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Extinct Eurasian rhinoceros *Coelodonta* and *Stephanorhinus* dental pathologies and tooth change modus

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ABSTRACT

Dental pathologies are described for four extinct rhinoceroses *Coelodonta antiquitatis* (Blumenbach, 1799) and *Stephanorhinus hemitoechus* (Falconer, 1868) of the Late Pleistocene Weichselian Glacial (MIS 3-5 d), *Stephanorhinus kirchbergensis* Jäger, 1839 of the Late Pleistocene Eemian Interglacial (MIS 5e), and *Stephanorhinus hundsheimensis* (Toula, 1902) from the Middle Pleistocene Cromerian Mosbach Interglacial (MIS 11) which material is mainly from the Rhine Valley megafauna migratory channel of Central Europe. All three extinct and even extant rhinoceros share similar ontogenetic P^4 pathologic misplacement pathologies. Those caused in some cases further dental abnormalities impacting the lower jaw dentition, even in rare cases including complete deformation of the lower jaw. In the browsing *Stephanorhinus* (*S. kirchbergensis, S. hundsheimensis*) the P^4 is more commonly misplaced; in the Mid-Pleistocene Mosbach *S. hundsheimensis* are three examples with similar misplacements on the right and left maxillaries, which have a similar genetic pool background of a local palaeopopulation. The grazer rhinoceros *C. antiquitatis* has a further pathology type with loss or even genetically pre-assessed non-development of the first upper or lower PM premolars or last M molars. The strong wear, damage, and loss of the anterior premolars in elderly individuals as ontogenetically based pathology, seem to result from intensive grazer and opal phytoliths abrasion. This loss finally resulted in irregularities of the permanent dentition and influenced wear stages and irregular abrasion angles of the tooth rows, affecting the upper and lower rows each others.

1. Introduction

Four rhinoceros species have been identified in the European Middle to Late Pleistocene: the browsers *Stephanorhinus hundsheimensis* (Toula, 1902) and *Stephanorhinus kirchbergensis* (Jäger, 1939), or the grazer *Stephanorhinus hemitoechus* (Falconer, 1868), and *Coelodonta antiquitatis* (Blumenbach, 1799) (e.g. Wüst, 1922; Lacombat, 2009; Van der Made, 2010) which have recently been subject to ancient DNA analyses in order to establish their phylogenetic relationships (cf. Welker et al., 2017). From those, pathological skulls and mandibles are described from eight sites of Germany (Fig. 1).

Knowledge about pathologies in those fossil Pleistocene rhinoceroses is very limited based on the two descriptions of a few recognized dental abnormalities by Garutt (1994) or Billia and Graovac (1999). Those dental pathologies were figured only for two specimens of the extinct woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799) and one extant *Diceros* skull all in subadult ages. In those cases, dental pathologies were defined as an “irregular eruption of the permanent P^4 in subadults” which was named “supernumerary” by Garutt (1994).

Wholly rhinoceroses *C. antiquitatis* are known from Germany by its holotype tooth (Blumenbach, 1799), one skeleton from the gypsum Karst of Middle Germany (Löscher, 1906) as redescribed in its pathological cranium herein (Fig. 2), a single incomplete skeleton from a gravel pit in northern Germany (Diedrich, 2008) and mainly single skulls, jaws or partly chew-damaged bones which are more and more identified to come from hyena den sites in cave entrances or at open air localities along river valleys (e.g. Diedrich, 2012, 2015). Abundant isolated bone material can be studied in many museums collections all over Germany coming from caves or gravel pit localities as figured herein with selected pathologic mandible and crania (Figs. 2–4). Especially, along the Lippe River in the Westphalian Bay (Heinrich, 1983; Siegfried, 1983) and along the Upper Rhine Graben (e.g. Jäger, 1939), uncountable rhinoceros

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Fig. 1. The geographic position of Middle to Late Pleistocene cranial pathologic rhinoceros remains sites in Germany being discussed herein.

