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# Dental paleopathology in fossil rhinoceroses: etiology and implications

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## Abstract

The identification and interpretation of paleopathological findings in the dentition of mammals have the potential to shed light on disturbed development and stress conditions. In combination with knowledge about the timing of dental development, dental pathologies can provide a unique opportunity to reconstruct specific phases in the life history of fossil taxa, as well as animal-environment interactions. The dental ontogeny of the extinct rhinoceros *Prosantorhinus germanicus* from the Miocene is well-known from an exceptionally preserved sample of juvenile dentaries. Two of the represented juvenile individuals each revealed a dental anomaly, which were analyzed macroscopically and via X-ray tomography in this study. One specimen documents decreased dental wear of deciduous cheek teeth, mandibular bone resorption as well as abnormal cemental deposition. At an early age, the extinct juvenile rhinoceros probably was affected by a gingival infection resulting from an accumulation of bacterial plaque. This led to a chronic gingivitis and eventually may have caused periodontitis. Furthermore, it suffered from inflammation-induced hypercementosis. Another specimen revealed an abnormal reduction in thickness of enamel in the deciduous cheek tooth. The enamel hypoplasia indicates stress experienced during the prenatal period. During a phase of environmental stress (e.g. increased fluoride exposure) or physiological stress (e.g. malnutrition) the function of the secretory ameloblasts was disrupted in the developing embryo. The present work shows that the analysis of dental paleopathologies is a useful means for retrospective assessment of specific phases in the life history of extinct animals. This adds to the picture of the living conditions of the extinct rhinoceros *P. germanicus*.

## Introduction

The mammalian dentition records a lot of information about the animal's diet, feeding strategy as well as individual age and, thus, has proved to be an organ system of great importance to study ecology, physiology and life history in extinct animals. In addition to normal development documented by a healthy dentition, dental pathologies may also shed light on disturbed development and stress conditions. Hence, the identification and interpretation of paleopathologies provide a unique opportunity to reconstruct specific phases in the life history of fossil taxa, as well as animal-environment interactions.

In general, dental pathologies are classified as traumatic or non-traumatic (Miles & Grigson, 2003). Traumatic damage primarily involves a physical injury of sudden onset, such as tooth fractures during combat (Garutt, 1997; Miles & Grigson, 2003). Secondarily, it may result in subsequent defects, such as root resorption, or chronic infections, such as periodontitis (chronic inflammation of the gum tissue) (Trope, 2002; Miles & Grigson, 2003; Shaddox & Walker, 2010; Langer *et al.*, 2016). Non-traumatic damage includes congenital defects, such as supernumerary teeth, enamel hypoplasia or acquired tooth defects, such as dental caries (Miles & Grigson, 2003; Touger-Decker & van Loveren, 2003; Koenigswald *et al.*, 2007).

Trauma to a developing tooth germ, some systemic diseases, a number of genetic disorders, and local inflammation can result in abnormal tooth morphology and/or enamel as well as dentin quality (e.g. Boy, Crossley & Steenkamp, 2016). The etiological factors for disturbance during dental development may also involve environmental parameters, such as flouride-induced changes, or physiological stress induced by malnutrition (e.g. Suckling & Thurley, 1984; Witzel *et al.*, 2008). Understanding the basic causes of pathologies in fossil teeth has, therefore, the potential to allow interpretation of life

history parameters in extinct animals. In combination with knowledge about the timing of dental development, the time period when the pathology occurred can be dated.

Böhmer, Heissig & Rössner (2016) recently took advantage of an exceptionally preserved sample of juvenile dentaries at different ontogenetic stages of the extinct rhinoceros *Prosantorhinus germanicus* from the Miocene fossil lagerstätte Sandelzhausen in Germany and reconstructed its tooth replacement pattern. The dental formula for *P. germanicus* is 1(?) 0 4/2 0 4 = 22 for juvenile and 1 0 3 3/2 0 3 3 = 30 for adult individuals: in contrast to the report by Peter (2002) that assigned the first postcanine position to the adult dentition. The analysis of the juvenile *P. germanicus* mandibles revealed a dental eruption sequence of (d2, d3), (d1, d4), m1, m2, p2, p3, p4, m3 (d1 is shed without successor); a pattern identical to that reported for the extant African rhinoceros, *Diceros bicornis* (Böhmer *et al.*, 2016). The comparison of the tooth eruption sequences in living and extinct rhinoceroses indicated that the sequence is quite conservative, but there is variation in the timing of the eruption of p2, p3 and m2; that is, the m2 erupts either before or after p2 and p3. The investigation of the teeth of *P. germanicus* allowed to evaluate the individual age-at-death of the fossil specimens. The juvenile mortality profile showed a trend of selective mortality at an age range of about 3 months to 3 years (Böhmer *et al.*, 2016). Two of the juvenile individuals each revealed a dental anomaly, which will be described in this study. One of the juvenile *P. germanicus* dentaries showed a defect in the mandibular bone supporting the teeth (lateral alveolar wall); the other dentary displayed a defect in the crown of a deciduous cheek tooth. The discussion of the potential causes for these paleopathologies will provide an opportunity for interpreting life-history parameters in the extinct rhinoceros comprising disturbed development and stress conditions.

