

Predation on *Allactaga major* (Teufelslucke, Lower Austria, Upper Pleistocene): carnivores or birds of prey

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Abstract

The first documented excavation of the Fuchsenlucke, also known as Teufelslucke (located in Lower Austria, Austria, northeast of Eggenburg, 314 m above sea level), started in 1890. During these years several excavations have been conducted uncovering a variety of fossil bones of different Upper Pleistocene age species. Cave bears, cave lions, and hyenas are among the findings of bigger vertebrates as well as their prey. Additionally, birds and other small mammals have been found. A stratigraphic classification, however, proved to be more difficult. In this article the mostly fragmented but only findings (postcranial elements) of *Allactaga major* (KERR, 1792), syn. *Allactaga jaculus* (PALLAS, 1779), will be analysed and discussed as leftovers from specific predators found on-site (*Bubo bubo* and *Vulpes vulpes*). The focus lies on recent information on *Allactaga major* combined with the assumption that most fossil findings of *Allactaga* are prey leftovers.

Zusammenfassung

Die ersten nachweislichen Grabungen der „Fuchsenlucken“, auch als Teufelslucken bekannt (Lage: Niederösterreich, Österreich, nordöstlich von Eggenburg, 314 m über dem Meeresspiegel), begannen um 1890. Im Laufe der Jahre brachten diese eine Vielzahl an Knochen diverser Tiere oberpleistozänen Alters hervor. Unter den Großsäugern befinden sich unter anderem Höhlenbären, Höhlenlöwen und die Hyänen sowie deren Beutetiere. Es wurden auch Kleinsäuger und Vögel entdeckt, jedoch gestaltet sich eine stratigraphische Klassifizierung dieser schwieriger. In diesem Artikel werden die hauptsächlich fragmentierten und einzigen Funde (postcraniale Elemente) von *Allactaga major* (KERR, 1792), syn. *Allactaga jaculus* (PALLAS, 1779), als Speisereste von spezifischen Prädatoren (*Bubo bubo* und *Vulpes vulpes*) analysiert und diskutiert. Der Fokus liegt auf rezenten Informationen von *Allactaga major* kombiniert mit der Annahme, dass die meisten fossilen Funde von *Allactaga* Speisereste sind.

Key words: *Allactaga*, Dipodidae, Upper Pleistocene, Teufelslucke

1. Introduction

The Teufels- or Fuchsenlucke in Lower Austria is placed at the northern side of the Koenigsberg near Roggendorf in Lower Austria. The cave has been known since 1890. It is famous for its cave hyena remains as well as for its huge variety in different taxa (ADAM et al., 1966, DÖPPES & RABEDER, 1997). Naturally the question occurred whether or not all these findings are of the same age since ADAM et al. (1966) already distinguished three different layers. Radiocarbon-dating was executed on cave hyena remains during the ancient DNA investigation of these animals and yielded an age around 38.060 +900/-810 years BP (VERA 2536) (ROHLAND et al., 2005); similar results gave the dating of the cave lion. Micromammals on the contrary were never tried and only judged on their evolutionary level between 13.000 to 10.000 years BP (DÖPPES & RABEDER, 1997).

Today, specimens from the genus *Allactaga* are mainly distributed in Asia and Eastern Europe (China, Mongolia, Pakistan, Afghanistan, Armenia, Azerbaijan, Georgia, Kazakhstan, Uzbekistan, Turkmenistan, Tajikistan, Syria, Iraq, Iran, Jordan, Saudi Arabia, Russia, Ukraine) (DON & REEDER, 2005). *Allactaga major*, the great Jerboa, is a typical inhabitant of steppes and fossil findings show temporary immigrations into Europe, one of them in the Late Glacial (VAUTHEY et al., 1973, JANOSSY, 1961). Therefore, a steppe layer was defined for a Late Glacial period in the Teufelslucke (DÖPPES & RABEDER, 1997). Since *Allactaga* is bound to very specific climatic conditions and habitat characteristics (dry steppes, low vegetation), the species was presumed to reach only western and central parts of Europe for short periods of the younger ice age (KAHLKE, 1981). Radiocarbon datings are still missing to confirm this.

