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ORIGINAL PAPER

Dental Eruption Series and Replacement Pattern in Miocene *Prosantorhinus* (Rhinocerotidae) as Revealed by Macroscopy and X-ray: Implications for Ontogeny and Mortality Profile

Christine Böhmer[1,2] · **Kurt Heissig**[1,2] · **Gertrud E. Rössner**[1,2,3]

Abstract Fossil evidence of complete sequences of dental ontogeny in extinct mammals is rare but contains valuable information on the animal's physiology, life history, and individual age. Here, we analyzed an exceptionally high number of juvenile dentaries at different developmental stages including highly fragile tooth germs of the extinct rhinoceros *Prosantorhinus germanicus* from the Miocene fossil lagerstätte Sandelzhausen in Germany. We used dental wear stages, eruption stages, and tooth germ development in order to reconstruct the tooth replacement pattern for *P. germanicus*. The results allow for the distinction of 11 dental eruption stages and document a tooth eruption sequence of (d2, d3), (d1, d4), m1, m2, p2, p3, p4, m3; a pattern identical to that reported for the extant African rhinoceros, *Diceros bicornis*. Moreover, our findings indicate that *P. germanicus* falls into the life history category of slow-growing, long-living mammals. The dental eruption stages of the fossil rhinoceros were correlated with data of living rhinoceroses in order to gain insight into the age-at-death distribution of *P. germanicus* at Sandelzhausen. The juvenile mortality profile of *P. germanicus* shows a trend of selective mortality at an inferred age range of about 3 months to 3 years. As this age range represents a life phase of increased natural risk of mortality, our findings indicate a gradual accumulation of corpses (attritional fossil assemblage). This result supports the interpretation of a taphocenosis found at the Sandelzhausen fossil site.

Keywords *Prosantorhinus germanicus* · Perissodactyla · Tooth wear · Dental development · Life history · Sandelzhausen

Introduction

Mammalian dentition is a highly evolved organ system and integral part of feeding strategy in which biological investment focused on quality (functional differentiation by heterodonty; functional efficiency by differentiated crown morphology, occlusion, and thecodont attachment; functional sustainability by enamel) not quantity (diphyodonty only instead of polyphyodonty). Diphyodonty, the replacement of the juvenile by the adult set of teeth, however, is a requirement for mammalian growth (reflected through larger tooth size, different crown morphology, and a higher tooth number). As this essentially entails ensuring functionality of mastication during dentition transition, a number of group specific modifications in dentition ontogeny evolved across mammals (Schultz 1960; Kindahl 1967; Ziegler 1971; Vigal and Machordom 1985; Luckett 1993; Smith 1994; van Nievelt and Smith 2005). This is facilitated by a strict, genetically determined spatiotemporal order of tooth development and eruption that links individual age with exact ontogenetic stages (e.g., Lowe 1967; Goddard 1970; Hitchins 1978; Morris 1978; Lubinski 2001; Hillson 2005; Ruscillo 2006; Anders et al. 2011). Accordingly, tooth ontogeny provides a measure of taxon specific individual age comprising phases of development, replacement, and wear. Yet, the usage of dentitions' ontogenetic stages as age indications requires exact knowledge on anatomical and age specifics in the ontogeny of species. However, complete

✉ Christine Böhmer
boehmer@vertevo.de

[1] Department of Earth and Environmental Sciences, Ludwig-Maximilians-Universität München, Richard-Wagner Straße 10, 80333 Munich, Germany

[2] SNSB–Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner Straße 10, 80333 Munich, Germany

[3] GeoBio-Center der Ludwig-Maximilians-Universität München, Richard-Wagner Straße 10, 80333 Munich, Germany

ontogenetic series with age details are unknown for most living mammals and data on extinct species are even sketchier. The fragmentary fossil record usually impedes gathering of full ontogenetic series and absolute individual age can only be inferred from correlation with living relatives. In this context, exceptionally rich fossil assemblages are a major source of evidence of dentition ontogeny.

In the present study, we took advantage of the Miocene fossil lagerstätte Sandelzhausen in Germany, which has revealed an exceptional high percentage of remains of juvenile individuals for many species (Fahlbusch 1976, 2003; Moser et al. 2009). In particular, the rhinoceros *Prosantorhinus germanicus* is remarkable for an extraordinary high number of juvenile dentaries at different developmental stages including highly fragile tooth germs (Fahlbusch et al. 1972; Peter 2002). The dental formula for *P. germanicus* was previously described as 1(?) 0 3/ 2 0 3=18 for juvenile and 1 0 4 3/ 2 0 4 3=34 for adult individuals (Peter 2002). *Prosantorhinus germanicus* is a representative of the extinct Teleoceratini lineage for which a hippo-like semiaquatic lifestyle is hypothesized, which is absent in extant rhinoceroses (Heissig 1972; Prothero et al. 1989; Cerdeño 1996). Thus, modern rhinos may be poor models for this extinct rhino. However, there is some debate with regard to the proposed ecological analogy between hippos and teleoceratines (e.g., Mihlbachler 2003). Dental ontogeny of rhinoceroses has been investigated in the living African species, the White rhinoceros (*Ceratotherium simum*) (Bigalke et al. 1950; Dittrich 1972, 1974; Hillman-Smith et al. 1986) and the Black rhinoceros (*Diceros bicornis*) (Anderson 1966; Goddard 1970; Dittrich 1974; Hitchins 1978), as well as in the extinct species *Stephanorhinus hundsheimensis* and *Aceratherium incisivum* (Eurasia) (Koenigswald et al. 2007), *Teleoceras proterum* and *Aphelops malacorhinus* (North America) (Mihlbachler 2003), and the woolly rhinoceros (*Coelodonta antiquitatis*) (Garutt 1994; Shpansky 2014), which is a rather small sample when considering the known total of 198 extant and extinct species of the family Rhinocerotidae (obtained from The Paleobiology Database, downloaded June 2015 using the family name Rhinocerotidae). Dental ontogenetic data reported in these studies include dental wear as well as the timing of tooth eruption, which are similar in living and fossil rhinos. Apart from variation in the eruption timing of p2, p3, and m2, the tooth eruption sequence for rhinocerotids follows a consistent pattern: (d2, d3), (d4, d1), m1, m2, (p2, p3), p4, m3 (parentheses enclose teeth with more or less simultaneous eruption) (Fortelius 1985).

Here, we intend to contribute to the study of evolutionary dental ontogeny in rhinocerotids by reconstructing the tooth replacement pattern of the extinct *P. germanicus* via analyzing dental wear stages of the deciduous teeth, eruption state of the postcanine dentition, and germ development inside the jaw. The evolution of diphyodonty, one apomorphy of mammals (Owen 1855; Peyer 1963; Ziegler 1971; Luo et al. 2004), resulted in heterochronic variation in the timing of molar eruption relative to that of the replacement teeth across specific mammalian growth patterns (Schultz 1960; Smith 1994, 2000). According to 'Schultz's rule,' rapidly growing mammals have all three molars erupted before any teeth are replaced, whereas slowly growing species start to replace the deciduous cheek teeth relatively early, at least before the last molar is erupted (Schultz 1960; Smith 1994, 2000). Based on the documentation of the ontogenetic stages of the fossil dentaries, our study will also test if *P. germanicus* falls into the life history category of slow-growing, long-living mammals like its extant relatives. Furthermore, the investigation of the teeth in *P. germanicus* will allow evaluating the individual age-at-death of the fossil specimens and, thus, will provide insights into the age-at-death distribution in the Sandelzhausen fossil site. This may reveal trends in mortality that will add to the interpretation of the taphocenosis of Sandelzhausen because the juvenile mortality profile reflects either a non-selective mortality due to a catastrophic event or a selective mortality favoring age classes with lower death risk at natural environmental stress.

Material and Methods

The analyzed material is housed at the Staatliche Naturwissenschaftliche Sammlungen Bayerns - Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG) in Munich. The study focuses on the lower dentition of *P. germanicus*, as maxillae with complete dentitions are rare. The documentation of the dental ontogeny in *P. germanicus* is based on 24 lower jaws with 56 in situ deciduous cheek teeth (four d1 and 52 d2–d4) representing 18 juvenile individuals and one subadult individual. Additionally, isolated deciduous cheek teeth were included in the analysis of dental wear. A total of 113 in situ and isolated deciduous cheek teeth (28 second deciduous premolars, 42 third deciduous premolars, 43 fourth deciduous premolars) were measured (see Appendix for a detailed list and SNSB-BSPG 1959 II numbers of the analyzed material).

d1–4 lower deciduous premolars, *m1–3* lower molars, *p1–4* lower permanent premolars

Reconstruction of Dental Ontogeny and Classification of Ontogenetic Stages

Qualitative macroscopic and radiological analysis (X-rays and CT scans) of all fossil mandibles was performed in order to comprehensively describe their ontogeny. Based on the number of erupted teeth, degree of dental wear, and presence of tooth germs inside the jaw, the mandibles' ontogenetic stages were interpreted and placed in a chronological order reflecting the eruption sequence and tooth replacement pattern of *P. germanicus*. According to this, we established 11 ontogenetic stages representing ten morphological events until reaching adulthood. In doing so, teeth were considered as starting eruption when emerging at the dorsal aspect of the mandible and as fully erupted, when the tooth crown appears fully dorsal to the mandible. Finally, reference data on the eruption sequence and replacement pattern in extant rhinoceroses obtained from a literature survey were used to correlate the age stages of *P. germanicus* with absolute ages. The documented timing and age range of morphological events during dental ontogeny of modern rhinos were associated with the dental eruption stages of the Miocene rhino. This allowed inferring absolute minimum and maximum individual ages of each dental eruption stage for *P. germanicus*.