In the literature, a variety of dental anomalies have been reported in living and extinct rhinoceroses. Malpositionings, irregular eruptions, supernumerary teeth (hyperdontia), dental asymmetries and tooth rotations have been described (e.g. Mead, 1999; Miles & Grigson, 2003; Koenigswald *et al.*, 2007; Romig, Lowder & Citino, 2011; Antoine *et al.*, 2012; Roohi *et al.*, 2015). In comparison to anomalies found in permanent teeth, reports on anomalies in deciduous teeth are relatively rare. Furthermore, this study is not limited to solely diagnose the paleopathological findings, but also explores the potential processes and mechanisms behind pathologies, complemented by knowledge of the dental ontogeny in *P. germanicus*.

## Materials and methods

The material is housed at the Staatliche Naturwissenschaftliche Sammlungen Bayerns - Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG) in Munich. The juvenile dentaries of *P. germanicus*, SNSB-BSPG 1959 II 3782 and 2261, were studied macroscopically and via X-ray microtomography (μCT) to identify dental defects in mandibular bone and teeth. The non-invasive methods allow to systematically describe the external and internal dental anatomy. The whole specimens were subjected to micro-tomographic analysis at the SNSB in Munich, using a phoenix|x-ray nanotom m (GE Sensing & Inspection Technologies GmbH, Wunstorf/Hannover, Germany) at 160 kV and 60 μA (1400 slices with 54.5 μm voxel size, and a 0.25 mm copper filter; specimen 1959 II 3782) and at 160 kV and 50 μA (1400 slices with 44.5 μm voxel size, and 0.2 mm aluminium filter; specimen 1959 II 2261). The data were visualized in VG Studio Max 2.0.

The dental terminology used in the present study follows the nomenclature used by Böhmer *et al.* (2016).

## Results

### SNBS-BSPG 1959 II 3782

Specimen 3782 is a left mandible containing several teeth *in situ*: two completely erupted deciduous cheek teeth (d3 and d4) and one permanent cheek tooth (m1) still largely in the crypt (Fig.1a). The right d4 in connection with some pieces of the mandibular bone is preserved as well. The d3 reveals dentin exposed on the occlusal surface due to wear. Although completely erupted, both d4 (left and right) are not worn. The m1 lacks wear because it has not reached functional occlusion yet. The radiological analysis revealed that premolar germs had not developed yet (Fig. 1b.). In *P. germanicus*, a full deciduous complement of deciduous mandibular teeth (d1-d4) with d2-d4 in wear, the m1 in eruption and the absence of permanent tooth germs, characterizes dental eruption stage 3 (correlated with an age range of 9 months to 3 years) (Böhmer *et al.*, 2016). In total, the study established 11 dental eruption stages representing ten morphological events until reaching adulthood. However, in contrast to dental eruption stage 3 (Böhmer *et al.*, 2016), d3 of specimen 3782 is only slightly worn and d4 shows no dentin in occlusal view. Moreover, specimen 3782 does not only differ in the degree of dental wear, but also in general appearance. The mandibular bone is more solid and heavy and the preserved teeth are more robust in comparison to other fossil specimens. Additionally, the bone around d3 and d4 shows damage, exposing tooth roots (Fig. 1d). Based the rounded shape of the bone damage and the lack of color change, we regard this as a pathology and not a taphonomic artefact. Above the mandibular bone, the roots of d4 are laterally covered by some small bits of minerals, which may be either part of the dental cementum or dental calculus (mineralized bacterial plaque).

Dental cementum is radiographically identified as an outer layer of the root. It is clearly identifiable in specimen 3782 (Fig. 1b), but appears much more developed and therefore thicker compared to other fossils of the sample. This contributes to the robust appearance of the teeth.

The radiological imaging shows that the pulps of d3 and d4 have blurry areas (Fig. 1b). This is in contrast to all other juvenile dentaries among the sample of *P. germanicus* as revealed by X-ray images (Böhmer *et al.*, 2016). The well-mineralized hard dental tissues, such as enamel and dentin, show a white to gray appearance on radiological images, whereas the pulp cavities usually show much less radiodensity and appear as dark gray areas.

