Early Agenian rhinocerotids from Wischberg (Canton Bern, Switzerland) and clarification of the systematics of the genus *Diaceratherium* (#37621)

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Early Agenian rhinocerotids from Wischberg (Canton Bern, Switzerland) and clarification of the systematics of the genus *Diaceratherium*

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Background. Wischberg is a Swiss locality in Bern Canton which has yielded numerous vertebrates remains from the earliest Miocene (= MN1). It has a very rich faunal diversity, one of the richest in Switzerland for this age. Among all the mammals reported in the original faunal list 70 years ago, three rhinocerotid species were identified. The material consists of two fragmentary skulls, cranial fragments, several mandibles, teeth and postcranial bones, in a rather good state of preservation.

Results. After reexamination of the material from this locality (curated in three different Swiss museums), and comparison with holotype specimens, we show that all rhinocerotid specimens from Wischberg can be referred to ~~just~~ two species. Most of the material can be attributed to the large size teleoceratine *Diaceratherium lemanense*, while only a few specimens, including a skull and mandible, belong to the much smaller sized *Pleuroceros pleuroceros*. We describe and illustrate for the first time most of these fossil remains. However, the systematics of the genus *Diaceratherium* is currently controversial, and we attempt to elucidate it based on our new observations, though a large-scale phylogenetic study should be done in the future to resolve it. The rhinocerotid association found in Wischberg is nonetheless typical of the MN1 biozone, which results from a faunal renewal occurring just before the end of the Oligocene.

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Abstract

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Introduction

The Aquitanian Lower Freshwater Molasse (USM) record of the Plateau Molasse is characterised within the central and eastern area of the Swiss North Alpine Foreland Basin (NAFB) by the floodplain deposits from the *Granitische Molasse* Formation, lateral equivalent of the *Molasse grise de Lausanne* Formation from the western area (Habicht 1987, Berger et al.

2005a, b, Schweizerisches Komitee für Stratigraphie und Landesgeologie 2014). These geological formations yielded many vertebrate localities, unfortunately recording mostly incomplete assemblages and only a few large mammal species (Scherler et al. 2013). However, Agenian land mammal associations are remarkably well documented in the locality of Wischberg (MN1; Schaub & Hürzeler 1948, Engesser & Mödden 1997), Engehalde (MN2; Becker et al. 2010) and Wallenried (MN2; Becker et al. 2001, Mennecart et al. 2016).

From the area of Langenthal (Bern Canton, Switzerland), Gerber (1932, 1936) first reported fossil rhinocerotids originating from the Wischberg locality (latitude 47.199157894°/longitude 7.763943664°; Fig. 1). A preliminary mammal list was provided by Schaub & Hürzeler (1948), including Eulipotyphla, Rodentia, Lagomorpha, Cainotheriidae, non-ruminant Artiodactyla, Ruminantia, Tapiridae and Rhinocerotidae. More recently, Lagomorpha have been reviewed by Tobien (1975) and part of large mammals by Becker (2003) and Scherler et al. (2011, 2013). Since the work of Engesser & Mödden (1997) on the mammal biozonation of the Lower Freshwater Molasse of Switzerland, the mammal assemblage of Wischberg (Tab. 1) can be considered as one of the most important and complete in the Swiss Molasse Basin, consistently pointing to an early Aquitanian age (MN1 biozone; Agenian European Land Mammal Age).

Figure 1:
General setting of Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).
(A) Map of a part of Western Europe showing the location of Switzerland and the Molasse Basin. (B) Enlargement of the Aquitanian palaeogeographical context of the Swiss Molasse Basin, with detailed location of Wischberg locality. Modified from Becker et al. (2010).

Table 1:
Mammal assemblage of Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, ~~Early~~ Miocene).

Contrary to Schaub & Hürzeler (1948), the cranio-mandibular, dental, and postcranial remains from Wischberg are here attributed to two different rhinocerotid species, instead of three. In this work, we first review the description and the identifications of the material, which can be assigned to the single-horned and short-limbed teleoceratine *Diaceratherium lemanense* (Pomel, 1853), and the small-sized ~~double~~-horned *Pleuroceros pleuroceros* (Duvernoy, 1853). Second, we examine the systematics of the genus *Diaceratherium*, which is currently contentious, and the ecological role of the Early Miocene Rhinocerotidae within the large herbivorous mammal communities of Western Europe.

Materials & Methods

The fossil materials from Wischberg were discovered between 1931 and 1947 in two pits of Aquitanian mottled marls and sands of the *Granitische Molasse* (Schaub & Hürzeler 1948) that

were exploited during the first half of the last century in Langenthal (Bern Canton, Switzerland). The sites are no longer accessible due to anthropogenic developments. The studied material includes twenty-five rhinocerotid specimens (and among them numerous casts) that are stored in the natural history museums of Bern (*Naturhistorisches Museum des Burgergemeinde Bern*) and Basel (*Naturhistorisches Museum Basel*) as well as in the local museum of Langenthal (where the original skull and a mandible of *Diaceratherium lemanense* are exposed). It is worth to clarify that the original specimens referred to *Pleuroceros pleuroceros*, except the semilunate NMBE5031537, are lost and the work on this taxon is based on the remaining casts.

The rhinocerotid specimens from Wischberg have been described by means of anatomical descriptions, comparative anatomy, and biometrical measurements. The sequence of described dental and osteological features follows Antoine (2002). The dental terminology follows Heissig (1969) and Antoine (2002), while dental and skeletal measurements were taken according to Guérin (1980). The locomotion type is based on the gracility index of the McIII and MtIII (100 x TDdia/L; Guérin 1980). All dimensions are given in mm and those between parentheses are estimated.

The stratigraphical framework is based on geological time scales and European Land Mammal Ages (ELMA) for the Neogene (Hilgen et al. 2012). Successions of Mammal Neogene units (MN) were correlated by Berger (2011) based on biostratigraphic and magnetostratigraphic data (BiochroM'97 1997, Engesser & Mödden 1997, Kempf et al. 1997, 1999, Mein 1999, Steininger 1999, Agustí et al. 2001).

Body masses of the rhinocerotid species found in Wischberg are estimated from dental measurements and particularly from the lower first molar (m1) area (length × width). Teeth are indeed the most frequent elements in the fossil record because of their higher fossilization potential. Teeth are also the subject of extensive studies in palaeontology and biology due to the diagnostic values of their morphology. Legendre (1989) developed several allometric equations for different groups of extant mammals which always show correlation coefficients higher than 0.95, indicating high correlations between the body mass and the occlusal area of the first lower molar. The equation used to estimate the body masses of rhinocerotids is based on the correlation established for perissodactyls by Legendre (1989).

Abbreviations

APD antero-posterior diameter, **Cc** calcaneus, **dia** diaphysis, **dist** distal, **H** height, **I/i** upper/lower incisor, **L** length, **M/m** upper/lower molar, **Mc** metacarpal, **MHNT** *Museum d'histoire naturelle de Toulouse*, **ML** *Museum Langenthal*, **MNHN** *Muséum National d'Histoire naturelle (Paris)*, **Mt** metatarsal, **NMB** *Naturhistorisches Museum Basel*, **NMBE** *Naturhistorisches Museum der Burgergemeinde Bern*, **P/p** upper/lower premolar, **prox** proximal, **SMNS** *Staatliches Museum für Naturkunde Stuttgart*, **TD** transversal diameter, **W** width.

Results

Systematic palaeontology

Class Mammalia Linnaeus, 1758
Order Perissodactyla Owen, 1848
Superfamily Rhinocerotoidea Gray, 1821
Family Rhinocerotidae Gray, 1821
Subfamily Rhinocerotinae Gray, 1821
Genus *Pleuroceros* Roger, 1898

Type species: *Pleuroceros pleuroceros* (Duvernoy, 1853)
Included species: *Pleuroceros blandfordi* (Lydekker, 1884)

Pleuroceros pleuroceros (Duvernoy, 1853)
Fig. 2-3, Tab. 2

Stratigraphical range: Latest Oligocene (?MP29/30) to Early Miocene (MN1-MN2), western and central Europe (Antoine & Becker 2013)
Occurrences:
- France: Billy-Base (Allier), ?MN29/30; Gannat, MN1 (type locality); Paulhiac, MN1; Pyrimont-Challonges, MN1; Saulcet, MN1; Laugnac, MN2; Montaigu-le-Blin, MN2; (Duvernoy 1853, Lavocat 1951, de Bonis 1973, Hugueney 1997, Ginsburg & Bulot 2000, Antoine et al. 2010, Antoine & Becker 2013, Scherler et al. 2013)
- Germany: Flörsheim, MN2; Pappenheim, MN2 (Schlosser 1902, Heissig 1999)
- Switzerland: Wischberg, MN1 (Schaub & Hürzeler 1948, Heissig 1999, Becker 2003)
Referred material: Skull with right P1-M3 and left P2-M3 (original specimen lost, cast NMBE5031553, cast NMB-AS77), fragmented mandible with right p4-m3 and left m1-2 (original lost, cast NMBE5026739, cast NMB-AS78), right semilunate (original NMBE5031537, cast NMB-AS3), right McIV (original lost, cast NMB-AS79) from Wischberg (Switzerland, MN1)

Figure 2:
***Pleuroceros pleuroceros* (Duvernoy, 1853) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).**
Partial skull NMBE5031553 in lateral (A), dorsal (B), medial (C) and occlusal (D) views and left-side fragment from the same individual in occlusal (E) view. Mandible fragments NMBE5026739 in labial (F), lingual (G) and occlusal (H) views with p4-m3 (right-side fragment) and m1-2 (left-side fragment). Scale bars = 10 cm.

Figure 3:
***Pleuroceros pleuroceros* (Duvernoy, 1853) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).**

Right semilunate NMBE5031537 in dorsal (A), proximal (B), distal (C), lateral (D) and medial (E) views and right McIV (cast NMB-AS79) in dorsal (F), lateral (G), ventral (H), medial (I) and proximal (J) views.

Table 2:
Dimensions [mm] of the cheek teeth of *Pleuroceros pleuroceros* (Duvernoy, 1853) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Description

Skull. NMBE5031553 is a cast of an incomplete, fragmented and transversally compressed skull comprising a part of the frontals, the area of the right zygomatic arch, the right P1-M3 and the left P2-M3. Few cranial characters are observable. We can note a remarkably curved upwards jugal bearing a *processus postorbitalis*, an infraorbital foramen situated above the P3, an anterior border of the orbit reaching the paracone of M1, an anterior base of the zygomatic process high above the M1 as well as the presence of a *processus ~~lacrymalis~~*.

Mandible. From the fragmented mandible NMBE5026739, the *corpus mandibulae* (height below m3 = 71.5) does not seem to bear a median sagittal groove (*sulcus mylohyoideus*). The retromolar space is short and the position of the *foramen mandibulare* (based on the transverse slimming of the *corpus* in cross section) is located below the teeth neck.