Quantification of Dental Wear

The degree of dental wear was used as indicator to evaluate the individual age-at-death of the fossil specimens represented by in situ and isolated deciduous cheek teeth. Crown morphology of d2, d3, and d4 are illustrated in Fig. 1a–c. Tooth crown terminology used in this study is based on the nomenclature proposed by Heissig (1968) and Peter (2002).

Dental wear on the deciduous teeth was quantified via morphometric analyses by considering two parameters. The first measured parameter is the crown height (H) within the anterior buccal cusp of the deciduous cheek teeth (Fig. 1d). The second parameter is the dentinal width (W) on the posterior occlusal surface of the teeth (Fig. 1e, f) that emerges and increases with progressive dental wear. The dentinal width of d2 was measured from the buccal boundary of the hypolophid perpendicular to the longitudinal axis of the lower jaw to the ring-shaped talonid-pit (Fig. 1e). In d3 and d4, the dentinal width was measured in the anterior part of the hypolophid representing the largest width before it curves lingually

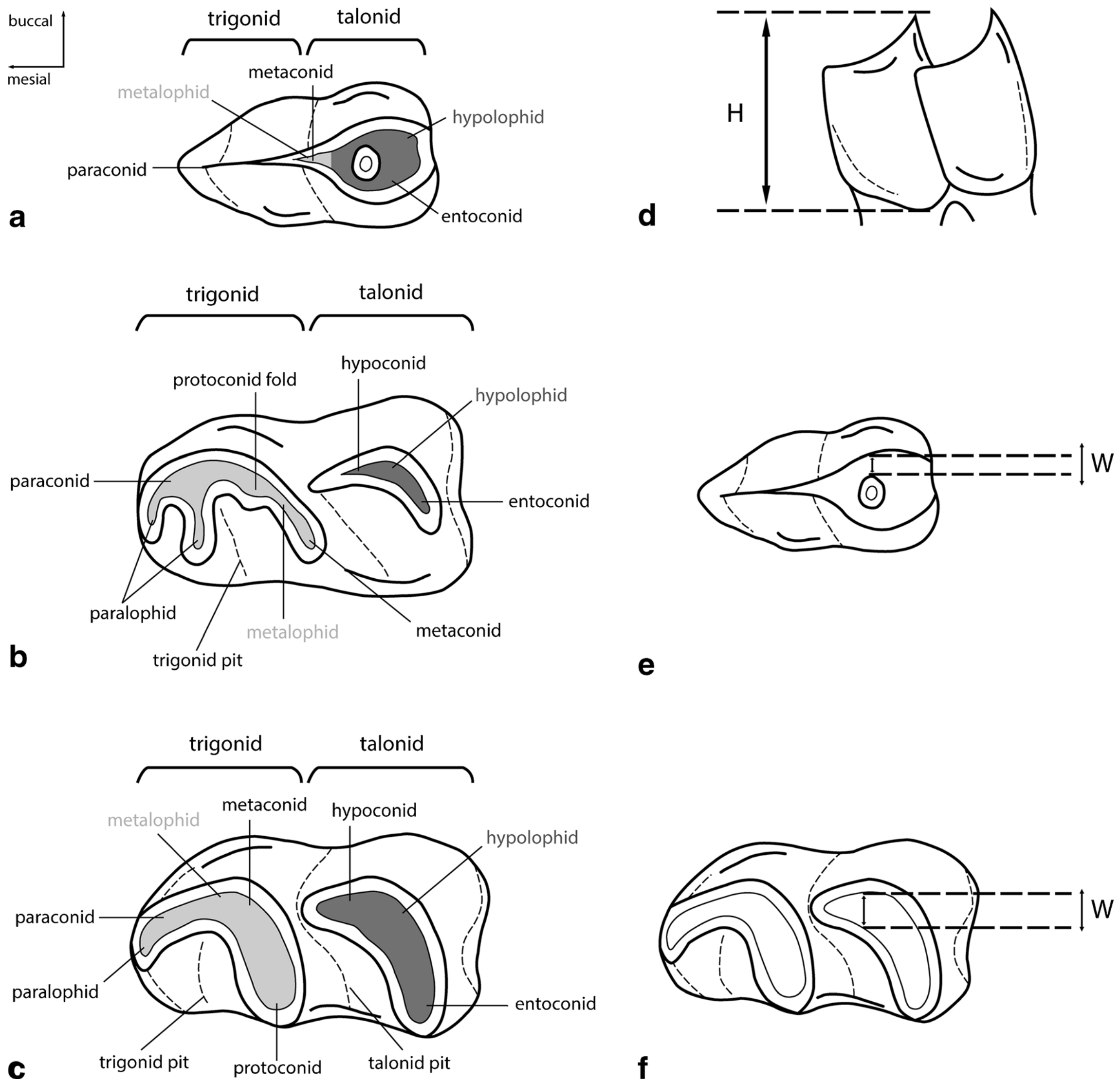

Fig. 1 Tooth crown elements of **a** d2; **b** d3; **c** d4 of the rhinoceros *Prosantorhinus germanicus* in occlusal view (after Heissig 1968; Peter 2002). Dental parameters measured on the deciduous teeth of *P. germanicus*: **d** H = crown height; **e**, **f** W = dentinal width

(Fig. 1f). The measurements were taken twice with a digital caliper rule and averaged resulting in the mean crown height (standard error 0.16 mm) and the mean dentinal width (standard error 0.07 mm) for each deciduous tooth.

Age-at-Death Distribution (Juvenile Mortality Profile)

In order to establish a juvenile mortality profile for *P. germanicus*, frequency distributions of represented ontogenetic stages of the fossil mandibles and wear stages of the in situ and isolated deciduous cheek teeth were calculated. The correlations with absolute individual age data of living rhinos enabled us to reconstruct the age-at-death distribution of the *P. germanicus* juveniles found at the Sandelzhausen site and to infer accumulation modi of the fossils via comparison with mortality trends of extant juvenile rhinos.

Results

Reconstruction of Dental Ontogeny and Classification of Dental Eruption Stages

The measured degree of dental wear of the in situ deciduous cheek teeth revealed the ontogenetic order of the represented individuals (Table 1), because individual age (time of usage) increases with increasing wear, i.e., decreasing crown height and increasing dentinal width.

Considering in addition the entity of erupted teeth, the fossil deciduous dentitions show, generally speaking, an association of low degree of dental wear with an incomplete/still developing milk dentition and the lack of permanent teeth, whereas a higher degree of dental wear of the deciduous cheek teeth is accompanied with the eruption of the permanent teeth of the adult dentition. In addition, the radiological analysis revealed the presence of tooth germs inside the fossil jaws (Fig. 2). As all radiological images show the roots of the corresponding erupted teeth in the jaw, thus, it is appropriate to assume that the presence or absence of tooth germs in the X-ray is diagnostic. The compilation of data allowed for a classification of a total of 11 dental ontogenetic stages for *P. germanicus* (Table 2). Among those stages, 6 and 8 needed to be inferred and extrapolated from earlier and later stages, because the direct fossil evidence is missing.

Specimen SNSB-BSPG 1959 II 2257 represents the youngest individual (stage 0) recorded. The only teeth present, second and third deciduous cheek teeth, are in eruption. The d2 is unworn, whereas d3 is worn in the region of the talonid, but the trigonid is still edged. Despite the fragmentary preservation of the mandible, the radiological analysis revealed evidence for the absence of the d1 and d4 (Fig. 2a). The X-ray image shows the roots of d2 and d3 in the bone, but confirms the absence of a d1 germ as well as of d4, p2, and p3 germs (Fig. 2a).