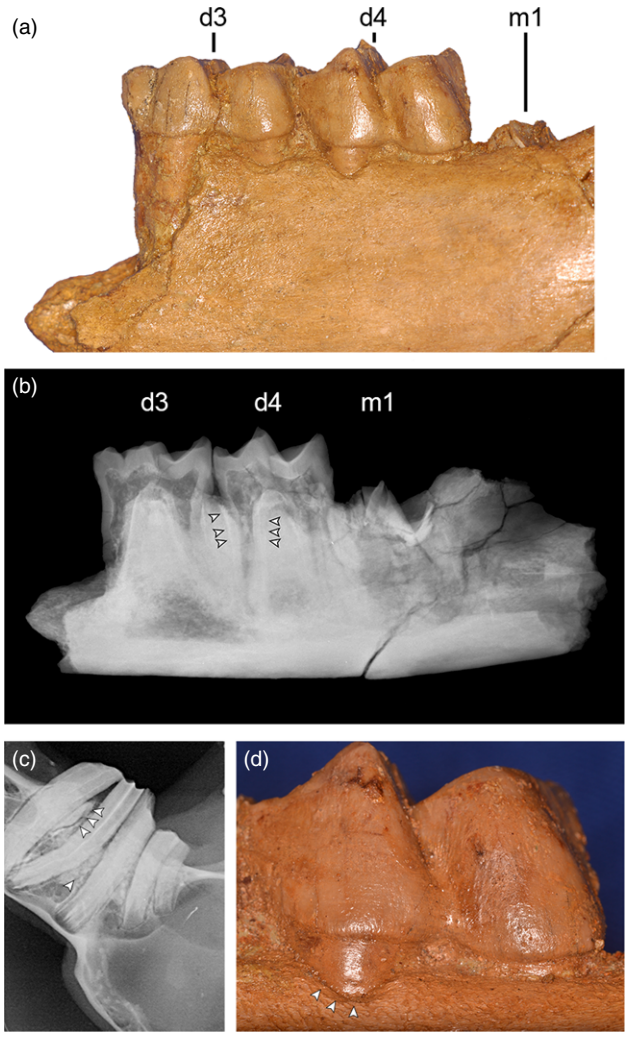


**Figure 1** SNSB-BSPG 1959 II 3782 of *Prosantorhinus germanicus*. (a) In lateral view: the left mandible contains two completely erupted deciduous cheek teeth *in situ* (d3 and d4) and one permanent cheek tooth (m1) that was in eruption. (b) The latero-lateral X-ray reveals very thick layers of cementum around d3 and d4. This may be the result of hypercementosis. (c) The latero-lateral X-ray of an extant rabbit displays hypercementosis. Hypercementosis is an excessive deposition of normal dental cementum on the tooth root and can affect either one or more teeth. (d) The detailed view of the mandible shows that the bone around d4 is damaged having resulted in exposed tooth roots (supposedly by mandibular bone resorption). Above the mandibular bone, the roots of d4 are laterally covered by some small bits of minerals, which may be either part of the dental cementum or dental calculus (mineralized bacterial plaque). [Colour figure can be viewed at wileyonlinelibrary.com]

### SNSB-BSPG 1959 II 2261

Specimen 2261 is a fragmentary left mandible containing three completely erupted deciduous cheek teeth *in situ* (d2, d3, d4) (Fig. 2a). The anterior and posterior parts of the jaw are broken, but the preserved fragment is almost complete. All teeth reveal dentin exposed on the occlusal surface with d2 and d3 displaying most progressed wear. Radiological analysis proved absence of premolar germs (Fig. 2b). Dental wear stage of the deciduous teeth, eruption state of the postcanine dentition, and state of tooth germ development indicate dental eruption stage 3 for specimen 2261 correlated with an age range of 9 months to 3 years. We hypothesize that the calve was still accompanied by its mother during this life stage (Böhmer *et al.*, 2016).

As usual in herbivorous mammals, one mental foramen is present below the d2 and the corresponding alveolar canal runs anteroposteriorly along the mandibular bone as revealed by the radiological image (Fig. 2a and b). It transmits the mental vessels and nerves (König & Liebich, 2012). The roots of the deciduous cheek teeth are partially exposed because the mandibular bone is damaged (Fig. 2c and d). In contrast to specimen 3782, the damaged bone is chiseled and displays changes in color which indicates disintegration.

A clearly visible, deep trench in the dental enamel encompasses the entire d4 (Fig. 2e). The $\mu$CT analysis reveals that this trench is confined to the enamel and does not affect the underlying dentin (Fig. 2f). We interpret this to indicate some degree of quantitative enamel deficiency (i.e. enamel hypoplasia). It occurs about 1.6 cm from the tip of the crown cusp. The width of the trench is 1 mm and reflects the duration of an assumed stress episode (Fig. 2e).

The distribution of the perikymata (see below) in the juvenile dentary of *P. germanicus* appears to be unevenly distributed over the entire crown surface (Fig. 2e). The spaces between the concentric ripples are greater at the cusp tips and smaller just below the trench becoming greater again towards the end of the crown.

Generally, during tooth development, the crown is formed by successive apposition of different enamel layers. The striae of Retzius (or incremental lines) (Retzius, 1837) end at the surface of dental enamel and appear as shallow furrows, known as perikymata (Figs. 2e and 3a). Moreover, since the formation of enamel begins at the cusp tips, striae of Retzius formed early in development do not intersect the tooth surface (Tafforeau *et al.*, 2007). They cover the underlying dentin in form of multiple semilunar cusps that overlap each other. Concomitant with an increasing size of the crown, the striae of Retzius end at the surface of dental enamel, where they appear as perikymata. The perikymata on the d4 of specimen 2261, therefore, represent late tooth crown development. The concentric ripples are long-period growth lines in the enamel and are spaced several days apart. In living rhinoceroses, an enamel apposition rate of approximately 10 $\mu$m/day has been reported (Tafforeau *et al.*, 2007).

