New rhinocerotid remains in the latest Oligocene–Early Miocene of the Swiss Molasse Basin

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Abstract
New specimens of rhinocerotids including a complete skull of *Diaceratherium asphaltense* and a series of associated dental and postcranial elements of *D. aginense* and *Pleuroceros pleuroceros* have been discovered in two localities of the Swiss Molasse Basin: Bühler (?latest Oligocene-earliest Miocene, Canton Appenzell-Ausserhoden) and Sous le Mont (Early Miocene, Canton Bern). The record of *D. asphaltense* in Bühler may push its First Appearance Datum back to the latest Oligocene. *Pleuroceros pleuroceros* and *Diaceratherium aginense* co-occur at Sous le Mont. This assemblage is typical of the Agenian age in Western Europe. Sous le Mont is the second Swiss occurrence of *P. pleuroceros* beside Wischberg (MN1).

Keywords
Systematics, Rhinocerotidae, *Diaceratherium*, *Pleuroceros*, Biostratigraphy, Oligocene, Miocene, Swiss Molasse Basin.

1. INTRODUCTION

Among Rhinocerotidae, *Pleuroceros* Roger, 1898 and *Diaceratherium* Dietrich, 1931 are rhinocerotine genera assigned to "Aceratheres *sensu lato*" (Antoine *et al.*, 2010; Becker *et al.*, 2013) and Teleoceratina (Heissig, 1989), respectively. Except for the early and puzzling "*Diaceratherium*" *massiliae* Ménouret & Guérin, 2009 from Marseille area (Early-Late Oligocene transition) and for scattered Asian records [*Pleuroceros blanfordi* (Lydekker, 1884) from the Early Miocene of Pakistan and Vietnam (Antoine *et al.*, 2010; Prieto *et al.*, accepted), the Late Oligocene *D.* cf. *lamilloquense* from Thailand (Marivaux *et al.*, 2004), and the Early Miocene *Diaceratherium fatehjangense* (Pilgrim, 1910) from Pakistan (*sensu* Boada-Saña, 2008)], these two genera range almost exclusively from the latest Oligocene to the Early Miocene of Western Europe (e.g. Cerdeño, 1993; Boada-Saña *et al.*, 2007; Becker *et al.*, 2009; Antoine *et al.*, 2010; Antoine & Becker, 2013).
Two new localities of the Swiss Molasse Basin, namely Bühler, Canton Appenzell-Ausserhoden and Sous le Mont, Canton Bern, have yielded rhinocerotid specimens including a splendid skull of *D. asphaltense* (Depéret & Douxami, 1902) at Bühler and a series of associated dental and postcranial elements of *D. aginense* (Répelin, 1917) and *P. pleuroceros* (Duvernoy, 1853) at Sous le Mont. In the present work, we describe these new specimens, discuss their systematic affinities, and propose an anatomical reconstruction of the head of *D. asphaltense*.

2. GEOLOGICAL SETTING

The skull of *Diaceratherium asphaltense* comes from a sandy outcrop located about 2 km north of the Bühler village on the road to Trogen (Fig. 1; folded Plateau Molasse, Canton Appenzell Ausserhoden, Switzerland). It has been extracted from its enclosing matrix by Urs Oberli from St. Gall and the outcrop was documented by the collaborators of the Archeology Office of Canton Thurgau under the request of the Canton Appenzell-Ausserhoden (Steiner & Pfifter, 2014). According to the Geological Atlas of Switzerland, the site is located at the southern border of the folded Plateau Molasse, just north of the Subalpine Molasse boundary (Ludwig
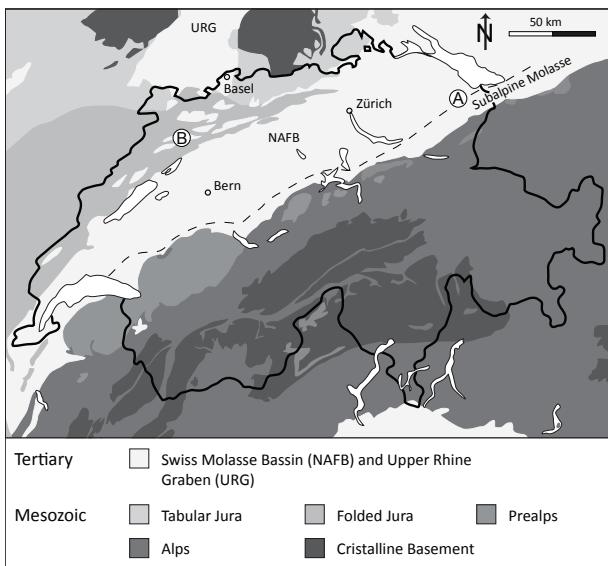
Fig. 1: Geographical and geological locations of the Rhinocerotidae localities from the Swiss Molasse Basin. A, Bühler (?latest Oligocene-earliest Miocene, folded Plateau Molasse, Canton Appenzell-Ausserhoden). B, Sous le Mont (Early Miocene, Jura Molasse, Canton Bern).

et al., 1949). Paleogeographically, the site is located north of the *Speer-Stockberg-Schüttung* alluvial fan and south of the vast Chattian-Aquitanian fluvial system of the *Genferseeschüttung* drained eastwards (Berger *et al.,* 2005). The sedimentary record consists of about 10 m of loose light-gray sandstone, deposited in 10-20 cm thick beds, with a 30° SE dipping. The sandstone deposits belong to the *Appenzeller Sandstein* Formation (syn. *Ebnater Sandstein*) of the USM (*Untere Süsswasser Molasse* = Lower Freshwater Molasse), assumed to be late Chattian in age (Habicht, 1987). Taking into account the latest Oligocene age of the surrounding mammal localities of the *Appenzeller Sandstein* Formation, such as Ebnat-Kappel (MP28; Engesser & Mödden, 1997) or Halsen (MP28-30; Scherler *et al.*, 2011), the Bühler locality could be dated to MP28-30. However, given the well-bounded stratigraphical range of *D. asphaltense* (it is strictly limited to MN1 localities; Becker *et al.*, 2009; Antoine & Becker, 2013) and the diachronic nature of fluvial sandstones, it would be also possible that these deposits are in fact dated from the MN1, and may then provide an earliest Miocene age for some deposits of the *Appenzeller Sandstein* Formation.