Table 1 Dental wear measurements (mm) of *Prosantorhinus germanicus* from Sandelzhausen fossil site

	d2		d3		d4	
SNSB-BSPG 1959 II	H	W	H	W	H	W
2257	14.9	0.0	19.7	0.9		
2279	15.1	1.3	19.5	1.2		
3782	–	–	15.9	0.9	19.4	0.0
4547	12.8	2.9	17.4	2.0	18.6	0.0
3106	–	–	–	2.1	21.6	1.7
2261	12.3	2.0	15.7	2.2	24.8	1.6
2253	14.5	1.7	15.7	2.7	22.6	1.3
4534	–	–	–	–	22.6	1.7
2255 left	–	–	15.6	2.6	20.4	2.1
2255 right	–	–	–	–	18.1	1.9
522	12.6	1.8	15.2	2.2	20.7	1.6
2281	11.8	2.2	15.1	2.2	22.0	1.8
1939	11.0	3.5	14.0	3.3	21.4	2.1
3715	–	–	13.6	2.7	22.9	1.9
2268	–	–	13.9	3.7	19.0	2.1
2251	10.5	5.2	12.4	3.4	17.8	3.2
3362	10.4	3.8	12.0	4.2	18.8	2.9
5978 left	8.1	6.3	10.5	5.2	17.1	3.9
5978 right	–	–	11.2	5.5	15.2	3.5
1	p2		10.0	5.7	11.9	5.7
2264	p2		8.0	8.7	–	3.2
2265	p2		7.6	7.8	14.0	3.4

Mandibles with in situ deciduous cheek teeth are listed in order based on decreasing crown height (H) and increasing dentinal width (W) of d3. Crown height and dentinal width are each given as the average of two independent measurements

Abbreviation: − not measurable

Stage 1 is defined by erupting d1 and d4, d2 and d3 in wear as well as presence of the m1 germ (Table 2). This is represented by specimen 4547, a complete hemimandible (Figs. 2b and 3). No premolar germs were found via the radiological images (Fig. 2b). Due to its fragmentary preservation, specimen 2279 holds only d2 and d3, but they are both fully erupted and in wear (Table 1), thus representing an equivalent stage to specimen 4547.

The successive morphological event (stage 2) comprises entirely erupted d1 and d4 and d2–d4 in wear (d1 lacked integration into occlusion). Additionally, the m1 germ is developed (Table 2). The latter is recorded in specimen 2261, which shows entirely erupted and slightly worn d2, d3, and d4 (Table 1). However, some uncertainty remains due to the fragmentary preservation of the hemimandible that does not allow for assessing a germ or erupting stage of m1.

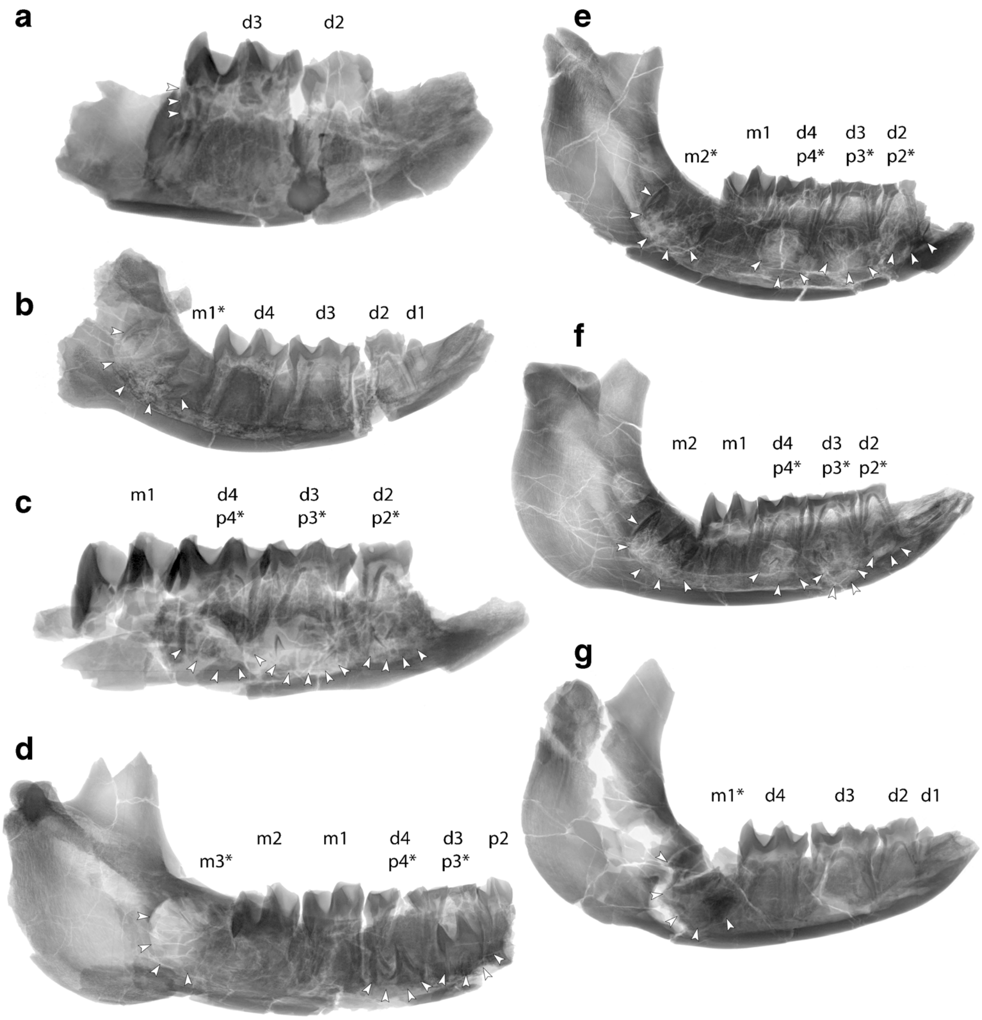

Fig. 2 Latero-lateral X-rays of dentaries of *Prosantorhinus germanicus* at different developmental stages. *Arrowheads* **a** indicate that the deciduous tooth is not completely erupted and **b-f** mark tooth germs inside the jaw. **a** left dentary SNSB-BSPG 1959 II 2257 (stage 0); **b** right dentary SNSB-BSPG 1959 II 4547 (stage 1); **c** left dentary SNSB-BSPG 1959 II 1939 (stage 4); **d** left dentary SNSB-BSGP 1959 II 2264 (stage 7); **e** right dentary SNSB-BSGP 1959 II 2251 (stage 5); **f** left dentary SNSB-BSPG 1959 II 5978 (stage 5); **g** right dentary SNSB-BSGP 1959 II 2253 (stage 3). *Abbreviations*: * = tooth germ

Stage 3 is characterized by the erupting m1 (Table 2). Specimens 2261, 3715, 522, 2253, 2255 (right and left), and 2281 all possess an m1 in beginning eruption along with completely erupted deciduous teeth (Fig. 3). The d2, d3, and d4 reveal dentine exposed on the occlusal surface due to progressive wear (Table 1). The exceptionally well-preserved hemimandibles 522 and 2253 display an entirely erupted d1 (Fig. 3). The radiological imaging revealed that the premolar germs were not

Table 2 Dental eruption stages as recorded for *Prosantorhinus germanicus* from Sandelzhausen fossil site, except for stages 6 and 8 which are inferred

Dental eruption stages								Condition of externally visible teeth	Tooth germs					
0		d2	d3					d2 and d3 erupting						
1	d1	d2	d3	d4				d1 and d4 erupting; d2 and d3 in wear	m1					
2	d1	d2	d3	d4				Full deciduous complement in wear	m1					
3	d1	d2	d3	d4	m1			Full deciduous complement; d2–d4 in wear; m1 erupting						
4	d1	d2	d3	d4	m1			Full deciduous complement; d2–d4 in wear; m1 not in wear		p2	p3	p4		
5		d2	d3	d4	m1			d1 shed; d2–m1 in wear		p2	p3	p4	m2	
6		d2	d3	d4	m1	m2		d2–m1 in wear; m2 erupting		p2	p3	p4		
7		p2	d3	d4	m1	m2		p2 erupting (replacing d2); d3–m1 in wear; m2 erupting			p3	p4		m3
8		p2	p3	d4	m1	m2		p2; d4–m2 in wear; p3 erupting (replacing d3)				p4		m3
9		p2	p3	p4	m1	m2	m3	p2–p3; m1–m2 in wear; p4 erupting (replacing d4); m3 erupting						
10		p2	p3	p4	m1	m2	m3	p2–m3 in wear						