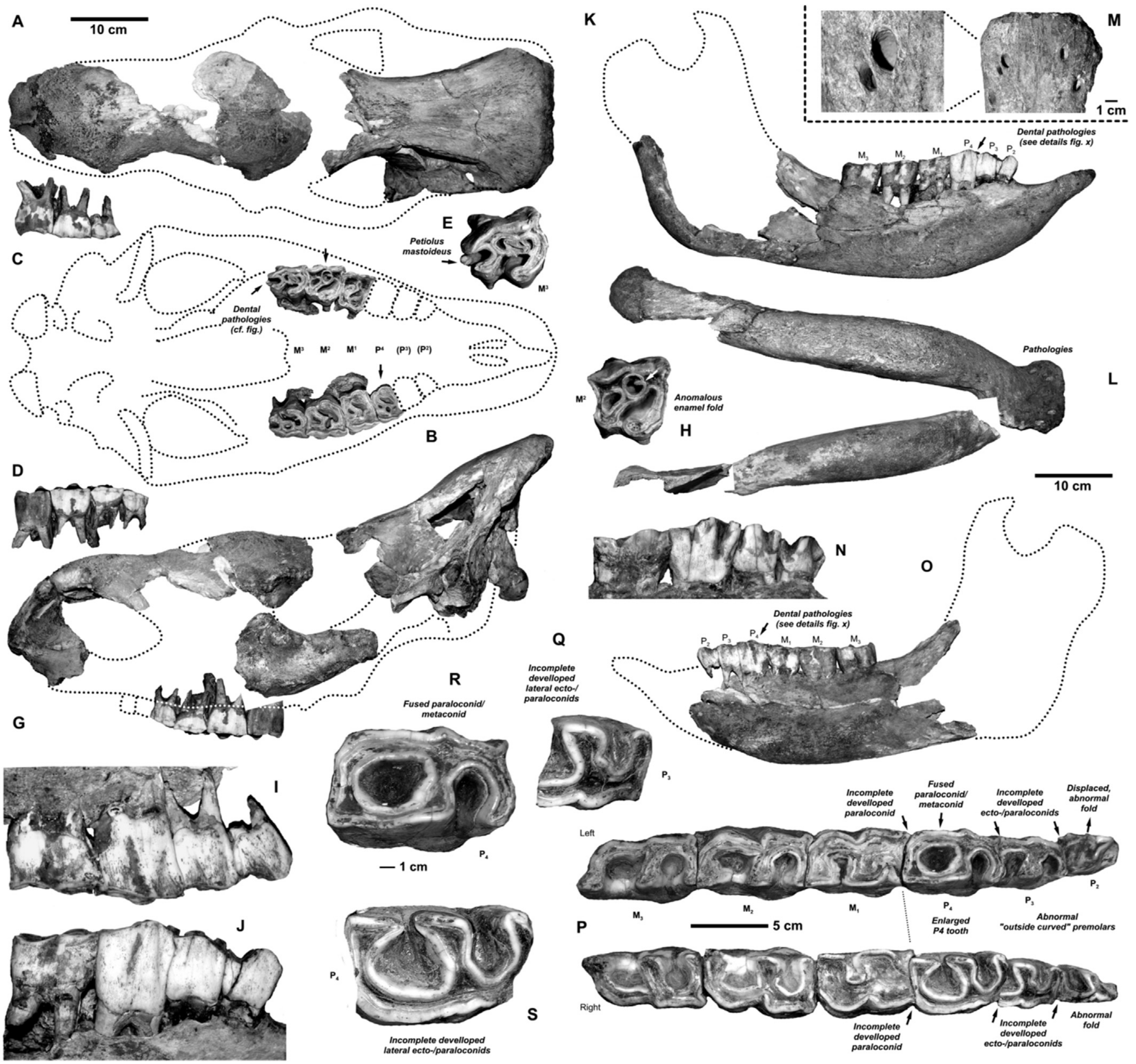

Fig. 2. *Coelodonta antiquitatis* (Blumenbach, 1799). Late Pleistocene (MIS 3-5 d), Pohlitz (Central Germany). A-J. Historical damaged skull in dorsal, ventral dentition and left lateral views, with dental pathologies on the right M^{2-3} (coll. NMG). K–O. Lower jaw in different views with dental pathologies/abnormalities of the premolar teeth of both mandibles. P–S. Detail views dental pathologies/abnormalities of the premolar teeth of both mandibles.

bones have been collected mainly from dumps in secondary position of gravel pits, from which some of the figured skulls come from. Abundant material has not been published or figured, yet. Mummies of *C. antiquitatis* are well known from the tar pits of Poland (Kubiak, 1994; Borsuk-Bialynicka, 1973; Kowalski, 2000) and as frozen mummies even with their horns from Siberia (e.g. Tolmachoff, 1929; Kirillova and Shidlovskiy 2010; Boeskorov et al., 2011).

The herein described Mid-Pleistocene *Stephanorhinus* skulls are also from a former sand pit near the West-German city Wiesbaden (Biebrich-Mosbach), which became famous for its *Mammuthus trogontheri* steppe fauna, which is recently also being revised to have been accumulated by spotted hyenas. Only *S. kirchbergensis* is known by a perfect preserved skeleton with nutrition content inbetween its teeth from the famous Interglacial skeleton Neumark Nord lake site in Middle Germany (cf. Van der Made, 2010).