Upper teeth. The dental wear of the tooth series is advanced. The premolar series is rather long compared to the molar series (LP3-4/LM1-3 > 50; Tab. 2). The dental structures are simple, without secondary enamel folds. The cheek teeth are brachydont (low-crowned), and the roots are long and distinct. The upper cheek teeth lack crista and medifossette. The paracone fold is present on all cheek teeth and strong on lesser worn teeth such as the M2-3. The premolars are molariform (*sensu* Heissig 1969) and lack any crochet, antecrochet and constriction of both protoloph and metaloph. The labial cingulum is reduced to the posterior part of the ectoloph and the lingual cingulum is reduced to the opening of the median valley. On P2–4 the postfossette is narrow and the metaloph is posterolingually oriented. The P1 is much narrower than P2 and triangular in occlusal view. On P2, the protocone is equally developed than the hypocone, and the protoloph is transverse, continuous and widely connected with the ectoloph. A crochet is always present on upper molars, but the metaloph is not constricted. The labial cingulum is weak and absent at the base of the paracone fold, whereas the lingual cingulum is reduced to the base of the posterior half of the protocone, reaching the opening of the median valley. The metastyle is long and the metacone fold is absent. On M1-2, the protoloph is slightly constricted and bears an antecrochet, the metaloph is short and the distal part of the ectoloph is straight. A weak mesostyle is present on M2. The M3 has a roughly triangular occlusal outline, though the ectoloph and metaloph are fused in a characteristic convex ectometaloph without posterior groove. The protoloph is rather transverse and straight, without constriction and antecrochet.

Lower teeth. On lower cheek teeth, the labial cingulum is reduced to a thin bulge at the base of the external groove and the lingual one is completely absent. The external groove is developed

and is vanishing above the neck. The trigonid is angular and forms a right dihedron. The metaconid and the entoconid are not constricted. The posterior valley is V-shaped, but wider on lower molars. The hypolophid of the lower molars is oblique and there is no lingual groove on the entoconid of m2-3.

~~**Semilunar**~~. The semilunate NMBE5031537 is rounded and eroded (DT=30.6, DAP= 53.2, H=38.8). The medial and lateral facets are not preserved, except for the flat, ovoid, and sagittally elongated proximal facet for the scaphoid. In proximal view, the ulna-facet is lacking and, in anterior view, the anterior side is smooth with an acute distal border. The proximal facet is very convex and short sagittally. The magnum-facet is roughly flat in its anterior half and concave posteriorly.

Metacarpals. The McIV NMB-AS79 is short and rather gracile (L = 112.3, DTprox = 32.6, DAPprox = 31.1, DTdia = 26.0, DAPdia = 15.2, DTdist = -, DAPdist = 28.8; IG = 23.0), sagittally flattened, with a short insertion for the m. interossei. It bears a salient insertion for the m. extensor carpalis, and a high and acute intermediate relief of the distal articulation. In proximal view, the proximal facet is triangular and the articulation facet for the McV on the lateral side is not preserved.

Remarks

Based on comparison with coeval rhinocerotid genera, the referred specimens point to a remarkably small rhinoceros, excluding an assignation to the teleoceratine *Diaceratherium*. Moreover, this genus differs by a developed external groove and a rounded trigonid on the whole lower cheek teeth series. The acerathere (*sensu lato*) *Mesaceratherium* differs by the lack of antecrochet and continuous lingual cingulum on P2-4, by the presence of a short metastyle and a concave posterior part of the ectoloph on M1-2 as well as a rounded trigonid, a transverse hypolophid on lower cheek teeth and a pentagonal outline of the proximal facet of the McIV (Heissig 1969, de Bonis 1973, Antoine et al. 2010). The species *Protaceratherium minutum* (Cuvier, 1822) is of similar size, but morphologically differs by a constricted metaconid and an angular V-shaped external groove on lower cheek teeth as well as the lack of a labial and continuous lingual cingulum, the presence of a usually multiple crochet on upper premolars, a rounded distal border of the anterior side of the semilunate, and a trapezoid outline of the proximal facet of the McIV (Antoine et al. 2010).

Pleuroceros shares many striking morphological similarities with these referred specimens, such as a reduced lingual cingulum on upper premolars, a lack of antecrochet on P2-3, a straight posterior part of the ectoloph on M1-2, and a smooth anterior side of the semilunate with an acute distal border. According to the dimensions, *Pleuroceros blanfordi* (Lydekker 1884) is ca. 15% larger than those of the studied material and differs by a lingual bridge on P2-4 (semimolariform upper premolars, *sensu* Heissig 1969), a transverse metaloph and a hypocone weaker than the protocone on P2, an usually constricted protocone on P3-4, the presence of an antecrochet on P4, a weak mesostyle on M2, a constricted metaconid on lower cheek teeth, and a continuous lingual cingulum on lower premolars (Antoine et al. 2010).

The dimensions as well as the postcranial, cranial and dental morphology of Wischberg specimens are in fact extremely similar to the type material and other specimens of *Pleuroceros pleuroceros* (Duvernoy, 1853) from Gannat (type locality, collection MNHN), notably by the shape of the jugal bearing a *processus postorbitalis*, the molariform upper premolars lacking antecrochet, the only slightly constricted protoloph on M1-2, the typically convex ectometaloph of M3, the absence of antecrochet and protocone constriction on the M3, the reduction of the labial cingulum, the rather smooth external groove and rounded trigonid on lower cheek teeth, as well as an acute distal border of the anterior side of the semilunate and a somewhat short and gracile McIV (Tab. 3; Duvernoy 1953, Roman 1912, de Bonis 1973, Antoine et al. 2010, pers. obs.).

Table 3:
Metapod lengths of *Pleuroceros pleuroceros* and *Diaceratherium* species.
Comparisons of the metapod lengths [mm] based on *Pleuroceros pleuroceros* (Duvernoy, 1853; McIV NMB-AS79) and *Diaceratherium lemanense* (Depéret and Douxami, 1902; MtIII NMBE5026811) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene) with those of *P. pleuroceros* from Paulhiac (MN1, France; McII and McIV in de Bonis 1973, p. 152 fig. 43.1 and p. 153 fig. 44.2), *D. lemanense* from Gannat (MN1, France; McII and McIV NMB GN39, MtIII NMB-GN40), *D. asphaltense* from Saulcet (MN1, France; McII, McIV and MtIII NMB-SAU1662) and Pyrimont-Challonges (MN1, France; type material, McII UCBL-213016, McIV UCBL-213011 and 213012 and MtIII UCBL-213016), and *D. tomerdingense* from Tomerdingen (MN1, Germany; type material, MCII SMNS-16155a, McIV SMNS-16155b).

Genus *Diaceratherium* Dietrich, 1931

Type species: *Diaceratherium tomerdingense* Dietrich, 1931
Included species: *Diaceratherium lemanense* (Pomel, 1853), *Diaceratherium aurelianense* (Nouel, 1866), *Diaceratherium asphaltense* (Depéret and Douxami, 1902), *Diaceratherium aginense* (Répelin, 1917), *Diaceratherium lamilloquense* Michel in Brunet et al., 1987, *Diaceratherium askazansorense* Kordikova, 2001

Diaceratherium lemanense (Pomel, 1853)
Fig. 4-7, Tab. 4-6

Stratigraphical range: Latest Oligocene (MP30) to Early Miocene (MN2), Western Europe (Antoine & Becker 2013)
Occurrences: See Tab. 7.
Referred material: Skull with left M1-M3 (original exposed in ML, cast NMBE5031538, cast NMB-AS75), right maxillary fragment with P3-M3 (original NMBE5031539), right and left I1

(original NMBE5031540), dental fragments of right I1 (original NMBE5031546), left i2 (original NMBE5031547), right P1 (original NMBE5031548), left P3 (original NMBE5031549), right P3 (original NMBE5031550), two left lower cheek teeth (originals NMBE5031551 and NMBE5031552), right hemi-mandible with i2 and p2-m3 (original NMBE5026738, cast NMB-UM6719), reconstructed incomplete mandible with left and right dental series with p2-m3 (original specimen exposed in ML, cast NMBE5031541, cast NMB-AS76), right femur (original NMBE5031542, cast NMB-UM6314), incomplete right tibia (original NMBE5031543), right tibia (original NMBE5031544, cast NMB-UM6315), right calcaneus (original NMBE5031545), two right astragali (original NMB-2017, original NMB-698), right MtII (original NMBE5026812), right MtIII (original NMBE5026811) from Wischberg (Switzerland, MN1)

Figure 4:
***Diceratherium lemanense* (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).**
Skull NMBE5031538 in laterodorsal (A), occlusal (B) and occipital (C) views. Right hemimandible NMBE5026738 in labial (D), lingual (E) and occlusal (F) views. Right maxillary fragment NMBE5031539 in labial (G), lingual (H) and occlusal (I) views. Scale bar = 10 cm.

Figure 5:
***Diceratherium lemanense* (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).**
Left I1 NMBE5031540 in occlusal (A), lingual (B) and labial (C) views. Right I1 NMBE5031546 in occlusal (D), lingual (E) and labial (F) views. Right I1 NMBE5031540 in occlusal (G), lingual (H) and labial (I) views. Left i2 NMBE5031547 in occlusal (J), lingual (K) and labial (L) views. Left P3 NMBE5031549 in occlusal (M) and lingual (N) views. Right P3 NMBE5031550 in occlusal (O) and lingual (P) views. Fragmentary right P1 NMBE5031548 in occlusal (Q), lingual (R) and labial (S) views. Fragmentary left p4 NMBE5031551 in occlusal (T), lingual (U) and labial (V) views. Scale bar = 1 cm.

Figure 6:
***Diceratherium lemanense* (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).**
Right femur NMB-UM6314 in anterior (A), medial (B), posterior (C) and lateral (D) views. Right tibia NMBE5031544 in anterior (E), medial (F), posterior (G) and lateral (H) views. Scale bar = 10 cm.

Figure 7:
***Diceratherium lemanense* (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).**

Right astragalus NMB-2017 in dorsal (A) and ventral (B) views. Right astragalus NMB-698 in dorsal (C) and ventral (D) views. Right calcaneus NMBE5031545 in dorsal (E), lateral (F), ventral (G) and medial (H) views. Right MtIII NMBE5026811 in anterior (I), lateral (J), posterior (K), medial (L) and proximal (M) views. Right MtII NMBE5026812 in proximal (N), anterior (O), lateral (P), posterior (Q), medial (R) views. Scale bar = 10 cm.

Table 4:
Dimensions [mm] of the anterior teeth of *Diaceratherium lemanense* (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Table 5:
Dimensions [mm] of the upper cheek teeth of *Diaceratherium lemanense* (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Table 6:
Dimensions [mm] of the lower cheek teeth of *Diaceratherium lemanense* (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Table 7:
Occurrences of *Diaceratherium* species in France, Switzerland and other countries. Modified from Becker et al. (2009) with additions from Duranthon (1990, 1991), Antoine et al. (1997), Boada-Saña et al. (2007), Antoine & Becker (2013), Mennecart et al. (2012) and Becker et al. (2018).

