The Miocene carnivore fauna of Schönweg-"Brüchl" (Austria, Carinthia): III. Tooth replacement in a basal hyaena

Die miozäne Raubtierfauna von Schönweg-„Brüchl" (Österreich, Kärnten): III. Zahnwechsel bei einem basalen Hyänenartigen

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Abstract

A fragmentary mandible of the basal hyena cf. *Protictitherium* sp. from the Miocene of the Schönweg-"Brüchl" locality (Lavanttal, district Wolfsberg, Carinthia) still shows three milk teeth and the second molar in the process of eruption. Using modern X-ray computer tomography methods, the adult premolars p4, p3, p2, canine and probably i3-i2 can be then studied. The dental eruption sequence might be similar to that of *Genetta genetta* and other viverrids. If confirmed by new finds, the occurrence of the genus *Protictitherium* at Schönweg-"Brüchl" would be the first in Austria, but also one of the oldest in Europe.

Keywords

Schönweg-„Brüchl", Miocene, Badenian, Mammalia, Carnivora, Hyaenidae, cf. *Protictitherium* sp.

Zusammenfassung

Ein fragmentarischer Unterkiefer des basalen hyänenartigen cf. *Protictitherium* sp. aus dem Miozän der Fundstelle Schönweg-„Brüchl" (Lavanttal, Bezirk Wolfsberg, Kärnten) zeigt noch drei Milchzähne und den zweiten Backenzahn im Durchbruchsprozess. Mit Hilfe moderner Röntgen-Computertomografie-Methoden können die Prämolaren p4, p3, p2, der Eckzahn und wahrscheinlich i3-i2 untersucht werden. Die Abfolge des Zahndurchbruchs könnte der von *Genetta genetta* und anderen Viverriden ähneln. Wenn dies durch neue Funde bestätigt wird, wäre das Vorkommen der Gattung P*rotictitherium* in Schönweg-"Brüchl" das erste in Österreich und eines der ältesten in Europa.

Schlüsselwörter

Schönweg-„Brüchl", Miozän, Badenium, Mammalia, Carnivora, Hyaenidae, cf. *Protictitherium* sp.

Introduction

The study of vertebrate fossils from the Schönweg-"Brüchl" locality (Lavanttal, district Wolfsberg, Carinthia, 14°48'01"E/46°44'37"N; Early Badenian, ~approx. 16 million years) has revealed a relatively diverse carnivore fauna (Prieto et al. 2022a, b, Morales et al. 2022). Indeed, five species have been recognized, including the rare genus *Sivanasua* whose particular tooth structure indicates a diet that is rather plant-based. The specific diversity of vertebrates opens an exceptional window on the Miocene continental ecosystems of Carinthia (Prieto et al. 2016, 2019), however, the quality of the fossil finds is also remarkable. Thus, a fragmentary mandible assigned to a basal hyena (cf. *Protictitherium* sp.; Prieto et al. 2022b) shows three milk teeth and a molar in the process of eruption. Using modern X-ray computer tomography methods, it is now possible to observe the permanent teeth at a very early stage, while they are still in the bone.

	Length	Width
i1	-	-
i2	-	-
c	2.40	1.85
p1	4.15	1.8
p2	4.50	2.00
p3	6.20	2.90
m1	-	-
m2	3.85	3.00
dp2	3.20	1.20
dp3	4.60	1.70
dp4	6.00	2.70

Tab. 1: Measurements (mm) of cf. *Protictitherium* sp. from Schönweg-"Brüchl".

Messungen (mm) von cf. *Protictitherium* sp. aus Schönweg-„Brüchl".

Methods

A micro-3D X-ray computer tomograph (μ-CT) from the University of Freiburg (Switzerland) was used to study invisible structures of the tooth and bone morphology from the inside. The material was scanned with a resolution of 14-30 μm. The resulting series of radiographs was further processed in the specialised software Amira 6.0. to virtually separate the bones and teeth and reconstruct their individual structures. The generated 3D models were used as a template for this study. The measurements were taken either directly with a sliding gauge or on the basis of digital photos. Teeth still in the mandibles were measured with the Amira 6.0 programme. The tooth measurements are given in mm and provided in Table 1. The abbreviations are the same as those used in Prieto et al. (2022b)

Results and Discussion

Description of the specimen and taxonomy

The right hemimandible is damaged. It was originally broken into several pieces and has been glued back together. The ramus ascendens is completely missing as well as some parts of the bone, showing thus part of the p3. The mandibular symphysis reaches the middle of the dp2. On the other side of the mandible, the mental foramen is clearly visible under the dp2, at somewhat half the height of the bone. The fossil shows the erupted decidual dentition dp2-dp4. In addition the m2 is only partially encrypted in the mandible. The two alveoli for m1 can be seen in occlusal view, but, inside the corpus mandibular, the roots cavities are poorly defined. Similarly, mesially to the dp2 one alveolus is present for the lost dp1. The alveolus of the dc is also preserved. The most anterior part of the mandible is damaged.