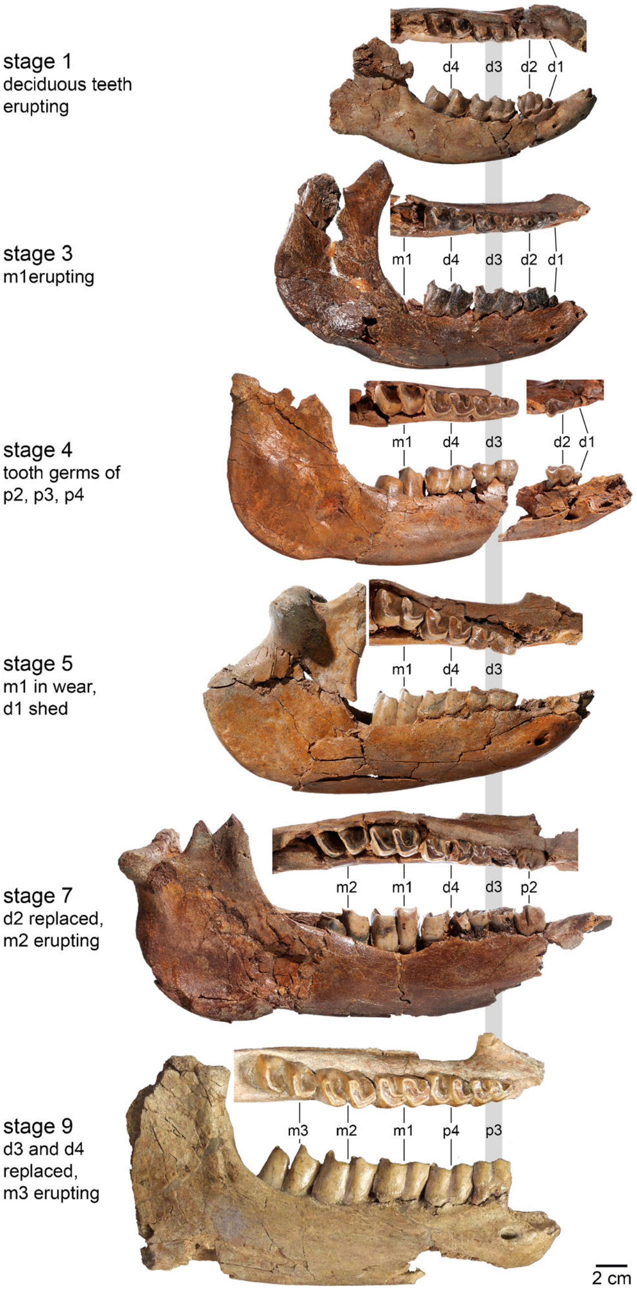

Fig. 3 Ontogenetic series based on state of dental development of the dentaries of *Prosantorhinus germanicus* in lateral and occlusal view. See Table 2 for detailed description of dental eruption stages as recorded for *P. germanicus*. Stage 1, SNSB-BSPG 1959 II 4547; stage 3, SNSB-BSPG 1959 II 2253; stage 4, SNSB-BSPG 1959 II 3362 (mirrored); stage 5, SNSB-BSPG 1959 II 5978; stage 7, SNSB-BSPG 1959 II 2264 (mirrored); stage 9, SNSB-BSPG 1959 II 2278 (mirrored)

developed yet (Fig. 2g). The fragmentarily preserved specimen 4534 holds a moderately worn d4 (Table 1) and an erupting m1 only with some remains of the surrounding fossil bone. No p4 germ was found via the radiological analysis. In total, these characteristics indicate stage 3 for 4534 as well.

The next morphological event is the presence of all premolar germs (stage 4). Specimens 1939, 2268, and 3362 each hold deciduous teeth showing advanced dental wear (Table 1) and a nearly completely erupted m1 that is unworn. The radiological analysis revealed all premolar germs embedded in the jaw bone below their functional precursors (Fig. 2c).

In contrast, specimens 2251 and 5978 (left and right) (stage 5) show fully functional first molars with wear marks (Fig. 3). 5978 is an exceptionally well-preserved mandible with left and right processes holding each d2, d3, d4, and m1, but it does not show any trace of the d1s, which suggests that the first deciduous cheek tooth was physiologically shed (Fig. 2f). The X-ray images display the premolar germs still in the jaw (Fig. 2e). Additionally, all three lower jaw halves contain an unerupted m2 (Fig. 2e, f).

The successive morphological event comprising the beginning eruptional phase of m2 before starting replacement of d2 (stage 6) (Table 2) is known from studies on recent rhinos (Anderson 1966; Goddard 1970; Hillman-Smith et al. 1986; Hitchins 1978; Tong 2001) (Table 4) but not recorded in the Sandelzhausen *P. germanicus* sample. However, specimens 1, 2264, and 2265 (stage 7) display advanced stages of dental eruption and tooth replacement (Table 2). Apart from clearly worn m1s, m2s are in eruption and p2s replace d2s (Fig. 3). In 2264, p2 is completely erupted, but not in wear yet (Fig. 3). The radiological images of all three specimens reveal the p3 germ in a higher position than the p4 germ (Fig. 2d). In addition, the radiological image of 2264 displays the germ of m3 (Fig. 2d).

Erupting p3 and the replacement of d3 while d4 was still in function is not recorded but it is likely that it was the next successive morphological event (stage 8) due to the more dorsal position of the p3 germ compared to the p4 germ as observed in 1, 2264 and 2265 (stage 7, Table 2) and observations in extant rhinos (Anderson 1966; Goddard 1970; Hitchins 1978; Hillman-Smith et al. 1986; Tong 2001) (Table 4).

Specimen 2278 (stage 9) does not hold any deciduous teeth, but p3, p4, m1, m2, and m3 (Fig. 3). The second molar was already in wear, whereas the m3 was still in eruption.

Specimen 3106 preserves only fragmentary pieces of the second, third, and fourth deciduous cheek teeth and shows the m1 in beginning eruption. The X-ray image revealed that d2, d3, and d4 are not shed but rather broken off. Furthermore, it proved the absence of premolar germs. This combination of characteristics indicates stage 3. However, 3106 additionally holds some pieces of the m2 germ, which is characteristic for stage 5, but this stage is further characterized by the presence of the premolar germs. In contrast to the fragmentary preservation of the deciduous cheek teeth, the mandibular bone in the respective area is complete and, thus, the radiological analysis confirmed the absence of any premolar germs.

Specimen 3782 (stage 2–3) is unusual because the bone appears to be more solid and heavier than that of the other fossils. Moreover, the deciduous cheek teeth are more robust. The m1 is in initial eruption and the premolar germs are not yet developed. In contrast to the other jaws possessing an erupting m1, 3782 has an unworn d4 (left and right). The third

Table 3 Tooth eruption sequences in living and extinct (†) rhinoceroses

Taxon	Tooth eruption sequence	Crown morphology	Reference
Ceratotherium simum	(d2, d3), d4, d1, m1, p2, (p3, p4, m2), m3	Hypsodont	Bigalke et al. (1950), Dittrich (1972), (1974), Hillman-Smith et al. (1986)
Diceros bicornis	(d2, d3), (d4, d1), m1, m2, (p2, p3), p4, m3	Brachydont	Anderson (1966), Dittrich (1974), Goddard (1970), Hitchins (1978)
†*Stephanorhinus hundsheimensis*	(d2, d3, d4, d1), m1, m2, (p2, p3), p4, m3	Brachydont	Koenigswald et al. (2007)
†*Aceratherium incisivum*	(d2, d3, d4, d1), m1, m2, (p2, p3), p4, m3	Brachydont	Koenigswald et al. (2007)
†*Teleoceras proterium*	[?d2], d3, d4, [?d1], m1, [?p2], p3, m2, p4, m3	Hypsodont	Mihlbachler (2003)
†*Aphelops malacorhinus*	[?d2], d3, d4, [?d1], m1, [?p2], p3, m2, p4, m3	Brachydont	Mihlbachler (2003)
†*Coelodonta antiquitatis*	d3, d2, d1, d4, p2, p3, m1, m2, p4, m3	Hypsodont	Garutt (1994), Shpansky (2014)
†*Prosantorhinus germanicus*	(d2, d3), (d1, d4), m1, m2, p2, p3, p4, m3	Brachydont	This study

Parentheses enclose teeth with more or less simultaneous eruption. There is no information available about the timing of eruption of d1, d2, and p2 in *Teleoceras* and *Aphelops*. Hypsodont = high-crowned cheek teeth, brachydont = low-crowned cheek teeth

deciduous tooth is also relatively little worn. Due to the apparent differences in comparison to the other mandibles, an assumed pathology in specimen 3782 appears to be reasonable. However, this specimen is currently under further investigation in order to verify this hypothesis.

Tooth Replacement Pattern of *Prosantorhinus germanicus*

In summary, the record of the ontogenetic series of juvenile *P. germanicus* mandibles from Sandelzhausen documents a dental eruption sequence of (d2, d3), (d1, d4), m1, m2, p2, p3, p4, m3 (Table 3). This pattern is characteristic for rhinoceroses in general (Fortelius 1985) and shows correspondence with the previously recorded tooth eruption sequences in living and extinct rhinos (Table 3). Considering 'Schultz's rule,' the tooth eruption sequence indicates that *P. germanicus* was a slowly growing species because the deciduous cheek teeth are replaced before the last molar is erupted.