## Discussion

### SNSB-BSPG 1959 II 3782: periodontal pathology or diagenetic alteration?

Specimen 3782 is exceptional among the sample of juvenile dentaries of *P. germanicus* from Sandelzhausen because of a low level of occlusal wear, unusual in the dental eruption stage represented (see Böhmer *et al.*, 2016), very robust appearance

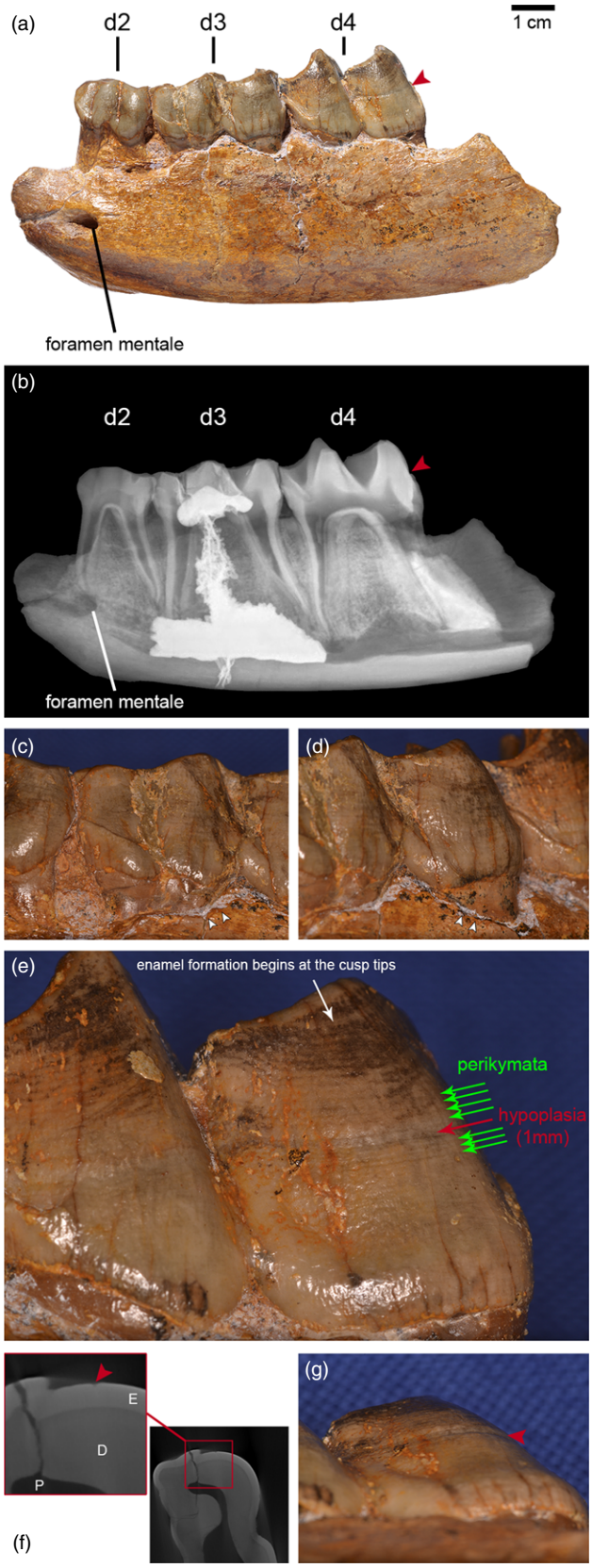


**Figure 2** SNSB-BSPG 1959 II 2261 of *Prosantorhinus germanicus*. (a) In lateral view: the left mandible contains three completely erupted deciduous cheek teeth *in situ* (d2, d3, d4). (b) The latero-lateral X-ray proved absence of premolar germs. (c and d) The detailed view of the mandible shows that the roots of the deciduous cheek teeth are partially exposed because the mandibular bone is damaged (supposedly by post-mortem destructive factors, such as erosion). (e) The striae of Retzius (or incremental lines) end at the surface of dental enamel and appear as shallow furrows, the perikymata, in d4. A clearly visible, deep trench in the dental enamel encompasses the entire d4. (f and g) The detailed view of the tooth and the µCT images reveal that this trench is confined to the enamel and does not affect the underlying dentin. Based on this, a linear enamel hypoplasia, a quantitative enamel deficiency, is assumed.

of the preserved teeth (in particular the tooth roots), bits of minerals suspected to be dental calculus, mandibular bone damage (lateral alveolar wall) exposing the tooth roots of the deciduous cheek teeth (d3 and d4), and blurry areas in the pulp cavities of d3 and d4. In living mammals, a common reason for decreased occlusal wear is a painful periodontal pathology such as gingivitis (gingival inflammation) and subsequent periodontitis (resorption of the alveolar bone around the teeth) (Page & Schroeder, 1982; Miles & Grigson, 2003). The aforementioned observations appear to support a periodontal pathology for specimen 3782. For reasons discussed below, we regard lifetime pathology as a more likely cause factor than post-mortem taphonomy.