Description

Skull. The skull NMBE5031538 is long and relatively narrow (Lcondyles-nasals = 575.5, Lcondyles-premaxilla = 615.5, Wfrontals = 158.5), belonging to a large-sized adult rhinocerotid. It is incomplete and laterally compressed. It lacks the zygomatic arches, the occipital crest as well as the anterior dentition and the right cheek teeth series, while only M1-3 are preserved in the left one. The dental remains are much worn, indicating an aged individual. The separated nasal bones are long, but less than the premaxilla, relatively thin, and bear a lateral apophysis. Roughness for a small nasal horn is preserved at the tip of the nasals. In lateral view, the *foramen infraorbitalis* and the posterior border of the U-shaped nasal notch are both located above the P3, while the anterior border of the orbit is above the M1/2 limit. The minimum distance between the posterior edge of the nasal notch and the anterior border of the orbit is 82.5 mm. The back of the cheek teeth reaches the posterior half of the skull. The *processus lacrymalis* seems to be slightly developed and the *processus postorbitalis* of the frontal is absent. The base of the *processus*

zygomaticus maxillari is high; it is about 2.5 centimetres above the neck of M2. The general dorsal profile of the skull is slightly concave, characterized by a nasal tip pointing downwards and by a slight posterior elevation of the parietal bones. In dorsal view, the postorbital constriction is very moderate, and the fronto-parietal crests are well-separated. The *processus postglenoidalis* is long, strong and transversally narrow. The articular surface of the latter defines a right dihedron in cross section. The *processus postglenoidalis* is curved forward and contacts the short *processus-posttympanicus*, partially closing the external auditory *pseudomeatus*. The *processus paraoccipitalis* is long and well developed. The *foramen magnum* is circular. A smooth median transverse ridge runs all over the occipital condyles, but there is no axial truncation.

Mandible. The hemi-mandible NMBE5026738 bears a very weak median sagittal groove (*sulcus mylohyoideus*) on the lingual side of the *corpus mandibulae*. The symphysis, probably thick, is not constricted at the diastema level. It is upraised (about 30° with respect to the *corpus mandibulae*) and its posterior border, as well as the *foramen mentale*, are located below p2. The *corpus mandibulae* displays a straight ventral border with a constant height below p2-p4 (height below p2 = 80.3) that gets slightly higher until m3 (height below m3 = 92.5). The *incisura vasorum* is weakly marked, the *angulus mandibulae* not much developed and the retromolar space rather long. The *foramen mandibulare* is located below the jugal teeth neck line. The other referred mandibular specimen (casts NMBE5031541 and NMB-AS76) is greatly reconstructed and the anterior part of the symphysis is missing. The *ramus mandibulae* (maximum height = 250.0) is inclined forward, with a *processus coronoideus* sagittally well developed. The *foramen mandibulare* is also located much below the jugal teeth neck line.

Anterior teeth. The anterior dentition is reduced to the chisel-tusk shearing complex of I1-i2, characteristic of the family Rhinocerotidae *sensu* Radinsky (1966). The referred I1 are almond-shaped in cross section and the i2 are tusk-like.

Upper cheek teeth. The cheek teeth are low-crowned (brachy~~o~~dont) and their roots are partly joined. There is neither cement nor enamel foldings on the crowns of cheek teeth. The enamel is thin and wrinkled. Due to the advanced dental wear and the fragmented state of upper cheek teeth remains, only few characters can be identified. The protocone of upper molars and premolars is not constricted. The lingual and labial cingulum are completely lacking on upper molars, while the lingual one seems to be strong and continuous on upper premolars. The P1 NMBE5031548 is biradiculate and does not bear labial cingulum. The P3-4 are molariform (sensu Heissig, 1969), the paracone fold seems poorly developed on upper molars and the M3 is quadrangular in occlusal view, with a transverse protoloph and a posterior groove on the ectometaloph.

Lower cheek teeth. The lower dental formula is 1i-3p-3m (there are neither alveoli nor any trace of contact with the d1/p1 on p2). The lower premolar series is long compared to the molar series (Lp3-4/Lm1-3 > 50; Tab. 6). The lingual cingulum of the lower cheek teeth is reduced to the base of the opening of the anterior valley as an extension of the anterior cingulum. The labial cingulum is only present at the base of the paraconid, while the posterior is only present on lower

premolars. The external groove is developed, oblique and vanishes before the neck. The trigonid is angular on lesser worn teeth and forms an acute dihedron with a rather developed lingual branch of the paralophid in occlusal view. The talonid valley is narrow and V-shaped on p2-m3. The p2 displays a developed paraconid and a constricted paralophid (spur-like), an open posterior valley, as well as marked anterior and external grooves of the ectolophid. The hypolophid is transverse on lower molars and the entoconid of the lower molars does not bear a lingual groove.

Femur. The femur (NMBE5031542) is ~~rather~~ slender (L = 499.0, TDprox = 187.5, APDprox = 69.0, TDdia = 66.0, APDdia = 55.0, TDdist = 132.0, APDdist = 130.5). The *trochanter major* is high, the articular facet of the head is slightly medially asymmetric, the *fovea capitis* is high and narrow, and the third trochanter is developed. In medial view, the anterior border of the diaphysis forms a slope break with the medial lip of the patellar trochlea. In anterior view, the distolateral epicondyle is low and well developed, the proximal border of the patellar trochlea is horizontal. The lateral lip is acute, while the lateral one is rounded.

Tibia. Two tibias are preserved: the specimen NMBE5031544 is complete and very well preserved while the other (NMBE5031543) is incomplete. In distal view, the anterodistal groove is well marked. The mediodistal gutter for the m. tibialis is present and shallow, and the posterior apophysis is high and rounded. In lateral view, the proximal articulation for the fibula is low and the diaphysis bears discontinuous contact marks for the fibula.

Astragal. Two astragali are preserved. They slightly differ by their dimensions (NMB-2017: TD = 85.5, APD = 41.5, H = 74.0; NMB-698: TD = 76.8, APD = 40.0, H = 70.5), but they are proportionally and morphologically homogeneous (NMB-2017: TD/H = 1.16, APD/H = 0.56; NMB-698: TD/H = 1.09, APD/H = 0.57). The fibula-facet is subvertical and transversally flat. The *collum tali* is high. In proximal view, the posteroproximal border of the trochlea is sinuous. In distal view, the trochlea is very oblique compared to the distal articulation and the posterior stop on the cuboid-facet is present on NMB-2017 (not observable in NMB-698). The lateral lip is very prominent, and the medial tubercle is low, salient, and laterally displaced. The calcaneus-facet 1 (*sensu* Heissig 1972) is very concave. The laterodistal expansion of this latter facet is lacking in NMB-698 (not observable in NMB-2017). The calcaneus-facet 2 is roughly oval, flat and wider than high. The calcaneus-facet 3 is transversally developed and separated from the calcaneus-facet 2 by a notch.

Calcaneum. The available calcaneus NMBE5031545 (TD = -, APD = 65.5, H = 124.4) is incomplete, the *sustentaculum tali* is not preserved. Both fibular and tibial facets are lacking. The *tuber calcanei* is high and slender in posterodistal view. The insertion for the m. fibularis longus is marked, forming a deep notch. The *processus calcanei* is long (APD = 51.5) and narrow (TD = 27.2). The cuboid-facet forms a transverse half-circle in distal view, and it is slightly convex anteroposteriorly.

Metatarsals. The metatarsals have a long insertion for the m. interossei, a salient insertion for the m. extensor carpalis, and a high and acute intermediate relief of the distal articulation. The MtIII NMBE5026811 is rather robust (L = 146.9, TDprox = 47.4, APDprox = 35.5, TDdia =

45.3, APDdia = 16.3, TDdist = 46.6, APDdist = 30.6; IG = 30.8), while the MtII NMBE5026812 is shorter and more slender (L = 130.6, TDprox = 31.7, APDprox = -, TDdia = 32.1, APDdia = 16.3, TDdist = 36.2, APDdist = 29.5). The MtII bears a narrow and sagittally-elongated proximal end. The mesocuneiform facet forms a half oval. An axially elongated posteromedial entocuneiform-facet joins the proximal facet. On the lateral side, the posterior ectocuneiform facet is oblique and lozenge-shaped while the anterior one is smaller and nearly vertical. The anterior and posterior MtIII-facets are poorly developed, flat, and vertical. The cuboid-facet of the MtIII NMBE5026811 is lacking. In proximal view, the anterior border has a sinuous articular facet, while it is concave in anterior view. The MtIV-facets are independent, the posterior one is distally displaced with respect to the anterior one. The diaphysis slightly widens distally, reaching its maximal width (TDdist max = 53.4) immediately above the distal articulation, especially due to a considerably developed distomedial tuberosity. No posterodistal tubercle is present on the diaphysis.

Remarks

Based on dimensions and morphology, the referred specimen cannot be assigned to the small-sized contemporaneous European rhinocerotids. *Protaceratherium minutum* (Cuvier, 1822) differs by smaller dimensions, a spindly symphysis, an angular trigonid with a right dihedron on lower cheek teeth, a continuous labial cingulum on lower premolars, an astragalus as high as wide and the contact between Cc1 and Cc2 facets (de Bonis 1973, Ginsburg et al. 1981). *Pleuroceros pleuroceros* (Duvernoy, 1853) also differs by smaller dimensions as well as a smooth and U-shaped external groove on lower cheek teeth, a continuous lingual cingulum on lower premolars, a very oblique fibula facet of the astragalus and a MtIII with a straight and horizontal proximal facet in anterior view (de Bonis 1973, Antoine et al. 2010). *Plesiaceratherium* Young, 1937 and *Mesaceratherium* Heissig, 1969 species are roughly of similar size. The former differs by a flattening of the ectolophid on lower cheek teeth, external roughnesses on p2-3, a ramus of the mandible inclined backwards, and metapodials much slenderer (Yan and Heissig 1986, pers. obs.). The latter differs by a strongly raised symphysis, an astragalus as high as wide and a proximal facet of the MtIII dorsoventrally elongated (Heissig 1969, de Bonis 1973).

The assignment of the referred specimens to the genus *Diaceratherium* is supported by their dimensions and their morphology. The nasals (long, thin and totally separated), the deep, U-shaped notch ending above P3, the orbital features (presence of a *processus lacrymalis*, anterior border above M1/2), the mandible (straight profile of the base of the *corpus mandibulae*), the dental remains (quadrangular M3, constricted paralophid and developed paraconid on p2) as well as the astragali (lateral lip larger than the medial one and a low, salient, and laterally displaced medial tubercle), are all characteristic of the genus *Diaceratherium* (Becker et al. 2009, 2010, 2018, Antoine et al. 2010, pers. obs.).