The documented dental ontogeny for *P. germanicus* indicates that d1 and d4 erupt more or less simultaneously. Furthermore, d1 is shed without successor before the replacement of d2, d3, and d4 begins. This suggests that the first mandibular cheek tooth is part of the deciduous dentition and thus the dental formula of *P. germanicus* is 1(?) 0 4/ 2 0 4=22 for juvenile and 1 0 3 3/ 2 0 3 3=34 for adult individuals (in contrast to Peter 2002). Correspondingly, the first mandibular cheek tooth is also part of the deciduous dentition in *C. simum* as indicated by the dental formula of *C. simum* 0 0 4/ 0 0 4=16 for juvenile and 0 0 3 3/ 0 0 3 3=24 for adult individuals (Hillman-Smith et al. 1986). The same applies to the fossil rhinos *S. hundsheimensis* and *A. incisivum* (Koenigswald et al. 2007) as well as *C. antiquitatis* (Garutt 1994). In contrast, the dental formula of *D. bicornis* 0 0 4/ 1–2 0 4=18–20 for juvenile and 0 0 4 3/ 0 0 3–4 3=26–28 for adult individuals (Hitchins 1978) reveals some variation with regard to the first postcanine position. In this regard, there is no information available for *T. proterum* and *A. malacorhinus*.

Correlation of Dental Eruption Stages

The comparison between dental eruption stages recorded for *P. germanicus* and age classes reported for living rhinos allows correlation of the dental eruption stages with individual age ranges (Table 4). In general, rhinos are born with only two deciduous cheek teeth, d2 and d3, and the other milk teeth erupt within 2 to 12 months in extant rhinos (Table 4) and by stage 1 in *P. germanicus*. The full deciduous dentition is developed and in function by about 1.5 years in the living rhinos (Table 4) and by stage 2 in *P. germanicus*. In parallel, the first molar develops as tooth germ (Table 4) and is finally in eruption until about 3 years in the extant rhinos (Table 4) and by stages 3–4 in *P. germanicus*. In *C. simum*, the second premolar begins to erupt between 3 and 4 years (Hillman-Smith et al. 1986). The third and fourth premolar erupt after p2 and the second molar erupts between 4 and 7 years of age (Hillman-Smith et al. 1986). All premolars are in wear by about 8 years in the White rhino (Hillman-Smith et al. 1986). In *D. bicornis*, the second molar starts to erupt before the premolars (Table 3) at about 4 years (Table 4). Subsequently, the second, third, and fourth premolar erupt in sequence between 5 and 8 years (Goddard 1970; Hitchins 1978). In *P. germanicus*, the eruption of m2 begins before that of the premolars (Table 3) at stage 6 and the premolars erupt in sequence between stages 7–9. In general, the third molar is the last tooth to erupt in rhinos (Table 3) between 8 and 11 years in living rhinos (Table 4) and at stage 10 in *P. germanicus*. On average, the extant rhinos reach a maximum age of about 35–40 years (Goddard 1970; Hillman-Smith et al. 1986; Hillman-Smith and Groves 1994).

Table 4 Correlation between dental eruption stages as recorded for *Prosantorhinus germanicus* from Sandelzhausen fossil site (see Table 2 for description of the dental eruption stages) and age classes of extant rhinoceroses (*Diceros bicornis*, *Ceratotherium simum*) based on dental data (eruption sequence, tooth replacement, dental wear)

Dental eruption stages with calibrated age ranges (*P. germanicus*)		Age class (*D bicornis*) (Goddard 1970)	Age class (*D. bicornis*) (Hitchins 1978)	Age (*D. bicornis*) (Anderson 1966)	Age class (*C. simum*) (Hillman-Smith et al. 1986)	Life stage (*C. simum*) (Hillman-Smith et al. 1986)
0	≤2 m	I (0 y)	I (n.s.)	Fetus	I (1.5–2 m)	Newborn infant
1	2 m–1 y	II–III (0.5–1.0 y)	II (n.s.)	+3 m	II–III (2–12 m)	Unweaned infant
2	3 m–1.5 y	II–III (0.5–1.0 y)	III (n.s.)	+3 m	IV (12–18 m)	Calve still nursing
3	9 m–3 y	IV (1.5 y)	IV (n.s.)	9 m	V (1.5–3 y)	Calve still accompanying mother
4	9 m–4 y	IV–V (1.5–2+/−0.5 y)	V (4 y)	9 m	VI (3–4 y)	Adolescent independent of mother, not yet reproductive mature
5	9 m–4 y	V (2+/−0.5 y)	V (4 y)	9 m	VII (3.5–4 y)	Adolescent independent of mother, not yet reproductive mature
6	14 m–7 y	VII (4+/−0.5 y)	V (4 y)	14–16 m	VIII (4–7 y)	Adolescent independent of mother, not yet reproductive mature
7	1.5–9 y	VIII (5+/−0.5 y)	VII (6–7 y)	18–20 m	VIII–IX (4–9 y)	Subadult (reproductive mature but not yet full weight)
8	2–9 y	IX (6+/−0.5 y)	VIII (6–7 y)	2 y	VIII–IX (4–9 y)	Subadult (reproductive mature but not yet full weight)
9	6.5–9 y	X (7+/−0.5 y)	IX–X (7–12 y)	7 y	VIII–IX (4–9 y)	Subadult (reproductive mature but not yet full weight)
10	≥7.5 y	XI (8+/−0.5 y)	XI (10 y)	Mature	X (8–11 y)	Adult

This helps to calibrate the dental eruption stages of *P. germanicus* with age ranges. In the extant rhinoceros *C. simum*, the age classes based on dental data were interrelated with life stages

Abbreviations: n.s. not specified, *m* months, *y* years

Dental Wear

Table 5 and Fig. 4 summarize the results of the quantitative dental wear analysis. Corresponding to their morphology, the deciduous teeth vary in their maximum crown height with d2 being the lowest and d4 being the highest tooth. There are teeth from all three tooth positions that do not show any signs of exposed dentin (four d2, one d3, ten d4). The tooth morphology influences the measured width of the dentin. The minimal dentinal width is about 1.0 mm for all three tooth positions. The absolute maximal dentinal width is measured in d3.

Plotting dentinal width against crown height reveals the relationship of both measurements in d2, d3, and d4 (Fig. 4a). Although the measurements confirm that dentinal width increases when crown height decreases (Fig. 4b), there is no significant correlation of crown height with dentinal width (r^2<0.90) (Fig. 4a). Both measures of dental wear provide additional information for more detailed determination of the individual age of an animal at death not only for tooth series, but also for isolated teeth.

Juvenile Mortality Profile

Both the frequency distribution of crown height and dentinal width of the in situ and isolated deciduous teeth (Fig. 5) as well as of the ontogenetic stages represented by the fossil mandibles (Fig. 6) indicate a similar juvenile mortality pattern for *P. germanicus*. The measurement of dental wear reveals a peak in worn d2 (Fig. 5a, d), moderately worn d3 (Fig. 5c, e), and unworn or slightly worn d4 (Fig. 5c, f). This indicates an increased mortality at ages in which all or at least the first two milk cheek teeth are in wear which corresponds to dental eruption stages 1–3 documented for *P. germanicus* (Table 2). The comparison with data of living rhinoceros shows that this correlates with relatively young age classes indicating an age range of about 2 months to 3 years (Table 4).

Table 5 Univariate analysis of the dental wear measurements (mm) of *Prosantorhinus germanicus* from Sandelzhausen fossil site

	H(d2)	H(d3)	H(d4)	W(d2)	W(d3)	W(d4)
Number of teeth	28	42	43	24	41	33
Minimum value	8.1	7.6	10.6	0.8	0.9	1.2
Maximum value	17.0	23.4	26.8	6.3	8.7	5.7
Mean value	12.93	15.35	19.36	2.56	2.94	2.78
Variance	4.75	13.31	16.52	2.37	3.35	1.31
Standard deviation	2.18	3.65	4.06	1.54	1.83	1.14

The total number of measurements of the isolated and in situ deciduous cheek teeth of *P. germanicus* differs between crown height (H) and dentinal width (W) because there are teeth that do not show any exposed dentin: 4 d2, 1 d3, and 10 d4