1.2. Material and Method

Allactaga major from the Teufelslucke is known by the following elements: a total number of 6 pelvic fragments, 7 right (3 juvenile, 4 fragments) and 11 left femora (3 complete, 8 fragments), 8 tibiae (2 complete, 6 fragments), 6 metapodia (4 complete, 2 fragments), 5 phalanges (partially fragmented). The materials are housed today in the Krahuletz-Museum (Eggenburg) and the Höbarth Museum (Horn), both in Lower Austria.

Micromammal assemblages are nowadays evaluated in archaeological excavations to analyse the paleoenvironment. In areas where Dipodidae are common, like Asia Minor, the general assumption is that they result from owl pellets (HASHEMI, 2006, CUPERE et al., 2009, TAL et al. 2018). Taphonomic processes without animal activities are also evaluated. The bones were judged by their bones surface modification, styles of limb bone breakage (ANDREWS & COOK, 1990, SCHIPMAN et al., 1981) and acid damage (TAL et al., 2018, CUPERE et al., 2009, WEISSBROD et al., 2005).

2. Results and comparison

There is a complete lack of cranial elements of *Allactaga* from the Teufelslucke as only postcranial bones were recovered during the excavations.

As a result, the adscription to *Allactaga* spp. happened solely according to the morphology of the larger postcranial elements and can be considered as *Allactaga major*. With the exception of one humerus fragment, the findings are strictly comprised of hind limb elements: femora with additional tibiae, metapodia and pelvic fragments. Judging from the size, some of them probably belonged together.

The pelvic remains were often fractured with stepped or even sawtoothed marks. Femora are mostly represented by the proximal part, four are complete and three more belong to juveniles, the distal epiphysis missing. Six tibiae are fractured at an obtuse angle, the other two are not broken. All remains show very few bone flaking and pittings. No gnawing or bite marks could be observed as well as no acid/digestive damage. In general, the bone surface is very well preserved (Fig. 1). Hence, reptilians like snakes and bigger lizards are ruled out as possible predators because they have strong acid-digestive juices affecting surfaces of bones and teeth (CZAPLEWSKI, 2011, FISHER, 1981). Therefore, animals leaving little to no digestive traces were closely considered.



Fig. 1: Fossil *Allactaga major* leftovers from Teufelslucke cave, Austria. a1: femora sin., a2: femora dex., b: metapodials, c: tibiae, d: humerus fragment.

a) Carnivores. Terrestrial carnivores such as the fox (*Vulpes vulpes*) or various mustelids were found in the Teufelslucke. These carnivores crush the bones significantly and leave typical bite marks

(ANDREWS & COOK, 1990, WETTSTEIN-WESTERSHEIMB, 1966). Fossil findings from *Allactaga major* from the Villa Seckendorff, Stuttgart, show these conical impressions most likely from small predators such as the red fox (KOENIGSWALD, 1985). Jerboa remains from the Teufelslucke, however, have no bite marks whatsoever and can therefore be ruled out (Fig. 2).

