %	12.00 %	16.00 %	59.00 %

male beavers become already sexually mature already with 1½ years, females with about 2½ to 3 years.

Because sex determination is not possible with cheek teeth, in the mortality profiles of our studied fossil samples sexually immature female beavers could be recorded also in age group 5, instead only up to group 4. However, in this case, the proportion prime adults would be even higher than calculated above.

Age groups of Trogontherium

Compare the following notes with Text-fig. 4. Age determinations of *Trogontherium* based on cheek teeth has been already presented by Schreuder (1929: pl. 7, figs 12 a–e, 14) who figured lower premolars from Tegelen in six successive stages of tooth development. Mohr (1954: 91, fig. 81 a–f) used these figures to define four age groups: very young (tooth base wide open, enamel folds visible), young (pulp cavity still open, but with restrictions), grown up (roots, nearly closed) and old (closed roots, tooth crown heavily worn). Unfortunately, this classification is hardly applicable, since it requires premolars with perfectly preserved tooth bases, which are usually rare in the fossil record.

Another age classification was applied to Mosbach 2 and Tegelen, based on occlusal patterns of different cheek teeth anchored in mandibles. Data were initially reported in the thesis of H. Mai (1977) and subsequently published by H. Mai (1979: Mosbach 2) and Guenther (1986: Tegelen). However, this method requires at least fairly large fragments of mandibles, which are not or only rarely available in our material.

Mayhew (1978b: 417, tab. 413) defined relative age groups based on "grinding surface pattern of the lower cheek teeth in relation to tooth crown height". Also, this method can hardly apply to our specimens, since most of them are incomplete teeth.

Here we present a relative age classification for *Trogontherium* (see also Text-fig. 4) modified from the above-mentioned approaches. A correlation of age groups with life years, as in extant beavers, is not possible yet.

- *Trogontherium* Age group 0: The dp4 is still in use.
- *Trogontherium* Age group 1: Cusps/ridges of the p4 crown are not or only very faintly worn.
- *Trogontherium* Age group 2: Tooth crown of p4 worn; chewing surface pattern still incomplete (e.g., confluence of meso- and hypoflexid that split off the chewing surface in anterior and posterior sections); with anterolingual flexid, if 5th striid present.
- *Trogontherium* Age group 3: Chewing surface of p4 with para-, meso-, meta-, hypoflexid and anterolingual flexid (if 5th striid present and worn).
- *Trogontherium* Age group 4: Chewing surface of p4 with meso-, meta- and hypoflexid or rarely with para-, meso- and hypoflexid, and one main fossettid (para- or metafossetid); with anterolingual flexid, if 5th striid present and worn.
- *Trogontherium* Age group 5: Chewing surface of p4 with two main enamel loops (meso- and hypoflexid) and two main enamel fossettids (para- and metafossetid); with anterolingual flexid, if 5th striid present and worn.

- *Trogontherium* Age group 6: Chewing surface of p4 with one main enamel loop (hypoflexid) and three main enamel fossettids (para-, meso- and metafossettids); with antero-lingual flexid, if 5th striid present and worn.
- *Trogontherium* Age group 7: Chewing surface of p4 with four main enamel fossettids (para-, meso-, meta- and hypofossettids); with antero-lingual flexid, if 5th striid present and worn.
- *Trogontherium* Age group 8: Chewing surface of p4 only with 4 (para-, meso-, meta- hypo-) fossettids and antero-lingual fossettid (if 5th striid is completely worn), only four main enamel fossettids, if 5th striid is lacking.

Still more deeply worn lower premolars were not available in the examined material from Tegelen, Mosbach 2 and Bilzingsleben II. H. Mai (1977: 7) reported from Mosbach 2 a heavily worn p4 with only two fossettids on the grinding surface, indicating that not all age groups of *Trogontherium* are represented in the here examined samples.

Results and discussion

Mortality profiles of the *Castor* samples

The high number of *C. fiber* lower premolars in Bilzingsleben II allowed it to analyse the samples from the border terrace and the alluvial fan separately. The two mortality profiles yielded similar unimodal frequency distributions with a maximum in age group 4 (about 43 %) (Tab. 2). However, the relatively high proportions of older individuals in the alluvial fan (age groups 5 and 6: ca. 44 %) exceed those from the border terrace (ca. 33 %; Tab. 2). Although the reasons for this are not clear, the remarkable similarity in the dominance of age group 4 justifies it to establish an overall mortality profile for *C. fiber* of Bilzingsleben II that can serve as a basis for discussions.