The Highway A16 construction through the Swiss Jura Mountains allowed for the discovery of the Sous le Mont mammalian locality, near Tavannes in 2008-2011 (Fig. 1; Jura Molasse, Canton Bern, Switzerland). More than 400 vertebrate remains were discovered, including unpublished rhinocerotid remains. The outcrop consists of a 16 m-thick section of molasse, subdivided in 3 m of calcareous and marly-calcareous deposits (*Calcaires*

delémontiens) topped by 7 m of marly deposits rich in *caliche* and 6 m of grey sandy and marly deposits, marked by an erosive base (Zulliger, 2008). Classically, deposits above the late Chattian *Calcaires delémontiens* of the USM are considered as Burdigalian marine deposits of the OMM (*Obere Meeresmolasse* = Upper Marine Molasse). However, the grey sandy and marly deposits at the top of the Sous le Mont section present no evidence of marine fauna, but are typical fluvial deposits instead, and encompass three fossiliferous levels rich in continental fossils (mammals, reptiles, birds, and charophytes). The vertebrate remains are either fragmented and rounded (attesting to a transport), or well preserved. The rhinocerotid remains come from the first and third levels; the taxonomical assemblages being similar in both cases, they are considered as contemporaneous (Mennecart, 2012). According to Mennecart (2012), the ruminant association (*Dremotherium feignouxi* and *Pomelomeryx gracilis*) consistently places the locality in the Agenian (MN1-2). The study of small mammal assemblage, still in progress, would support a late Agenian age (MN2; Burkart Engesser, pers. com. 2009; Mennecart, 2012). Lithostratigraphically, this record is among the first evidences for Aquitanian-earliest Burdigalian continental deposits of the USM in the South-Central Jura Molasse.

3. MATERIAL AND METHODS

The complete rhino skull from Bühler is stored in the collection of the Natural History Museum Sankt Gallen ("*Naturmuseum St. Gallen*", Switzerland). Although stored in the collection of the JURASSICA Museum (Porrentruy, Switzerland) as a long-term loan, specimens from the locality of Sous le Mont belong to the Natural History Museum of Bern ("*Naturhistorisches Museum der Burgergemeinde Bern*", Switzerland). The fossils have been described and identified by means of anatomical descriptions, comparative anatomy, and biometrical measurements. Dental and osteological features described correspond basically to cladistic characters used and listed by Antoine (2002). The dental terminology follows Heissig (1969) and Antoine (2002), while measurements were taken according to Guérin (1980). All dimensions are in mm and those between parentheses are estimated.

The gracility index (Guérin, 1980; Becker *et al.*, 2009) was calculated for the MtII SLM008-135. Comparison was made with other diacerathere species, *Mesaceratherium paulhiacense* (Richard, 1937) and *P. pleuroceros*. Given that this index and the gracility categories were originally intended to be calculated on central metapods, they have been tentatively adapted to the shorter length of medial metacarpals.

The stratigraphical framework is based on geological time scales and European Land Mammal Ages (ELMA) for the Paleogene (Vandenberghe *et al.*, 2012) and Neogene

(Hilgen *et al.*, 2012). Successions of Mammal Paleogene levels (MP) and 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; Legendre & Lévêque, 1997; Mein, 1999; Steininger, 1999; Agustí *et al.*, 2001). The concerned period ranges from the latest Arvernian (latest Oligocene, MP28-30) to the Agenian (Early Miocene, MN1-2).

Abbreviations
FAD First Appearance Datum. **M/m** upper/lower molar, **P/p** upper/lower premolar. **APD** antero-posterior diameter, **dia** diaphysis, **dist** distal, **H** height, **L** length, **prox** proximal, **TD** transversal diameter, **W** width, **Mc** metacarpal, **Mt** metatarsal. **MHNG** "Muséum d'histoire naturelle Genève", **MHNT** "Muséum d'histoire naturelle Toulouse", **MJSN** JURASSICA Museum (formerly "Musée jurassien des sciences naturelles"), **NMB** "Naturhistorisches Museum Basel", **NMBE** "Naturhistorisches Museum der Burgergemeinde Bern", **NMSG** "Naturmuseum St.Gallen", **UCBL** "Université Claude Bernard - Lyon 1".

4. SYSTEMATICS

The suprageneric arrangement follows that proposed by Antoine *et al.* (2010).