The generated 3D model shows in the mandible different stages of development the adult premolars p4, p3, p2, canine and probably i3-i2.

The dp4 is a molariform tooth, with a sharp trigonid, a highly developed metaconid, the talonid is wide and basined, with an entoconid almost as tall as the metaconid. The tooth has a morphology very close to the dp4 of *Protictitherium* from Batallones site (Spain). The dp3 is a premolariform tooth, with a strong mesial cuspid, high and sharp main cusp and an enlarged postero-lingual area. The dp2 is a unicuspid tooth, with a low cusp slightly elongated distally.

The morphology of the incisors and the canine are still rudimentary. On the contrary, the three premolars (p2-p3), although still without roots, already have a well-shaped crown morphology. The three premolars have a high and relatively robust main cusp and the p2 has a small mesial cusp. The p3 is similar to the previous one, but additionally it has a well-developed distal basal cusp. The p4 differs from the previous ones due to the development and complexity of its distal part, in which there is a strong secondary cusp and a very well-developed disto-lingual widening. The mesial secondary cusp is also stronger than the other two premolars.

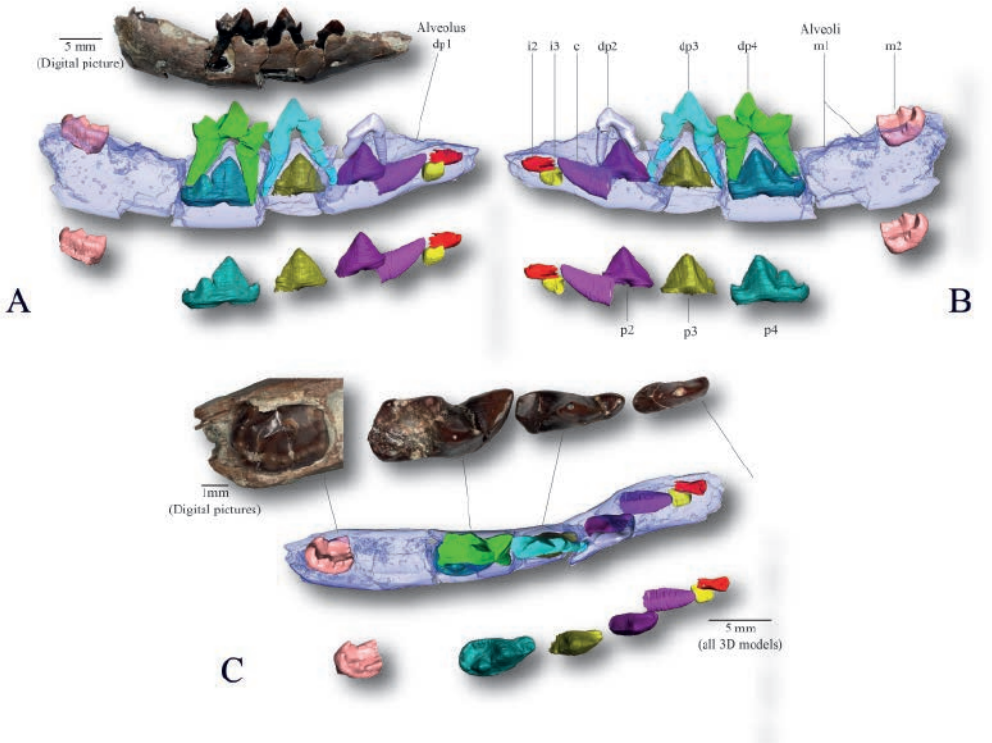

Fig. 1:
cf. *Protictitherium* sp. from Schönweg-"Brüchl". Generated 3D models and digital pictures of the right hemimandible. Three deciduous teeth (dp2-dp4) and the m^2 are directly observable. The X-ray computer tomography allows the reconstruction of the permanent teeth that are still in the bone (two incisors, a canine and three premolars). The first molar is missing. A. labial views. B. lingual views. C. Occlusal views.