2. Material and methods

In this study, the new undescribed Late Pleistocene Weichselian Glacial (MIS 3-5 d) *C. antiquitatis* crania and mandibles can be added from the Upper Rhine Graben Valley gravel pits or the Pohlitz site in the Thuringian Mountains (Germany) (Fig. 1). This material allows extending the knowledge of the dental change in more detail of both genera, *Coelodonta* and *Stephanorhinus*, and their cranio-dental pathologies. First pathologic *S. kirchbergensis* skull

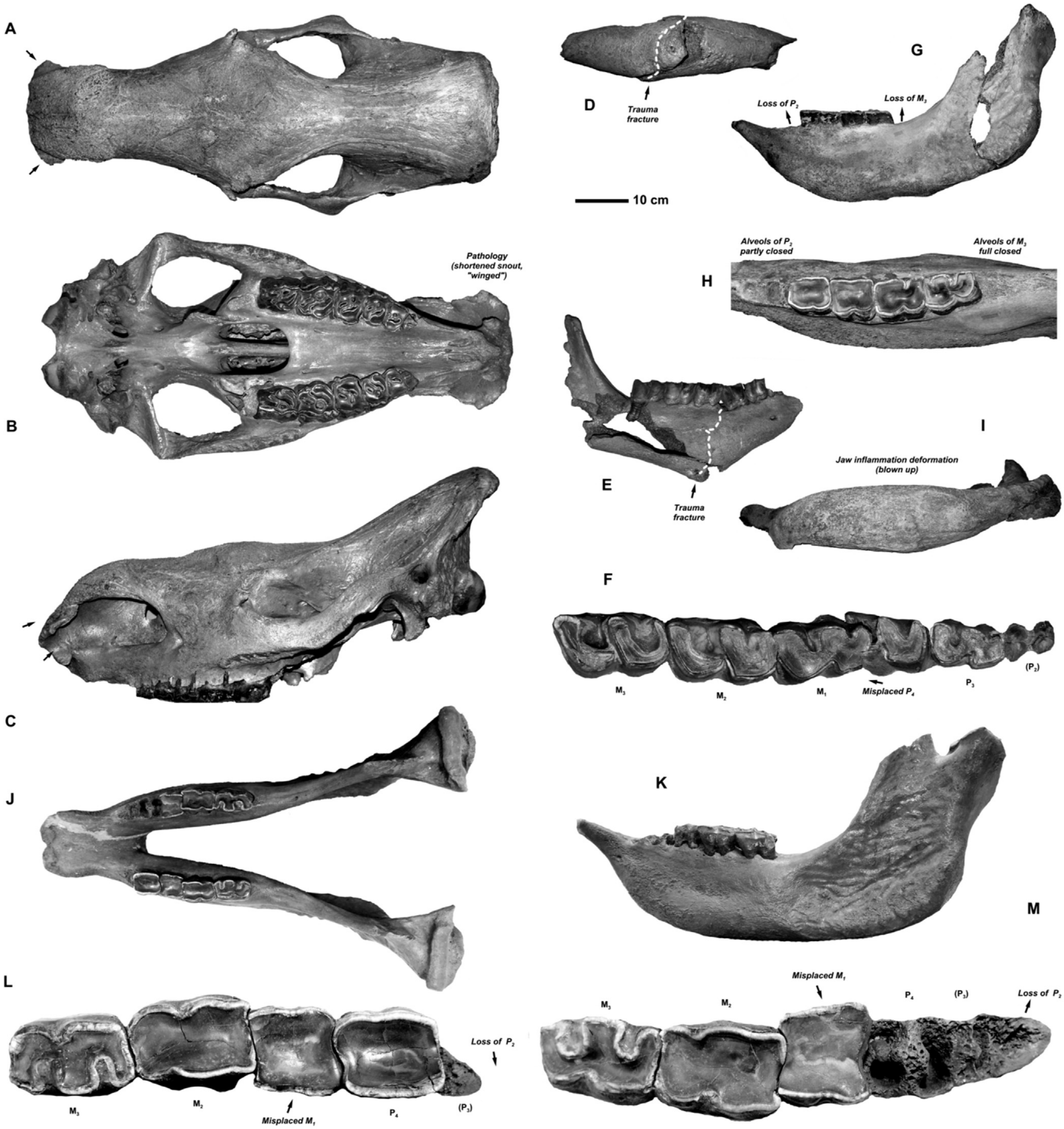

Fig. 3. A-C. *Coelodonta antiquitatis* (Blumenbach, 1799), Late Pleistocene. A-C. Skull from Bobenheim-Roxheim gravel pit Willersinn with rostrum shortening and nasal wing-like pathologies (coll. ME). dorsal, ventral, lateral left. D-F. Mandible with fracture and dental pathologies on lower jaws of *Coelodonta antiquitatis* (Blumenbach, 1799), Late Pleistocene, from Bobenheim-Roxheim gravel pit Willersinn (coll. ME), Upper Rhine Graben, West-Germany, dorsal and dental details. G-I. Left mandible (mirrored) from Bensheim with lost P_2 and M_3 and blown up mandible as a result of the root canal inflammations (coll. HH), ventral, lateral mandible tooth row details. J-M. *Stephanorhinus hemitoechus* (Falconer, 1868), Late Pleistocene, lower jaw from the Upper Rhine Graben without exact locality (coll. NMM), lateral, ventral, and right tooth row details.

records are figured from the Eemian Interglacial MIS 5e. Similar pathologic *S. hundsheimensis* skulls from the late Middle Pleistocene (Cromerian MIS 13–15) Mosbachian Interglacial site are further discussed. Both groups of grazer (*Coelodonta*) and browser (*Stephanorhinus*) specialized rhinoceroses are compared in their dental pathology differences to extant *Diceros* species of Africa.