Order Perissodactyla Owen, 1848
Family Rhinocerotidae Gray, 1821
Subfamily Rhinocerotinae Gray, 1821
Tribe Rhinocerotini Gray, 1821
Subtribe Teleoceratina Hay, 1902
Genus *Diaceratherium* Dietrich, 1931

Diaceratherium asphaltense
(Depéret & Douxami, 1902)
Fig. 2

Stratigraphical range: ?latest Oligocene-earliest Miocene (?MP28-30–MN1).
Occurrences: France, Switzerland (Depéret & Douxami, 1902; Schaub & Hürzeler, 1948; Hugueney, 1997; Heissig, 1999; Becker *et al.*, 2009; Ménouret & Guérin, 2009; Antoine & Becker, 2013).
Referred material: Subcomplete skull (NMSG-F13607).
Description: The Bühler skull NMSG-F13607 is incomplete. It lacks the basioccipital and the basicranium, part of the molar series, and the tip of the premaxilla. The dental remains are much worn, pointing to an aged individual. In dorsal view, the general outline of the skull is brachycephalic with well-divergent zygomatic arches (*sensu* Antoine, 2002; maximum zygomatic width/ nasal-occipital length ratio = 0.57), but with relatively narrow frontal bones (*sensu* Antoine, 2002; zygomatic

width/ frontal width = 1.99). The nasal bones are totally separated, long and thin, and rough spots for a small nasal horn are identified at the anteriormost part of the nasals. The postorbital constriction is moderate, marked by well-separated fronto-parietal crests (minimum distance = 47.5 mm) and the occipital crest is concave. In lateral view, the zygomatic arch is moderately high with a high anterior base of the processus zygomaticus maxillary. The processus postorbitalis of the squamosal and the processus lacrymalis are developed. The general dorsal profile of the skull is very concave, characterized by a nasal tip pointing downwards and a strong posterior elevation of the occipital crest. The postglenoid and posttympanic apophyses are in contact, and the external auditory pseudomeatus is partially closed. The back of the toothrow reaches the posterior half of the skull. The nasal notch, deep and U-shaped, ends above P3. The anterior border of the orbit is located above the M1. The minimal distance between the posterior edge of the nasal notch and the anterior border of the orbit is 81 mm. The anterior tip of the processus zygomaticus maxillari is somewhat projected laterally in ventral view. Anterior dentition is not preserved; premolar series are complete, from P1 to P4, while the molar series only preserve M1-2 on the right labial side and M1-3 on the left labial side. Due to the advanced wear of the teeth, only few characters can be identified: wrinkled enamel, low crowned cheek teeth, joined roots, weak trace of cement on left M2, long premolar row (*sensu* Antoine, 2002; IP/M = 0.59), absence of labial cingulum, continuous lingual cingulum on premolars, anterolingual cingulum on P1, protocone and hypocone equals and separated on P2-4, and a strong paracone fold on M1. The biometrical dimensions of the Bühler skull are shown in Tabl. 1.
Remarks: The assignment of the skull NMSG-F13607 to *Diaceratherium* is undisputable, notably thanks to the nasals (long and thin, totally separated and deep U-shaped notch reaching P3) and the orbit features (presence of a processus placrymalis, anterior border above M1). In comparison with *D. lamilloquense*, the skull of which is unknown, P2 clearly differs in having a protocone weaker than the hypocone, related to it by a lingual bridge and by a transverse metaloph (Michel, 1983: p. 15, figs 4a-b). According to Roman (1912: pl. VIII, fig. 1), Becker *et al.* (2009: p. 16, fig. 3) and Becker *et al.* (2010: p. 100, fig. 3C), the skull NMSG-F13607 differs from that of *Diaceratherium lemanense* in having a dolichocephalic outline in dorsal view, a more pronounced occipital elevation, lesser developed concavity of the occipital crest ("forked" in *D. lemanense*, *sensu* Antoine, 2002), frontoparietal crests more distant (usually fused into a "sagittal crest" in *D. lemanense*, *sensu* Antoine, 2002), a base of the processus zygomaticus maxillari high, as well as a processus postorbitalis on the zygomatic arch and a median nasal horn (Becker *et al.*, 2009). With respect to *D. aurelianense*, the occipital elevation is still more pronounced whereas the zygomatic arch is

Fig. 2: *Diaceratherium asphaltense* from Bühler (?latest Oligocene-earliest Miocene, Canton Appenzell-Ausserhoden, Switzerland). A and B, Skull NMSG-F13607 in lateral view. C, same in dorsal view. D, same in ventral view.

Tableau 1: *Diaceratherium asphaltense* (Depéret & Douxami, 1902). Dimensions of the skull (NMSG-F13607) from Bühler, ?latest Oligocene-earliest Miocene (Canton Appenzell-Ausserhoden, Switzerland). Dimensions in parentheses are estimated.

Skull dimensions	(mm)	Teeth dimensions	L x W (mm)
Nasal-occipital length	580.0	P1	25.0 x 23.5
Front of orbit-occipital length	354.0	P2	30.0 x 40.5
Nasal notch length	201.0	P3	32.0 x 47.5
Nasal notch-front of orbit length	81.0	P4	(38.5 x 52.0)
Minimum width of frontoparietal crest	47.5	M1	(37.0 x -)
Frontal width	167.0	M2	(- x -)
Zygomatic width	332.0	M3	38.0 x -
Occipital crest width	149.0	Length P1-M3	128.0 (n=1)
Skull height (above P1)	163.0	Length P1-4	121.0 (n=2)
Skull height (above P4/M1)	183.0	Length P3-4	68.5 (n=2)
Skull height (above M3)	178.0	Length M1-3	117.0 (n=1)
Zygomatic W / frontal W	1.99	LP3–4 / LM1-3	0.59 (n=2)
Zygomatic W / occipital-nasal L	0.57		

lower (Nouel, 1866: pl. 2). The cranial characters of *D. aginense* and *D. asphaltense* are very similar to those of NMSG-F13607. *Diaceratherium aginense* only differs from the Bühler specimen in displaying a completely closed external auditory pseudomeatus, an anterior tip of the processus zygomaticus maxillary with a very progressive divergence in ventral view, and in lacking a posterior groove on the processus zygomaticus (specimens from Laugnac; Répelin, 1917: pl. I, figs 1-2 and pl. IV, figs 1-2). Likewise, dental remains differ in showing a weak paracone fold on M1-2 (Répelin, 1917: pl. III, fig. 1 and pl. IV, figs 1-2).

