Supernumerary teeth in a subadult rhino mandible (*Stephanorhinus hundsheimensis*) from the middle Pleistocene of Mosbach in Wiesbaden (Germany)

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with 6 figures and 3 tables

Dedicated to Prof. Dr. Kurt Heißig, Munich, in honor of his 65th birthday for his many contributions to the paleontology of the rhinos

Abstract: A well preserved subadult rhino mandible from Mosbach 2 can be attributed to *Stephanorhinus hundsheimensis* based on a metrical and morphological analysis. A comparison to tooth eruption of living *Diceros bicornis* suggests an individual age for the animal of about 7 years at death. The described mandible shows a significant tooth anomaly: two teeth occupy the p3 position on each side of the mandible. Comparisons with three younger juvenile *Stephanorhinus hundsheimensis* from Mosbach 2 show the sequence of tooth eruption for the species and allow us to determine that the anomalous teeth are not persistent milk teeth but are supernumerary teeth, which are morphologically intermediate between normal p2 and p3. The animal's occlusion was compromised to some degree by the anomaly, and the functional disadvantage may have been critical during a harsh period.

Keywords: Rhinocerotidae • Perissodactyla • tooth eruption • dental anomaly • life history • middle Pleistocene • Germany

Zusammenfassung: Der gut erhaltene Unterkiefers eines jungadulten Nashorns aus Mosbach 2 kann aufgrund der morphologischen Merkmale und der Abmessungen *Stephanorhiuns hundsheimensis* zugeordnet werden. Nach der Abfolge, in der die Zähne beim Zahnwechsel in der Kauleiste erscheinen, war das Tier - verglichen mit *Diceros bicornis* - etwa 7 Jahre alt. Der Unterkiefer zeigt eine auffallende Anomalie in der Zahnreihe: In der Position des unteren p3 sind auf beiden Seiten jeweils zwei Zähne vorhanden. Aus dem Vergleich mit drei weiteren Kiefern von *Stephanorhinus hundsheimensis* aus Moosbach 2 kann der Zahnwechsel rekonstruiert und gezeigt werden, dass es sich bei den überzähligen Zähnen nicht um persistierende Milchzähne sondern um eine Verdoppelung der Zahnanlagen handelt. Morphologisch vermitteln diese Zähne zwischen p2 und p3. Die Funktion des Gebisses war zwar nicht schwerwiegend gestört, aber dennoch kann sich eine solche Anomalie während einer besonders schwierigen Nahrungssituation als Nachteil erwiesen haben.

Schlüsselwörter: Rhinocerotidae • Perissodactyla • Zahnwechsel • Zahnanomalie • Lebensgeschichte • Mittel-Pleistozän • Deutschland

Introduction

The Mosbach Sands of Wiesbaden (Hessen, Germany) are well known for significant remains of Pleistocene mammals. Fossils were found during intensive quarry-ing through the sands to reach the discontinuously underlying Tertiary limestone, which was exploited industrially for cement fabrication. Although the quarrying of the limestone has stopped, that of the sands continued and intensive observation through the Landesamt für

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Denkmalpflege Hessen produced several significant finds (KELLER 2003; HEMMER et al. 2003). In this paper we report a well preserved mandible of a subadult rhino recovered in 2001 by one of the authors (T.K.). The specimen is of particular interest because of a striking anomaly in the dentition which raises questions of cause and effect. Was the pathology produced by an incomplete exchange of the milk dentition, malpositioned permanent teeth or split tooth germs? Was the abnormality so severe as to affect tooth function to a degree that the animal was handicapped and died? In order to understand this pathology, the mode of tooth exchange in the mandible of *Stephanorhinus hundsheimensis* had to be compared with other juvenile mandibles from Mosbach 2, housed in the Naturhistorisches Museum Mainz.

Repository: The acronyms of collections we used material from are
BSPG = Bayerische Staatsammlung für Paläontologie und Geologie, München;
LfDH = Landesamt für Denkmalpflege Hessen, Wiesbaden;
NHMM = Naturhistorisches Museum, Mainz;
NHMW = Naturhistorisches Museum, Wien.

The locality and the stratigraphic position of the Mosbach 2 fauna

The "Mosbach Sande" is one of the classical sites of Pleistocene faunas in Germany. As early as 1841, H. v. MEYER described fossil remains of *Hippopotamus* found when digging sands near the village of Mosbach (later incorporated in the larger village Biebrich and now part of Wiesbaden). The quarrying of the Mosbach sands was driven by the exploitation of the underlying Tertiary limestone, which was used for the industrial production of cement. BRÜNING (1970) documented several historical stages of the progressive quarrying of the limestone. The exploitation of the limestone has ended but some sand is still quarried. The Mosbach sands produced a great number of fossils. About 65 mammals and birds and have been described from this locality. Faunal lists are given by KAHLKE (1961), BRÜNING (1978), TOBIEN (1980), VON KOENIGSWALD & TOBIEN (1987, 1990), VON KOENIGSWALD & HEINRICH (1999), and HEMMER et al. (2003). The Mosbach sands are the type locality for several mammalian taxa, e.g. *Equus mosbachensis* REICHENAU, 1903, *Ursus deningeri* REICHENAU, 1904, *Canis lupus mosbachensis* SOERGEL, 1925, *Arvicola mosbachensis* SCHMIDTGEN, 1911, *Microtus subarvalis* HELLER, 1933, *Pitymys schmidtgeni* HELLER, 1933, "*Cervus*" *reichenaui* KAHLKE, 1995 (= *C. elaphoides* KAHLKE, 1960). A more recent description of the outcrop at Wiesbaden Weisenau which contains the Tertiary limestone and the Mosbach sands is given by KELLER & RADTKE (2007).

The Mosbach sands were deposited in the confluence of the rivers Rhine and Main. They now lie 35–60 m above the rivers, indicating a down cutting of the rivers and an uplift of the Taunus, as part of the Rheinisches Schiefergebirge. The sands from Mosbach contain several levels of different sedimentology and climatic oscillations (BRÜNING 1978). Three faunal levels Mosbach 1, Mosbach 2, and Mosbach 3, of Pleistocene age have been differentiated (KAHLKE 1961; TOBIEN 1980; VON KOENIGSWALD & TOBIEN 1987). While the lowest one (Mosbach 1) is of early Pleistocene age, the main faunal assemblage (Mosbach 2 and Mosbach 3) represent early phases of the middle Pleistocene.

The sands from Mosbach 2 were traditionally regarded as "early Pleistocene" (e.g. ADAM 1952, 1966; TOBIEN 1957; SCHÜTT 1970). After the boundary between lower and middle Pleistocene became defined as the palaeomagnetic boundary between Brunhes and Matuyama at about 780.000 years, however, and KOCI et al. (1973) determined polarity to be normal in the Mosbach sands, they must be reallocated to the middle Pleistocene. Biostratigraphically, the Mosbach 2 fauna, providing the main bulk of fossils, is characterized by the large vole *Arvicola cantianus* (VON KOENIGSWALD & TOBIEN 1987, 1990). [The name *Arvicola mosbachensis* SCHMIDTGEN, 1911 preferred by MAUL et al. (2000) in a careful description of the variability of the Mosbach population, is regarded as a younger synonym of *Arvicola cantianus* (HINTON, 1910).]