However, an attribution of the studied material to a specific taxon within this genus remains difficult. Apart from *"Diaceratherium" massiliae* Ménouret and Guérin, 2009, whose generic

attribution remains doubtful by several non-*Diaceratherium* morphological features (Antoine & Becker 2013), between five and seven species are usually considered as valid in the literature (e.g. Heissig 1999, Boada-Saña et al. 2007, Becker et al. 2009, Antoine & Becker 2013).
The type species *Diaceratherium tomerdingense* differs by the presence of a reduced lingual cingulum under the protocone and at the opening of the median valley on M1-2 as well as an almost vertical external groove of lower premolars in labial view that does not vanish before the neck. Furthermore, though its metacarpals cannot be directly compared to the metatarsals from Wischberg, their length is much closer to those of *D. aginense* from Laugnac, than to those from *D. lemanense* from Gannat (Tab. 3). Since in Wischberg the metatarsal's length is very close to those for Gannat (*D. lemanense*), we assume that the metacarpals from Wischberg must have been similar correlatively, and thus much longer than those from *D. tomerdingense* (Dietrich 1931, pers. obs.).
The latest Oligocene diacerathere, *D. lamilloquense*, from La Milloque differs by the presence of lingual cingulum under the protocone of M3, an angular trigonid on lower cheek teeth, and a high proximal articulation for the fibula on the tibia (Michel 1983, Brunet et al. 1987). The specimens from Castelmaurou differ by the presence of labial cingulum in the external groove of m2 and m3, a posterior facet for the MtII on the MtIII (Duranthon 1990).
The skull NMBE5031538 and mandible NMBE5026738 differ from the type material of *D. asphaltense* from Pyrimont in having slightly stouter nasals, a moderate postorbital constriction of the skull, more distant frontoparietal crests, as well as a higher *corpus* of the mandible and a lower position of the *foramen mandibulae* on the ramus (Depéret and Douxami 1902, pers. obs.).
Concerning the postcranial remains, some differences can be noted with *D. asphaltense* from Pyrimont and Saulcet, such as a dorsoventrally reduced proximal facet of the MtIII for the ectocuneiform, a laterally compressed distal facet of the calcaneus for the cuboid and a slender *tuber calcanei* (Depéret and Douxami 1902, pers. obs.).
Diaceratherium aginense from Laugnac (type locality) differs from the Wischberg material in displaying a completely closed external auditory pseudomeatus, a reduction of lingual cingulum on upper molars, a more developed ectolophid groove of lower cheekteeth, a strong lingual groove on the *corpus mandibulae*, a shorter posterodistal apophysis of the tibia, stouter metapodials and a very concave navicular facet of the astragal in anterior view (Répelin 1917, pers. obs.).
In *Diaceratherium aurelianense*, labial cingulum can be present on lower molars, the postorbital process of the frontals is absent, the lesser trochanter of the femur is more developed and the metapodials are more robust with a low and smooth intermediate relief in distal view (Mayet 1908, Cerdeño 1993, pers obs.).
Finally, the Early Miocene Kazakh species *Diaceratherium askazansorense* differs by a larger size of the lower molars, a posteriorly increasing height of the horizontal ramus, more hypsodont teeth, a higher *colum talli* of the astragal and a shorter and wider *tuber calcanei* (Kordikova 2001).

519 The cranio-dental and postcranial characters of the diacerathere from Wischberg are in fact
520 morphologically indistinguishable from those of *D. lemanense* from Gannat (type locality). The
521 nasals are small, and same sized as the type skull from Gannat, as well as the remaining nasal
522 bone of the type species *D. tomerdingense*, but much shorter than those of *D. asphaltense* from
523 Pyrimont, Bühler and Saulcet. Like the specimen from Gannat NMB Gn. 40, the proximal facet
524 of the MtIII is sagitally elongated and concave in anterior view. The astragal from this same
525 individual is very similar to the two specimens from Wischberg and is also wider than high. As
526 in *D. lemanense* from Montaigu (NMB S.G.18480), the *ramus mandibulae* is inclined forward,
527 with a sagittally well developed *processus coronoideus*. The lingual and labial cingulum are also
528 absent on lower cheek teeth. The material from Wischberg only differs by a slightly smaller size
529 compared to the type material. Therefore, we attribute the referred specimens from Wischberg to
530 *D. lemanense*.
531

532 ## Discussion

533 **Systematic implications**

534 The systematic of the genus *Diaceratherium* is far from consensual. Four species in particular
535 are contentious and often subject to synonymies: *D. lemanense*, *D. asphaltense*, *D.*
536 *tomerdingense* and *D. aginense*.
537 According to Antoine & Becker (2013) and Becker et al. (2018), *D. tomerdingense* is a junior
538 synonym of *D. aginense* and this latter is likely to be a junior synonym of *D. asphaltense*. More
539 recently, Becker et al. (2018) still accepted the synonymy of *D. tomerdingense* and *D. aginense*,
540 but maintained *D. asphaltense* as valid whereas, according to de Bonis (1973) and Boada-Saña et
541 al. (2007), *D. asphaltense* and *D. tomerdingense* should be considered as junior synonyms of *D.*
542 *lemanense*. However, no clear justification is ever provided, except for the synonymy of *D.*
543 *asphaltense* and *D. lemanense* by the phylogenetic analysis of Boada-Saña (2008). Yet, the
544 coding of *D. asphaltense* in this latter work is based on photographs of the type material from
545 Pyrimont-Challonges (Boada-Saña, 2008: tab. 1) and should be confirmed by direct
546 observations.
547 These synonymies probably derive from the absence of differential diagnoses between these four
548 species, and of designated type for *D. lemanense*. Indeed, a skull referred to *"Acerotherium"*
549 *lemanense* from the type locality of Gannat (Roman 1912, Pl. VIII fig. 1-3) was unfortunately
550 mistakenly considered as a reference specimen for comparison by Becker et al. (2009, 2018)
551 whereas Boada-Saña (2007) had designated another skull and mandible from Gannat (MNHN
552 AC 2375 and MNHN AC 2376 respectively) as lectotype. Regrettably, both skulls from Gannat
553 may belong to two different taxa, which led to unfortunate comparisons of specimens and
554 erroneous taxonomic attributions. The skull used by Becker et al. (2009, 2018) as reference
555 material of *D. lemanense* (FSL-213944) is remarkably similar to the skull attributed to *D.*
556 *lemanense* from Eschenbach (NMSG–P2006/1), but after direct observation could both be
557 referred to *Plesiaceratherium* Young, 1937, another genus of Miocene rhinocerotid.

Moreover, cranial remains from Saulcet (NMB-SAU-1662) and Bühler (NMSG-F13607) have been referred to *D. asphaltense* (Becker et al. 2009, 2018), based on similarities with the type skull of *D. asphaltense* from Pyrimont-Challonges (FSL-212997bis), but also on indisputable dissimilarities with the non-*Diaceratherium* skull from Gannat (FSL-213944) and from Eschenbach (NMSG–P2006/1). Currently, the question of the synonymy of *D. lemanense* and *D. asphaltense*, as suggested by Boada-Saña et al. (2007), is still pending.

Finally, another systematic interpretation has been recently proposed by Heissig (2017), who referred the species *D. aurelianense* to the genus *Prosantorhinus* because of characters not found in other species of the genus *Diaceratherium*. These characters are "the deeply concave skull profile with upslanting nasals, a wide nasal incision of medium depth, and the triangular last upper molar." Similarities between the two genera had already been expressed by Cerdeño (1996) who referred some specimen previously attributed to *D. aurelianense* to the genus *Prosantorhinus* but keeping both taxa as valid. Antoine et al. (2018) have also recently attributed all the material previously referred as *Diaceratherium aurelianense* from Béon 2 to *Prosantorhinu*s aff. *douvillei*, which indicates indeed similarities between these two taxa, as also already noted by Mayet (1908). However, Antoine et al. (2018) subsequently expressed numerous anatomical differences between these two taxa, including the 20% size difference of the MtIV, which is a character that specifically distinguishes these two genera. Moreover, the characters used by Heissig (2017) seem quite labile to confirm the attribution of the species *D. aurelianense* to the genus *Prosantorhinus.* Indeed, a recently described skull of *Diaceratherium asphaltense* does show a deeply concave skull and slightly upslanted nasals (Fig. 8), though not as much as the skull of *D. aurelianense*. Another skull of *D. asphaltense* from Saulcet has a similar morphology, but it is true that *D. lemanense* and *D. aginense* do not show such an upslanted nasal bone (though for this latter species the skulls illustrated by Répelin (1917) are heavily reconstructed, and the global shape is very misleading). Finally, the M3 is indeed more triangular in *D. aurelianense* than in other species of the genus, but it could be a character specific to this species. Therefore, to the best of our knowledge, the four above-mentioned problematic *Diaceratherium* species should be considered as valid (just like *D. lamilloquense* and *D. askazansorense*), and *D. aurelianense* could still belong to the genus *Diaceratherium* (as presented in Tab. 7), until a comprehensive phylogenetic analysis at Teleoceratina scale is carried out.

Figure 8:
Comparison of the skulls of *Diaceratherium*.
(A) *D. asphaltense* (NMSG-F13607) from Bühler (MP30-MN1; Becker et al. 2018). (B) *D. apshaltense* (NMB Sau 1662) from Saulcet (MN1). (C) *D. aurelianense* (MNHN.F.1888-4, holotype) from Neuville-aux-Bois (MN3), original drawing from Heissig (2017). (D) *D. aurelianense* (MHNT.PAL.2013.0.1001, cast of the holotype), from Neuville-aux-Bois (MN3). (E) *D. aginense* (MHNM 1996.17.111.1, "skull B", lectotype) from Laugnac (MN2), original drawing from Heissig (2017). (F) *D. aginense* (FSL collection) from Laugnac

(MN2). (G) *D. lemanense* (MNHN-AC-2375, holotype) from Gannat (MN1). (H) *D. lemanense* (cast NMBE5031538) from Wischberg (MN1).

Palaeobiogeographical and biostratigraphical implications

The record of two Rhinocerotid species in Wischberg is typical of the Agenian time period, which is a period rather rich in rhinocerotoid diversity in Western Europe (Antoine & Becker 2013). The records of *Pleuroceros pleuroceros* and *Diaceratherium lemanense* are typical from the MN1 biozone since Gannat (France) is the type locality of both taxa. In addition, both taxa have in common an Asian sister species: *Pleuroceros blanfordi* both from the Early Miocene of Pakistan (Antoine et al. 2010) and *Diaceratherium askazansorense* from the Early Miocene of Kazakhstan (Kordikova 2001).

Furthermore, the presence of *Diaceratherium lemanense* in Wischberg extends the record of this genus in Switzerland. Indeed, though the species *D. lemanense* was found in numerous French localities, Wischberg is the only record of this species in Switzerland during the MN1 biozone (Tab. 7). The genus *Diaceratherium* has a rather long record in Europe, from the ~~Late~~ Oligocene to the early middle Miocene, and it ~~crosses the Oligo-Miocene boundary. It is after this limit that this genus extensively diversifies,~~ with the presence of four different species during MN1: *D. tomerdingense* (type species), *D. lemanense*, *D. asphaltense* and *D. aginense*. However, this high diversity may be potentially artificial if synonymy occurs either between *D. aginense* and *D. tomerdingense* or between *D. asphaltense* and *D. lemanense*. As discussed previously, a comprehensive systematic and phylogenetic revision of this genus would be needed to solve this matter.

Palaeoecology and diversification

The Agenian rhinocerotid fauna from Wischberg includes two co-occurring species: the large-sized graviportal *Diaceratherium lemanense*, and the small-sized mediportal *Pleuroceros pleuroceros*. The two taxa also differ by their body masses (Tab. 8), one being a megaherbivorous with a body mass over 10^3 kg (Owen-Smith 1988).

Table 8:

~~Estimation~~ of rhinocerotid species body mass from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene), based on the allometric correlations with the occlusal surface of the first lower molar (Legendre, 1989).