This age profile from Bilzingsleben II is broadly in line with those from Weimar-Ehringsdorf and Weimar-Taubach (Text-fig. 2, Tab. 2). Again, the peak of the frequency distribution is found in both samples in age group 4 with ca. 46 %, but the proportions of individuals of the remaining age groups are slightly different. Following our tentative calibration of the age groups, the mortality profiles of *C. fiber* from the three Thuringian sites are dominated with ca. 42 % to 46 % by suspected 2–2½ years old beavers.

The three profiles of *C. fiber* (Text-fig. 2) do not conform the well-known "U-shaped" basic mortality type that is referred to as "attritional" or "normal" mortality due to "normal or routine ecologically related (accidental) death of population members" (Lyman 1994: 118). They also differ from the "L-shaped" basic mortality type referred to as "catastrophic" or "mass" mortality pattern "including individuals" killed more or less instantaneously (Lyman 1994: 118).

We also created a ternary diagram following basically the method introduced by Stiner (1990) for large mammals and modified here for the assessment of the age distribution in *C. fiber*. Stiner's (1990: 309) approach is based on a three age groups model (juvenile, prime adult, old adult) and "marked by an elevated proportion of prime adults relative to juvenile and old individuals". Juveniles include here age groups 0–2 (up to ±1½ years), prime adults age groups 3–4 (between ±1½
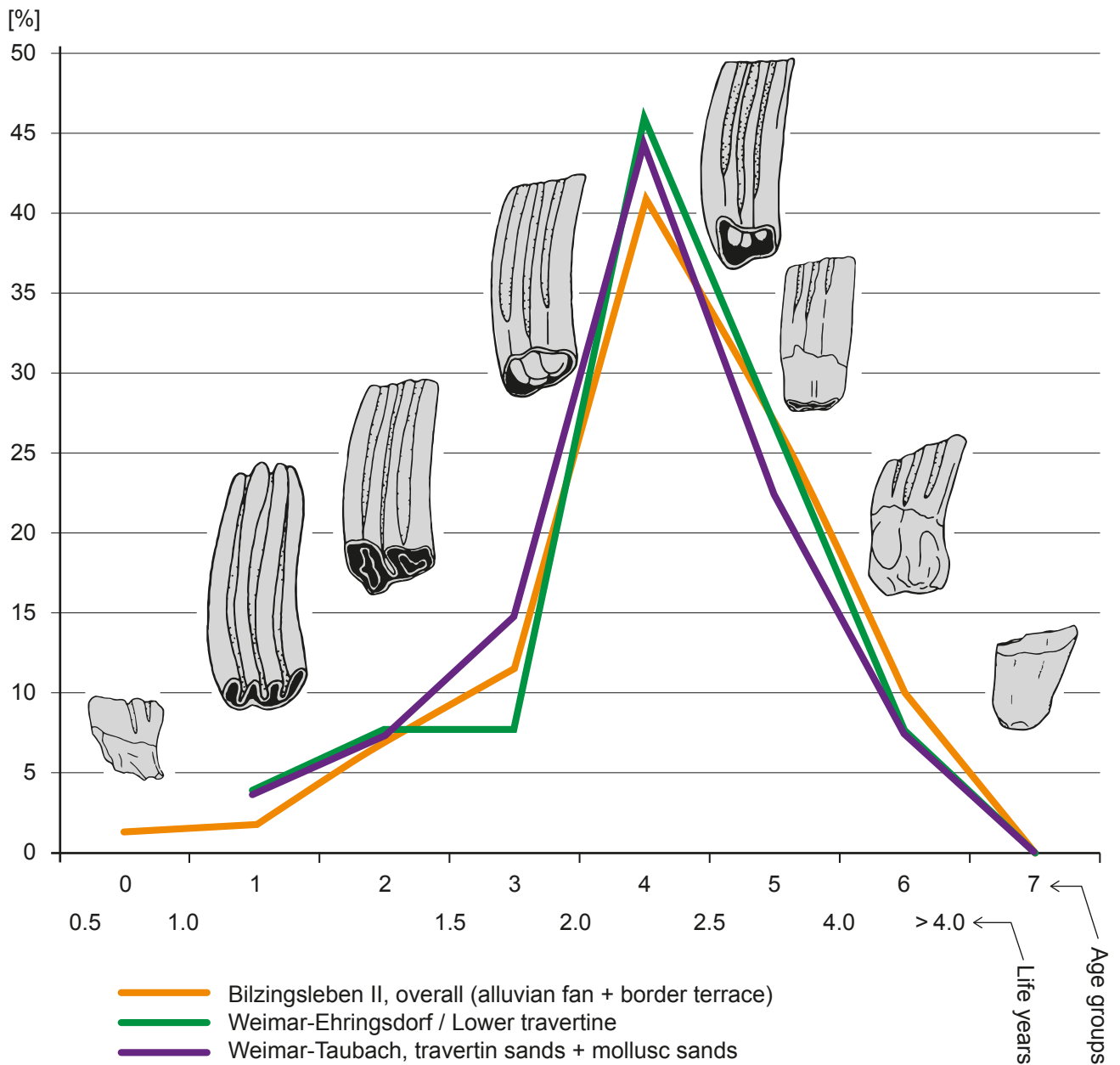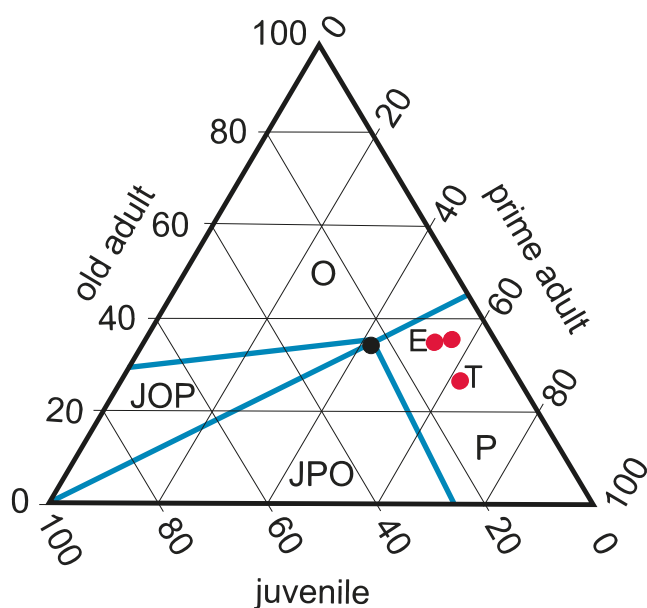
Text-fig. 2. Mortality profiles (relative abundance of age groups) of *Castor fiber* based on dp4 and p4 from the fossil sites of Bilzingsleben, Weimar-Ehringsdorf and Weimar-Taubach, supplemented by tentative correlations of age groups with beaver life years. Data from Table 2.