The *Arvicola cantianus* faunas, and thus Mosbach 2, do not represent the earliest biostratigraphic stage within the middle Pleistocene. They are antedated by the *Mimomys savini* faunas such as Süssenborn and Voigtstedt in Thüringen, or the classical Cromer Forest bed of West Runton (Great Britain) (VON KOENIGSWALD & KOLFSCHOTEN 1996).

Within the *Arvicola cantianus* faunas, two levels can be distinguished. The "older *Arvicola cantianus* faunas" are characterized by a high diversity among the small mammal fauna while the "younger *Arvicola cantianus* faunas" lack specific taxa like *Talpa minor*, *Drepanosorex savini* and *Pliomys* (VON KOENIGSWALD & HEINRICH 1999). The reduction of diversity is related to the Elsterian glaciation. Thus the Mosbach 2 fauna represents a late stage of the Cromerian. At present, no well supported correlation to the MIS stratigraphy can be given.

Among the "older *Arvicola cantianus* faunas" of the late Cromerian, Mosbach 2 is regarded as somewhat younger than famous fauna of Mauer near Heidelberg (ADAM 1952). In addition to rhino *Stephanorhinus hundsheimensis*, which characterizes the Mauer fauna, in Mosbach 2 there occurs the most derived *Stephanorhinus kirchbergensis*. But recently SCHREIBER (1999) found indications that *S. kirchbergensis* might occur in Mauer as a very rare faunal element as well.

Ecologically, the Mosbach 2 fauna represents interglacial conditions as witnessed by the occurrence of *Hippopotamus amphibius* and *Sus scrofa*. The ecological significance of the occurrence of *Lemmus* and *Prae-*

ovibos schmidtgeni is uncertain at this stratigraphic level. The separation of younger sediments, referred to as Mosbach 3, is problematical (KELLER & RADTKE 2007), but they include some arctic elements like *Gulo gulo* and *Rangifer tarandus*. Traditionally these cold adapted species were regarded as an indicator of the onset of the Elsterian but minor oscillations of the late Cromerian cannot be excluded and these species might indicate decreasing temperatures. However, none of these rare faunal elements indicating a cold climate were found during the stratigraphically controlled collection of the last years. On the other hand, a redeposition from older sediments is unlikely given the skull fragment with attached antler of *Rangifer tarandus* figured by BRÜNING (1978).

The new rhino mandible and its systematic attribution

Stephanorhinus hundsheimensis, Mosbach-Collection, Landesamt für Denkmalpflege Hessen, LfDH 5/01. The mandible (hereafter called Mandible 1) was found in 2001 in place, just above the basal conglomerate of the second fluviatile cycle. The geographical coordinates of the locality are 50°02'39.80" N and 8°16'55.54" E (KELLER et al. 2004; KELLER & RADTKE 2007).

Mandible 1 is a juvenile, with left and right dentaries containing p2-m3, with m3 unerupted (Fig. 1). Wear stages of the various teeth are discussed below (see "individual age of Mosbach Mandible 1"). On both sides, two teeth occupy the p3 position, neither with a perfectly normal appearance. The abnormality is symmetrical, with a similar lingual pair and a similar buccal pair. For ease of description, those which probably erupted first are termed p3a (lingual pair) and those which probably erupted later, p3b (buccal pair). The morphology and development of p3a and p3b are described below (see "the dental anomaly").

The mandible remains fused at the symphysis, but both ascending rami were broken off before final imbedding. Thus is it likely that the Mandible 1 underwent some transportation downstream in the river before coming to rest. A redeposition from older sediments is unlikely because of the very good preservation.

In the Mosbach fauna two rhinos have been identified and described: *Stephanorhinus hundsheimensis* (TOULA, 1902) and the distinctly larger *Stephanorhinus kirchbergensis* (JÄEGER, 1839). The most common species is *Stephanorhinus hundsheimensis*. In most earlier faunal lists and in museum catalogues this species it appears under the name *S. etruscus* (FALCONER, 1868). The identification as *S. hundsheimensis* dates back to MAZZA et al. (1993). This attribution was confirmed recently by LACOMBAT (2006). The rhino populations of Süssenborn (KAHLKE 1969) and Voigstedt (KAHLKE 1965) formerly described as "*Stephanorhinus etruscus*" represent *Stephanorhinus hundsheimensis* as well (MADE 2000; LACOMBAT 2003, 2006). HEMMER et al.

(2003) used the name *Stephanorhinus etruscus hundsheimensis* for the smaller rhino from Mosbach.

The morphological characters, especially the V-shaped anterior and posterior valleys of premolars and molars and the difference in their depth correspond with *Stephanorhinus hundsheimensis*, which is the most common rhino in Mosbach 2. The measurements of the teeth (Tab. 1, Fig. 2) were compared with those from Süssenborn (KAHLKE 1965), Voigtstedt (KAHLKE 1969) and Mauer (Schreiber 1999). The teeth of the Mosbach Mandible 1 fit well into the range of *Stephanorhinus hundsheimensis*, despite the supernumerary tooth. The dimensions of the dentition of *Stephanorhinus kirchbergensis* are distinctly larger (Fig. 2).

Age stages of *Stephanorhinus hundsheimensis* from Mosbach

On initial inspection it is not clear whether the anomaly at p3 results from unshed deciduous teeth, malpositioned permanent teeth or supernumerary teeth, especially since the individual died during active tooth eruption. To discern the nature of the anomaly, we compared the Mosbach Mandible 1 to several juvenile fossil rhinos from the Pleistocene and also to tooth eruption as observed in the living black rhinoceros, *Diceros bicornis* (see below). We restrict our investigation of tooth eruption to the mandible since the fragile maxilla is much rarer in the fossil record.

Tooth emergence and life history of living Rhinocerotidae

Dental formulae of living Rhinocerotidae vary somewhat, 0-2/0-1, 0/0-1, 3-4/3-4, 3/3, over the four genera *Dicerorhinus*, *Rhinoceros*, *Diceros* and *Ceratotherium* (see THENIUS 1989; NOWAK 1991); African rhinos (*Diceros* and *Ceratotherium*) share missing or rudimentary anterior teeth (HILLMAN-SMITH & GROVES 1994), whereas the Asian rhinos *Dicerorhinus* and *Rhinoceros* and some extinct rhinos had more substantial anterior teeth (THENIUS 1989). Like other Perissodactyla, rhinos may retain a first premolar, a tooth which has disappeared in many mammalian lineages. Living mammals which retain a first premolar show only a single tooth generation at that locus, with the single exception of the tapir, which replaces a maxillary DP1 (LUCKETT 1993). Those that have considered a range of mammals (KINDAHL 1967; ZIEGLER 1971; LUCKETT 1993) allocate the first premolar to the deciduous dentition, regarding it as a late developing deciduous tooth; it often emerges after the deciduous and before permanent dentitions (SMITH 2000). GODDARD (1970) notes that dp1 appears through the gum fairly late in *Diceros*, around the time dp4 appears; dp1 was eventually lost in 80 % of mandibles of young adults. Presumably dp1 retains an important function in the deciduous dentition for youngest animals.

p2

p3a/p3b

p4

m1

m2

(m3)