To cover a wide-range of rhinoceros species, and as much as possible different dental pathologies, rhinoceros skulls and mandibles were studied from Mid-Late Pleistocene Central European sites mainly along the Rhine River Valley where some ten thousands of rhino bones were found the past hundreds of years by gravel pit dump collecting, bag hoe finds, or excavating. Other hyena open air den sites with rhino guilt concentrations are another important source in Germany, such as the hyena den gypsum karst

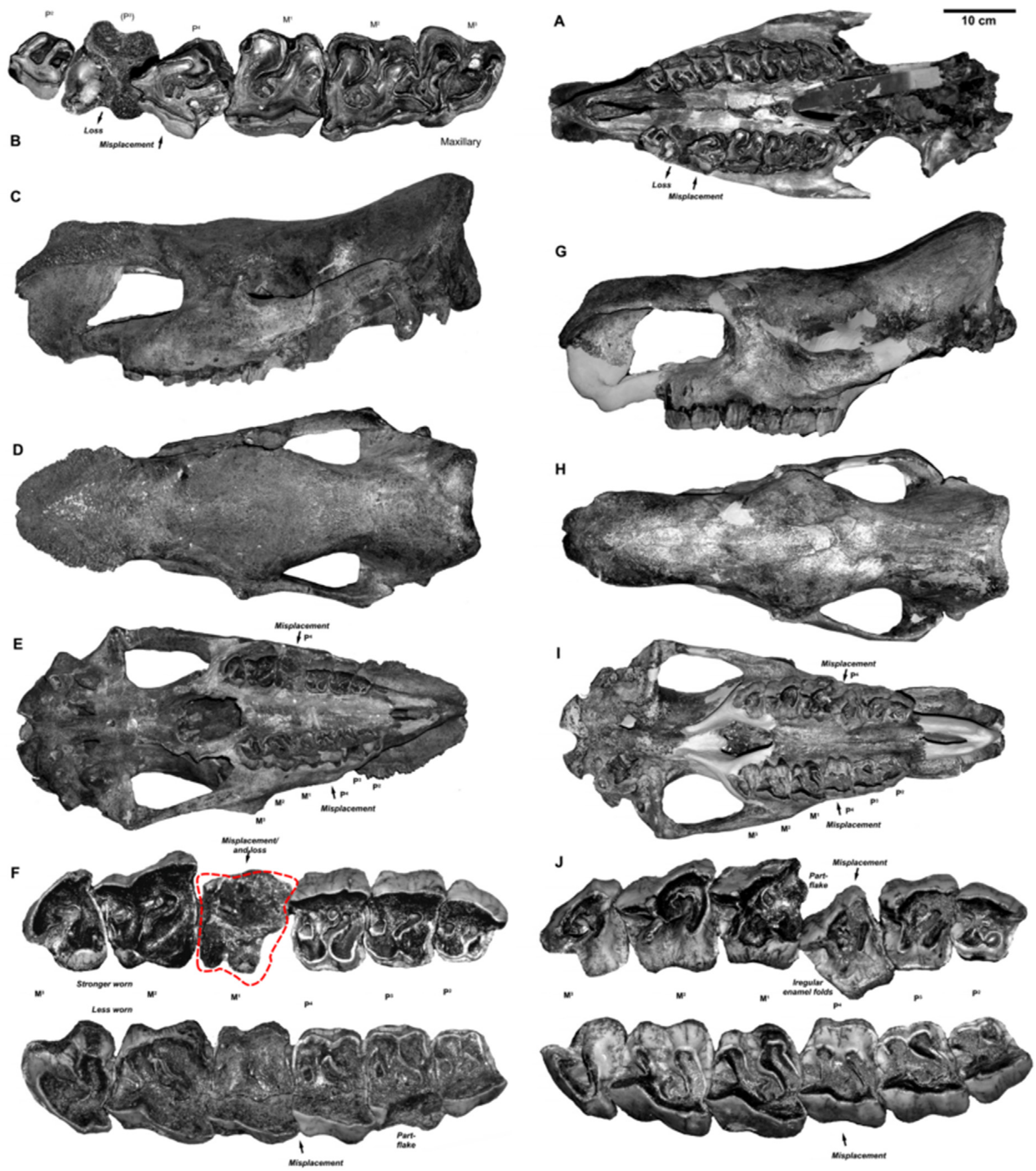

Fig. 4. A-B. *Stephanorhinus kirchbergensis* Jäger, 1939 skull from (coll. ME), ventral, and right tooth row detail. *Stephanorhinus hundsheimensis* (Toula, 1902). C–F. Skull from Mosbach (coll. NMM), dorsal, ventral, lateral right (mirrored), and dentition details. G-J. Skull from Mosbach (coll. NMM), dorsal, ventral, lateral right (mirrored), and dentition details.