In a healthy mammalian dentition, the tooth roots are covered by layers of cementum (avascular mineralized tissue secreted by cementoblasts) in order to secure the connection of the teeth to the alveolar bone in concert with the surrounding periodontal ligaments (Peyer, 1968; Hillson, 2005). This gives the teeth a certain flexibility and a firm fixation as well. The development of dental cementum (cementogenesis) begins after the eruption of the tooth (Yamamoto *et al.*, 2016). Since cementoblasts arrange tissue matrix in very thin uniform layers, the cementum usually forms a relatively regular surface. In general, the deposited cementum of deciduous teeth is not as developed as that of permanent teeth. Although it is difficult to exclude a bias due to fossil preservation, the mineral bits on the root of d4 in *P. germanicus* are irregular and quite thick. Thus, they may not be part of the cementum. Alternatively, the irregular surface of the root of d4 may be the result of dental calculus deposits. Dental calculus is calcified dental plaque, composed primarily of minerals deposited between and within remnants of microorganisms (White, 1997). It can occur both above (supragingival) and below (subgingival) the gumline (White, 1997). In the case of specimen 3782, it may be subgingival calculus because the mineral bits are limited to the root surface of d4. However, dental calculus is generally rare among juvenile animals. The distinction between cementum and calculus is very difficult since, once highly mineralized, calculus can become cement-like in terms of physical hardness (White, 1997). In terms of mineral density, statistical differences ($P < 0.05$) were observed in humans between normal cementum (1250-1340 mg/cc), cementum affected by