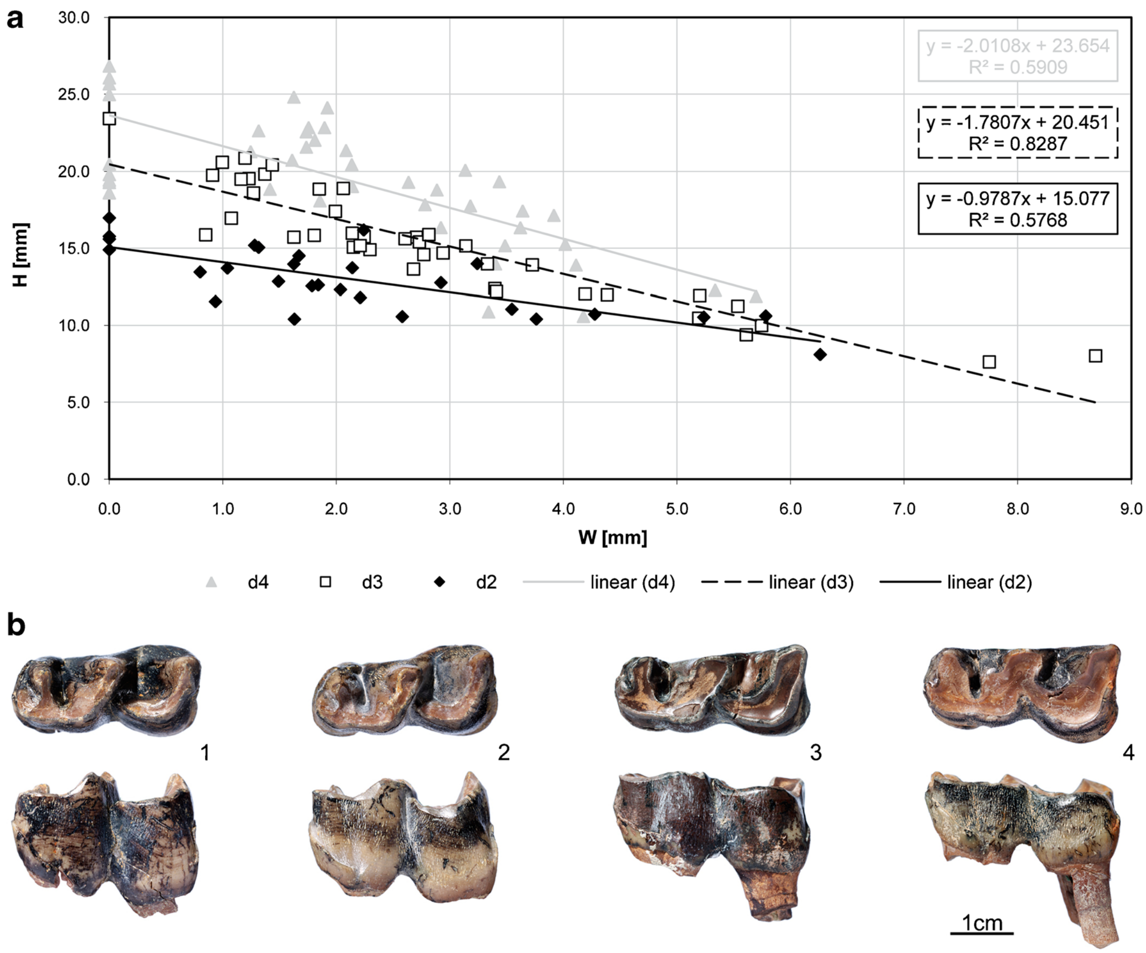

Fig. 4 Dental wear in *Prosantorhinus germanicus*. **a** Linear regression plot of measured crown height (*H*) and dentinal width (*W*) of the isolated and in situ deciduous cheek teeth of *P. germanicus* (28 d2, 42 d3, 43 d4); **b** visualization of morphological change in d3 of *P. germanicus* with progressive dental wear due to crown height reduction and increasing dentin exposure (*top row*: occlusal view, *bottom row*: lateral view). The depicted deciduous teeth display different degrees of dental wear. 1, SNSB-BSPG 1959 II 4518; 2, SNSB-BSPG 1959 II 2470; 3, SNSB-BSPG 1959 II 2454; 4, SNSB-BSPG 1959 II 2463; 5, SNSB-BSPG 1959 II 2452

The juvenile age-at-death distribution based on the fossil mandibles reveals a tendency towards an increased mortality at dental eruption stages 2–3 (37 % of the represented individuals) (Fig. 6). The highest mortality (stages 2–3) corresponds to an age range of about 3 months to 3 years (Table 4).

Discussion

Dental Ontogeny in Rhinocerotids

The combined qualitative macroscopic and radiological analysis of the excellently preserved fossil mandibles with dentition of *P. germanicus* clearly revealed the anatomical changes that occur during dentition ontogeny of this extinct rhinoceros (Table 2, Figs. 2 and 3) and contributes to the evolutionary history of dental ontogeny in rhinocerotids. The comparison of the tooth eruption sequences reported for living and extinct rhinoceroses including *P. germanicus* indicates that the sequence is quite conservative with regard to the eruption of the deciduous cheek teeth, the first and third molar, but there is variation in the timing of the eruption of p2, p3, and m2 (Table 3). In *C. simum*, *T. proterum*, *A. malacorhinus*, and *C. antiquitatis*, at least one premolar (p2, p3) is replaced before m2 erupts, whereas in *D. bicornis*, *S. hundsheimensis*, *A. incisivum*, and *P. germanicus*, m2 erupts before p2 and p3 (Table 3). The woolly rhino (*C. antiquitatis*) reveals an additional peculiarity of dental ontogeny because it replaces the second and third deciduous cheek teeth even before the first molar is in eruption (Table 3). This difference in dental eruption sequence may be due to the tooth crown morphology because rhinocerotids with hypsodont cheek teeth appear to erupt the second and third premolar before the second molar, whereas in rhinos with brachydont cheek teeth the m2 erupts before p2 and p3 (Table 3). As hypsodont cheek teeth are generally indicative of grazers that feed on highly abrasive

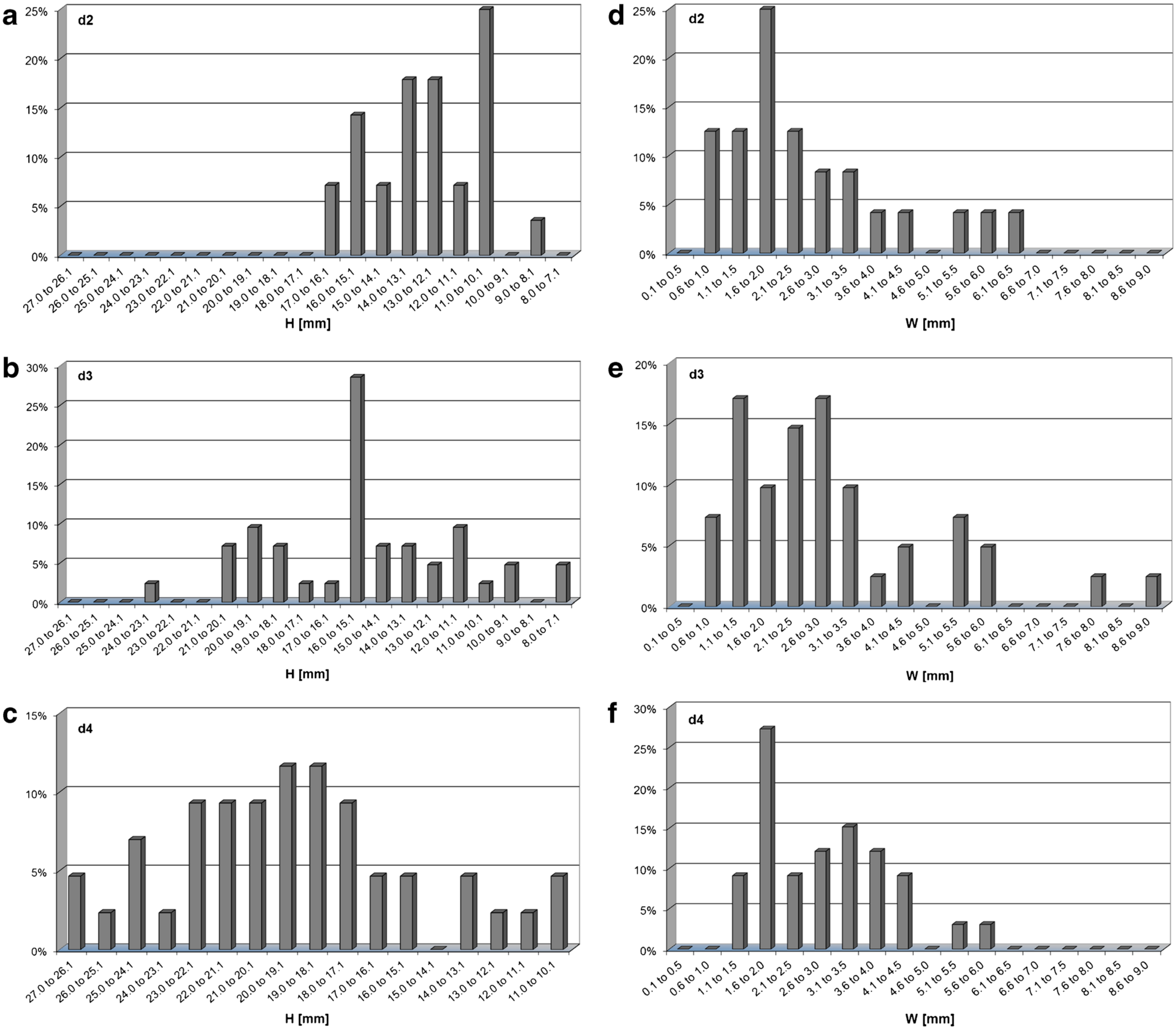

Fig. 5 Frequency distribution of measured dental wear of the isolated and in situ deciduous teeth of *Prosantorhinus germanicus*; **a** crown height in d2; **b** dentinal width in d2; **c** crown height in d3; **d** dentinal width in d3; **e** crown height in d4; **f** dentinal width in d4

roughage and hypsodonty usually applies to the adult dentition and not the milk teeth, one interpretation for the accelerated eruption of the premolars may be that the young rhinos experience high dental wear during grazing and, thus, the deciduous premolars have to be replaced relatively early.