At last, cranio-dental characters of NMSG-F13607 are morphologically undiscernable from those of *D. asphaltense*, either from Wischberg (Schaub & Hürzeler, 1948: p. 363, fig. 4; Becker, 2003: p1. IV, figs a1-2), Pyrimont-Challonges (Depéret & Douxami, 1902: pl. I, figs 1-2), or Saulcet (Becker *et al.*, 2009: p. 18, fig. 4a). This fully supports the referral of this skull to *D. asphaltense*.

Diaceratherium aginense (Répelin, 1917)
Figs 3A-H and 4E

1931. *Diaceratherium tomerdingense* Dietrich.

Stratigraphical range: Early Miocene (MN1-2).
Occurrences: France, Germany, Switzerland (Duvernoy, 1853; Pomel, 1853; Roman, 1912, 1924; Répelin, 1917; Lavocat, 1951; de Bonis, 1973; Tobien, 1980; Brunet *et al.*, 1987; Duranthon, 1991; Engesser & Mödden, 1997; Hugueney, 1997; Heissig, 1999; Ginsburg, 2000; Ginsburg & Bulot, 2000; Becker, 2003; Boada-Sañã *et al.*, 2007; Becker *et al.*, 2009, 2010; Antoine & Becker, 2013).

Referred material: Two fragmented left M1/2s (MJSN SLM008-133, SLM011-286); fragmented right d2 (MJSN SLM010-1), fragmented left m2/3 (MJSN SLM011-51); thoracic vertebra (MJSN SLM011-52); incomplete left humerus (MJSN SLM011-194); right MtII (MJSN SLM008-135).
Description: Dental remains consist only of a worn and rounded metaloph of a left M1/2 (SLM008-133) and of a postfossette of M1/2 (SLM011-286). Their crown is low. Enamel is wrinkled and arborescent. Observable features are a developed crochet, a continuous short metaloph, a high lingual cingulum surrounding the hypocone, a marked constriction notching the base of the anterior side of the hypocone, a posterior profile of the ectoloph probably concave and a postfossette narrow and deep. The d2 (L > 20.0; W > 14.0) is two-rooted and without a cingulum. It displays a constricted paralophid (spur-like) and a developed paraconid as well as rather shallow anterior and external grooves on the ectolophid. The fragmented left m2/3 (W = 28.5) corresponds to the anterior part of the tooth. Cingula are missing and the trigonid is rounded, forming a right dihedron in occlusal view.

The thoracic vertebra SLM011-52 is preserved by its spinous process (APD = 50.0; H = 42.0), its body (APD = 55.5; TDanterior = 44.0; Hanterior = 38.5) and its vertebral foramen (TD = 30.0; H = 25.0), the dimensions of which match those of a medium to large-sized rhinocerotid.

The humerus SLM011-194 preserves only the diaphysis and distal articulation. It was short and robust. The available dimensions are TD = 60.5 and minimum APD of the diaphysis = 43.5. The fossa olecrani is high and the median constriction of the trochlea is shallow (egg cup-shape *sensu* Antoine, 2002).

The MtII SLM008-135 (L = 113.0; TDprox = 33.5; APDprox = 43.5; APDdia = 21.0; TDdia = 29.5; TDdist = 36.5; APDdist = 39.5) is stout, with a long and robust insertion for the musculi interossei, reaching the distal half of the shaft. In anterior view, the proximo-anteromedial tuberosity is salient, the proximal end is narrow and the anterior border very concave with lateral and medial borders roughly of the same height. The proximal mesocuneiform facet is roughly isosceles triangle-shaped. A high oval posteromedial facet for the entocuneiform, strongly developed, clearly joins the proximal facet. On the lateral side, the anterior MtIII-facet is well developed, flat, vertical and approximately in the same plan as the tiny anterior ectocuneiform facet. The posterior MtIII-facet is low and circular. There is no posterior ectocuneiform facet. The diaphysis is oval in cross-section and transversally elongated. The distal end is the most robust part of the bone. The distal articulation is roughly anteroposteriorly elongated in distal view, with both medial and lateral epicondyles strongly developed. The intermediate relief is slightly salient in distal view, especially with respect to the medial lip of the pulley, but almost not visible in anterior view.

Remarks: The referred material fits in dimensions and morphology with those of *Diaceratherium* (e.g. postfossette narrow and deep on upper cheekteeth, trigonid rounded forming a right dihedron on lower cheek teeth, as well as a high fossa olecrani and an egg-cup shaped distal articulation on the humerus; Boada-Saña, 2008; Becker *et al.*, 2010). Also, the presence of an elongated entocuneiform-facet on the MtII is typical of teleoceratines (Fig. 4).