sinkhole at Pohlitz, Thuringia (Fig. 1). The Rhine River Valley region (Westphalian Bay and Upper Rhine Graben regions) has by far the most-bone-rich open-air site density in Central Europe (Germany). This is due to dense active gravel pits nearby the large cities in the North, such as Bottrop, and in the South with Mainz, Wiesbaden, Darmstadt, and Mannheim, further down to Karlsruhe. The local natural history museums (Bottrop, Mainz, Wiesbaden, Darmstadt, Karlsruhe, and Stuttgart) and some active private collectors (Hartnagel, Menger) keep the largest Rhine gravel pit bone collections. Those have been screened by the author many years for Pleistocene rhinoceros material (Fig. 2). The Middle Pleistocene spotted hyena den bone assemblage of Mosbach (Cromerian, MIS 13–15) Rhine River terrace were checked for rhino pathologies (coll. Mainz, Wiesbaden and Darmstadt) (Fig. 3).

In total, in both cases of the screened *Coelodonta* and *Stephanorhinus* cranial material, the dental pathological material is less than 0.1% of the total skull/jaw material each. On the postcranial, pathologies have not been identified yet.

Woolly rhinoceros calves to elderly individual age classifications are estimated herein on dental row material from several different

German sites (Fig. 5). Those allow presenting in *Coelodonta* and *Stephanorhinus* the tooth change stages and its time estimation of abnormality appearance. The individual age classification of young calf, old calf, subadult, adult and elderly is based on the tooth change modus presented for the mandible and maxillary dentition tooth rows of deciduous and permanent teeth (Fig. 4). The results are compared to modern (cf. Dittrich, 1974) and Late Pleistocene *C. antiquitatis* dental change described by Garutt (1994), which latter can be extended herein much in more detail, whereas it is presented for the first time in *Stephanorhinus*.

Abbreviations of studied collections: Private collections H. Hartnagel in Bensheim, Germany (**HH**) and F. Menger in Geinsheim, Germany (**ME**). Naturkundemuseum Gera (**NMG**). Naturhistorisches Museum Mainz (**NMM**).

3. Results

3.1. Skull of Coelodonta from Pohlitz skeleton

The right maxillary of a *C. antiquitatis* cranium comprises the M^{1-3} and the left one the P^4-M^3 (Fig. 2). In some historic casts of the tooth rows, the P^4 was incorrectly fixed and misidentified as P^3 which simply results from the pathology and unusual use as described herein. After the historical descriptions, two upper premolar teeth became lost during time and were not able to be relocated in the collection anymore. From the right upper molar teeth, the M^3 has developed posterior a Petiolus mastoideus (Fig. 2E). This causes an un-normal and sinuous occlusal surface of all last molars (see the labial view in Fig. 2C and D - to compare with the slightly convex one). The M^2 tooth has an anomalous enamel fold (Fig. 2B). The left tooth row is only pathological in the P^4, which is much more used in its anterior surface (Fig. 2B). This exactly correlates to the lower jaw pathologies, especially the left P_4. The upper and lower dentitions fit exactly in their "bite" after correcting the P^4 position. The lower jaw includes all six teeth in each mandible. The symphyses have four (two on each side) unusual oval openings ("foramina") (Fig. 2M). On both tooth rows, the P_2 is not in the normal place and curves labial (right) or is even misplaced (left) about 2–3 mm (Fig. 2P). Both tooth rows have no plain occlusal chew surface as it is usual in more or less normal dentitions (e.g. Fig. 2I and J, mandibles in lateral views with a plain occlusal surface). In both tooth rows, the P_4 is too high erupted and builds together with the adjacent teeth a triangle-like occlusal surface in lateral view (Fig. 2I, J, N). In both jaws, the M_{2-3} are more or less developed normally. All four anterior teeth are deformed or have incomplete enamel folds. The right M_3 has a non-developed anterior paraconid. The right P_3 have incomplete developed ecto-/paraconids (Fig. 2Q). The enamel fold in the P_2 is completely abnormal and has a strong anterior angled position. The left M_1 is again with an incomplete paraconid (Fig. 2P). The strange fusion between paroconid and metaconid in the left P_4 is note worthy, which has no explanation yet.

3.2. Skull/mandibles of Coelodonta from the Rhine Graben

Fig. 3D–E shows the trauma fracture of the mandible in *C. antiquitatis*. It is blown up between and below the P and M and has a strange angled form in lateral view (Fig. 3E). The bone surface is granular nearby the callus (thickening area, Fig. 3E, I) which is a typical surface structure within the bone healing process. The P_2 loss and rostrum shortening and nasal wing-like pathology is remarkable (see arrows in Fig. 3A). A lower jaw that would fit the skull with loss/non-development of both P_4 teeth and completely closed alveoli is another unique dental pathology record. It remains unclear, if those belong together as finds from the same pit. In both, the skull and mandible, the anterior premolars were either not developed or were lost at a subadult individual age estimated on the full-fused alveoli (Fig. 3J-M). Another left mandible from another site of the Rhine Graben has a similar loss of the P_2 (Fig. 3G and H), which alveoli are still in the closing process. Furthermore, the M_3 must have been lost already before, which alveoli are completely refilled.