Table 2. Provenance and numbers of the studied lower premolars of *Castor fiber* and their assignment to age groups.

| Localities | n | Age groups | | | | | | | Σ |
	%	0	1	2	3	4	5	6	
Weimar-Taubach (Travertine Sands)	n	–	1	2	4	12	6	1	26
	%	–	3.85	7.69	15.38	46.15	23.08	3.85	100
Weimar-Ehringsdorf (Lower Travertine)	n	–	1	2	2	12	7	2	26
	%	–	3.85	7.69	7.69	46.15	26.93	7.69	100
Bilzingsleben II (Border terrace)	n	1	2	12	24	66	36	15	156
	%	0.64	1.28	7.69	15.38	42.31	23.08	9.62	100
Bilzingsleben II (Alluvial fan)	n	2	1	3	1	32	21	10	70
	%	2.86	1.43	4.29	1.43	45.71	30	14.29	100
Bilzingsleben II (Overall)	n	3	3	15	25	98	57	25	226
	%	1.33	1.33	6.64	11.06	43.36	25.22	11.06	100

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and 2½ years), and old adults age groups 5–7 (more than ±2½ years). However, the original method of ternary diagrams has received some methodological criticism in the past, like the unclear demarcation of L- and U-shaped zones, the use of individual age groups of different durations etc. Also, in our example we can see that a sharp separation between prime and old adults is not always possible, since it depends on the time of sexual maturity, which varies (see above). Therefore, it cannot be excluded that in age group 5 (normally containing old adults) also juvenile female beavers may have been recorded. In addition, sex determination in *C. fiber* is not possible on the basis of teeth. In order to overcome such uncertainties, Discamps and Costamagno (2015) evaluated

and modified the method of Stiner and introduced four zones (Juveniles-Old-Prime dominated zone, Juveniles-Prime-Old dominated zone, Old dominated zone, and Prime dominated zone) resulting in more robust interpretations of the relative abundance. These species-specific zones are delimited by lines leading from a reference point to the corners of the diagram triangle. In our case the reference point is the intersection of the percentage values of the three age groups of the extant sample of *C. fiber* from Campbell (2009) (Text-fig. 3, Tab. 3).