5 cm

A

B
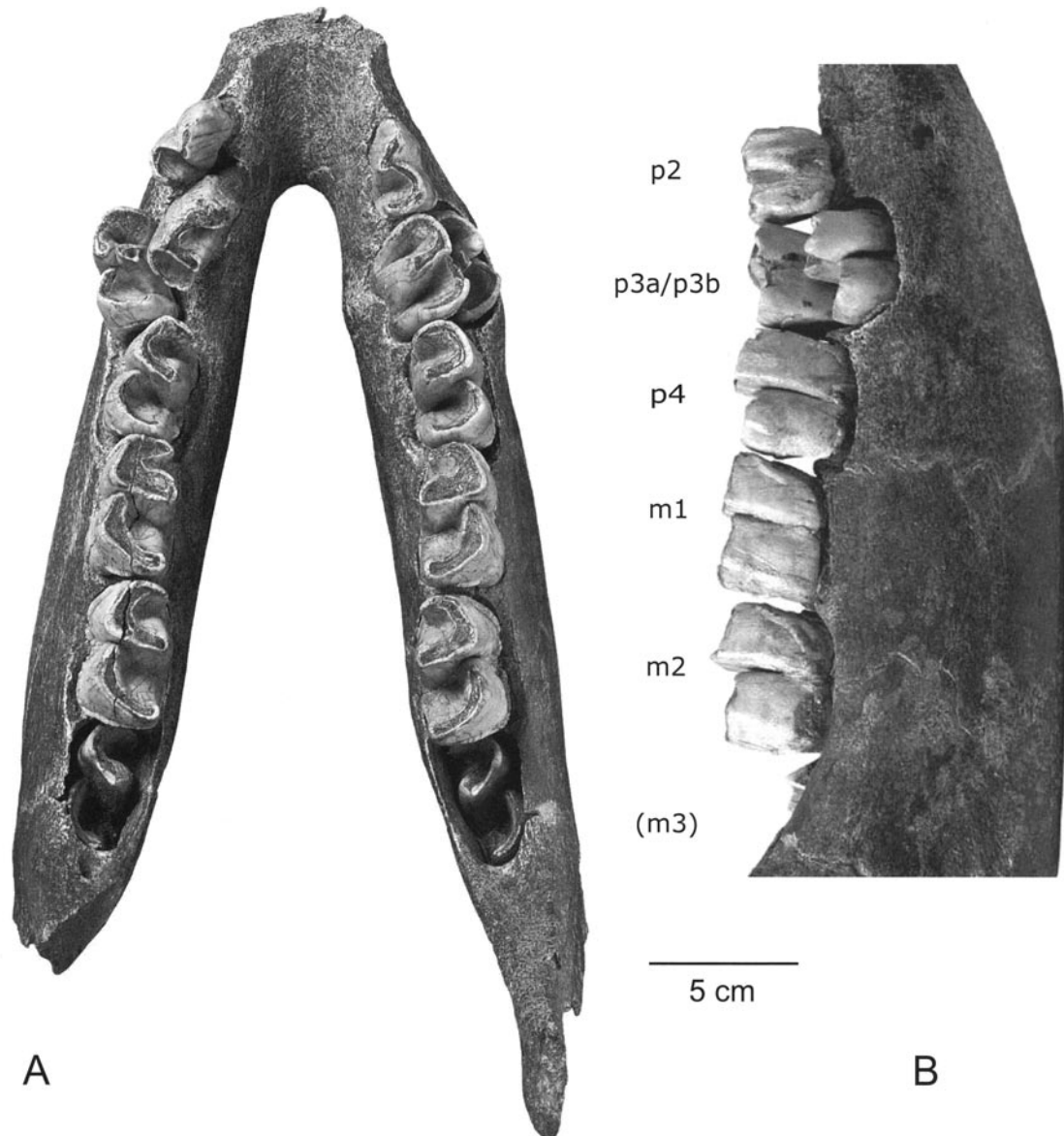
Fig. 1. *Stephanorhinus hundsheimensis* from Mosbach 2, Mandible 1 (LfDH 5/01), with a symmetrical anomaly in the p3 position. – **A**: occlusal view. – **B**: lateral aspect of the right ramus.
Abb. 1. *Stephanorhinus hundsheimensis* aus Mosbach 2, Unterkiefer 1 (LfDH 5/01) zeigt eine symmetrische Zahn-anomalie in der Position des p3. – **A**: Aufsicht. – **B**: Seitenansicht des linken Unterkieferastes.

Tab. 1. *Stephanorhinus hundsheimensis* from Mosbach 2, dental measurements of Mandible 1 in mm. Length p2–p4: lingual side 109.5 mm, buccal side 112.7 mm

	p2 sin/dex	p3a sin/dex	p3b sin/dex	p4 sin/dex	m1 sin/dex	m2 sin/dex
lingual length	(28.1) / 28.4	31 / –	– / 32.6	35.6 / 34.4	41.9 / 41.8	45.1 / 45.7
buccal length	30.3 / 30.4	31.4 / (28.5)	34.6/ –	(40.7) / 38.5	41.6 / 41.2	43.1 / 43.5
anterior width	17 / 17.7	(18.5) / 22.2	– / –	25.5 / 25.1	27.3 / 26.3	28.4 / 28.7
distal width	– / 21.5	22.7 / 22.8	26.5 / –	28.6 / 27.1	30.7 / 29.3	30.8 / 29.4
ant. valley depth	– / –	– / –	– / 14.8	18.5 / 19.9	8.9 / 10.1	19.4 / 17.2
post. valley depth	– / 13.2	11.6 / 14.6	– / –	19.2 / 21.5	17.9 / 18.5	21.6 / 21.1
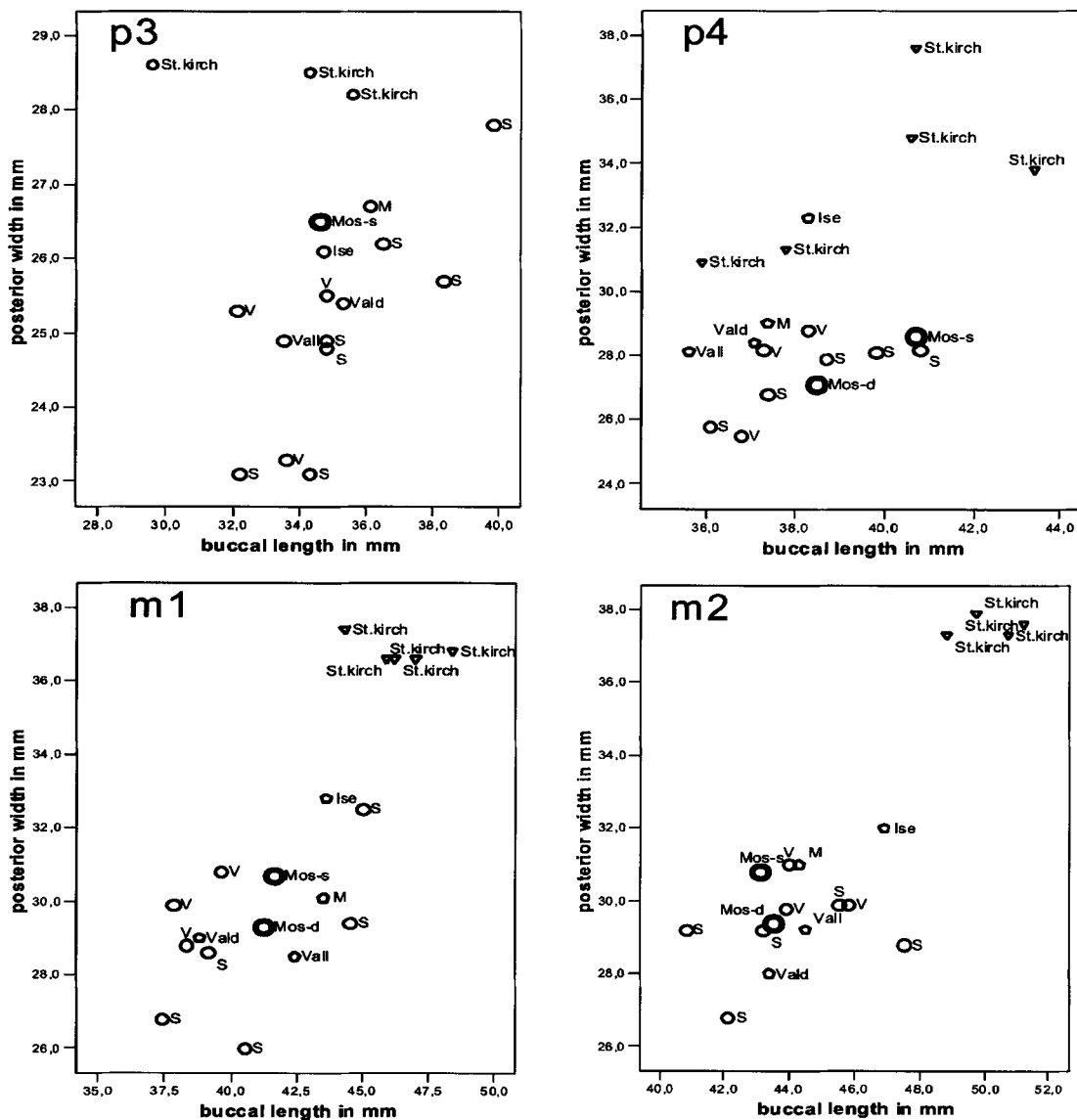
Fig. 2. *Stephanorhinus hundsheimensis* and *Stephanorhinus kirchbergensis* dental measurements. In tooth size, especially m1 and m2, *Stephanorhinus hundsheimensis* differs from *S. kirchbergensis*. Mandible 1 from Mosbach 2 clearly falls within the range of *S. hundsheimensis*.