Among diaceratheres, the MtII SLM008-135 differs from those of *D. lamilloquense*, *D. lemanense*, and *D. asphaltense* by a higher robustness and a long insertion of the m. interossei. Even if *D. aurelianense* and *"D." massiliae* are considered as being graviportal, their metapods also differ in being clearly more robust in *D. aurelianense* and in having a short insertion for the m. interossei in *"D." massiliae* (Cerdeño, 1993; Ménouret & Guérin, 2009; pers. obs.). According to the morphology, dimensions and gracility index, the medial metatarsal SLM008-135 is closer to the specimen of *D. aginense* from Laugnac illustrated by de Bonis (1973: fig. 34.2), which can be considered as robust (Fig. 5). As

a consequence, we tentatively refer our available material from Sous le Mont to *D. aginense*. Furthermore, the MtII SLM008-135 belonged to an old individual, evidenced by a long and robust insertion for the musculi interossei and pathologies such as fibrous, candle wax and lumpy bone texture, the presence of several exostoses, and a variation in foramen sizes and shapes (Fig. 3H), commonly found in massive rhinocerotids (Stilson *et al.*, 2016). These pathologies may explain the difficulties encountered to identify the specimen, as its original shape looks distorted. Also, no example has been found in any compared material of such a posteriorly displaced MtIII-facet associated to an absence of a posterior ectocuneiform facet, but it could potentially result from the advanced age of the individual.

From the Tabl. 2 and Figs 4-5, it must be noted that the MtII NMB-UM2565 from Rickenbach assigned to *D. lamilloquense* by Mennecart *et al.* (2012: fig. 4) seems to be closer to *D. asphaltense* from Saulcet and Wischberg by its dimensions and gracility index. Based on these new observations, we suggest to use a conservative approach and to attribute this latter specimen to *Diaceratherium* sp. instead.

Subfamily Rhinocerotinae Gray, 1821
Unnamed clade
Genus *Pleuroceros* Roger, 1898

***Pleuroceros pleuroceros* (Duvernoy, 1853)**
Fig. 3I-K

Stratigraphical range: ?latest Oligocene-Early Miocene (?MP30–MN2).
Occurrences: France, Germany, Switzerland (Duvernoy, 1853; Schlosser, 1902; Schaub & Hürzeler, 1948; Lavocat, 1951; de Bonis, 1973; Hugueney, 1997; Heissig, 1999; Ginsburg & Bulot, 2000; Becker, 2003; Ménouret & Guérin, 2009; Antoine *et al.,* 2010; Antoine & Becker, 2013).
Referred material: Fragmentary left m2/3 (MJSN SLM011-60); left magnum (MJSN SLM011-66); left proximal epiphysis of tibia (MJSN SLM011-176).
Description: The lower molar SLM011-60 (L > 35.0; W > 21.0; H = 29.0) is low-crowned, the enamel is wrinkled and a thin layer of cement is present in variable quantity.

Fig. 3: *Diaceratherium aginense* (A-H) and *Pleuroceros pleuroceros* (I-K) from Sous le Mont (Early Miocene, Canton Bern, Switzerland). A, left humerus MJSN SLM011-194 in anterior, posterior, lateral and medial views. B, dorsal vertebra MJSN SLM011-52 in anterior and lateral views. C, right d2 MJSN SLM010-1 in occlusal, lingual and labial views. D, fragment of left M1/2 MJSN SLM008-133 in occlusal and lingual views. E, right MtII MJSN SLM008-135 in anterior, posterior, lateral, medial, proximal and distal views. F, fragment of left M1/2 MJSN SLM011-286 in occlusal and posterior views. G, left m2/3 MJSN SLM011-51 in occlusal and labial views. H, proximal part of the right MtII MJSN SLM008-135 in posterior view, showing pathologies (track wear and candle wax exostose). I, left proximal epiphysis of tibia MJSN SLM011-176 in posterior and proximal views (arrow indicating the proximal articulation with the fibula). J, left magnum MJSN SLM011-66 in anterior (left), distal (top-middle), proximal (top-right), medial (bottom-middle) and lateral (bottom-right) views. K, left m2/3 MJSN SLM011-60 in occlusal and labial views.
◄

The external groove is developed, smoother at mid-crown height, and vanishing above the neck. The trigonid is angular and forms a right dihedron in occlusal view. The metaconid is constricted. The anterior and posterior valleys are V-shaped in lingual view, the latter being wider and deeper than the former. The labial cingulum is nearly absent, with only a tiny bead at the base of the external groove. The talonid is lingually shifted in respect to the trigonid and the hypolophid is oblique.

The referred magnum is subcomplete (TD = 37.5; H =

Tableau 2: Compared MtII gracility index (sorted by ascending order) of MJSN SLM008-135 (Sous le Mont, Canton Bern, Switzerland) and of *Diaceratherium* species, *Pleuroceros pleuroceros* and *Mesaceratherium paulhiacense* (true cursorial anatomical type).

Taxon	N°	Specimen	Locality	L (mm)	W (mm)	Gracility Index
M. paulhiacense	1	Ph.1012 (Bonis, 1973, fig. 41.2)	Paulhiac	136.0	18.5	13.61
P. pleuroceros	2	Ph.430 (Bonis, 1973, fig. 47.4)	Paulhiac	111.0	18.0	16.22
D. lamilloquense	3	MHNT.PAL.2014.0.2564.4	Castelmaurou	132.2	22.0	16.64
	4	MHNT.PAL.2014.0.2564.1	Castelmaurou	131.5	24.0	18.25
D. lemanense	5	NMB-S.9.18260	Montaigu	127.5	25.5	20.00
	6	NMB-GN40	Gannat	134.0	27.0	20.15
D. asphaltense	7	NMB-Sau1662	Saulcet	119.5	27.0	22.59
D. sp.	8	NMB-UM2565 (Mennecart *et al.*, 2012, fig. 4)	Rickenbach	119.0	28.0	23.53
D. asphaltense	9	NMBE-5026812	Wischberg	128.0	32.0	25.00
D. aginense	**10**	**MJSN SLM008-135**	**Sous le Mont**	**113.0**	**29.5**	**26.11**
	11	Lg. M. (Bonis, 1973, fig. 34.2)	Laugnac	106.5	29.5	27.70
D. aurelianense	12	MNHN-NEU95 (Cerdeño, 1993, tabl. IV)	Neuville-aux-Bois	101.5	30.5	30.05
	13	NMB-SO229	Artenay	106.5	33.0	30.99