3.3. Skulls of Stephanorhinus from Mosbach and the Rhine Graben

One *S. hemitoechus* lower jaw from the Late Pleistocene (Weichselian) of the Upper Rhine Graben is from an elderly individual that has strongly worn teeth (Fig. 3J, M). The anterior teeth are missing most probably not as a result of natural loss, whereas the alveoli of the P_2 are already closed, which is similar to the *C. antiquitatis* mandibles. In both grazers, the P_2 is the first tooth that is damaged and lost. One Late Pleistocene Eemian aged skull from the Rhine Graben of *S. kirchbergensis* has the right P^4 position abnormality (Fig. 4A and B), which is found similar in both tooth rows of two Middle Pleistocene (Cromerian) *S. hemitoechus* crania from Mosbach (Fig. 4C–J). Two *Stephanorhinus* individuals died in the similar early adult age (in the time shortly after the P^4 tooth change), whereas one *S. hundsheimensis* individual lived with this tooth misplacement until elderly age.

3.4. Ontogenetic tooth changes in Coelodonta and Stephanorhinus

To understand abnormalities in dental pathologies, the "normal" tooth change modus is presented as detailed as possible for both genera (Fig. 5). The tooth change stages in grazing woolly rhinoceros *C. antiquitatis* is based on material from the German sites Bad Wildungen, Selm-Ternsche, Krölpa, Bobenheim-Roxheim, and others. Tooth change stages in browsing *S. hundsheimensis* is based on material from Mosbach (Fig. 6). In general, in both extinct rhinoceroses, the change modus is as expected similar. Both start with the eruption of the four deciduous teeth from anterior to posterior, the upper and lower dm1 to dm 4, which are the teeth in young calves. The "milk" teeth are replaced then starting opposite, from posterior. First the M1/M1 and then the M2/M2 rise behind the worn upper and lower dm1-4 teeth in the older calf stage. The tooth loss begins in the subadult age class. First, the P2-3/P2-3 are replaced by the permanent premolars for which no examples are found in any collection. Then, the P4/P4 exchanges the dm4 and the M3/M3 rises up more or less simultaneous. This phase is the most problematic in genetically related dental pathologies of *Stephanorhinus*, but not in *Coelodonta*. The problems in Stephanorhinus are obviously the few spaces for the P4/P4, which is not yet to understand on the few material. In early to late adults, the dental abrasion causes different pictures of the lophes, which in some of the teeth completely disappear after full tooth wear (Fig. 5).

4. Discussion

4.1. ? genetically P^4 eruption pathology

Dental pathologies were figured only on two subadult *Coelodonta* skulls and one extant *Diceros* skull (Dittrich, 1974; Garutt, 1990). In all those described cases, the dental problems are caused by an "irregular eruption of the permanent upper jaw P^4" (Garutt, 1990, 1994). The P^4 was in one case laterally and horizontally positioned in the maxillary, in another case it grew beside the milk molar (= supernumerary: Garutt, 1990). This P^4 anomaly can be reported herein again with one of the preserved, but strongly used last premolars of the Pohlitz cranium. The lower jaw dentition of the Pohlitz specimen, especially the P_4, is erupted much too high