St. kirch. = *Stephanorhinus kirchbergensis* from the late Pleistocene of the Oberrheinebene near Darmstadt; O = *Stephanorhinus hundsheimensis*: Ise = Isernia (mean), M = Mauer (mean); Mos-s and Mos-d Mosbach Mandible 1 (left and right); S = Süssenborn; V = Voigtstedt; Val = Valdarno (mean). Additional data from KAHLKE (1965, 1969; LACOMBAT 2006; SCHREIBER 1999 and SYRING (pers. comm.)).

Abb. 2. Zahnproportionen von *Stephanorhinus hundsheimensis* und *Stephanorhinus kirchbergensis*. In den Zahnmaßen, besonders am m1 und m2, unterscheidet sich *Stephanorhinus hundsheimensis* von *S. kirchbergensis*. Der Unterkiefer 1 aus Mosbach 2 liegt eindeutig im Schwankungsbereich von *S. hundsheimensis*.

Living members of this family mature slowly, with potential life spans of 4 and even 5 decades (HUTCHINS & KREGER 2006). A complete picture of maturation is not available for any one species: tooth eruption is known primarily from the African rhinos *Diceros bicornis* (GODDARD 1970) and *Ceratotherium simum* (HILLMAN-SMITH et al. 1986), whereas mother-infant behaviour is best described for the Indian *Rhinoceros unicornis* (LAURIE 1982; HUTCHINS & KREGER 2006). GODDARD (1970) observed mandibular tooth emergence in the black rhino, *Diceros bicornis,* combining

observations on 15 individuals of known age with those from 500 mandibles of unknown age. He reported that *Diceros* is born without teeth erupted; dp2–dp3 cut the gum in a few months and all deciduous teeth are fully erupted by the first year. The m1 cuts the gum at about 1½ to 2 years of age, the m2 at about 4 years, premolars exchange sometime between 4–6 years, and the m3 cuts the gum around 7 years. It may be years, however, before all four third molars are fully at occlusal level. In both living rhinos and fossil rhinos from the Quaternary, milk teeth are retained until heavily worn, until only an

Tab. 2. Tabulation of GODDARD's (1970) age stages of *Diceros bicornis* mandibular tooth eruption.

		Tooth position						
Class	Mean age in years	dp1	p2	p3	p4	m1	m2	m3
I	0	d	d					
II	0.5	d	D	D	d			
III	1.0	d	D	D	d			
IV	1.5	d	D	D	D	m crest		
V	2+/-0.5		D	D	D	m		
VI	3 +/-0.5		D	D	D	M		
VII	4 +/-0.5		D(1p)	D(1p)	D	M	m	
VIII	5+/-0.5		D/p	D/p	D	M	m	
IX	6+/-0.5		P	P	p/P	M	M	
X	7+/-0.5		P	P	P	M	M	m
XI	8+/-0.5	Lost in 80%	P	P	P	M	M	M

d, deciduous tooth emerged at least above alveolus; D, deciduous tooth erupted and in wear.

p, permanent premolar emerged at least above alveolus; P, permanent premolar fully erupted and in wear; m, molar emerged at least above alveolus; M, molar fully erupted and in wear.

enamel rim surrounds the dentin (GODDARD 1970; LOU-GUET 2005).

Tooth emergence bears a functional relationship to weaning in mammals (SMITH 1991 and unpubl. data). Wild *Rhinoceros unicornis* calves are reported to begin eating plant foods by ca. 2–3 months (LAURIE 1982), which coincides with dates given for emergence of dp2–dp3 in other rhino species (GODDARD 1970). Weaning data that exist appear similar across the living rhinos: an intense nursing period is noted for the first two months (*Ceratotherium, Rhinoceros*), with decreasing frequency after one year (*Rhinoceros*, probably *Ceratotherium*); until 18 months (*Rhinoceros*) or even two years (*Diceros*); calves are reportedly driven off by the mother at least a week before birth of the next calf (*Rhinoceros, Ceratotherium*) (LAURIE 1982; NOWAK 1991). *Rhinoceros* calves typically parted with their mother at about three years of age (LAURIE 1982), although they may associate with her longer if not replaced by another calf (HUTCHINS & KREGER 2006). Even with such variation, we can pose that weanlings possess a minimum of a complete deciduous dentition; some will have added newly cut m1 (Tab. 2).