Although loss of the replacement tooth at the first premolar position is known for living rhinoceroses, the tooth is either exclusively present in juveniles or it is retained within the adult stage (Foster 1965; Goddard 1970; Hitchins 1978; Groves and Grubb 2011). In some mammals, the interpretation of the first postcanine position as d1 or p1 is sometimes difficult, if based on the degree of tooth wear (e.g., Vera and Cerdeño 2014). However, d1 in *P. germanicus* was not in functional occlusion and thus, lacks wear. Based on the eruption sequence, our results suggest that the first mandibular cheek tooth belongs to the primary dentition in the extinct rhino *P. germanicus*. The first cheek tooth shows only a single tooth generation and is thus not replaced. The comparison of the radiological images of specimens 4547 and 5978 suggests that d1 is physiologically shed (Fig. 2b, f). This is very likely because the latter mandible is well preserved and therefore the first deciduous premolar is not lost due to the fossilization process. In the case of a tooth breakage, we would expect at least the presence of the alveolus in the jaw. However, the X-ray shows no alveolus of d1. This indicates either a dental anomaly, namely that the first deciduous tooth did not develop in this specimen; or the alveolus was ossified after d1 was shed. Re-ossification occurs relatively quickly in mammals; e.g., in rats, the re-ossification of the alveolus occurs within two to four weeks after tooth extraction (Raposo-Amaral et al. 2010).

Life History of *Prosantorhinus germanicus*

Following 'Schultz's rule,' which describes that mammals replace teeth in a pattern relative to their life history (Schultz 1960; Smith 1994, 2000), *P. germanicus* falls within the slow-growing, long-living species such as the living rhinoceroses because it starts to replace the deciduous cheek teeth before the last molar is erupted (Table 3). The same also applies to the other studied extinct rhinos suggesting that they grew slowly and were long-lived as well (Table 3). Although there is some debate with regard to the ecological interpretation (Mihlbachler 2003), *P. germanicus* differs somewhat from the other rhinos because it was a relatively small, short-legged species and is assumed to have had a hippo-like semiaquatic, herd-forming lifestyle (Heissig 1972; Prothero et al. 1989; Cerdeño 1996). However, according to 'Schultz's rule,' hippos, horses, and pigs are also slow-growing, long-living mammals (Smith 2000). In contrast, fast-growing artiodactyls such as the springbok (*Antidorcas*), the pronghorn (*Antilocapra*), or the common duiker (*Sylvicapra*) show eruption of all three molars before any teeth are replaced (Smith 2000). Although 'Schultz's rule' appears to be a good indicator for growth rate and life history in a number of mammals (e.g., Jordana et al. 2013), it has to be noted that exceptions to this rule have been reported for lemurs (Godfrey et al. 2005). 'Schultz's rule' assumes that the relative timing of molar eruption depends on the size of the jaw and, thus, on the absolute growth rate of the jaw, which is used as indicator for the general growth rate of the animal (Schultz 1960; Smith 1994, 2000). However, there are processes that allow the formation and eruption of permanent teeth in a jaw that might appear to be too small to accommodate them (Godfrey et al. 2005). Furthermore, other factors such as diet, environment, brain and body size are considered to affect dental growth and eruption sequence (Harvati and Frost 2007).

Although the living African rhinos, *C. simum* and *D. bicornis*, vary slightly in dental ontogeny, there is correspondence between tooth eruption sequence and life stage (e.g., Dittrich 1974). Comparing the age data reported for the extant rhinos by Goddard (1970), Hitchins (1978), and Hillman-Smith et al. (1986) reveals only little range, whereas the results reported by Anderson (1966) differ significantly from the other data and reveal some discrepancies as previously noted (e.g., Dittrich 1974; Hitchins 1978).

Taphonomic Interpretation and Juvenile Mortality Profile

Although Sandelzhausen mainly yielded disarticulated vertebrate skeletons, the preservation of fragile fossils and the absence of transport marks on most skeletal remains indicate that transport over long distances is unlikely (Fahlbusch et al. 1972). The sediments of the Upper Freshwater Molasse in which the fossils occur represent a limnofluvial paleoenvironment with seasonal inundations (Fahlbusch et al. 1972; Schmid 2002; Moser et al. 2009; Böhme 2010). The mammal remains were washed in from the moist subtropical woodland habitat and deposited within a relatively short time (Fahlbusch et al. 1972 and references therein; Fahlbusch 2003; Moser et al. 2009). There is evidence for accumulation of the fossils through deposition of episodic influx within a fluvial plain (Fahlbusch et al. 1972;

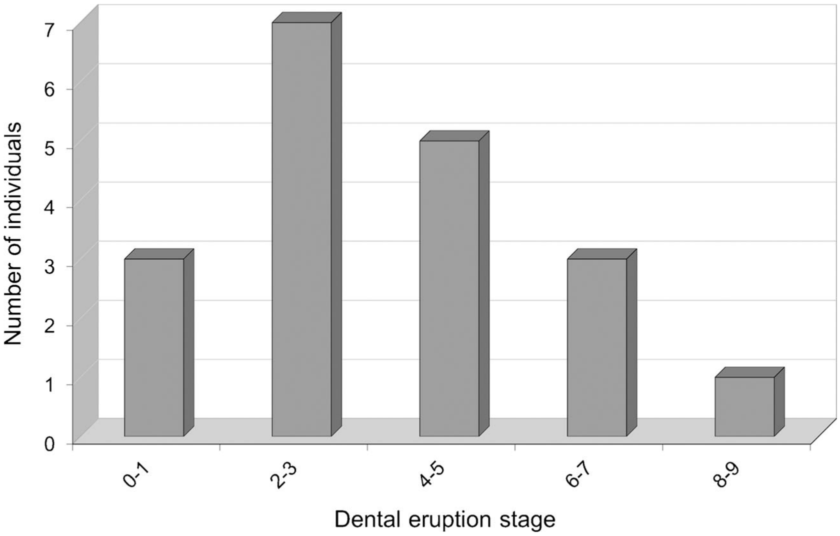

Fig. 6 Juvenile mortality profile of 19 individuals of *Prosantorhinus germanicus* represented by 24 mandibles from Sandelzhausen fossil site. The age-at-death distribution is based on the dental eruption stages (see Table 2)

Fahlbusch 1976). Although previous analyses indicate that the deposits of Sandelzhausen accumulated over a period of several decades to thousands of years (Schmid 2002), the exact duration of fossil deposition remains unclear (Fahlbusch 2003). Due to the uniform mammal fauna of Sandelzhausen, a deposition period of millions of years can be excluded, but the fossil lagerstätte may represent a single short-term event (Fahlbusch 2003).

In young animals the sequence of tooth eruption and replacement provides a highly informative method to determine the life stage of the individual. In general, there are two theoretical types of fossil accumulation with respect to the age-at-death distribution: the catastrophic and the attritional fossil assemblage (Kurtén 1953; Van Valen 1964; Voorhies 1969; Klein and Cruz-Uribe 1983; Lyman 1994). The first model reflects a catastrophic event that caused non-selective mass mortality (Klein and Cruz-Uribe 1983). The mortality profile typically displays the age structure of a natural population indicated by the dominance of individuals at reproductive age (Klein and Cruz-Uribe 1983; Anders et al. 2011). In contrast, the attritional fossil assemblage reflects selective mortality induced by mortality factors such as predation, accidents, disease, and starvation (Klein and Cruz-Uribe 1983). In this model, the mortality profile differs from the age structure of the living population because it shows peaks that correspond to ages in which death rates are the highest (Klein and Cruz-Uribe 1983). The most vulnerable members of a population are juvenile and/or old individuals and, thus, they outnumber members of intermediate age classes (Klein and Cruz-Uribe 1983).