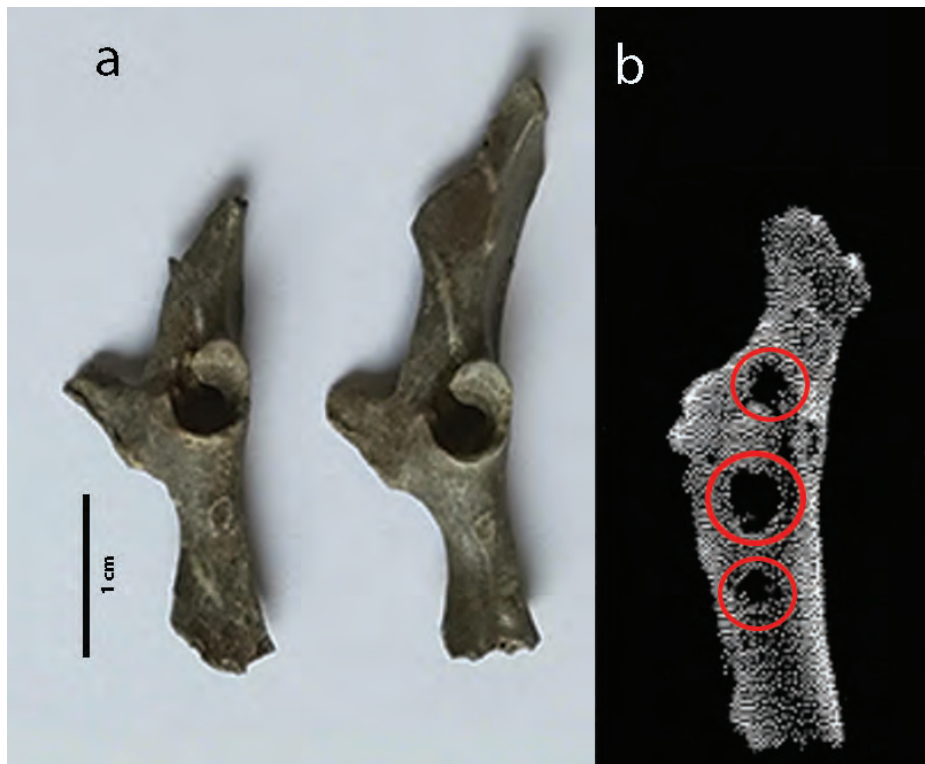


Fig. 2: a) Pelvic fragments without any bite mark traces from Teufelslucke cave. b) Fossil *Allactaga major* pelvic fragments from Villa Seckendorff with conical teeth impressions (KOENIGSWALD, 1985).

b) Diurnal birds. These do not swallow their prey as a whole but work their way from the head to the bottom, often leaving parts when not hungry enough or if parts are of no nutritional value (ANDREWS & COOK, 1990). If bones are eaten, then the articulations surface is often completely dissolved depending on the species (BOCHENSKI et al., 1998, GENG et al., 2009, CUPERE et al., 2009, TAL et al., 2018). In the Teufelslucke, *Aquila heliaca* (eastern imperial eagle), *Buteo buteo* (common buzzard) and *Falco tinnunculus* (common kestrel) are documented. Kestrels specialize on small prey ranging from 20g to 40g (GENG et al., 2009) and *Allactaga major* is well out of reach with an adult weight of 300g to 350g (TSYTSULINA et al., 2016). Buzzards seem to favour voles and lagomorphs but in case of low mammalian prey, they concentrate on birds and reptiles (SELAS, 2001). In any case, they prefer diurnal prey, while *Allactaga* is crepuscular to nocturnal. The imperial eagle has a wide variety of prey, just like the buzzards, and in Europe they are known to hunt ground squirrels, hamsters, lagomorphs but also birds and reptiles. The fragmentation and digestive traces they produce is much

higher than in the eagle owl (BOCHENSKI et al., 1998). Therefore, it seems reasonable to rule out the eagle as a possible predator of *Allactaga*.

c) **Eagle owl (*Bubo bubo*)**. In connection with *Allactaga*, birds of prey such as owls and more specifically the eagle owl (*Bubo bubo* (LINNAEUS, 1758)) are potential predators and were also described to be found in the same layers (WETTSTEIN-WESTERSHEIMB, 1966).

Bubo bubo inhabits mountainous areas with rocky ground but also occurs in open lowlands often close to rivers and lakes where it nests in trees. Both cover and perches overlooking wide areas are important for this species. Closed forests often appear to be less nutritious with respect to micromammals and as a result the eagle owl today prefers border areas of forested areas and open areas (PIECHOCK, 1985). Especially small to medium-sized mammal species dominate the diet of *Bubo bubo* (in West-Mongolia), including Cricetidae, Dipodidae and Arvicolidae (HOFFMANN, 1988).

The fossil bones from *Allactaga major*, however, show no traces of any digestive juices (Fig. 3).