The result shows that all three fossil samples of *Castor* are located within the "Prime dominated zone". This is an argument that these samples have been influenced by human hunting activity. However, this diagram alone might not be decisive (Discamps and Costamagno 2015), but it is convincing in combination with other evidence.

The prime dominated mortality pattern was initially considered typically "of cervid, bovid and equid remains in some archaeological records", where Stiner (1990: 316) also noted that humans "appear to be the only agencies that regularly produce prime-biased mortality in prey, making this pattern more specific to cause than the other types of death patterns". It is also worthy to note that this mortality pattern has been associated "with selective ambush hunting" such as "hide and wait and/or short chase" (Stiner 1990: 317, 322). Thus, we imply the *C. fiber* samples reflect remnants of human hunting.

Already Kretzoi (1975, 1977) interpreted the beaver remains of Weimar-Ehringsdorf and Weimar-Taubach as hunting prey of man. This conclusion was supported by the fact that in both sites fossil hominin remains and artifact inventories prove the temporary presence of the Palaeolithic man in the former travertine landscapes. A direct human's use of these animals is indicated by cut marks on some lower jaws and postcranial skeletal remains of *C. fiber* from Weimar-Taubach (Bratlund 1999).

The interpretation of the beaver remains as hominin hunting prey was also applied to *C. fiber* of Bilzingsleben II, since no substantial differences were observed between the beaver mortality profiles of these three travertine sites (Heinrich 1991: 50, fig. 56). This interpretation is retained here because beavers were doubtless an attractive prey for Palaeolithic humans, not only in terms of food, but also of the recovery of fur. *Castor* and *Trogontherium* were the largest native rodents in Eurasia at that time. Extant Eurasian beavers can weigh up to 30 kg and more (e.g., Djoshkin and

Text-fig. 3 Ternary diagram of the relative abundance (in %) of juvenile, prime adult, and old adult specimens in samples of *Castor fiber* (data from Table 3). The red dots indicate the Pleistocene samples of Bilzingsleben II (B), Weimar-Ehringsdorf (E), and Weimar-Taubach (T), the black dot represents an extant population from Telemark in Norway (data from Campbell 2009). Abbreviations of zones (after Discamps and Costamagno 2015): JOP – Juveniles-Old-Prime dominated zone, JPO – Juveniles-Prime-Old dominated zone, O – Old dominated zone, P – Prime dominated zone. The diagram shows the position of all three fossil samples in the prime dominated zone.

Table 3. Tentative subdivision of fossil premolar samples from *Castor fiber* of Thuringia showing the proportions of juveniles, prime- and old-adults, supplemented by data of an extant beaver population from Norway (Campbell 2009).