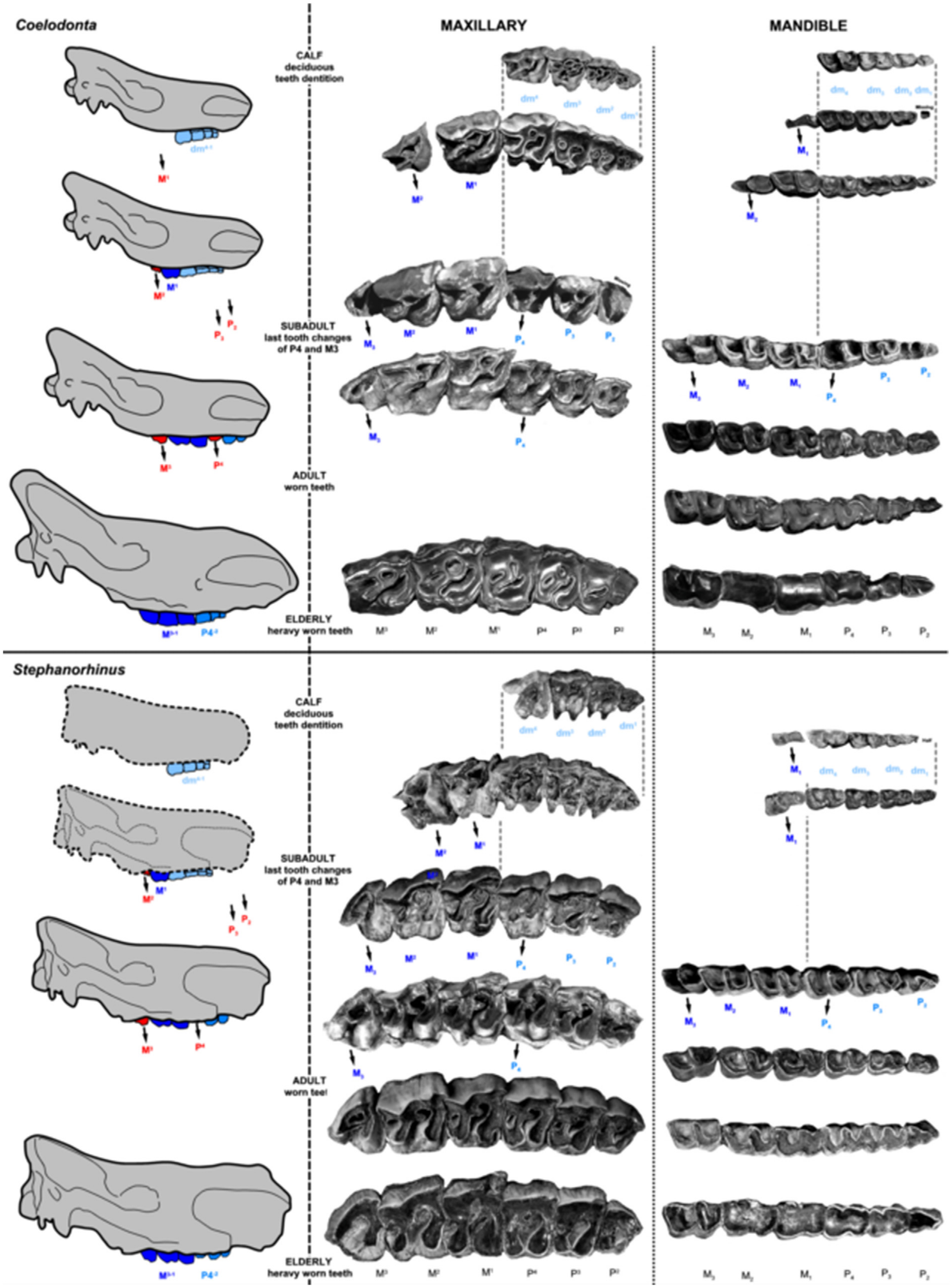

Fig. 5. A. Tooth change stages in woolly rhinoceros *Coelodonta antiquitatis* based on material from the German sites Bad Wildungen, Selm-Ternsche, Krölpa, Bobenheim-Roxheim, and others. B. Tooth change stages in *Stephanorhinus hundsheimensis* based on material from Mosbach.