This rhinocerotid association is comparable in composition to some contemporaneous Western European localities such as Gannat, Paulhiac, Pyrimont-Challonges and Saulcet. This sympatric association is characteristic of the MN1 biozone and results from the faunal renewal starting at MP28 in Western Europe (Scherler et al. 2013). It is a period marked by the beginning of a major worldwide diversification phase of Rhinocerotidae that lasted until the Late Miocene (Cerdeño 1998), and during which perissodactyls reach the maximum body size and mass among terrestrial

mammals (Smith et al. 2010). This rhinocerotid diversification may be due to the extinction of other megaherbivorous competitors in Europe such as the Anthracotheriinae (latest Oligocene, Scherler 2011, Scherler et al. 2018) or the Amynodontidae (Late Oligocene, Malez & Thenius, 1985). As for the other European perissodactyls, except for the Tapiridae, which are present in Europe until MN4, Palaeotheriidae are extinct since MP25 (Rémy 1995), Chalicotheriidae only re-appear during MN2 (Coombs 2009), Equidae first appear with *Anchitherium* in MN3 (Kaiser 2009, Alberdi & Rodríguez 2012) and Eggysodontidae disappear in MN1 (Scherler et al. 2013). However, none of those reached sizes over 10^3 kg during this time. Within the Artiodactyla only nine genera were present in Europe during MN1 (Scherler et al. 2013) and all of them were smaller than the smallest rhinocerotids (Scherler 2011, Mennecart 2012). Finally, the proboscideans, another group of megaherbivores who will later dominate the megaherbivore communities, do not appear in Europe until ~~MN4~~ (Antoine et al. 1997, Göhlich 1999). As a result, the earliest Miocene is a period during which rhinocerotids are the dominating largest herbivores and the only megaherbivores in Europe (Rössner & Heissig 1999, Scherler et al. 2013). This observation is of particular interest since, like extant African megaherbivores, Early Miocene rhinocerotids likely had large food intake requirements and could have been able to subsist on low-quality (i.e. high fibre) food resources (Demment & van Soest 1985, Owen-Smith 1988, Illius and Gordon 1992). Furthermore, due to their size, Early Miocene megaherbivorous rhinocerotids are expected, like extant ones, to display specific life-history attributes, physiology and ecological characteristics related to their body mass (Blueweiss et al. 1978, Brown et al. 2004), such as larger geographic ranges, higher potential for dispersal (e.g., Brown 1995, Gaston 2003), lower mortality rates and better resistance to limiting environmental factors (Erb et al. 2001). As a result, megaherbivores are considered to be a separate trophic guild among large herbivores (Fritz et al. 2002), possibly better adapted to ecosystems with high plant biomass but low-quality vegetation (Bell 1982).

The beginning of the Miocene is marked by a short glacial event (Mi-1; Zachos et al. 2001). This sudden climatic event has induced significant changes in the European vegetation, promoting fibre-rich plants associations. We observe indeed a lower proportion of C4 plants during the MN1 than during the Oligocene (Urban et al. 2010) and an increase of mesothermic vegetations at the expense of megathermic ones (e.g. Mosbrugger et al. 2005, Bessedik et al. 1984). Janis (1976) hypothesized that perissodactyls (hindgut fermenters) were able to overcome competition of other ~~herbivorous large~~ mammals by their ability to tolerate more fibrous herbage. This could explain the diversification of rhinocerotids at the beginning of the Miocene, for which large size might have increased their ability to monopolise resources (Fritz et al. 2002) and extract nutrients from specific feeding niches (Illius & Gordon 1992). The evolutionary success and rapid diversification of rhinocerotids during the earliest Miocene could consequently be linked to this particular environmental change, triggered by the short glaciation event but also by the absence of other megaherbivores. After the late Oligocene faunal renewal (Scherler et al. 2013), the earliest Miocene, and especially the first one million-year period (MN1), may have been a crucial time period for the Rhinocerotidae, and especially megaherbivorous taxa, to start

diversifying by occupying new ecological niches available at that time. Further analyses taking into account all European rhinocerotids, with their masses and anatomical features, will be necessary to test this hypothesis and better understand this unique transition in the European assemblages of megaherbivores at the beginning of the Miocene.

Conclusions

Based on comparisons, the rhinocerotid specimens from Wischberg, a typical Agenian (MN1) locality, can be attributed to two different taxa: *Diaceratherium lemanense* and *Pleuroceros pleuroceros*. Though Schaub & Hürzeler 1948 had identified a third taxon, *Diaceratherium asphaltense*, we believe that it should be attributed to the ~~other contemporaneous~~ species, *D. lemanense*, based on morphological differences with the holotype material from Pyrimont-Challonges (MN1, France). Furthermore, we believe that all *Diaceratherium* species found at the present time in the literature could be considered as valid, until an extensive revision of this genus is performed, preferentially through a phylogenetic analysis.

Acknowledgements

We are greatly indebted to all curators of the collections visited during this work, who kindly helped us during our visit: Manuela Aiglstorfer and Reinhard Ziegler (SMNS), Christine Argot and Guillaume Billet (MNHN), Christophe Borrely (MHNM), Loïc Costeur (NMB), Jana Fehrensen (ML), Yves Laurent (MHNT), Ursula Menkveld-Gfeller (NMBE), Emmanuel Robert (FSL). We are very grateful to Patrick Röschli (JURASSICA Museum) for preparing the plates.

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Table 1(on next page)

Mammal assemblage of Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

After Schaub & Hürzeler (1948)	After Tobien (1975), Scherler et al. (2013) and this study
Talpidarum indet.	Talpidae indet.
Erinaceus priscus	*Amphechinus edwardsi*
Lagomorphum aff. *Piezodus*	*Piezodus tomerdingensis*
Cricetodon cf. *hochheimensis*	*Eucricetodon* cf. *hochheimensis*
Cricetodon collatus	*Eucricetodon collatus*
Plesiosminthus myarion	*Plesiosminthus myarion*
Rhodanomys schlosseri	*Rhodanomys schlosseri*
Rhodanomys sp. nov.	*Rhodanomys* sp. nov.
Eomyidarum gen. nov.	*Ritteneria* sp.
Gliridarum gen. nov.	Gliridae indet.
Cainotherium laticurvatum	*Cainotherium latircurvatum*
Elomeryx minor	*Elomeryx minor*
Palaeochoerus meissneri	*Hyotherium meissneri*
Amphitragulus sp.	*Amphitragulus elegans*
Tapirus intermedius var. *robustus*	*Eotapirus broennimanni* (adult specimens)
Tapirus brönnimanni	*Eotapirus broennimanni* (juvenile specimens)
Aceratherium lemanense	*Diaceratherium lemanense*
Diceratherium asphaltense	*Diaceratherium lemanense*
Diceratherium pleuroceros	*Pleuroceros pleuroceros*

1

Table 2(on next page)

Dimensions [mm] of the cheek teeth of *Pleuroceros pleuroceros* (Duvernoy, 1853) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Pleuroceros pleuroceros casts NMBE5031553 and NMB-AS77				casts NMBE5026739 and NMB-AS78			
Upper tooth row	L_{P3-4}	L_{M1-3}	L_{P3-4}/L_{M1-3} x 100	Lower tooth row	L_{p3-4}	L_{m1-3}	L_{p3-4}/L_{m1-3} x 100
left	53.5	94.0	56.9				
right	54.0	95.0	56.8	right	-	101.5	-
Upper cheek teeth	L	W	H	Lower cheek teeth	L	W	H
right P1	15.1	15.1	-				
left P2	23.2	26.8	-				
right P2	24.0	27.1	-				
left P3	25.7	34.6	-				
right P3	27.8	36.6	-				
left P4	27.8	37.8	-				
right P4	27.1	37.2	-	right p4	28.0	19.9	
left M1	31.8	38.1	-	left m1	30.5	18.2	
right M1	31.0	35.8	-	right m1	29.0	(19.0)	
left M2	37.5	40.3	20.2	left m2	34.5	21.3	
right M2	39.0	41.3	19.1	right m2	33.6	21.0	
left M3	32.0	37.5	23.7				
right M3	33.8	38.3	-	right m3	36.9	20.8	

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Table 3(on next page)

Metapod lengths of *Pleuroceros pleuroceros* and *Diaceratherium* species.

Comparisons of the metapod lengths [mm] based on *Pleuroceros pleuroceros* (Duvernoy, 1853; McIV NMB-AS79) and *Diaceratherium lemanense* (Depéret and Douxami, 1902; MtIII NMBE5026811) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene) with those of *P. pleuroceros* from Paulhiac (MN1, France; McII and McIV in de Bonis 1973, p. 152 fig. 43.1 and p. 153 fig. 44.2), *D. lemanense* from Gannat (MN1, France; McII and McIV NMB GN39, MtIII NMB-GN40), *D. asphaltense* from Saulcet (MN1, France; McII, McIV and MtIII NMB-SAU1662) and Pyrimont-Challonges (MN1, France; type material, McII UCBL-213016, McIV UCBL-213011 and 213012 and MtIII UCBL-213016), and *D. tomerdingense* from Tomerdingen (MN1, Germany; type material, MCII SMNS-16155a, McIV SMNS-16155b).

Pleuroceros pleuroceros and *Diaceratherium* species
Metapod length

Species	Locality	McII	McIV	MtIII
Pleuroceros pleuroceros	Wischberg	-	112.3	-
	Paulhiac	126.0	112.5	-
Diaceratherium lemanense	Wischberg	-	-	146.9
Diaceratherium lemanense	Gannat	150.0	132.5	153.0
Diaceratherium asphaltense	Saulcet	135.0	124.0	131.5
Diaceratherium asphaltense	Pyrimont-Challonges	129.5	122.0 117.0	127.0
Diaceratherium tomerdingense	Tomerdingen	116.5	100.0	-

Table 4(on next page)

Dimensions [mm] of the anterior teeth of *Diaceratherium lemanense* (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Diaceratherium lemanense							
Upper incisors (I1)	APD	TD	H	Lower incisors (i2)	APD	TD	H
NMBE5031540 (left)	50.2	18.5	18.2	NMBE5031547 (left)	-	-	43.0
NMBE5031540 (right)	-	17.5	17.1	NMBE5026738 (right)	31.9	24.0	41.2
NMBE5031546 (right)	-	17	16.0				

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Table 5(on next page)

Dimensions [mm] of the upper cheek teeth of *Diaceratherium lemanense* (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Diaceratherium lemanense Original NMBE5031539, casts NMBE5031538 and NMB-AS75			
Upper tooth row	L_{P3-4}	L_{M1-3}	L_{P3-4}/L_{M1-3} x 100
right	(68.0)	126.9	(53.6)
Upper cheek teeth	L	W	
right P4	(34.5)	(42.6)	
left M1	39.2	-	
right M1	39.7	47.0	
left M2	47.1	51.1	
right M2	44.0	50.5	
left M3	48.0	52.6	
right M3	46.1	-	

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Table 6(on next page)

Dimensions [mm] of the lower cheek teeth of *Diaceratherium lemanense* (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Diaceratherium lemanense original NMBE5026738, cast NMB-UM6719				casts NMBE5031541 and NMB-AS76			
Lower tooth row	L_{p3-4}	L_{m1-3}	L_{p3-4}/L_{m1-3} x 100	Lower tooth row	L_{p3-4}	L_{m1-3}	L_{p3-4}/L_{m1-3} x 100
right	78.0	137.0	56.9	left	77.0	130.0	59.2
				right	76.5	133.5	57.3
Lower cheek teeth	L	W		Lower cheek teeth	L	W	H
right p2	30.0	20.1		left p2	28.5	-	24.2
				right p2	28.0	16.9	26.9
right p3	36.0	25.0		left p3	38.2	22.1	-
				right p3	36.1	24.0	-
right p4	40.5	29.5		left p4	36.5	29.0	-
				right p4	38.5	26.5	
right m1	42.8	28.5		left m1	39.5	28.7	-
				right m1	40.5	26.5	
right m2	46.0	30.5		left m2	44.2	30.5	27.5
				right m2	46.8	29.8	28.0
right m3	49.5	28.5		left m3	47.5	28.5	31.0

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Table 7 (on next page)

Occurrences of *Diaceratherium* species in France, Switzerland and other countries.