To assess the individual age of the Mosbach Mandible 1, we begin by seriating several juvenile fossil rhinos of the Mosbach site housed in the Naturhistorisches Museum Mainz, matched against available age data from living rhinos. Mandibles are described below in order from youngest to oldest.
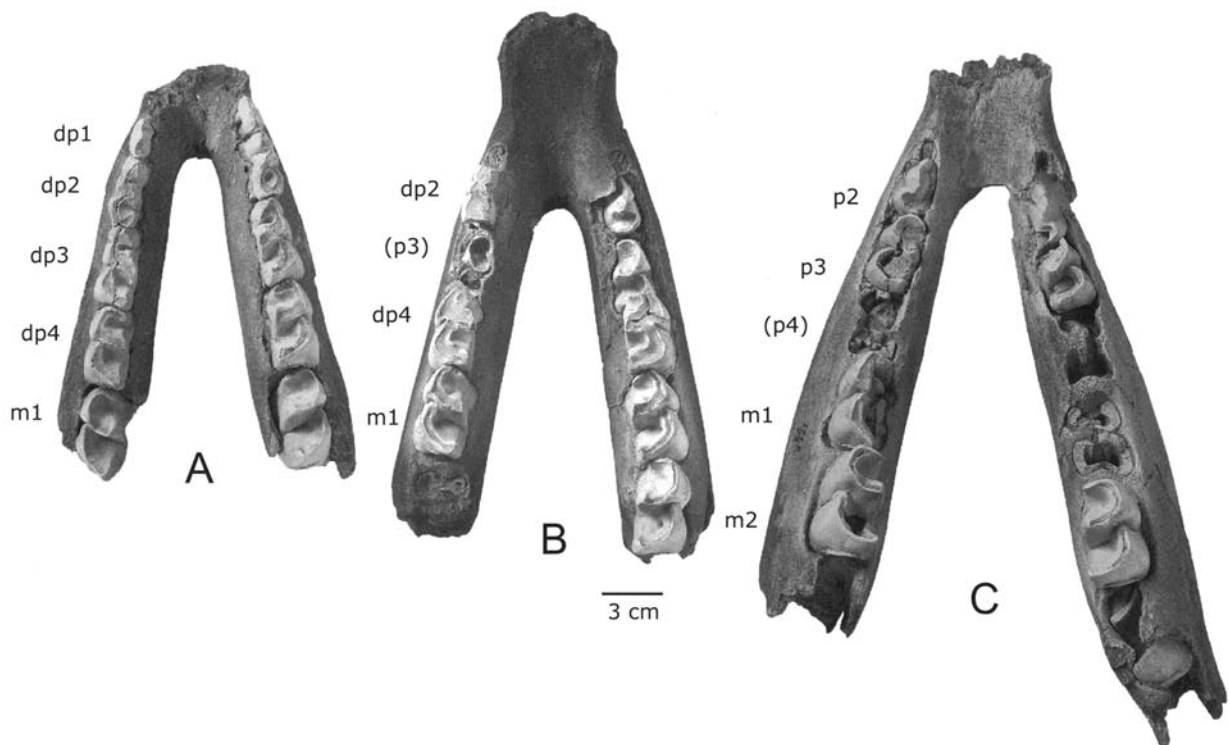
Mandible 2
(Figs. 3A, 5A)

Stephanorhinus hundsheimensis ("*Rhinoceros etruscus*"), Naturhistorisches Museum Mainz, NHMM 1957/37, partial symphysis with right and left dentaries containing dp1, dp2, dp3, dp4 and erupting m1.

Description and age attribution: In Mandible 2, all deciduous teeth are fully emerged and in wear. The dp1 are small with a bifid root. The dp2–4 are elongated, narrow and low crowned, with cingula absent on buccal and lingual faces. Moderate wear lessens from dp2–dp4. Dentin is exposed on the entire length of the dp4 hypolophid. The m1 crown has emerged from the alveolus, and may have just cut the gum (although first molar position in the reconstruction is probably too high). Within the jaw, CT scan reveals the crypts in which permanent premolars will form, large and oval underneath dp2 and dp3 roots, but small and circular underneath dp4, clearly in an early stage of development (Fig. 5A). By analogy with *Diceros bicornis*, this individual corresponds to GODDARD's class IV, which includes black rhinos with a mean age of 1.5 years (Tab. 2). Given what is known about rhino life history, this individual is likely a death at weaning.

Mandible 3
(Fig. 3B, 5B)

Stephanorhinus hundsheimensis ("*Rhinoceros etruscus*"), Naturhistorisches Museum Mainz, NHMM 1938/71, symphysis with left and right dentaries containing

Fig. 3. *Stephanorhinus hundsheimensis* from Mosbach 2. Three age stages of juvenile animals. – **A**: Mandible 2 (NHMM 1957/37) is about 1.5 years of age. – **B**: Mandible 3 (NHMM 1938/71) is about 5 years. – **C**: Mandible 4 (NHMM 1968/72) is of about 5+ years in comparison to *Diceros bicornis*.
Abb. 3. *Stephanorhinus hundsheimensis* aus Mosbach 2. Drei Altersstadien junger Individuen. – **A**: Unterkiefer 2 (NHMM 1957/37). Sein Alter beträgt etwa 1,5 Jahre. – **B**: Unterkiefer 3 (NHMM 1938/71), dessen Alter etwa 5 Jahre beträgt. – **C**: Unterkiefer 4 (NHMM 1968/72) auch im Alter von 5+ Jahren, gemessen an *Diceros bicornis*.

left dp1 root, dp2, dp3 root, dp4, m1, m2 (roots) and p2–p4 crowns within the jaw; the right side has dp1 root, dp4, m1, m2, with p2 and p3 crowns visible in a cut out. The symphysis shows four small depressions, two on each side, which suggests the presence of rudimentary incisors butts, as is occasionally observed in rhinos without incisors (Thenius 1955).

Description and age attribution: Mandible 3 is an older juvenile with m1 and m2 fully erupted and in wear. All deciduous crowns may have been present in life. CT scan (Fig. 5B) clearly shows well developed crowns of p2, p3, and p4 within the jaw; the small remaining root for the dp1 is also visible along with the lack of a replacing tooth at this position. At p2 and p3, roots are approximately half formed and much of alveolar bone between deciduous and permanent crowns has been resorbed. The permanent p4, however, lags in development: root development has hardly begun and the crown lies well below the dp4.

Notably, the one remaining dp2 is well worn to the point that dentin exposure is confluent over trigonid and talonid (Fig. 3B). The m1 is worn on the protolophid and hypolophid, but trigonid and talonid remain distinct. On m2, the trigonid and talonid show first signs of contact with their antagonist.

By analogy with *Diceros bicornis*, this individual is in Goddard's class VIII, ca. age 5 years; compared to

living rhinos, this juvenile would be feeding independently and probably separated from its mother.

Mandible 4

(Fig. 3 C)

Stephanorhinus hundsheimensis ("*Rhinoceros etruscus*"), Naturhistorisches Museum Mainz, NHMM 1968/72 [483 Mo], symphysis with right and left dentaries containing right dp1 root, p2–p3 erupting, m1 (roots), m2, and m3 crown unerupted; on the left are preserved broken roots of all deciduous teeth dp1–dp4, with p2–p3 crowns erupted through alveolus, and m1 and m2.