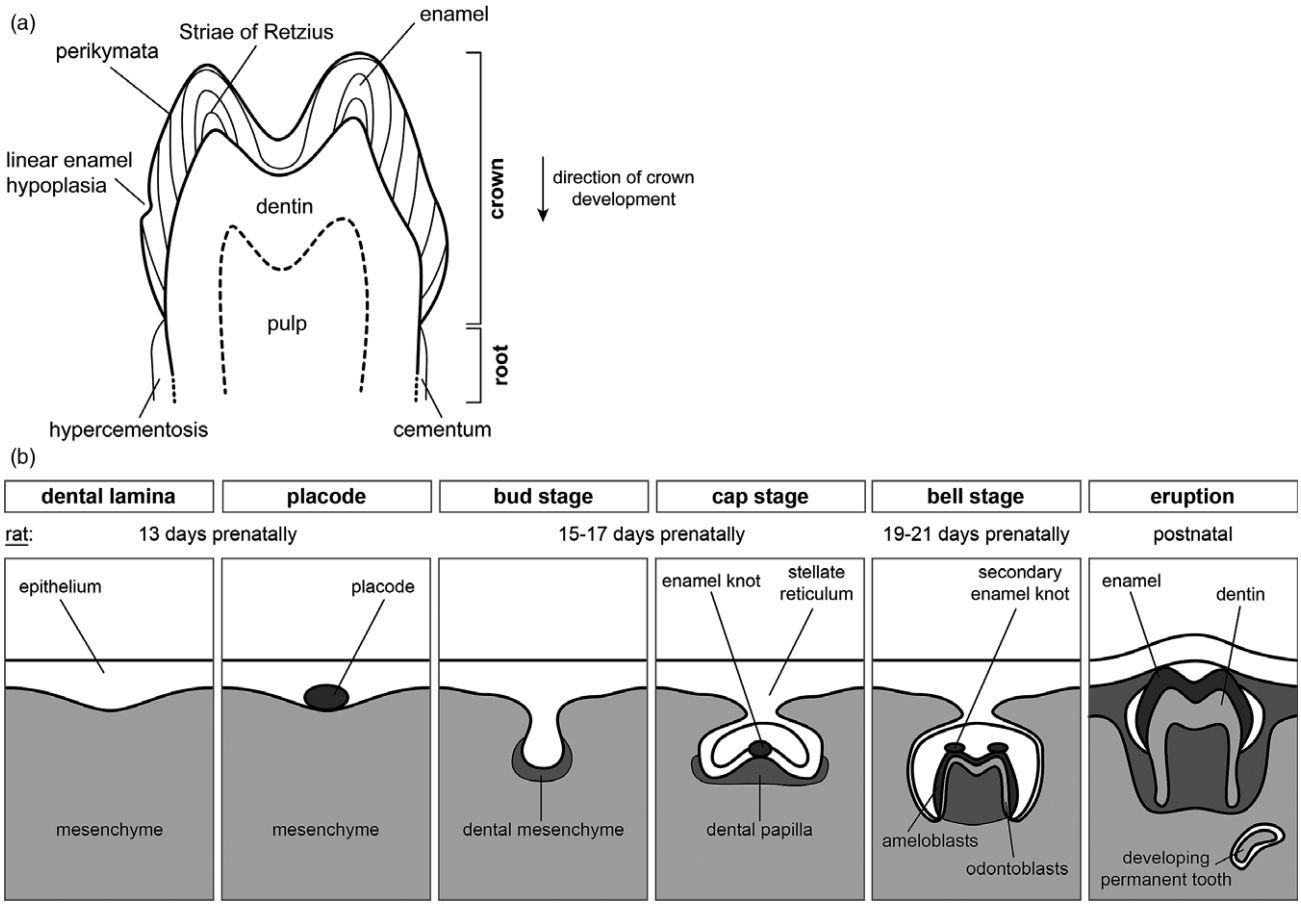


**Figure 3** Tooth structure and development. (a) Schematic illustration of a longitudinal section through a tooth. (b) Generalized tooth development in mammals. Timing of tooth development in the rat is based on Khaejornbut *et al.* (1991).

periodontitis (1100-1220 mg/cc) and calculus (1290-1770 mg/cc) (Djomehri *et al.*, 2015). Although compositionally and structurally different, the mineral density of calculus overlapped with that of normal dentin (1470-1605 mg/cc) (Djomehri *et al.*, 2015). If this applies to rhinoceroses as well, the bits of minerals covering the roots of d4 in *P. germanicus* may be calculus if they radiologically manifest as being as dense as dentin. Indeed, the bits of minerals appear to be more or less similar in density as compared to dentin (Fig. 1b). Interestingly, an association of dental calculus with periodontal pathologies is well reported in the literature (e.g. Page & Schroeder, 1982; White, 1997; Miles & Grigson, 2003), which adds to the picture of the fossil rhinoceros.

Soft bacterial films and hard plaques often cause secondary periodontal diseases. Plaque-induced periodontitis is a chronic inflammatory condition that progressively destroys attachment of the teeth and can lead to marked bone and finally tooth loss. Bone loss can occur either in vertical or horizontal direction. Vertical bone loss begins as widening of the periodontal ligament space and progresses parallel to the tooth root, whereas horizontal bone loss occurs parallel to the alveolar margin (Campbell *et al.*, 2016). It seems reasonable to interpret the mandibular bone damage that exposes the tooth roots of the deciduous cheek teeth as vertical alveolar bone loss due to periodontitis (Fig. 1a). Since the damage does not resemble fractured bone and the overall preservation of the fossil is very good, the bone loss appears not to be the result of the excavation work or the product of the fossilization process.

It is interesting to note that the radiological imaging shows that the pulps of d3 and d4 have multiple blurry areas (Fig. 1b). This is in contrast to all other juvenile dentaries among the sample of *P. germanicus* as revealed by the X-ray images (Böhmer *et al.*, 2016). Normally, tooth cavities are less dense than the mineralized tissues, that is, enamel and dentin, and, thus, the pulp appears dark in the radiological image. The blurry pulp cavity in specimen 3782 does not resemble any pathological findings in living animals. Therefore, it may be the result of diagenetic processes during fossilization. In case of an assumed pulpitis, apical bone resorption should be present or reactive formation of tertiary dentin (irritation dentin).

Very thick layers of cementum around d3 and d4 are clearly identifiable in the radiological image of specimen 3782 (Fig. 1b). This gives the deciduous teeth and, in particular, the tooth roots a robust appearance. This may be the result of hypercementosis. Hypercementosis is an excessive deposition of normal dental cementum on the tooth root and can affect

either one or more teeth (Leider & Garbarino, 1987). The increased thickness of the cementum results from abnormal cementogenesis (Page & Schroeder, 1982; Leider & Garbarino, 1987; Consolaro, Consolaro & Francischone, 2012). The etiological factors are not completely understood to date, but they include localized trauma, inflammation, periodontitis, excessive tooth eruption, osteitis deformans (a chronic bone disorder), or may occur idiopathically (Page & Schroeder, 1982; Leider & Garbarino, 1987; Woodmansey, Naidu & Lerner, 2011; Boy *et al.*, 2016). Abnormal cementogenesis can also be an adaptive response to an increased periodontal functional demand because increased or abnormal mechanical forces may stimulate cemental deposition and subsequent hypercementosis (Purkait, 2005; Consolaro *et al.*, 2012). Excessive cement formation is part of a newly recognized dental disease in horses that affects primarily the incisors (equine odontoclastic tooth resorption and hypercementosis, EOTRH) (Staszyk *et al.*, 2008; Moore, Schroeder & Staszyk, 2016). It has been reported that both periodontal inflammation and an abnormal strain on the incisors might be the initiating trigger of this disease that is combined with progressive tooth resorptions (Staszyk *et al.*, 2008; Moore *et al.*, 2016).

Supported by other anatomical features, the thickening of dental cementum observed in the Pleistocene *Coelodonta* was interpreted to indicate a progressive adaptation of the woolly rhinoceros as a very efficient grazer, under increasingly cold climatic conditions (Kahlke & Lacombat, 2008). On basis of the low level of occlusal wear in relation to the dental eruption stage as well as the aforementioned pathological observations, the adaptive response hypothesis may not apply to the juvenile dentary of *P. germanicus*.