Localities	n/%	Juvenile	Prime-adult	Old-adult	Σ
Weimar-Taubach (Travertine Sands)	n	3	16	7	26
	%	11.54	61.54	26.92	100
Weimar-Ehringsdorf (Lower Travertine)	n	3	14	9	26
	%	11.54	53.84	34.62	100
Bilzingsleben II (overall)	n	21	123	82	226
	%	9.3	54.42	36.28	100
Extant, Telemark (south Norway)	n	203	377	245	825
	%	24.6	45.7	29.7	100
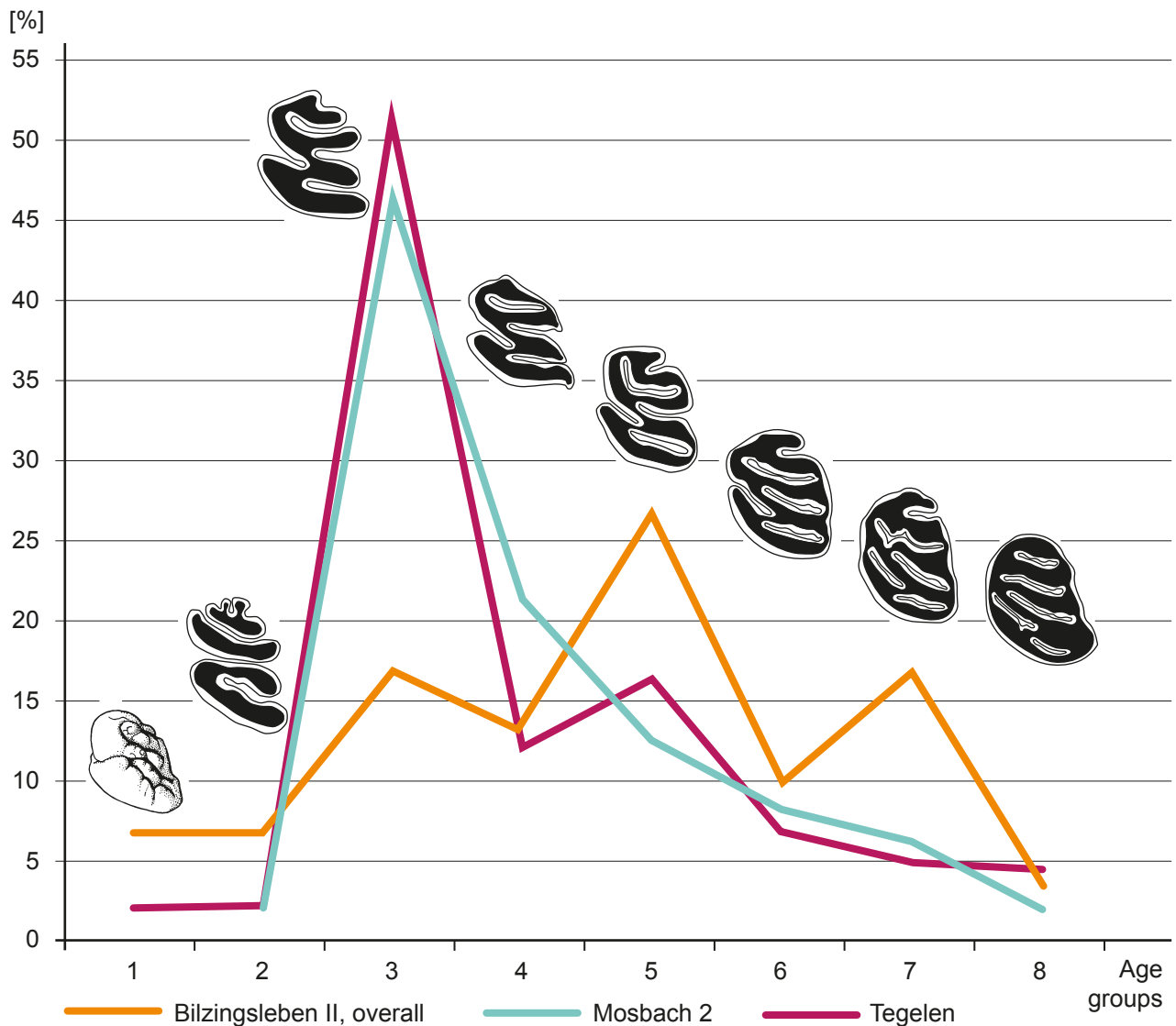
Text-fig. 4. Mortality profile (relative abundance of age groups) of *Trogontherium* based on dp4 and p4 from the fossil sites of Bilzingsleben II, Mosbach 2 and Tegelen. Data from Table 4.

Safanow 1972, Busher 2016), and the similarly large or even slightly larger *T. cuvieri* should have reached a similar or higher weight. In addition, it can be assumed that beavers were much easier to kill than larger mammals hunted by Palaeolithic humans at that time.

As noted above, human hunting is indicated by the mortality profiles of *C. fiber* that show similarities with the so-called "prime dominated mortality pattern" (sensu Stiner 1990). The dominance of the prime adults could therefore possibly be related to the natal dispersal of about two years old or a little older beaver, since the predator risk was likely higher for these animals, as there were no lodges or dens available in the search for new habitats, which could have offered them save shelter. Since parent beavers regularly

Table 4. Provenance and numbers of the studied lower premolars of *Trogontherium cuvieri* and *T. boisvilletti* and their assignment to age groups.