Fig. 4: MtIIs of *Diaceratherium* species in posterior views. Arrows indicate the elongated entocuneiform facet. A, *D. lamilloquense* from Castelmaurou (MHNT.PAL.2014.0.2564.1). B, *D. lemanense* from Gannat (NMB-GN40). C, *D. asphaltense* from Wischberg (NMBE-5026812). D, *D. asphaltense* from Saulcet (NMB-Sau1662). E, *Diaceratherium* sp. from Rickenbach (NMB-UM2565). F, *D. aginense* from Sous le Mont (MJSN SLM008-135).
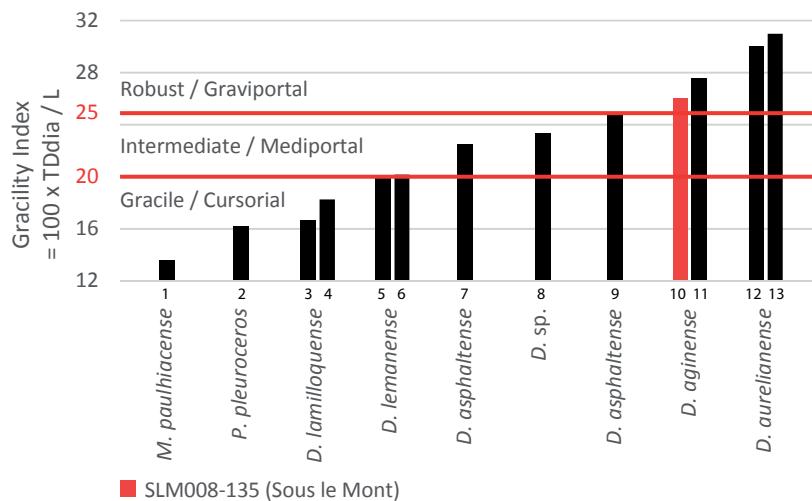
Fig. 5: Gracility index of MtII MJSN SLM008-135 and of *Diaceratherium* species, *Pleuroceros pleuroceros* and *Mesaceratherium paulhiacense* (true cursorial anatomical type). Numbers under columns correspond to the numbers and specimens in Tabl. 2.

52.5; Hanterior = 33.5; APD = 75.5). The anterior side is barely higher than wide. The proximal border is straight in anterior view. The articular process for the semilunate is high and semicircular in lateral view. On the medial side, the anterior indentation is very shallow and the separation of the articular facets (semilunate, trapezoid, McII) is smooth. On the lateral side, the unciform-facet is rectangular, anteroposteriorly narrow, and it joins the semilunate-facet nearly in the same plan, without apparent separation. The distal McII-facet is trapezoid. The posterior tuberosity is curved and short (34.0) in respect to the APD.

The left proximal epiphysis of tibia is strongly rounded: almost no features are preserved. The dimensions are modest (APDprox = 57.0; DTprox = 72.0). On the lateral side, the proximal articulation with the fibula is high. Grooves of the extensor and of the anterior tibial tuberosity (*sensu* Barone, 1999) are deep and narrow. In proximal view, the latter tuberosity is similarly anteriorly developed on its lateral and medial sides. The proximal medial and lateral articular facets are posteriorly little developed.

Remarks: The referred specimens correspond to the smallest rhinocerotid from Sous le Mont. They cannot be assigned to *Diaceratherium* or to *Mesaceratherium*, due to a clearly smaller size and an angular trigonid on lower cheek teeth. Their gracility is intermediate between *Mesaceratherium* (more gracile) and *Diaceratherium* (more robust; de Bonis, 1973; Antoine *et al.*, 2006, 2010). These remains differ from *Protaceratherium* in having a slightly larger size, a magnum lower and wider in anterior view and a less developed labial cingulum on lower cheek teeth (Roman, 1924; de Bonis, 1973: p. 160, fig. 7; Cerdeño, 1989). The smallest species of *Prosantorhinus*, *P. germanicus*, has a similar size, but its anatomical type is clearly stouter. Moreover, its lower cheek teeth bear

a more developed labial cingulum, a rounded trigonid forming an acute dihedron and a smooth external groove (Heissig, 1972).

The available remains share the closest affinities with *Pleuroceros* representatives, although being of smaller dimensions and having an external groove more developed than in *P. blanfordi* from Pakistan (Antoine *et al.*, 2010). On the other hand, dental features are strikingly similar to those of *P. pleuroceros* specimens from coeval European localities of Gannat and Wischberg (Roman, 1912: pl. VI, figs 4-5; Schaub & Hürzeler, 1948; Becker, 2003: p1. IV, fig. d). They can be referred to as this latter species based on the presence of a much reduced lingual cingulum, a dihedral and angular trigonid, a developed external groove, and a metaconid slightly constricted on lower molars. Also, the referred magnum and tibia match well the size and the morphological pattern of *P. pleuroceros*. In particular, the magnum figured by de Bonis (1973: p. 153, fig. 5) from Paulhiac presents similar features such as an anterior side barely higher than wide, a proximal border straight in anterior view, a very shallow anterior indentation on the medial side, with strongly connected unciform- and semilunate-facets on the lateral side. Accordingly, we tentatively attribute the referred specimens to *P. pleuroceros*, in particular because of the strict resemblance of SLM011-60 with the lower molars of Wischberg (NMBE- 5026739) and Gannat (Roman, 1912: pl. VI, figs 4-6) and of SLM011-66 with the magnum of Paulhiac (de Bonis, 1973: p. 153, fig. 5).