In summary, specimen 3782 appears to display a painful, pathological condition that involves the deciduous teeth and the surrounding mandibular bone. At an early age, the juvenile individual probably was affected by a gingival infection resulting from an accumulation of bacterial plaque. Impacted food might have been the primary cause for the local bacterial infection. Subsequently, the bacterial plaque may have been calcified forming dental calculus, which further contributes to the accumulation of even thicker dental calculi. Chronic gingivitis and apically ascending progressive periodontitis may have caused severe damage of the tooth-supporting tissues which finally lead to wide spread alveolar bone resorption. As a consequence of that, the formation of cementum may have increased in order to stabilize the teeth again or it may just be a reaction to the local inflammation and bone lysis which are accompanied by infected necrotic debris. Based on this, specimen 3782 may have suffered from inflammation-induced hypercementosis - similar to the above mentioned equine odontoclastic tooth resorption and hypercementosis (EOTRH) or a similar disease seen in pet rabbits suffering from malocclusion with an abnormal strain on the cheek teeth (Fig. 1c).

## SNSB-BSPG 1959 II 2261: enamel hypoplasia or hypomineralization?

Specimen 2261 is exceptional among the sample of juvenile dentaries of *P. germanicus* from Sandelzhausen because of a clearly identifiable enamel defect in d4 (Fig. 2a). Unlike other hard tissues, such as bones, dental enamel does not undergo remodeling or repair once formed (e.g. Hillson, 2005). Therefore, developmental defects of enamel are a permanent record of disturbance during enamel development (Salanitri & Seow, 2013).

### Enamel development (amelogenesis)

Two principal phases during the formation of mammal dental enamel (amelogenesis) can be differentiated: secretion phase and maturation phase (Tafforeau *et al.*, 2007; Bartlett, 2013; Robinson, 2014). Correspondingly, two types of enamel defects resulting from enamel organ dysfunction are distinguished: enamel hypoplasia and enamel hypomineralization. Enamel hypoplasia is a quantitative defect during the secretion phase of amelogenesis associated with a reduced thickness of enamel (Sarnat & Schour, 1941; Suckling, 1989; Kierdorf *et al.*, 2012). It refers to inadequate deposition of enamel matrix and affects one or several teeth. It can occur as pits and furrows (linear enamel hypoplasia) or it can affect the entire cusp of the tooth (plane-form and cuspal enamel hypoplasia) (Ogden, Pinhasi & White, 2007). Enamel hypomineralization is a qualitative defect during the maturation phase associated with normal thickness of enamel, but subsequent inadequate mineralization of the enamel matrix (Chadwick & Cardew, 1997; Jalevik & Noren, 2000; Fearne, Anderson & Davis, 2004). It results in alteration of enamel opacity and often affects several or all teeth. The deficient mineralization may secondarily cause a quantitative defect because the enamel is soft and may be worn more rapidly.

The observations made for specimen 2261 support a linear enamel hypoplasia because a reduction in thickness of enamel is clearly identifiable (Fig. 2e-g). A secondary quantitative defect as a result of enamel hypermineralization appears unlikely since the juvenile dentary of *P. germanicus* generally did not experience a lot of wear and, thus, a deficiently mineralized area of enamel may not be worn rapidly.

Since enamel deposition stops just before tooth eruption and therefore no further enamel layers are deposited on the crown following the breakthrough, enamel hypoplasia in deciduous teeth indicates stress experienced during the prenatal period (Sarnat & Schour, 1941). The exact timing of the quantitative enamel defect depends on the dynamics of tooth development and eruption. Knowledge of the timing of tooth development enables a relatively accurate estimation of the timing of the disturbance (Simmer & Hu, 2001) and, thus, enables reconstruction of the relative period in which the defect occurred because the disturbance happened prior to tooth eruption.

### Timing of tooth development

The timing of tooth development has not been studied in rhinoceros fetuses, but it is well-known for mice, rats and humans (Deutsch & Pe'er, 1982; Khaejornbut, Wilson & Owens, 1991; Caton & Tucker, 2009). In general, mammalian tooth development begins with the appearance of the dental lamina (or odontogenic band) within the dental epithelium (Smith, 2003; Jernvall & Thesleff, 2012) (Fig. 3b). The initial