Description and age attribution: Mandible 4 is one slight step advanced in development over Mandible 3. It also shows a juvenile with m1 and m2 fully erupted, just as exchange of the milk dentition is about to take place. The first premolar space is disappearing, with dp2 encroaching on its socket. In form, the unworn p3 is significantly more molarized than p2, which has only a weak external sulcus of little depth demarcating mesial and distal halves of the tooth; p3, in contrast, has a deep external sulcus that forms scroll shapes of trigonid and talonid, resembling a molar. Our CT scan (not shown) reveals the permanent premolars within the jaw. Their development is more advanced than in Mandible 3:
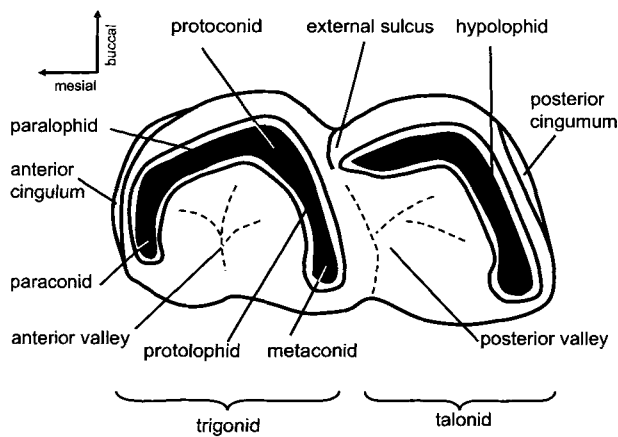
Fig. 4. Terminology for rhinoceros tooth elements in lower molars and molariform premolars according to THENIUS (1989) and LACOMBAT (2006).

Abb. 4. Bezeichnung der Zahnelemente für die unteren molariformen Prämolaren und Molaren.

roots are long on p2–3 and p4 has significant root development, and has erupted into position directly beneath the dp4. By analogy with *Diceros bicornis*, this is an older juvenile, also in GODDARD's class VIII, circa age 5+ and independent of its mother.

Individual age of the Mosbach Mandible 1

Tooth eruption sequence of Mosbach juvenile rhinos largely fits into descriptions and age stages of the living black rhino, *Diceros bicornis*. Judging from the normal Mandibles 2, 3 and 4, permanent tooth emergence order appears as: m1 m2 (p2 p3) p4 m3, a sequence also found in living rhinos (Tab. 3), although our specimens differ from GODDARD's modal pattern by showing full eruption of m2 before deciduous crowns are replaced. With some variation (p2 m2 order), rhinos erupt permanent premolars after the eruption of the m2 and before that of the m3. In this, rhinos resemble some long-lived generalized mammals like living primates, pigs, and the hippo; in contrast, most ungulates postpone emergence of premolars until after the eruption of the m3 (SMITH 2000). Within living perissodactyls, the tapir is most similar to the rhino whereas the zebra stands out as different, completing the dentition after m3. The eruption sequence of the postcanine permanent dentition in *Diceros* and *Stephanorhinus* seems to be valid for most fossil rhinos, whether they have enlarged incisors (*Aceratherium incisivum*) or not (*Prosantorhinus germanicus*) (Tab. 3).

For the Mosbach rhinos, development of p2 and p3 is closely in synchrony, and must have emerged quite

Tab. 3. Sequence of emergence of mandibular cheek teeth in living and fossil rhinos, compared with representatives of the other families of living Perissodactyla (tapir and zebra); ( ) indicates that internal order is uncertain.

Taxon	Deciduous teeth (<1 yr)	Permanent teeth
Rhinocerotidae		
Diceros bicornis GODDARD, 1970	(dp2 dp3) (dp4 dp1)	m1 m2 (p2 p3) p4 m3
Ceratotherium simum HILLMAN-SMITH et al., 1986	(dp2 dp3) dp4 dp1	m1 p2 (m2 p3 p4) m3
Stephanorhinus hundsheimensis Mosbach 2 - this study	(dp2 dp3 dp4 dp1)	m1 m2 (p2 p3) p4 m3
Prosantorhiunus germanicus Sandelzhausen, BSPG 1959 II 1	(dp2 dp3 dp4 dp1)	m1 m2 (p2 p3) p4 m3
Aceratherium incisivum Prottes, NHMW 1986/141	(dp2 dp3 dp4 dp1)	m1 m2 (p2 p3) p4 m3
Tapiridae		
Tapirus terrestris SIMPSON, 1945 and SMITH unpub.	(dp2 dp3) (dc dp4)	m1 p2 p3 m2 p4 m3
Equidae		
Equus burchelli SMUTS, 1974	(dp2 dp3) dp4 dp1	m1 m2 (p2 p3) m3 p4

Tooth emergence is cutting the gum; eruption to occlusal level may be substantially later. – Note on incisors: the complete sequence for *T. terrestris* is m1 (i1 i2) i3 c p2 p3 m2 p4 m3 and for *E. burchelli* is: m1 m2 i1 (p2 p3) m3 i2 (c p4) i3. We can say nothing about incisor emergence in living rhinos, but among some fossil rhinos with greatly enlarged incisors (HEISSIG 2006), they are replaced after deciduous premolars, e.g. in *Prosantorhinus germanicus* (Kurt Heißig and WvK, pers. obs.).

closely in time. These specimens give no direct information on sequence of emergence of the deciduous teeth, although a front to back sequence of dp2, dp3, dp4 would be in line with the degree of wear on the youngest juveniles. This is the background for our interpretation of Mandible 1.

Description and age attribution: Mosbach 1 represents a juvenile older than Mandibles 2–4. Here, first and second molars are fully erupted with significant wear. Third molar crowns are developed with cusp tips just emerging above alveolus, but CT scan shows root development had not yet begun (Fig. 5C). Left and right sides possess four premolars, crowded and doubled at the p3 position. On comparing Mandibles 2–4 above, it becomes clear that

the four premolars bear no characteristics of deciduous teeth: they are high crowned, short in mesiodistal length and possess buccal cingula. Significantly, all premolars are lightly worn, whereas at this age, any remaining deciduous premolars should be worn to an extreme point (compare the younger Mandible 3). No further tooth crowns are within the jaw, instead, CT scans and a traditional x-ray (Fig. 5C) show premolar roots that appear to have completed growth in length, with root ends closed on all except p4, where root apices remains open.