Modified from Becker et al. (2009) with additions from Duranthon (1990, 1991), Antoine et al. (1997), Boada-Saña et al. (2007), Antoine & Becker (2013), Mennecart et al. (2012) and Becker et al. (2018).

P-MN zones	Taxa	Localities		
		France	Switzerland	Others
MN4	*D. aurelianense*	Artenay		Areeiro da Barbuda (Portugal), Areeiro de Santa Luzia (Portugal), Eggingen-Mittelhart 3 (= *D.* cf. *aurelianense*; Germany), Quinta da Carrapata (Portugal), Quinta da Noiva (Portugal), Quinta da Trindade (Portugal), Quinta das Pedreiras (Portugal), Quinta do Narigão (Portugal), Vale Pequeno (Portugal)
MN3	*D. aurelianense*	**Neuville-aux-Bois**, Beaulieu, Chilleurs-aux-Bois, Chitenay, Esvres, La Brosse, Les Beilleaux, Les Buissonneaux, Marsolan, Mauvières, Navère, Ronville	Brüttelen, Cheyres, La Molière	Horta das Tripas (= *D.* cf. *aurelianense*; Portugal), Molí Calopa (Spain), Rubielos de Mora (Spain), Wintershof-West (Germany)
MN2/3	*D. askazansorense*			**Askazansor** (Kazakhstan)
MN2	*D. aginense*	**Laugnac**, Auterive, Beaupuy, Calmont-St-Cernin, Cintegabelle, Grépiac, Montaigu-le-Blin, Pouvourville, Venerque	Engehalde, La Chaux, Lausanne, Sous-le-Mont	Hessler (Germany)
	D. aurelianense			Loranca del Campo (= *D.* cf. *aurelianense*; Spain)
	D. lemanense	Barbotan-les-Thermes, Cindré, Gans, Laugnac, Montaigu-le-Blin, Selles-sur-Cher, St-Gérand-le-Puy	Engehalde	Budenheim (Germany), Ulm-Michelsberg (Germany)
MN1	*D. aginense*	Gannat, Paulhiac		
	D. asphaltense	**Pyrimont-Challonges**, Saulcet		

	D. lemanense	**Gannat**, Bazas, Bézac, Caignac, Casteljaloux-Balade, Cindré, Ginestous, Grenade-sur-Garonne, Labastide-Beauvoir, Pechbonnieu, La Roche-Blanche-Gergovie, Paulhiac, Pech David, Randan, St-Loup Cammas, St-Michel-du-Touch, Saulcet, Saverdun, Toulouse Borderouge, Toulouse Embouchure	Wischberg	Finthen (Germany), Oppenheim (Germany), Weisenau (Germany)
	D. tomerdingense			**Tomerdingen** (Germany)
MP30/MN1	*D. asphaltense*		Bühler	
MP30	*D. lemanense*	Billy, Gannat « sommet », Thézels (= *D.* aff. *lemanense*), Toulouse-Borderouge		Rott bei Bonn (Germany)
MP29	*D. lamilloquense*	**La Milloque**, Castelmaurou, Castelnau d'Estretefonds, Dieupentale	Rickenbach	

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Table 8(on next page)

Estimation of rhinocerotid species body mass from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene), based on the allometric correlations with the occlusal surface of the first lower molar (Legendre, 1989).

Rhinocerotidae from Wischberg	mean L m1	mean W m1	Estimated body mass (g)
Diaceratherium lemanense NMBE5026738	42.8	28.5	1'730’049
Diaceratherium lemanense casts NMBE5031541 and NMB-AS76	40.5	26.5	1’417’016
Pleuroceros pleuroceros casts NMBE5031553 and NMB-AS77	29.7	18.6	504’352

1

Figure 1

General setting of Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

(A) Map of a part of Western Europe showing the location of Switzerland and the Molasse Basin. (B) Enlargement of the Aquitanian palaeogeographical context of the Swiss Molasse Basin, with detailed location of Wischberg locality. Modified from Becker et al. (2010).

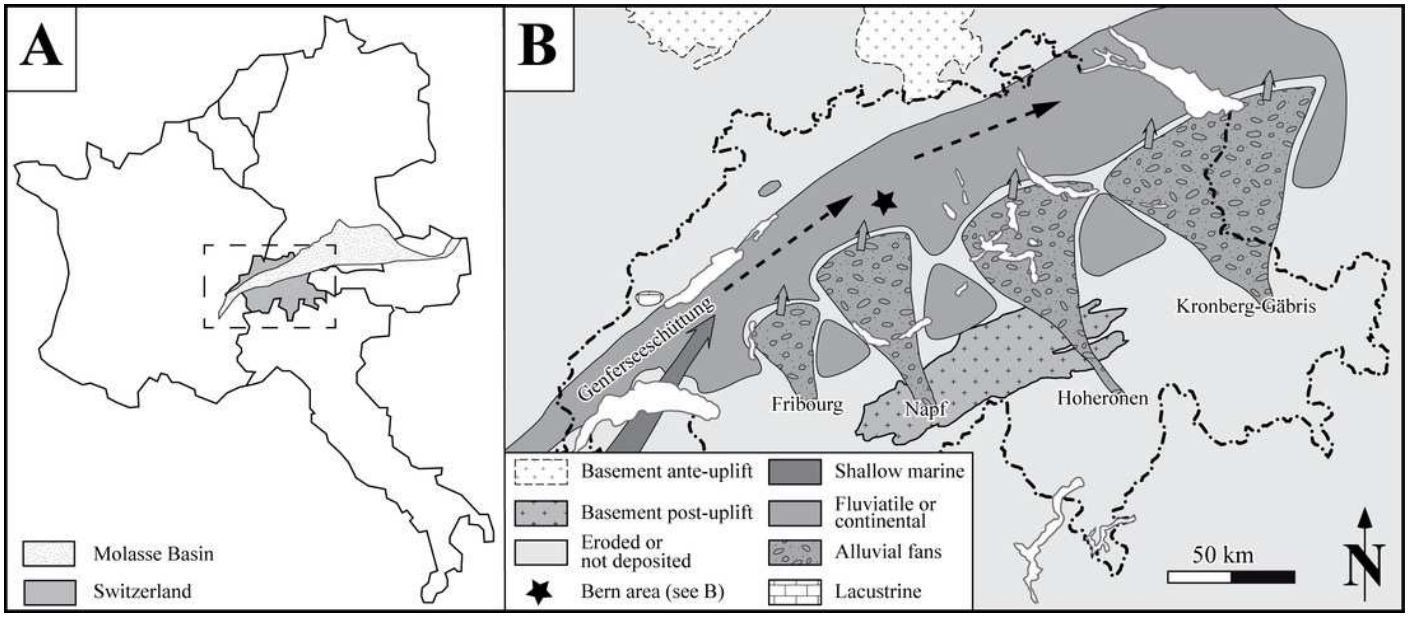


Figure 2

Pleuroceros pleuroceros (Duvernoy, 1853) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Partial skull NMBE5031553 in lateral (A), dorsal (B), medial (C) and occlusal (D) views and left-side fragment from the same individual in occlusal (E) view. Mandible fragments NMBE5026739 in labial (F), lingual (G) and occlusal (H) views with p4-m3 (right-side fragment) and m1-2 (left-side fragment). Scale bars = 10 cm.

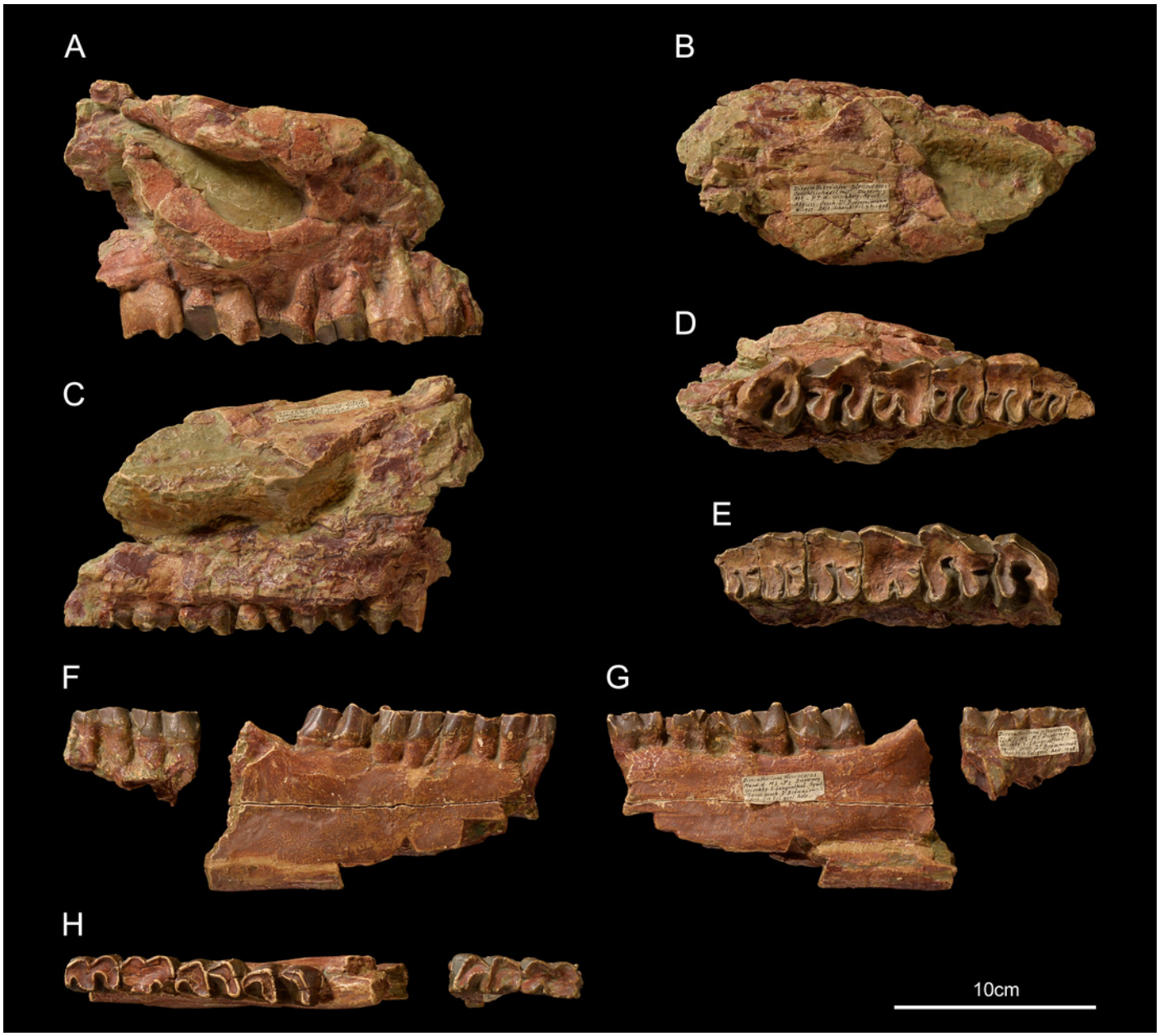

A
B
C
D
E
F
G
H
10cm

Figure 3

Pleuroceros pleuroceros (Duvernoy, 1853) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Right semilunate NMBE5031537 in dorsal (A), proximal (B), distal (C), lateral (D) and medial (E) views and right McIV (cast NMB-AS79) in dorsal (F), lateral (G), ventral (H), medial (I) and proximal (J) views.