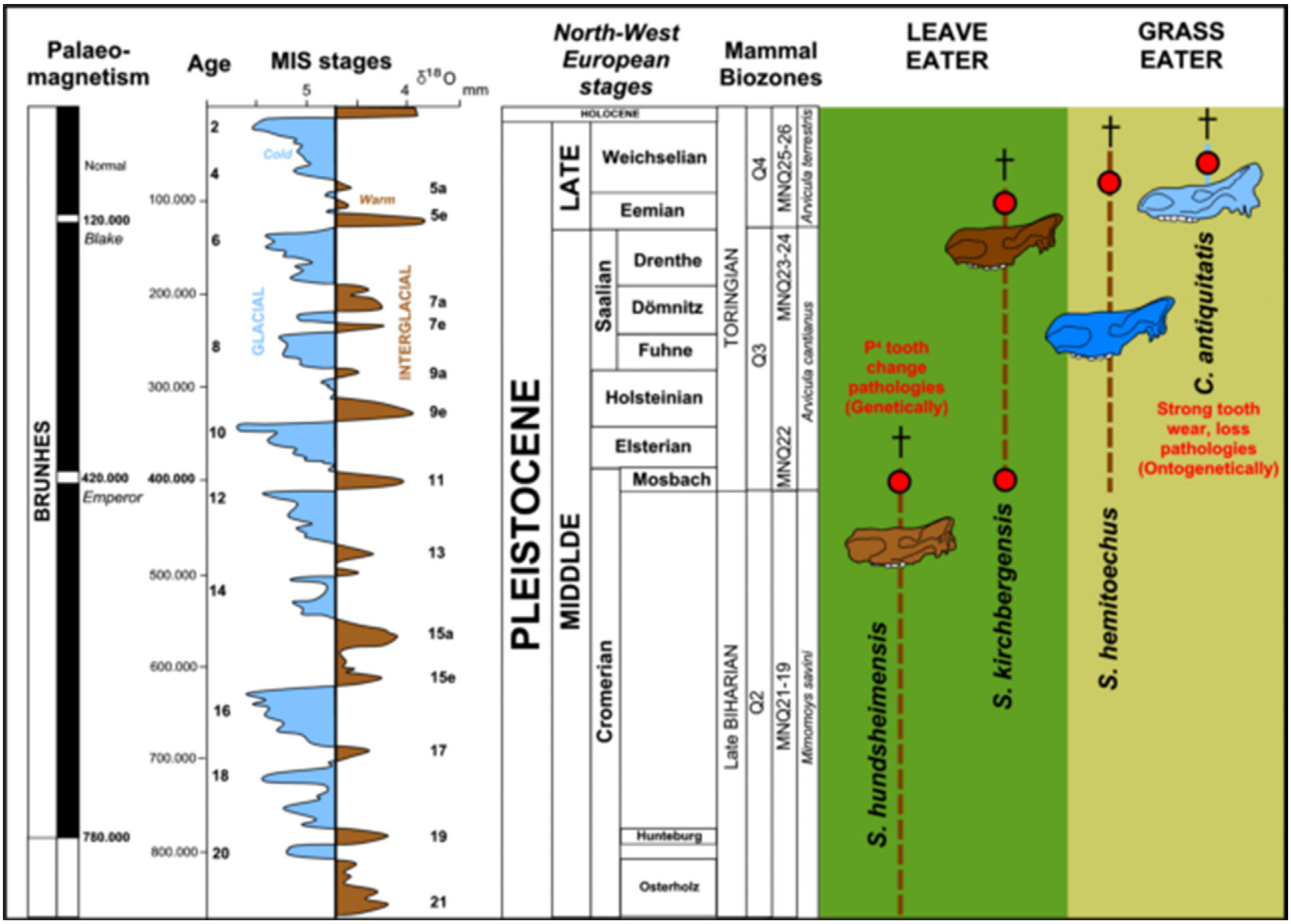

Fig. 6. Dental pathology differences in browsers (*S. hundsheimensis*, *S. kirchbergensis*) genetically, and grazer (*S. hemitoechus*, *C. antiquitatis*) ontogenetically based.

in both mandibles causing in lateral view a triangular occlusal surface, that made regular rotation chewing difficult to impossible with causing other dental/jaw defects. Unfortunately, the lower jaw joints at the Pohlitz mandible and skull are missing due to modern damage and only one articulation surface is present in the skull, so deformation or inflammation of the joints cannot be tested well. The symphyses of the mandibles are angled about 5° in anterior view correlating to the mandible deformations. Other dental abnormalities are also found in the form of irregularly worn right and left dentitions (cf. Garutt, 1994). Finally, dental and cranial abnormalities figured for the Rhine Graben material (Fig. 3) are without comparisons yet. The few dental pathological materials must be added with further finds, but herein the tooth modus and time of the P^4 "problem" are compiled for the main ontogenetic and tooth change stages (Fig. 5).

4.2. Wear damage and loss of the anterior premolars

This is the typical and most common dental pathology in elderly individuals of *C. antiquitatis* (and one *S. hemitoechus*) as ontogenetically related pathology that seems to result from intensive grazing and opal phytoliths abrasion (Fig. 6). Grass as main food source is well documented in stomach contents of Siberian frozen wholly rhinoceros mummies (Tolmachoff, 1929; Tikhonov et al., U. 1999; Tiunov and Kirillova, 2010; Boeskorov et al., 2011).

5. Conclusions

The normal dental change mode in both extinct Pleistocene rhinoceros genra *Coelodonta* and *Stephanorhinus* are compiled from early calf to elderly age classes. Based on the results, the unique hypothesis is proposed that the relationships between dental pathology is either result of genetically or ontogenetically influences. Four main dental pathologies are recorded in the fossil Late Pleistocene Eurasian woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799). 1. The most common is the maxillary P^4 late or misplaced rotated appearance, which results in the too high eruption of the P_4 antagonist. This can continue in a chain reaction of further dental palaeopathology: positions or absence of enamel folds or development of a Petiolous mastoideus on the posterior part of the M^3. After some years, the entire occlusal surface becomes non-plain, instead of triangular in the lower and opposite in the upper jaw. It finally can cause a complete tooth row misplacement and lower jaw deformation. 2. Supernumerary (permanent tooth erupts besides row) is recorded only once in *Coelodonta*. 3. Missing tooth (lost tooth), here the P^2 or P_2, caused also irregular tooth wear, whereas the teeth are worn anteriorly stronger, posteriorly lesser. This situation seems to correlate with a snout deformation and its shortening (? fight damage as trauma result in males). 4. Irregular tooth wear on both sides. In *Stephanorhinus kirchbergensis* and *Stephanorhinus hundsheimensis* the main dental pathology is a misplacement of the P^4 affecting the adjacent teeth. In *S. hundsheimensis* of Mosbach one individual did not survive long after the P4 misplacement, another lived to elderly age. In *Stephanorhinus*, the P^4 misplacements seem to relate to genetic background because of similar appearance. Based on DNA phylogenetic cladograms, both *Stephanorhinus* species are closest in their evolution and seem to share the same genetic driven tooth change pathologies (Fig. 6). Most probably, an evolution shortening trend of the maxillary caused the displacement of the last changing tooth. The P^4 misplacement is not yet recorded in the grazer *S. hemitoechus*, which has instead similar dental abrasion and loss damages as found on the grazer *Coelodonta*.

Author contribution

All collection studies, research and graphic work was made by the author.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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