On the right side (Fig. 1B), p3a is somewhat integrated into the tooth row with occlusal wear, although the crown tips to the buccal with roots bulging into the internal mandible. Heavily chipped buccal cusps suggest some malocclusion with the antagonist. On this side
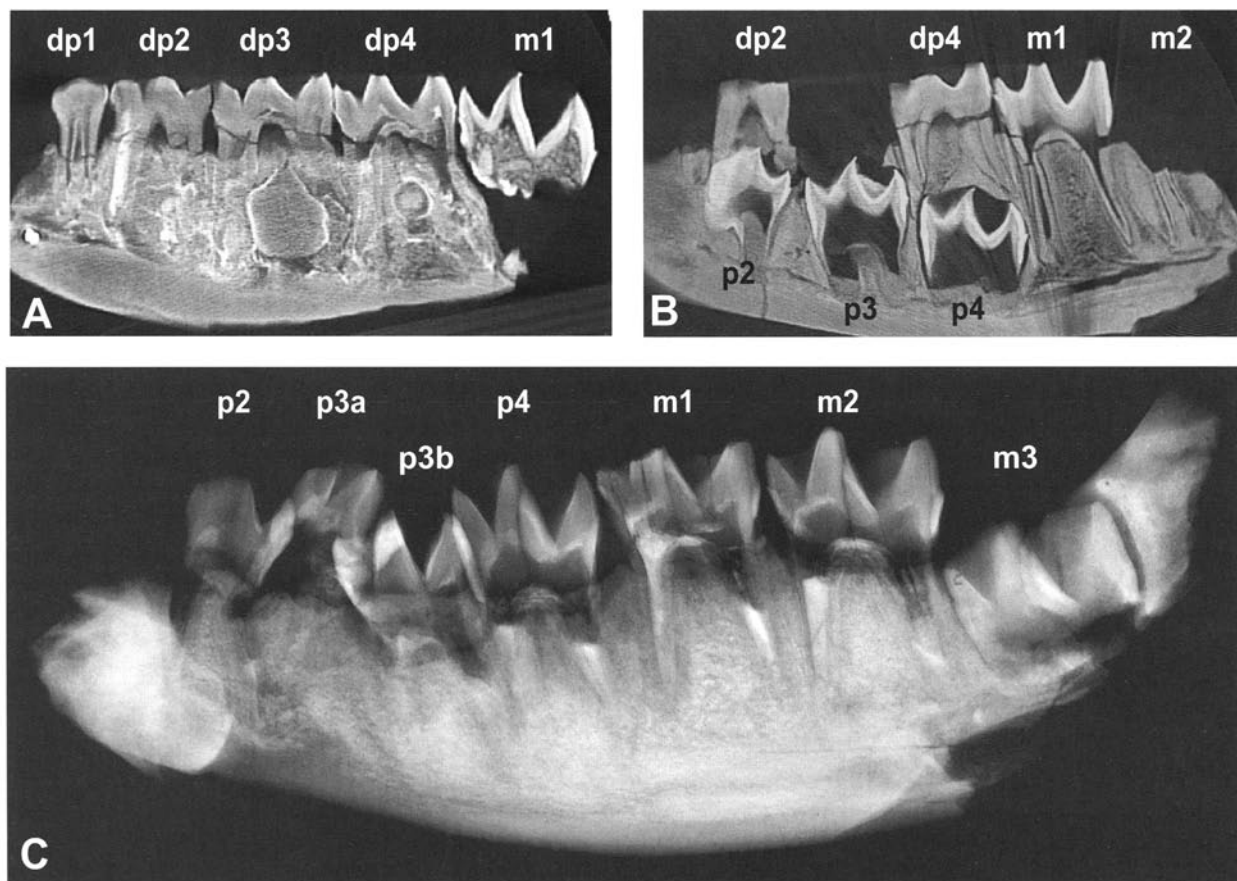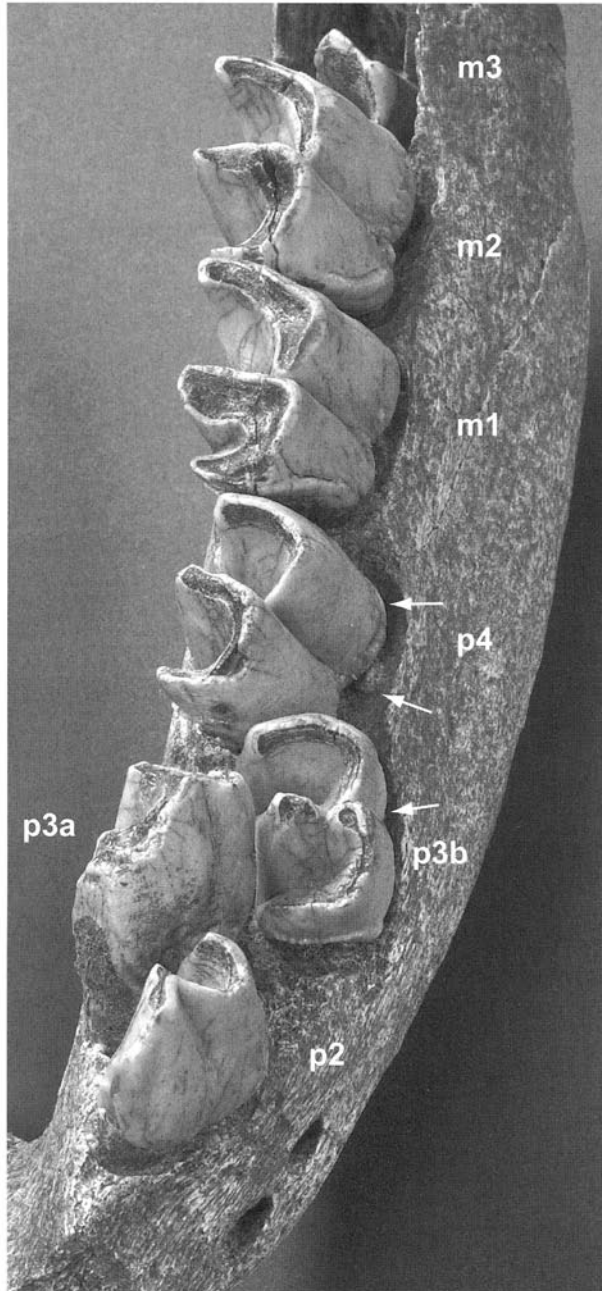

Fig. 5. *Stephanorhinus hundsheimensis*, Mosbach 2, CT scans and x-ray of the mandibular dentition in different age stages. – **A**: CT-scan of the left ramus of Mandible 2 (NHMM 1957/37), about 1.5 years old. The crypts for the germs of the permanent premolars are visible beneath the deciduous teeth dp3 to dp4 (an adjacent scan section showed crypt beneath dp2). – **B**: CT-scan of the left ramus of Mandible 3 (NHMM 19638/71), about 5 years in age. The permanent premolars are well developed beneath the deciduous dentition. – **C**: X-ray of the left ramus of Mandible 1 (LfDH 5/01), about 7 years in age. The tooth exchange is completed at this age, and dp1 is gone. The x-ray shows the two teeth in the position of the p3 as an anomaly, but no further teeth.

Abb. 5. *Stephanorhinus hundsheimensis* aus Mosbach 2, CT-scans and Röntgenaufnahmen der Unterkieferbezahnung verschiedener Altersstufen. – **A**: CT-scan des linken Kieferastes von Unterkiefer 2 (NHMM 1957/37), der etwa 1,5 Jahre alt wurde. Die Kavernen für die Zahnkeime der Dauerbezahnung sind unter den Milchzähnen (dp1–dp4) sichtbar. – **B**: CT-scan des linken Kieferastes von Unterkiefer 3 (NHMM 19638/71), Alter etwa 5 Jahre. Die Keime der permanenten Prämolaren sind gut unterhalb der Milchzähne ausgebildet. – **C**: Röntgenaufnahme des linken Kieferastes von Unterkiefer 1 (LfDH 5/01), im Alter von etwa 7 Jahren. Der Zahnwechsel ist abgeschlossen und der dp1 ausgefallen. Die Röntgenaufnahme zeigt die verdoppelten Zähne in der Position des p3 als Anomalie, aber keine zusätzlichen Zähne.

the p3b, deep to the occlusal plane, shows polish wear around the protoconid, suggesting the tooth had cut through the gum, but no wear to indicate any tooth-to-tooth contact.

On the left side (Fig. 6) the p3a is displaced more sharply with its anterior root exposed. The occlusal sur-

Fig. 6. *Stephanorhinus hundsheimensis* from Mosbach 2, Mandible 1 (LfDH 5/01): the dental anomaly in the right ramus of the mandible, showing the cleft in the protolophid of p3b, and indication of an infected gum margin (arrows).