Figure 4

Diaceratherium lemanense (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Skull NMBE5031538 in laterodorsal (A), occlusal (B) and occipital (C) views. Right hemimandible NMBE5026738 in labial (D), lingual (E) and occlusal (F) views. Right maxillary fragment NMBE5031539 in labial (G), lingual (H) and occlusal (I) views. Scale bar = 10 cm.

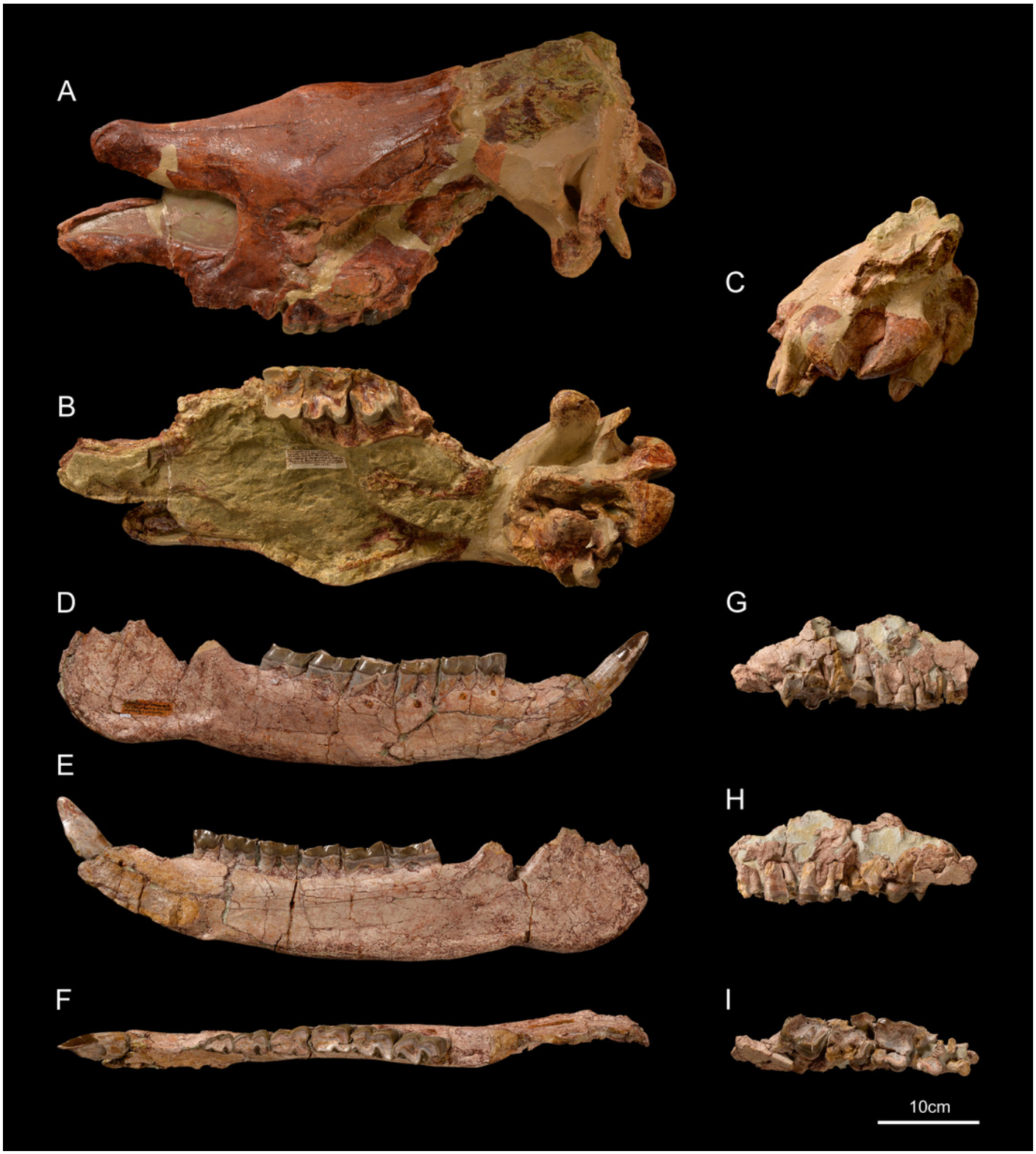
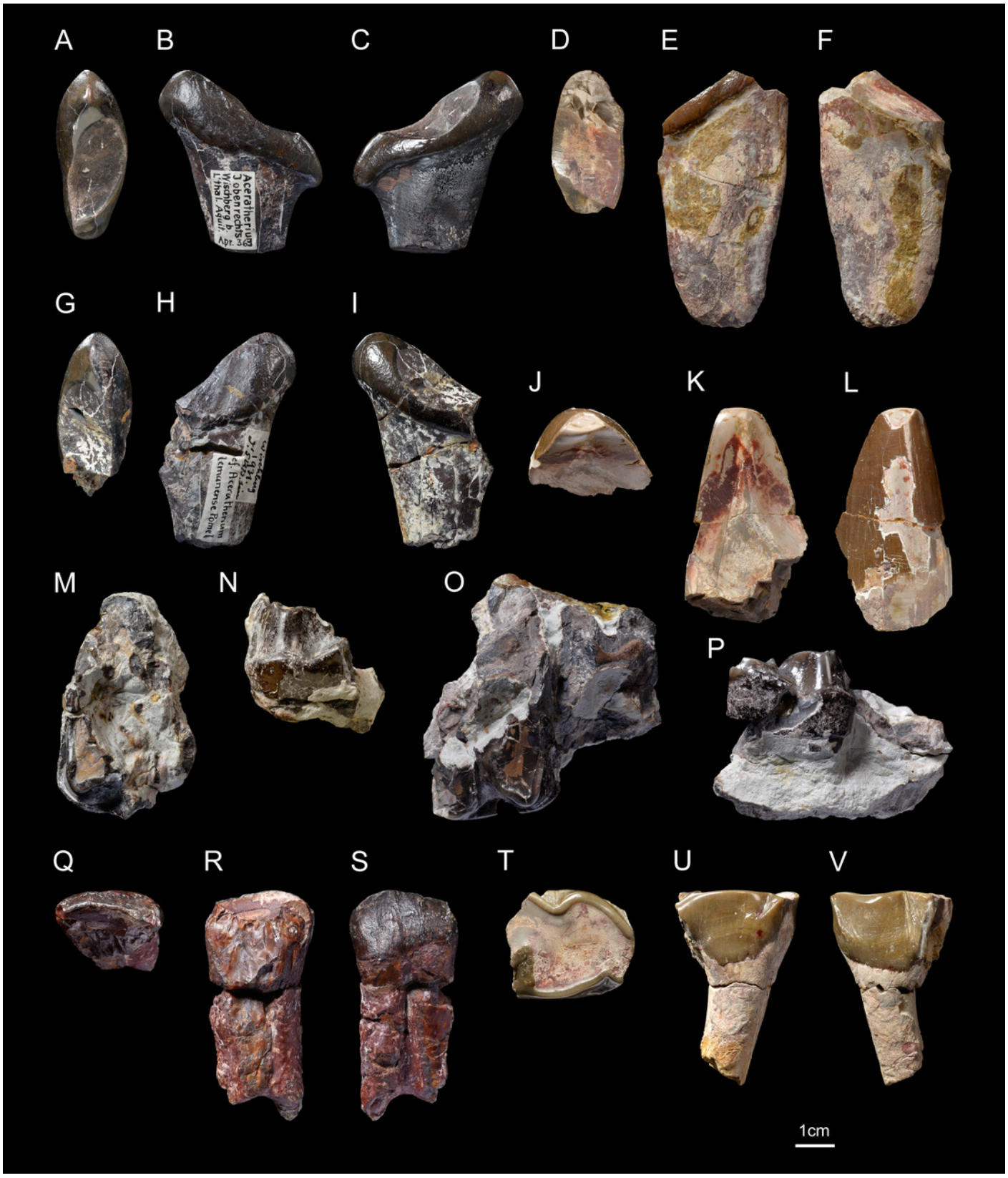

A
B
C
D
E
F
G
H
I
10cm

Figure 5

Diaceratherium lemanense (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Left I1 NMBE5031540 in occlusal (A), lingual (B) and labial (C) views. Right I1 NMBE5031546 in occlusal (D), lingual (E) and labial (F) views. Right I1 NMBE5031540 in occlusal (G), lingual (H) and labial (I) views. Left i2 NMBE5031547 in occlusal (J), lingual (K) and labial (L) views. Left P3 NMBE5031549 in occlusal (M) and lingual (N) views. Right P3 NMBE5031550 in occlusal (O) and lingual (P) views. Fragmentary right P1 NMBE5031548 in occlusal (Q), lingual (R) and labial (S) views. Fragmentary left p4 NMBE5031551 in occlusal (T), lingual (U) and labial (V) views. Scale bar = 1 cm.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R
S
T
U
V
1cm

Figure 6

Diaceratherium lemanense (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Right femur NMB-UM6314 in anterior (A), medial (B), posterior (C) and lateral (D) views. Right tibia NMBE5031544 in anterior (E), medial (F), posterior (G) and lateral (H) views. Scale bar = 10 cm.