5. DISCUSSION

The earliest undoubtful European representatives of *Diaceratherium*, i.e., *D. lamilloquense* (Michel, 1983;

Brunet *et al.*, 1987; Duranthon, 1990), were generalist browsers with quite slender limbs, although the more diverging species have later developed a trend to short-legged ("brachypod") anatomical type – particularly marked in *D. aurelianense* (Nouel, 1866) from the Orleanian of Western Europe (Heissig, 1999; Antoine *et al.*, 2000; Becker *et al.*, 2009; Scherler *et al.*, 2013). *Diaceratherium* was first named by Dietrich (1931), based on associated remains from Tomerdingen (MN1) assigned to *D. tomerdingense* Dietrich, 1931 (junior synonym of *D. aginense* following Antoine & Becker 2013 and contrary to Boada-Saña *et al.*, 2007). Depéret

A

B

C

20cm

50cm
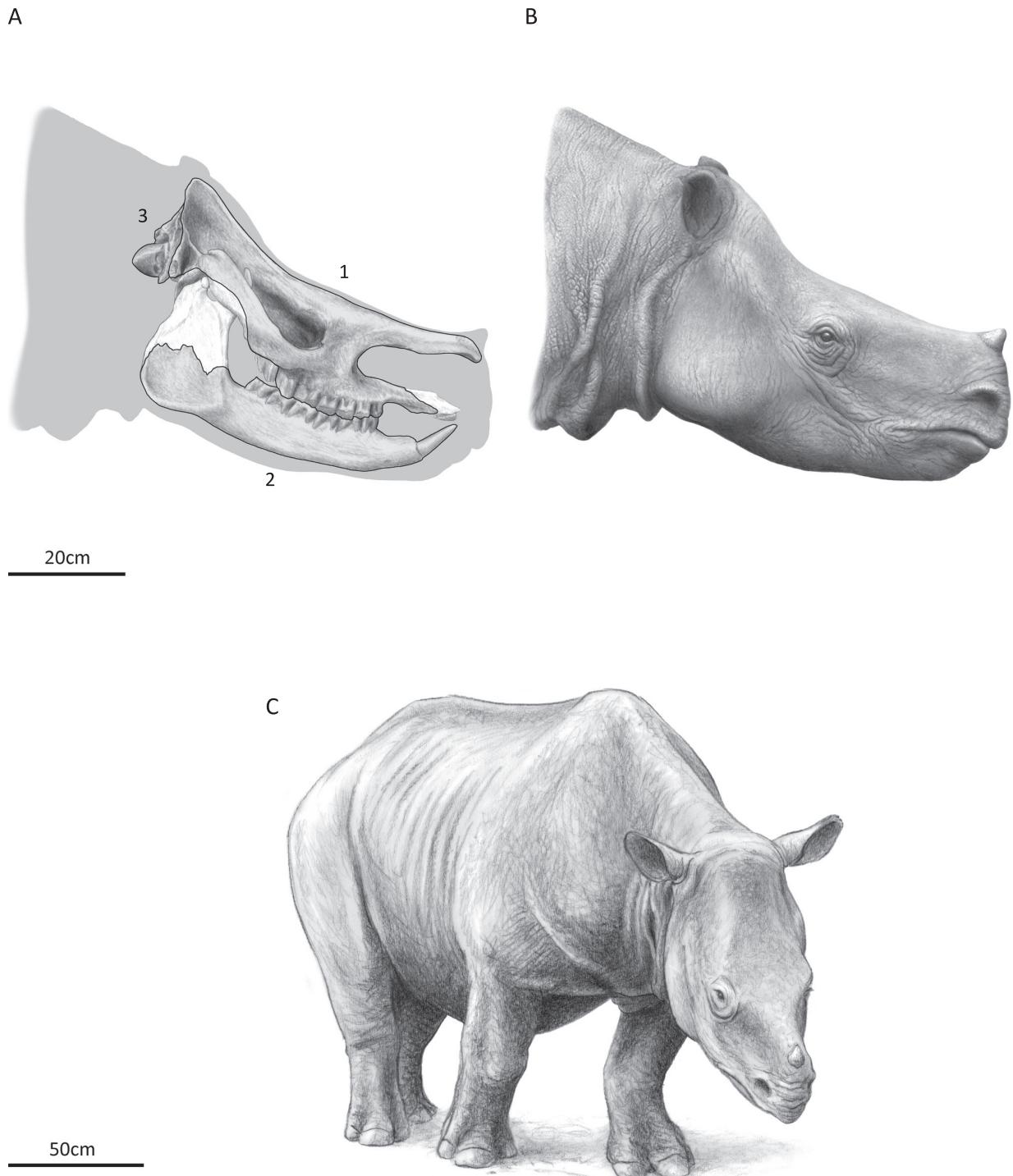
Fig. 6: *Diaceratherium asphaltense*. A, scientific drawing of the skull, based on (1) Bühler (skull NMSG-F13607), (2) Wischberg (mandible NMBE-5026738) and (3) Saulcet (skull NMB-Sau1662) specimens. White areas are reconstructed. B, reconstruction of the head based on A. C, sketch of the complete animal in three-quarter view, based on B and postcranial dimensions from specimens of Saulcet (skeleton NMB-Sau1662). Illustration by Patrick Röschli.