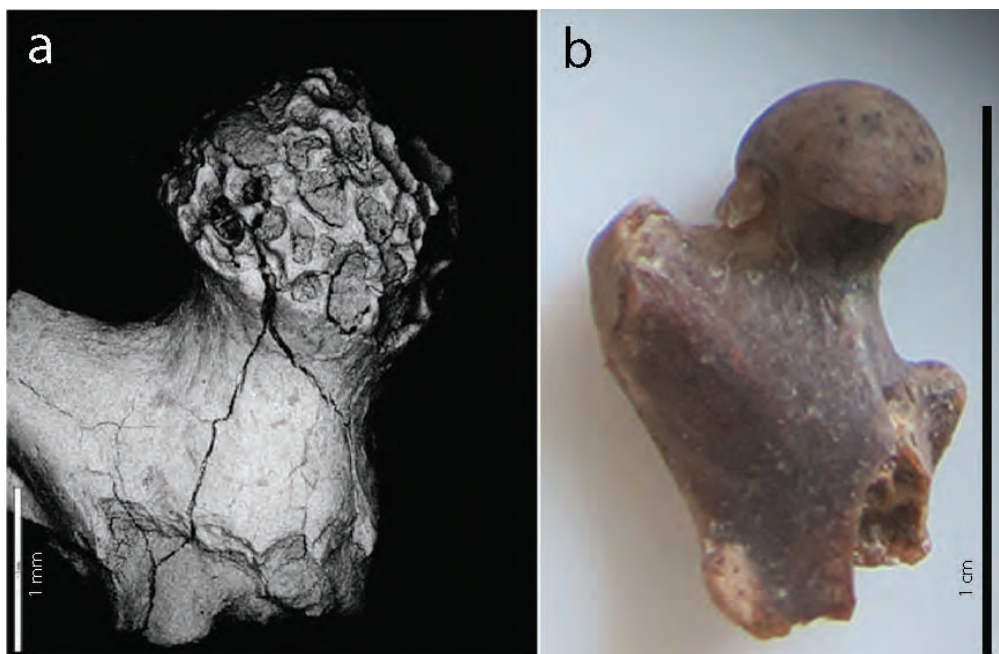


Fig. 3: a) Femur head from the Niche assemblage with acid digestion marks from ed-Wal Terrace (WEISSBROD et al., 2005). b) Femur head without any digestion marks from *Allactaga major* from Teufelslucke cave.

The lack of these missing structures and the actually good preservation of the fragmented bones could be an indicator for an eagle owl as they typically leave little chemical or physical damage to prey bones in comparison to other birds of prey (CZAPLEWSKI, 2011, GLUE, 1970). Larger prey is often torn apart by *Bubo bubo* (BEZZEL & OBST, 1976, HOFFMAN, 1988) and similar to large diurnal birds, they tear off elements of no nutritious value and discard them. This might be the reason for most findings being limb bones.

Fossil findings of *Bubo bubo* bones from the Teufelslucke reinforce this idea as both eagle owl and great jerboa remains were found in the same site (ADAM et al., 1966)

Bubo bubo has an enormous diversity in its diet, unlike other owls that hunt for specific animals (PIECHOCKI & MÄRZ, 1985). Leftovers from *Allactaga* are underrepresented in pellets from eagle owls in Mongolia even though this area is the species' main distribution site (KOENIGSWALD, 1985), which would explain the very few *Allactaga* remains in the Teufelslucke compared to other rodents.

3. Conclusion

Only the hind limb bones of *Allactaga major* were recovered in the Teufelslucke and they consist primarily of femora suggesting a selected accumulation by a predator. As findings show neither digestive nor bite marks many predators can be excluded. Judging from the bone damage only *Bubo bubo* comes into question as possible predator. This includes the possibility that prey was torn apart while eating and the bones were not digested at all.

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5. References

- ADAM, K. D., BERG, F., EHRENBURG, K., LEHMANN, U., SOERGEL, E., THENIUD, E., WETTSTEIN-WESTERSHEIMB, O. & ZAPFE, H. (1966). Die Teufels- oder Fuchsenlucken bei Eggenburg (NÖ.) Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Denkschriften, **112**. Band. Wien: Springer Verlag.
- ANDREWS, P. & COOK, J. (1990). Owls, caves and fossils: predation, preservation and accumulation of small mammal bones in caves, with analysis of the Pleistocene cave faunas from Westbury-di Mendip, Somerset, UK. University Chicago Press.
- BEZZEL, E. & OBST, J. (1976). Zur Ernährung und Nahrungswahl des Uhus (*Bubo bubo*). Journal für Ornithologie **117**: 210-238.