Taxon	Localities	n	Age groups								Σ
		%	1	2	3	4	5	6	7	8	
T. cuvieri	Bilzingsleben II (overall)	n	2	3	4	4	9	2	4	1	29
		%	6.9	10.34	13.79	13.79	31.03	6.9	13.79	3.45	100
	Mosbach 2	n	–	1	22	9	8	5	4	5	54
		%	–	1.85	40.74	16.67	14.81	9.26	7.41	9.26	100
T. boisvilletti	Tegelen	n	1	3	24	9	8	4	6	–	55
		%	1.82	5.45	43.64	16.36	14.55	7.27	10.91	–	100

chase away their approximately two years old youngs in spring, the very high proportion of suspected 1½–2½ years old individuals (age groups 3 and 4) presumably resulted from hominin-generated serial predation, "which refers to regular and habitual killing of prey animals in the same loci, which are favoured by predators because of … localized abundance of prey" (Haynes 1988: 219). The relatively high proportion of adult animals from age groups 5 and 6 may also be due to behavioural patterns, as adult beavers stay for foraging and tree felling longer on land than juveniles, and were, therefore, an easier and more frequent target of hunt.

Mortality profiles of the *Trogontherium* samples

Remains of *Trogontherium* are much less numerous than those of *Castor* in Bilzingsleben II. A reason could be that at that time animals of the first genus were rarer in the fauna than those of the second one, but this remains speculative and cannot be proven with certainty. It would also be conceivable that *Trogontherium* was more difficult to capture because it lived more hidden and was much more agile on land than *Castor* due to its better cursorial properties (Fostowicz-Frelik 2008).

Also, the assessment of the mortality profiles of *Trogontherium* is trickier, as the genus became already extinct in Europe during the Middle Pleistocene, whereas *Castor* is still widespread in the Northern Hemisphere. Habit and life style of *Trogontherium* are therefore to be reconstructed with dental and skeletal features, whereby the associated faunas and floras, the sedimentary context, etc. provided further useful data. Habit reconstructions are given, for instance, by Schreuder (1951: 416, fig. 414) for *T. boisvilletti* and more recently by Fostowicz-Frelik (2008: 775, fig. 777) for *T. cuvieri*.

Because of the small number of *Trogontherium* finds in Bilzingsleben II only an overall mortality profile of all p4 from the find horizon could be established (Text-fig. 4). The proportion of younger individuals of the age groups 1 to 4 is approximately 45 %, while older individuals of the age groups 5 to 8 are represented more frequently with ca. 55 % (Tab. 4). Striking differences exist to the mortality profiles from fluviatile deposits of Mosbach 2 and Tegelen. Here, younger individuals of the age group 1–4 dominate the samples (Mosbach 2: ca. 59 %, Tegelen: ca. 67 %), while the proportions of older animals (age groups 5–8) are only around 41 % (Mosbach 2) and ca. 33 % (Tegelen) (Text-fig. 4).

In any case, it is important to note that the relative frequencies in the non-hominin bearing sites Tegelen and Mosbach 2 are rather similar to each other, in contrast to Bilzingsleben II. Even if no statements can be made about the taphonomic biases in Tegelen and Mosbach 2, it seems obvious to relate the differences in mortality profiles to Bilzingsleben II to the presence or absence of hunting people.

Implications for the site formation of Bilzingsleben II

The results of the present study as well as additional taphonomic observations on the remains of *Castor* and *Trogontherium*, casts doubt the validity of the mass flow hypothesis for the fossil site of Bilzingsleben II (Müller

and Pasda 2011, Pasda 2012), according to which various sediments of different origin were mixed with components of former land surfaces.

A first objection is the fossil distribution. An earlier mapping had revealed that remains of both *T. cuvieri* and *C. fiber* display two striking concentrations located on the border terrace and in the alluvial fan of Bilzingsleben II (Heinrich 1997b: 129, fig. 3). Their positions coincide with excavation areas interpreted as anthropogenic activity zones (Mania 1991, Mania and Mania 2002, Mania and Altermann 2017). These accumulations contain, along with other finds, synchronous-autochthonous and synchronous-allochthonous components that come from animals captured inside and outside of the camp site area, but whose skeletal remains were embedded there together. The remains of *Trogontherium* are likely only synchronous-allochthon, as this beaver probably lived outside the site area (see above). After embedding, the skeletal remains of both components were only slightly re-deposited by post-depositional taphonomic processes, such as smaller waters running through the alluvial fan or the final flooding of the Palaeolithic find horizon.