Abb. 1: cf. *Protictitherium* sp. aus Schönweg-„Brüchl". Erstellte 3D-Modelle und digitale Bilder des rechten Hemimandibels. Drei Milchzähne (dp2-dp4) und der m^2 sind direkt zu sehen. Die Röntgen-Computertomographie ermöglicht die Rekonstruktion der permanenten Zähne, die sich noch im Knochen befinden (zwei Schneidezähne, ein Eckzahn und drei Prämolaren). Der erste Backenzahn fehlt. A. Labiale Ansichten. B. Linguale Ansichten. C. Okklusale Ansichten.

The only partially erupted definitive *in situ* tooth is a m2. It has a subrounded occlusal shape, with a wide central valley surrounded by cusps and clearly resembles the m2 of *Protictitherium*.

Overall, the morphology of the dentition shows a great proximity to *Protictitherium*, although additional material is necessary for a more precise determination. Other few isolated teeth from Schönweg-"Brüchl" have been assigned cf. *Protictitherium* sp. by Prieto et al. (2022b), but do not allow any precise conclusion either. This genus considered to be a basal hyaenid. *Protictitherium* appears as early as the end of the lower Miocene (MN 4) in Spain (Morales et al. 2015), France (Werdelin & Solounias 1996) and Germany (Sach 2014). Thus, the possible occurrence

of the genus at Schönweg-"Brüchl" would be the first in Austria, but also one of the oldest occurrences in Europe. *Protictitherium* is then an element of the European and Anatolian faunas during the middle and late Miocene, and can be as abundant as in the pseudokarst natural carnivore traps from Batallones in Spain (Fraile Gracia 2016).

Tooth replacement

Compared to the studies of fossil permanent teeth, little attention has been paid to the milk dentition of extinct mammals. However, studies have shown the importance of the knowledge of these fossils for the taxonomy and the understanding of evolutionary processes (e.g., Zack 2012, Bastl et al. 2014, Borths & Stevens 2017).

Based on the fossil from Schönweg-"Brüchl", the eruption sequence of the basal hyaenid cf. *Protictitherium* sp. can be interpreted as follow: the deciduous teeth are still functional while the two alveoli of the m1 are open (m1 may be -at least partially- out) and the m2 is in advanced stage of eruption. The dp1, here lost, is not replaced and probably arrives very early (Slaughter et al. 1974). Also probable is that the last tooth to erupt would be the canine, after the incisors and the permanent premolars. The dental eruption sequence, then ?dp1-m1-m2-p2-p3-p4, might be similar to that of *Genetta genetta* and other viverrids (Slaughter et al. 1974). The relative position of the premolars in the Austrian mandible - p2 higher than p3, higher than p4 - is in agreement with such a replacement. Indeed, the antero-posteriorly sequential replacement of the premolars is common in carnivores (Luo et al. 2004).

In modern hyenas the eruption sequence is different (m1-p2-p4-p3, and they lack the m2; Slaughter et al. 1974, Jimenez et al. 2019). Some Hyaeninae fossils also show a similar emergence of m1 and m2, like for instance the lectotype of *Hyaenictis graeca* from Pikermi (Greece, MN12; Koufos 2022: fig. 3b). In this specimen, the very small m2 is already erupted, and the m1 is on its way out. This is also shown on numerous other Hyaenidae (Baryshnikov & Averianov 1995). Jimenez et al. (2019) propose five ontogenetic stages based on tooth wear and dental replacement for *Crocuta crocuta* from the Pleistocene of NE Spain. It is worth mentioning that this model cannot be exactly applied to cf. *Protictitherium* sp. Indeed, in Schönweg-"Brüchl", the roots of the premolars are not/poorly developed, the same being true for the m2. This characteristic recalls the hemimandibles of juvenile individuals of stage 3 of Jimenez et al. (2019). At this stage, the m1 may have either just started to erupt or is not visible, but the alveoli are in an advanced state of opening. This is not clear for cf. *Protictitherium* sp. because the tooth is lost. In *C. crocuta* the cusps on the dp2 are unworn. This is not the case in the Austrian fossil where the main cusp is even more worn than in the other two deciduous teeth. The dp3 and dp4 are indeed slightly worn, the talonid of the dp4 showing the most advanced wear. In the strongly specialized dentition of the bone cracking spotted hyaena, the p3 plays a primordial role (e.g., Tseng & Binder 2010). In less specialized forms, the dp4 plays the role of a decidual carnassial and could be maintained in the mandible until the definitive m1 becomes functional (Slaughter et al. 1974).

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