With regard to mammals in general, Sandelzhausen is remarkable for the high number of juvenile remains (milk teeth as well as limbs with unfused epiphyses) (Fahlbusch et al. 1972). Focusing on juvenile *P. germanicus*, both, the dental wear analysis of the in situ and isolated deciduous teeth (Fig. 5) as well as the dental eruption stage analysis of the fossil mandibles (Fig. 6) revealed an increased mortality of *P. germanicus* at an inferred age range of about 3 months to 3 years. This age range represents unweaned infants, calves that are still nursing and/or still accompanying their mother (Table 4). The increased mortality at this life stage might indicate an attritional fossil assemblage because the percentage of individuals at ages with the highest natural risk of mortality is relatively higher (Kurtén 1953; Klein 1982). In general, there are two age phases of increased mortality: a juvenile phase characterized by a high rate of mortality, followed by an adult phase in which the rate of mortality is initially low but rises with increasing age (Caughley 1966). Although caution is needed when comparing *P. germanicus* with modern rhinos, there are findings indicating that teleoceratines share a link between mortality risks and life-history stages that is identical to that of the modern rhino *Diceros* (Mihlbachler 2003). Focusing on the non-adult stage in extant rhinoceroses, the life stage that is associated with the highest risk of mortality includes inexperienced yearlings. The analysis of an extant rhinoceros population (about 300 individuals: 52.2 % adults, 21.2 % subadults, and 26.6 % calves) resulted in minimum annual mortality rates of 5.6 % perinatal, 8.5 % for calves, 1.2 % for subadults, and 3.4 % for adults (Laurie 1982). Survival over the first year of life is at risk by multiple causes. Although the intake of solid food increases, extant rhinoceroses depend on their mother until the age of 1 to 1.7 years, because the young animals are still supplied with maternal milk (weaning period or mixed feeding phase) (Langer 2008). This transitional period is critical during the development of young herbivores because they have to establish a functional microbial population in the digestive tract in order to digest plant cell wall material (Savage 1977; Langer 1988). Although cows vigorously protect their offspring (Goddard 1966), juvenile survival is also decreased by predation. Subadult rhinoceroses (3 to 5 years) are usually capable of defending against predators, whereas calves of extant African and Asian rhinoceroses (<2 years) are particularly at risk of being killed by lions, hyenas, and tigers (Goddard 1966; Berger and Cunningham 1995 and references therein; Brain et al. 1999; Hutchins and Kreger 2006 and references therein). The differential response of adult and juvenile survival to environmental variation revealed that vital rates of young herbivores are in general highly sensitive to limiting environmental factors, such as extreme weather conditions (Gaillard et al. 1998). As the reproduction in extant rhinoceroses is asynchronous, the inter-calving intervals are not restricted to yearly time increments (Hillman-Smith and Groves 1994; Hrabar and Du Toit 2005). Depending on environmental conditions, the inter-calf interval usually ranges from 2 to 3 years (Laurie 1982; Hillman-Smith and Groves 1994 and references therein). Pregnancy is generally 15 to 16 months (Miller 2003). This implies that the mother cow meets a male when her current offspring is about 1–1.7 years. The mating behavior is accompanied by aggression and the young is sometimes attacked by the male rhinoceros with consequential death (Laurie et al. 1983; Hillman-Smith and Groves 1994).

In summary, the juvenile mortality profile of *P. germanicus* as revealed by the present study is in accordance with a fossil deposition period of Sandelzhausen of several decades or thousands of years because it corresponds to an attritional fossil assemblage. The juvenile age-at-death distribution of the fossil rhino does not reflect the age structure of a natural population as expected by a catastrophic event resulting in non-selective mass mortality, but displays selective mortality at certain ages indicating a gradual accumulation of corpses.

Conclusion

The analysis of the juvenile *P. germanicus* mandibles from Sandelzhausen revealed a dental eruption sequence of (d2, d3), (d1, d4), m1, m2, p2, p3, p4, m3 and allowed for a classification of a total of 11 dental eruption stages for the Miocene rhino. From the results of the present study, we conclude that the tooth replacement pattern reconstructed for *P. germanicus* suggests that the extinct rhino was a slow-growing, long-living species considering 'Schultz's rule.' The ecological interpretation of *P. germanicus* as either rhino-like or hippo-like is still under debate, but according to 'Schultz's rule,' modern rhinos as well as hippos, horses, and pigs are slow-growing, long-living mammals (Smith 2000). The tooth eruption sequence of *P. germanicus* is similar to the other living and fossil rhinos studied to date, but is identical to that of the extant African rhino, *D. bicornis*. Thus, it appears reasonable to correlate the dental eruption stages of the fossil rhino with age data of extant rhinos, in particular *D. bicornis*. Both approaches to reveal the juvenile mortality pattern (dental wear of isolated and in situ teeth as well as dental ontogeny of the fossil mandibles) indicate a selective mortality of *P. germanicus* at age classes that are more vulnerable at natural environmental conditions. The present contribution to the study of evolutionary dental ontogeny in rhinocerotids, thus, supports a gradual accumulation model for Sandelzhausen coinciding with the hypothesis of Schmid (2002).

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Appendix

Table 6 *Prosantorhinus germanicus* specimens measured in this study to evaluate dental wear

Collection number BSPG 1959 II	Left/right	Teeth			Isolated/ in situ
522	Left	d2	d3	d4	In situ
1939	Left	d2	d3	d4	In situ
2251	Right	d2	d3	d4	In situ
2253	Right	d2	d3	d4	In situ
2261	Left	d2	d3	d4	In situ
2281	Left	d2	d3	d4	In situ
3362	Left	d2	d3	d4	In situ
4547	Right	d2	d3	d4	In situ
5978	Left	d2	d3	d4	In situ
2257	Left	d2	d3		In situ
2279	Left	d2	d3		In situ
1	Left		d3	d4	In situ
2255	Left		d3	d4	In situ
2264	Left		d3	d4*	In situ
2265	Right		d3	d4	In situ
2268	Right		d3	d4	In situ
3106	Right		d3*	d4	In situ
3715	Left		d3	d4	In situ
3782	Right		d3	d4	In situ
5978	Right		d3	d4	In situ
2255	Right			d4	In situ
3782	Left			d4	In situ
4534	Left			d4	In situ
2465	Right	d2			Isolated
2494	Right	d2			Isolated
2495	Left	d2			Isolated
2496	Right	d2			Isolated
2497	Left	d2			Isolated
2755	Right	d2			Isolated
2757	Left	d2			Isolated
2758	Left	d2			Isolated
2759	Right	d2			Isolated
2760	Right	d2			Isolated
2761	Right	d2			Isolated
2762	Left	d2			Isolated
2764	Left	d2			Isolated
3915	Right	d2			Isolated
4747	Left	d2			Isolated
5192	Right	d2			Isolated
No. Nr. (PQ 6-B 50 ü. Basis)	Left	d2			Isolated
2452	Left		d3		Isolated

Table 6 (continued)

Collection number BSPG 1959 II	Left/right	Teeth	Isolated/ in situ
2453	Right	d3	Isolated
2454	Left	d3	Isolated
2456	Right	d3	Isolated
2457	Left	d3	Isolated
2460	Right	d3	Isolated
2461	Right	d3	Isolated
2462	Right	d3	Isolated
2463	Left	d3	Isolated
2465	Right	d3	Isolated
2466	Left	d3	Isolated
2468	Right	d3	Isolated
2470	Left	d3	Isolated
2473	Right	d3	Isolated
3136	Right	d3	Isolated
4493	Right	d3	Isolated
4507	Left	d3	Isolated
4518	Left	d3	Isolated
4523	Right	d3	Isolated
4537	Left	d3	Isolated
4539	Left	d3	Isolated
No. Nr. (NB 7-B)	Right	d3	Isolated
No. Nr. (NB6/B 55 ü. Basis)	Left	d3	Isolated
297	Left	d4	Isolated
2474	Right	d4	Isolated
2475	Right	d4	Isolated
2476	Left	d4	Isolated
2477	Right	d4	Isolated
2478	Left	d4	Isolated
2479	Right	d4	Isolated
2481	Left	d4	Isolated
2483	Left	d4	Isolated
2484	Left	d4	Isolated
2485	Right	d4	Isolated
2487	Left	d4	Isolated
2488	Left	d4	Isolated
2489	Right	d4	Isolated
2490	Right	d4	Isolated
2491	Left	d4	Isolated
2492	Left	d4	Isolated
2493	Right	d4	Isolated
3166	Right	d4	Isolated
3662	Left	d4	Isolated
4488	Right	d4	Isolated
4529	Right	d4	Isolated
No Nr. (29-T/-10)	Right	d4	Isolated

Specimen BSGP 1959 II 2278 is a subadult individual, but already replaced all deciduous teeth. Teeth marked with an asterisk (*) allowed only a single measurement (crown height or dentinal width, respectively)

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