Secondly, it should be noted that there are no significant differences in the preservation of the beaver remains of Bilzingsleben II, neither between *Castor* and *Trogontherium*, nor between the finds from the border terrace and the alluvial fan. If the mass flow hypothesis (Beck et al. 2007, Pasda 2009, 2012, Müller and Pasda 2011) would be really true, significant differences in colouring and preservation of the skeletal elements would have to be expected, which is however, not the case.

The main objections to doubt the mass flow hypothesis, however, come from the almost identical mortality profiles of *C. fiber*, established for the three Thuringian travertine sites. It is completely out of the question that mass flow of fossil-bearing deposits is capable to produce accidentally a beaver mortality profile like that of Bilzingsleben II, which is identical to those from the *Castor*-bearing deposits of Weimar-Ehringsdorf (LT) and Weimar-Taubach (travertine sands) with absolutely no evidence of turbulent gravitational mass flow. It is highly unlikely that the original age structure of any mortality profiles would survive mass flow and re-deposition without substantial changes.

With analogue arguments, we doubt the inundation hypothesis of Steguweit (2003). The not-human induced samples of *Trogontherium* from the fluvial deposits of Tegelen and Mosbach 2 show mortality profiles with an overrepresentation of juvenile individuals. If the find horizon of Bilzingsleben II was a fluviatile deposit, such a predominance of juveniles would be expected also there. However, this is not the case. This also corresponds well with observations on the molars of *Elephas antiquus* from Bilzingsleben II, which show no sanding marks due to rolling in flowing waters (Guenther 1991: 149).

Conclusions

In order to provide new arguments to the controversial discussion about the site formation of the renowned locality Bilzingsleben we produced mortality profiles of death assemblages of beavers based on lower premolars

(dp4, p4). The Middle Pleistocene *Castor* remains from Bilzingsleben II and Weimar-Ehringsdorf as well as the Late Pleistocene beaver fossils from Weimar-Taubach yielded almost identical, unimodal age frequency histograms. This indicates similar taphonomic filters that were effective in the site formation of these Thuringian localities. Their mortality profiles are characterised by an overrepresentation of supposed ±2–2½ year old beavers indicating these beaver accumulations are most likely cumulative products of hominin prey age selection. Eventually, the mortality profile of *Trogontherium* of Bilzingsleben II showing high proportions of adult individuals differs substantially from those of the non-hominin generated assemblages of Tegelen and Mosbach 2 that are marked by high proportions of juvenile individuals. This difference is probably also due to hominin habitual killing of prey animals in Bilzingsleben II. Since there are no indications of turbulent gravitational mass flows or inundations in the beaver-bearing deposits of Weimar-Ehringsdorf and Weimar-Taubach, and considering the identity of the mortality profiles of *Castor*, mass flow and inundation cannot be used to explain the site formation of Bilzingsleben II.

In summary, it can be therefore said that mortality profiles of beavers provide valuable independent criteria for the evaluation of the site formation. The structure of these mortality profiles reveals that the Palaeolithic hunters focused on prime-aged animals, captured probably at the natal dispersal of about two-year-old beavers. If that is indeed the case, the beaver remains are most likely results of serial hominin prey age selection.

However, many questions remain open for future research. Steele (2003) summarises the general limitations of studying age distribution in fossil assemblages as follows: the difficulty of estimating the age at death of individuals, pre- and post-depositional biases, and the reconstruction of the age structure and behaviour of prey animals. Only some of these aspects could be clarified by the present study, as not all methodological approaches could be used. For example, data of basal cement-layer counting, which probably provide more accurate age information, were not available. Furthermore, the interaction of Pleistocene beavers, which might have an influence on our data, still raises numerous questions. A verification of the present results requires further examinations of samples from other Pleistocene hominin and non-hominin generated sites as well as from extant beaver populations, using non-invasive methods for individual age determinations. In addition, it should be examined to what extent other beaver cheek teeth such as the upper P4 and M3 and the lower m3 can be used for such investigations.

Acknowledgements

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