Abb. 6. *Stephanorhinus hundsheimensis* aus Mosbach 2, Unterkiefer 1 (LfDH 5/01): Die Zahnanomalie des rechten Kieferastes mit dem unterbrochenen Protolophid am p3b. Der Kieferrand unter dem p3b und dem p4 zeigt eine Rinne, die wohl auf eine Entzündung des Zahnfleisches zurückgeht (Pfeile).

face of the p3b, which lies deep to the tooth row, shows distinct wear on the trigonid indicating some tooth-to-tooth contact. As this seems hardly possible in a normal occlusal cycle of a regular dentition, this wear pattern suggests that the left tooth row of the maxilla was disturbed to some degree as well. On both sides the p4 is fully erupted with slight attrition on the hypolophid; as noted above, its open roots suggest fairly recent emergence. The m1 and m2 are substantially more worn than in Mandible 4 (above).

Without regard to the anomaly, the individual fits GODDARD's stage X, *Diceros bicornis* of a mean age of about 7 years. Living rhinos of this age are of large size; males and females are sexually mature and females are near age of first calving (HILLMAN-SMITH & GROVES 1994). By this stage of tooth development, most *Diceros bicornis* have shed dp1 (GODDARD 1970), and judging from the Mosbach 2–4 mandibles, the dp1 alveolus is gradually subsumed by advancing cheek teeth. Thus the Mosbach Mandible 1 juvenile was past the period of exchange of the milk dentition and the additional tooth is an anomaly.

The dental anomaly

In Mandible 1 the p2 morphology is normal, much less molarized than a typical p3 and p4, with the paralophid undeveloped. Trigonid and talonid are separated by a slight external sulcus.

Left and right p3a share well developed paralophid, but one somewhat narrower than in a normal p3. Normally p3 is fully molarized with a well developed external sulcus separating trigonid and talonid, as can be seen in Mandible 4 or in a Munich specimen (BSPG 1982 XIV 1) illustrated by HEISSIG (2006). Here, in contrast, the external sulcus is weak, almost as weak as in p2. Thus p3a morphology shares characteristics of p2 and p3. The left p3a shows an additional abnormality: the base of the paralophid shows a groove or depression, possibly impression of the tooth germ of the adjacent p3b. On the left side p3a is positioned with its anterior root lingually to the p2 and slightly mesial to p3b.

Both p3b are mesiodistally longer than p3a. The p3b are substantially molarized teeth with anterior and posterior cingula and share a well developed external sulcus dividing the tooth into trigonid and talonid, characters which resemble normal morphology. Both p3b, however, show a fairly deep cleft of the protolophid, the crest that usually unites the protoconid and the metaconid. On the right side where the protolophid is unworn, the metaconid even has two small additional crests.

Because the p3b pair resembles normal p3 morphology to a higher degree than the p3a, we regard the p3a pair as supernumerary. Notably, the p3a are not simple duplicates of p3 but blend morphology expected for p2 and p3.

Supernumerary teeth have been reported widely in mammals (e.g. HALL 1940; KRAPP 1969, 1973; JUNGERS

& GINGERICH 1980; LAVELLE & MOORE 1996) and are particularly well documented in humans (see review in RAJAB & HAMDAN 2002). There is no standard percent of supernumerary teeth across mammals, the percent varying between closely related species and even between populations. For example, they are much rarer in humans (ranging between <1–4 % in populations) than in the gorilla (8 %), according to LAVELLE & MOORE (1996). Large scale surveys among artiodactyls report frequencies of about 2 % (LOE et al. 2006). Supernumerary teeth can be single, paired and bilaterally semi-symmetrical, or multiple; morphologically they may be "supplemental", resembling teeth in the nearest dental field, or they may be simplified or malformed (RAJAB & HAMDAN 2002). Molars added at the end of the tooth row are one of the most common forms of supernumerary tooth, and in one terrestrial mammal, *Otocyon*, the bat-eared fox, these supplementary molars have evolved to become the norm (GUILDAY 1962).

Extra premolars similar to the Mosbach condition can be seen in examples from the maxilla (MOPAGER et al. 2002) and mandible (AÇKGÖZ et al. 2006) in humans. Large studies available for humans find that supernumerary teeth are far more common in males than in females (2 : 1 or more) and are associated with larger teeth (RAJAB & HAMDAN 2002). Supernumerary teeth are well known to recur in families and have some heritability, although they do not appear to be inherited in simple Mendelian fashion (BROOK 1984). More than five such teeth, however, is often a sign of presence of another syndrome (AÇKGÖZ et al. 2006). Discussion continues on their aetiology as to the contributions of genes and the environment.

HATAB et al. (1994) interpreted supernumerary teeth as a "localized and independent hyperactivity of the dental lamina". In the case of the Mosbach Mandible 1, the anomalous teeth could represent of bud of tooth lamina, that, due to its locus in the premolar field, developed into a tooth that resembles anterior premolars in general, although not any one precisely. The intermediate form of the Mosbach supernumerary teeth fits with morphogenetic field theory, which proposes that morphology is not only due to the genetic code but reflects as well epigenetic information from position in the tooth row (GLASSTONE 1963). In the Mosbach Mandible 1 the anomaly occurs on both sides almost symmetrically, suggesting its basis was set early in development.

In the Mosbach Mandible 1, CT scan and traditional x-rays show no other supernumerary teeth (Fig. 5C). It remains possible that the individual had supernumeraries in the maxilla also, a situation not unknown in humans. In humans, supernumeraries of the deciduous dentition are far rarer than those of the permanent teeth (MOPAGER et al. 2002), so it is also quite possible that the Mosbach individual had a normal deciduous dentition.

Functional aspects of the dental anomaly

The reconstruction of pathological features in fossil mammals is often limited since only a very limited part of the skeleton, often only one bone, is available, whereas proper interpretation of the disease or injury would require evaluation of the entire skeleton (VON KOENIGSWALD & SCHMITT 1987). Similarly, for the Mosbach 1 mandible we are limited by the lack of the maxilla in evaluating occlusion. A careful investigation, however, suggests that the maxilla may also have had some disturbance. Conditions on the right side were the least severe where the supernumerary tooth is integrated into the tooth row; the left side shows a more definite pathology. Chipped wear is widespread over the p3a and left p3b, but not present on p4–m2, suggesting it results from traumatic occlusion rather than post-mortem damage. Lastly, the alveolar bone on the left side shows regression and rounding that suggests infection spread from the region of the supernumerary tooth to that of p3 and p4 (Fig 6).

However the dental anomaly arose, there is no question that it gave the Mosbach individual a significant pathologic occlusion. The malocclusion was apparently of short duration: all premolars are lightly worn, and in any case were probably erupted for a year or less before death (comparing *Diceros bicornis*).

LOE et al. (2006) investigated consequences of anomalous dental conditions in red deer, *Cervus elaphus*. In good years they could not show an effect, but in poor years, animals with some dental anomalies were in poorer condition, especially among females.

The rhinoceros is a herbivore of large body size that must comminute a large amount of forage or browse per day. Moreover, as a non-ruminant herbivore with hindgut fermentation, they must take in huge quantities of plant material per day to compensate for low efficiency of digestion, and reportedly spend much of their active hours foraging (HUTCHINS & KREGER 2006). The severity of the malocclusion must have compromised comminution of plant material in the Mosbach individual, and in turn, its nutrition. The short duration of the condition makes it not unlikely that it contributed to the animal's death.

Acknowledgments

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