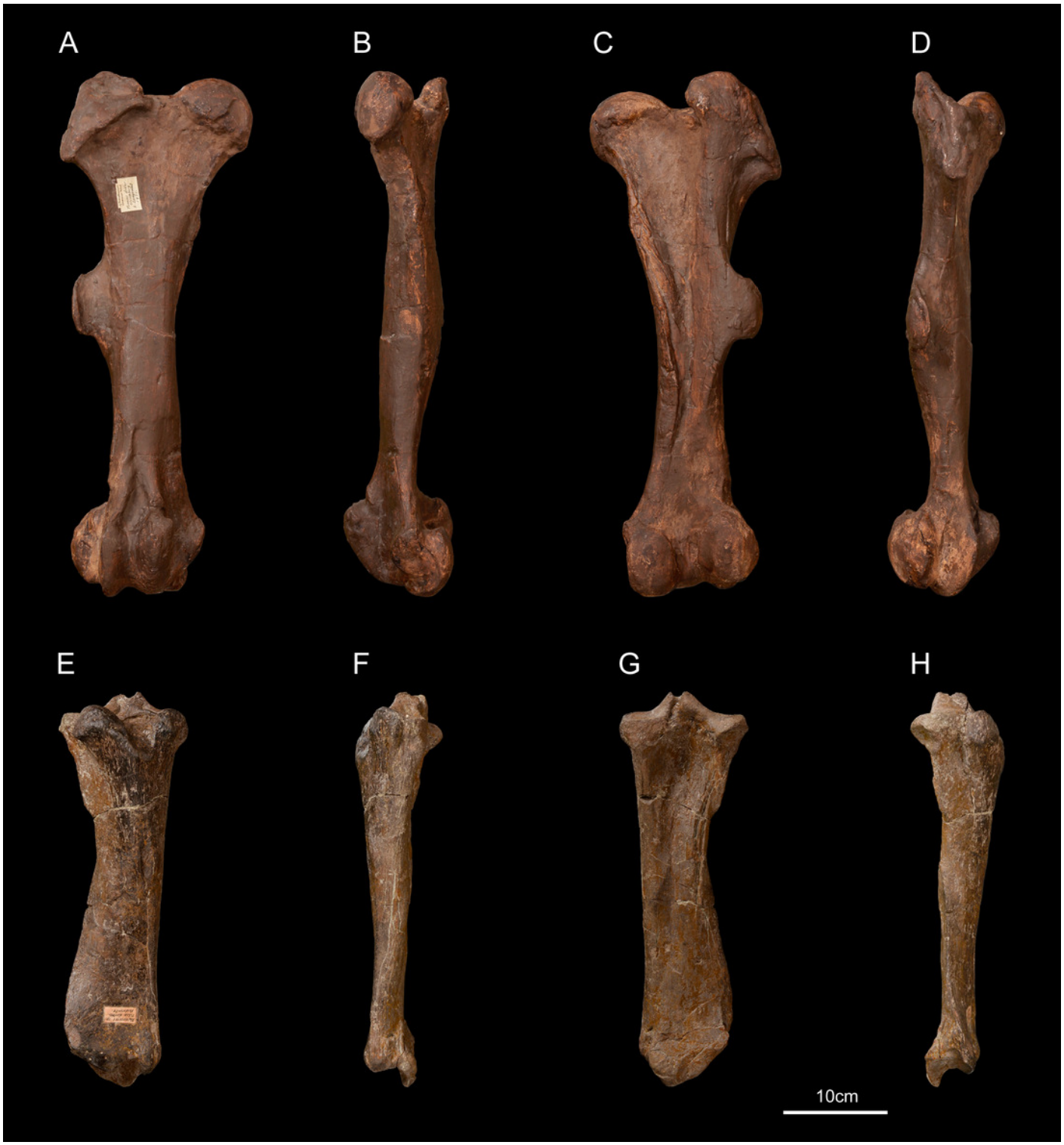

A
B
C
D
E
F
G
H
10cm

Figure 7

Diaceratherium lemanense (Depéret and Douxami, 1902) from Wischberg locality, Bern Canton, Swiss Molasse basin (MN1, Agenian, Early Miocene).

Right astragalus NMB-2017 in dorsal (A) and ventral (B) views. Right astragalus NMB-698 in dorsal (C) and ventral (D) views. Right calcaneus NMBE5031545 in dorsal (E), lateral (F), ventral (G) and medial (H) views. Right MtIII NMBE5026811 in anterior (I), lateral (J), posterior (K), medial (L) and proximal (M) views. Right MtII NMBE5026812 in proximal (N), anterior (O), lateral (P), posterior (Q), medial (R) views. Scale bar = 10 cm.

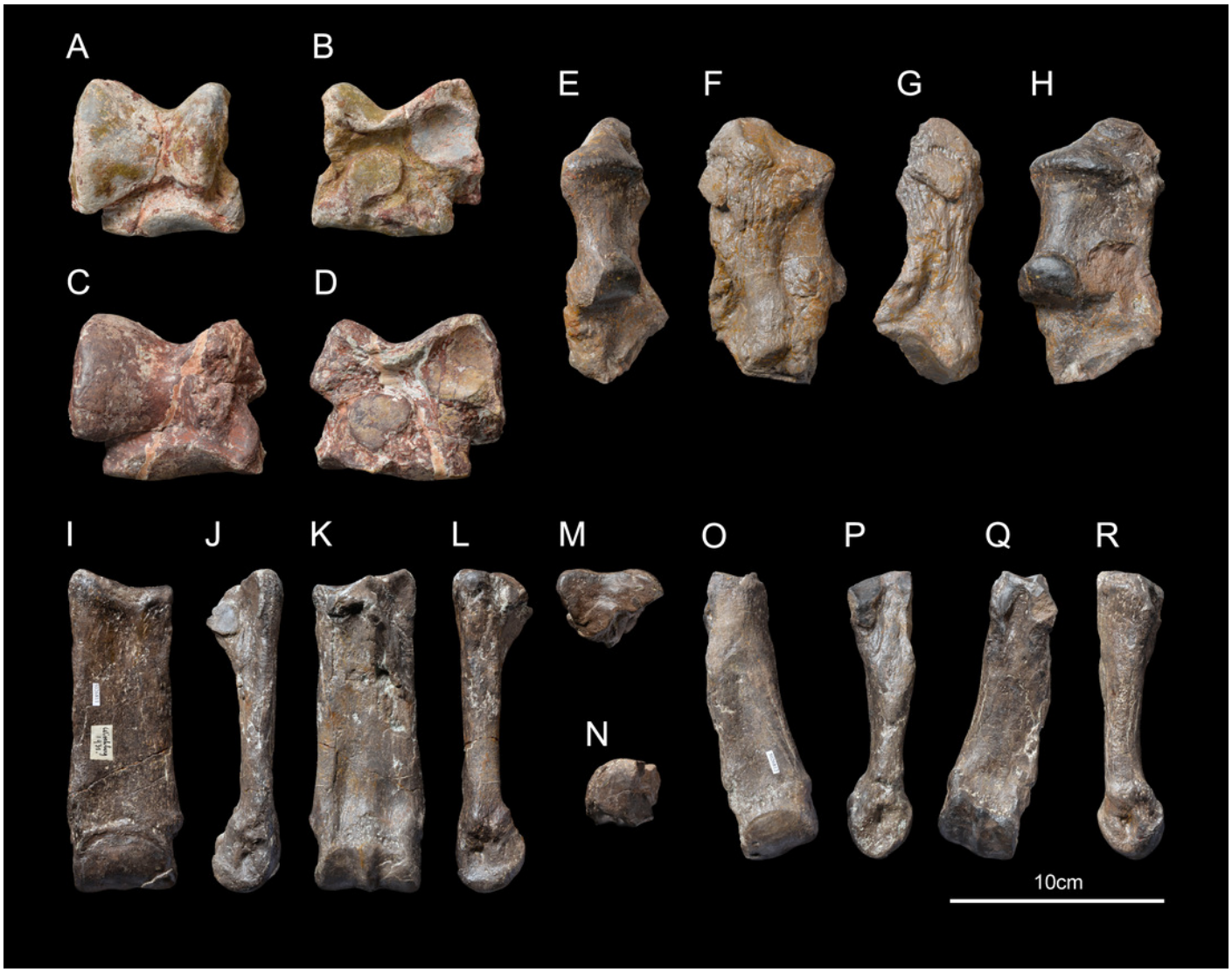
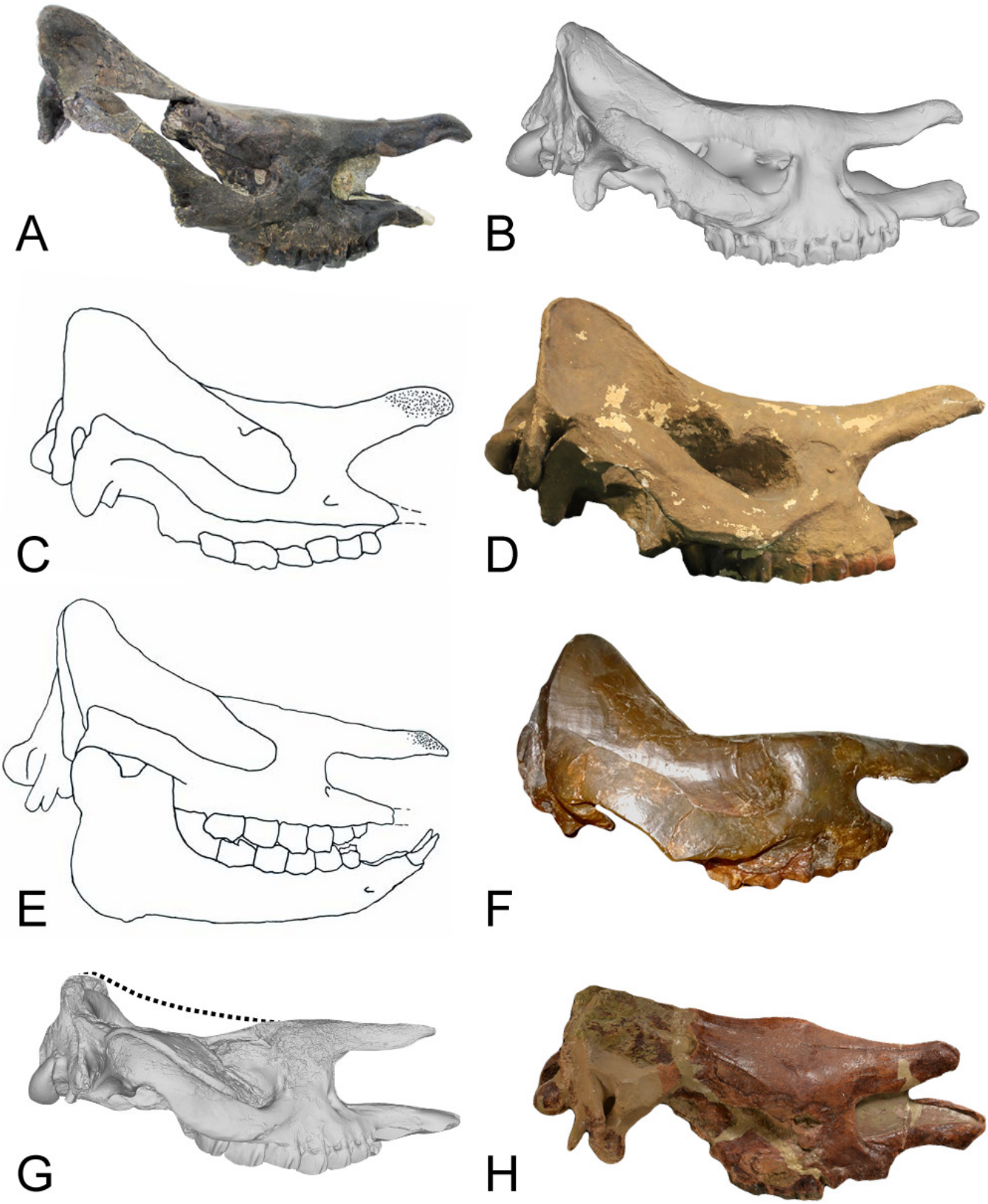


Figure 8

Comparison of the skulls of *Diaceratherium*.

(A) *D. asphaltense* (NMSG-F13607) from Bühler (MP30-MN1; Becker et al. 2018). (B) *D. apshaltense* (NMB Sau 1662) from Saulcet (MN1). (C) *D. aurelianense* (MNHN.F.1888-4, holotype) from Neuville-aux-Bois (MN3), original drawing from Heissig (2017). (D) *D. aurelianense* (MHNT.PAL.2013.0.1001, cast of the holotype), from Neuville-aux-Bois (MN3). (E) *D. aginense* (MHNM 1996.17.111.1, “skull B”, lectotype) from Laugnac (MN2), original drawing from Heissig (2017). (F) *D. aginense* (FSL collection) from Laugnac (MN2). (G) *D. lemanense* (MNHN-AC-2375, holotype) from Gannat (MN1). (H) *D. lemanense* (cast NMBE5031538) from Wischberg (MN1).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