- BOCHENSKI, Z., HUHTALA, K., JUSSILA, P., PULLIAINEN, E., TORNBERG, R. & TUNKKARI, P. (1998). Damage to Bird Bones in Pellets of Gyrfalcon *Falco rusticolus*. *Journal of Archaeological Science* **25**: 425-433.
- CUPERE D., B., THYS, S., NEER V., W., ERVYNCK, A., CORREMANS, M. & WAELEKENS, M. (2009). Eagle Owl (*Bubo bubo*) Pellets from Roman Sagalassos (SW Turkey): Distinguishing the Prey Remains from Nest and Roost Sites. *International Journal of Osteoarchaeology* **19**: 1-22.
- CZAPLEWSKI, N. J. (2011). An owl-pellet accumulation of small Pliocene vertebrates from the Verde Formation, Arizona, USA. *Palaeontologia Electronica* Vol. **14**, Issue 3: 33.
palaeo-electronica.org/2011_3/4_czaplewski/index.html .
- DON, E. W., & REEDER, M. (2005). *Mammal Species of the World. A Taxonomic and Geographic Reference*. Baltimore: The Johns Hopkins University Press.
- DÖPPES, D., & RABEDER, G. (1997). Pliozäne und pleistozäne Faunen Österreichs. *Mitteilungen der Kommission für Quartärforschung der österreichischen Akademie der Wissenschaften, Band 10*. Wien: ÖAW.
- FISHER, D. (1981). Crocodylian scatology, microvertebrate concentrations, and enamelless teeth. *Paleobiology* **7**: 262-275.
- GENG, R., ZHANG, X., OU, W., SUN, H., LEI, F., GAO, W. & WANG, H. (2009). Diet and prey consumption of breeding Common Kestrel (*Falco tinnunculus*) in Northeast China. *ScienceDirect* **19**: 1501-1507.
- GLUE, D. (1970). Avian predator pellet analysis and the mammalogist. *Mammal Review* **1**.
- HASHEMI, N., DARVISH, J., MASHKOUR, M. & BIGLARI, F. (2006). Rodents and Lagomorphs remains from late Pleistocene and early Holocene Caves and Rochshelter sites in the Zagros region, Iran. *Iranian Journal of Animal Biosystematics* **1**: 25-33.
- HOFFMAN, R. (1988). The contribution of raptorial birds to patterning in small mammal assemblages. *Paleobiology* **14**: 81-90.
- JANOSSY, D. (1961). Die Entwicklung der Kleinsäugerfauna Europas im Pleistozän (Insectivora, Rodentia, Lagomorpha). *Zeitschrift für Säugetierkunde* **26**: 1-11.
- KAHLKE, H. (1981). *Das Eiszeitalter*. Leipzig/Jena/Berlin: Urania-Verlag.
- KOENIGSWALD, W. v. (1985). Die Kleinsäuger aus der Allactaga-Fauna von der Villa Seckendorff in Stuttgart-Bad Cannstatt aus dem frühen letzten Glazial. *Stuttgarter Beiträge zur Naturkunde. Serie B (Geologie und Paläontologie)*. **110**: 1-40.
- PIECHOCKI, R. & MÄRZ, R. (1985). *Der Uhu*. Wittenberg Lutherstadt: Ziemsen Verlag.
- ROHLAND, N., POLLACK, J. L., NAGEL, D., BEAUVAL, C., AIRVAUX, J., PÄÄBO, S. & HOFREITER, M. (2005). The Population History of Extant and Extinct Hyenas. *Molecular Biology and Evolution* **22**(12): 2435-43.
- SELAS, V. (2001). Predation on reptiles and birds by the common buzzard, *Buteo buteo*, in relation to changes in its main prey, voles. *Canadian Journal of Zoology* **79** (11): 2086-2093.
- SHIPMANN, P., BOSLER, W. & DAVIS, K.L. (1981). Butchering of Giant Geladas at an Acheulian site. *Current Anthropology* **22**(3): 1-10.

- TAL, F., WEISSBROD, L., TEPPER, Y. & BAR-OZ, G. (2018). A glimpse of an ancient agricultural ecosystem based on remains of micromammals in the Byzantine Negev Desert. *R. Soc. open sci.* **5**: 171528.
- TSYTSULINA, K., FORMOZOV, N., ZAGORODNYUK, I. & SHEFTEL, B. (2016). *Allactaga major*. The IUCN Red List of Threatened Species 2016: e.T857A115052919. retrieved 29.07.2019
- VAUTHEY, M., VAUTHEY, P., & CHALINE, J. (1973). Le Quaternaire - L'Histoire humaine dans son environnement. *Revue archéologique du Centre de la France*, tome **12**, fascicule 3-4: 323-324.
- WEISSBROD, L., DAYAN, T., KAUFMAN & D. WEINSTEIN-EVRON, M. (2005). *Journal of Archaeological Science* **32**: 1-17.
- WETTSTEIN-WESTERSHEIMB, O. (1966). Kleinere Wirbeltiere. In: K. D. ADAM, F. BERG, K. EHRENBERG et al. *Die Teufels- oder Fuchsenlucken bei Eggenburg (NÖ.)*. Wien. Springer-Verlag: 89-92.

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