stage of tooth development is detectable at 13 days prenatally in the rat (Khaejornbut *et al.*, 1991). After the establishment of dental placodes (the first signaling centers of the tooth) along the dental lamina, the morphology of individual teeth unfolds during three developmental stages: the bud, cap and bell stage (Tucker & Sharpe, 2004; Jernvall & Thesleff, 2012). During the bud stage, the tooth germs begin to form by the invagination of the epithelium into the underlying mesenchyme (Jussila & Thesleff, 2012) (Fig. 3b). Subsequently, enamel knots are created at the tip of the tooth bud at the future location of each tooth cusp, forming the cap stage of tooth development (Tucker & Sharpe, 2004; Jernvall & Thesleff, 2012). Both stages occur during about 15-17 days of prenatal life in the rat (Khaejornbut *et al.*, 1991). At the bell stage of development (19-21 days prenatally in the rat), the ameloblasts (secreting enamel) and the odontoblasts (secreting dentin) form in adjacent layers (Tucker & Sharpe, 2004; Jussila & Thesleff, 2012) (Fig. 3b). The size and shape of the tooth crown is fixed when the organic matrices of enamel and dentin mineralize at the epithelial-mesenchymal interface (Jussila & Thesleff, 2012). The tooth erupts after the biomineralization process ends and the permanent tooth develops lingually to the deciduous tooth from an extension of the dental lamina (Jernvall & Thesleff, 2012; Jussila & Thesleff, 2012). In the rat, birth of the offspring occurs at 22 days of embryo development and eruption of the teeth occurs postnatally (Khaejornbut *et al.*, 1991). Similar to living rhinoceroses, *P. germanicus* is born with two deciduous cheek teeth, d2 and d3, and the other milk teeth erupt within 2 to 12 months (Böhmer *et al.*, 2016). The full deciduous dentition is developed and in function by about 1.5 years (Böhmer *et al.*, 2016). The development of d4 likely occurs before birth of the embryo and, thus, the enamel hypoplasia of specimen 2261 took place *in utero*. This suggests that the linear enamel hypoplasia reflects stress primarily experienced by the mother. During a phase of environmental stress (e.g. increased fluoride exposure) or physiological stress (e.g. malnutrition) (e.g. Sarnat & Schour, 1941; Kierdorf & Kierdorf, 1997; Chollet & Teaford, 2010; Salanitri & Seow, 2013), the function of the secretory ameloblasts was disrupted in the developing fetus.

The limnofluvial deposits of the Miocene fossil lagerstätte Sandelzhausen are part of the Upper Freshwater Molasse (Fahlbusch, Gall & Schmidt-Kittler, 1972; Schmid, 2002; Fahlbusch, 2003; Böhme, 2010). The paleoenvironment is characterized as a wetland with forest and woodland hinterland as well as periodically flooded river plains with seasonal grass cover (Schmid, 2002; Eronen & Rössner, 2007). The brachydont *P. germanicus* was a browser and preferentially lived in more closed forest environments (Peter, 2002; Tütken & Vennemann, 2009). An environmental stress-induced enamel hypoplasia appears reasonable in the case of *P. germanicus* because the seasonality might have caused recurrent droughts that contributed to nutritional stress in the extinct rhinoceros. Similar incidences of enamel hypoplasia in deciduous and permanent teeth have been reported in a number of studies including extinct rhinoceroses (Mead, 1999; Roohi *et al.*, 2015), giraffids (Franz-Odendaal, Chinsamy & Lee-Thorp, 2004), pigs (Dobney, 2000), sheeps and goats (Kierdorf *et al.*, 2012), bisons (Niven, Egeland & Todd, 2004), notoungluates (Braunn, Ribeiro & Ferigolo, 2014), and primates (Skinner, 1996; Lukacs, 2001).

Starting around the Middle-Late Miocene transition, the paleoenvironment changed from wetland forests to drier and more open woodlands in this region (Eronen & Rössner, 2007; Calandra, Göhlich & Merceron, 2010). Although it is not possible to deduce a large-scale climate change (drying and opening) on basis of a single dentary with enamel hypoplasia, this highlights the potential of analyzing a larger sample of teeth in order to evaluate the frequency of hypoplasia. For instance, poor environmental conditions associated with browser-habitat destruction may have resulted in the prevalence of enamel hypoplasia (Franz-Odendaal *et al.*, 2004; Roohi *et al.*, 2015).

## Conclusion

Paleopathology is the study of features caused by disease on organismic remains from past times. The present work demonstrates that the analysis of mammalian dental abnormalities is worthwhile in detecting paleopathologies of the dental system and their causes. Moreover, the complex ontogeny of the mammalian dentition (composition of three different hard tissues, implementation in the skeletal system, integrated replacement and wear) and related differentiated features makes dental paleopathology an effective tool for retrospective assessments. Identification of the causative agent and cascade effects allow for detailed reconstruction and timing of specific harmful events in the life history of extinct mammals. Provided that samples are large enough, this may even help to reconstruct the evolutionary history of dental apparatus diseases and seasonal environmental or physiological phases of stress of a population or community. Specimen 3782 revealed a periodontal disease, whereas specimen 2261 displays a linear enamel hypoplasia that is an indicator for a period of physiological stress during tooth development. Since amelogenesis of d4 in *P. germanicus* probably took place *in utero*, the hypoplasia detected in the juvenile rhinoceros is an indicator of maternal stress. Last, but not least, better knowledge of dental pathologies may unravel invalid species based on dental pathologies. For instance, at first sight the robust appearance of specimen 3782 may have raised the question if the fossil represents a species other than *P. germanicus*. However, as the present work demonstrated the appearance is related to pathology and not to differences in systematic origination.

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