& Douxami (1902) have described "*Diceratherium asphaltense*" based on the presence of lateral rugosities on the type skull of Pyrimont-Challonges (MN1), then assigned to *Pleuroceros asphaltense* by Wood (1929), and further referred to as *Diaceratherium asphaltense* by Dietrich (1931) and his followers. Due to nasal bones being totally separated in diaceratheres, this feature has often been interpreted as testifying to the presence of small paired nasal horns (e.g. Depéret & Douxami, 1902; Becker *et al.*, 2009; Antoine & Becker, 2013). However, direct observations of the nasal bones of *D. asphaltense* from the type locality Pyrimont-Challonges, as well as Bühler, Saulcet, and Wischberg, have shown the presence of weak symmetric protuberances, shaping a single small bump, which should be alternatively interpreted as the attachment of a small single and axial nasal horn. We propose here an anatomical reconstruction of *D. asphaltense* matching this hypothesis (Fig. 6). It is based on a composite skull including specimens from Bühler (skull NMSG-F13607), Saulcet (skull NMB-Sau1662) and Wischberg (mandible NMBE-5026738), as well as on the postcranial skeleton from Saulcet (NMB-Sau1662). The head posture is based on functional morphology following the study of Bales (1996) and comparison with extant rhinoceroses, particularly *Dicerorhinus sumatrensis*, which shares the closest cranial morphologies (occipital side and zygomatic arch of the skull, ventral border and angular of the mandible). Classically, this head posture is typical of regular browsers, feeding on tree and shrub foliage both above the ground and at ground level (Janis, 1988).

Concerning the record of *Diaceratherium asphaltense*, its presence in Bühler could either push back its FAD to the latest Oligocene (following Habicht, 1987) or alternately point to a longer sedimentary record for the *Appenzeller Sandstein* Formation (i.e., persisting until earliest Miocene times), given the known stratigraphical range of the species. The distribution of *Pleuroceros pleuroceros* is now more extended in Switzerland, as Sous le Mont represents the second Swiss occurrence beside Wischberg (MN1). The *Pleuroceros pleuroceros–Diaceratherium aginense assemblage* recorded in Sous le Mont (Bern Canton) is typical from the Western European Agenian age (Fig. 7; Antoine & Becker, 2013). These two brachydont species differ by their size and their anatomical type: small to medium-size, cursorial – to mediportal after Antoine & Becker (2013) – and three-toed manus for *P. pleuroceros* versus medium to large-size, graviportal with quite short-limbs and four-toed manus for *D. aginense*. They are both typical browsers
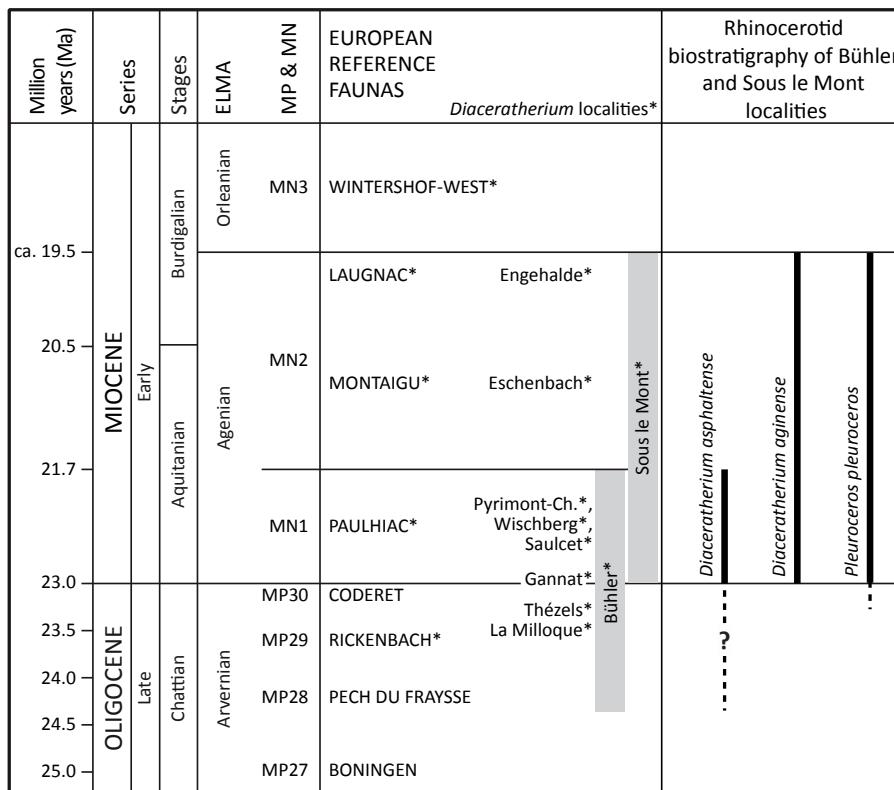

Fig. 7: Biostratigraphy of the Rhinocerotidae of Bühler (Canton Appenzell-Ausserhoden, Switzerland) and Sous le Mont (Canton Bern, Switzerland), according to the European reference faunas (capital) and *Diaceratherium* localities (regular). ELMA, European Land Mammal Ages; MP, Mammal Paleogene Levels; MN, Mammal Neogene Units. See Material and methods part for stratigraphical correlation and calibration. Modified from Becker *et al.* (2009, 2010).

and forest dwellers, but *D. aginense* could show more affinities towards soft and humid grounds (Antoine & Becker, 2013).

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