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The Early Miocene teleoceratine *Prosantorhinus* aff. *douvillei* (Mammalia, Perissodactyla, Rhinocerotidae) from Béon 2, Southwestern France

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Abstract
Béon 2 locality, near Montréal-du-Gers in the Garonne Basin, SW France, yields a middle Orleanian mammalian assemblage coeval to that of Artenay in the Loire Basin (early MN4). Two rhinocerotid species were previously mentioned at Béon 2: the small and slender rhinocerotine *Protaceratherium minutum* (Cuvier, 1822) and a large-sized and short-limbed teleoceratine provisionally referred to as *Diaceratherium aurelianense* (Nouel, 1866) prior to accurate preparation. The latter taxon is documented by a complete skull, isolated teeth, and postcranial elements unearthed in 1994-1998, showing the closest morphological affinities to *Prosantorhinus douvillei* (Osborn, 1900) instead, but differing from it in several cranio-dental and postcranial aspects (e.g., median ridge absent on the occipital condyle, sulcus mylohyoideus present on the corpus mandibulae, i1 with a developed crown, P2 molariform with a thick protocone and a protoloph joining the ectoloph, constricted protocone on M3, p2 with an unconstricted paralophid and a lingually open posterior valley, axis-facets transversally concave on the atlas, magnum with a long posterior tuberosity, fibula-facet more oblique and expansion of the Cc1 facet wide and low on the astragalus). The concerned remains are described and illustrated for the first time here, allowing for a new taxonomic assignment for this teleoceratine (*Prosantorhinus* aff. *douvillei*). A calcaneus from Béon 2 is further assigned to an unidentified representative of *Plesiaceratherium*. The revised Béon 2 rhinocerotid assemblage consists of three species: *Prosantorhinus* aff. *douvillei* (dominant), *Protaceratherium minutum*, and *Plesiaceratherium* sp. (large-sized).

Keywords
Montréal-du-Gers, Orleanian, Teleoceratina, *Plesiaceratherium* sp., systematics, paleobiogeography.

Résumé
Le téléocératiné *Prosantorhinus* aff. *douvillei* (Mammalia, Perissodactyla, Rhinocerotidae) du Miocène inférieur de Béon 2 (Gers, France).- Le gisement de Béon 2, à Montréal-du-Gers (bassin de la Garonne, sud-ouest de la France), livre une faune de mammifères de l'Orléanien moyen contemporaine de celle d'Artenay dans le bassin de la Loire (base de la MN4). Deux espèces de rhinocérotidés y ont précédemment été mentionnées: le petit rhinocérotiné gracile *Protaceratherium minutum* (Cuvier, 1822) et un téléocératiné de grande taille et brachypode attribué à *Diaceratherium aurelianense* (Nouel, 1866), avant préparation fine du matériel disponible. Ce dernier taxon est documenté par un crâne complet, des dents isolées et des éléments postcrâniens découverts en 1994-1998. Il présente finalement d'étroites affinités avec *Prosantorhinus douvillei* (Osborn, 1900), mais en diffère par plusieurs caractères crânio-dentaires et postcrâniens (en particulier, absence de l'arête médiane sur le condyle occipital, présence du sulcus mylohyoideus sur le corpus mandibulae, i1 avec une couronne développée, P2 molariforme avec un protocône puissant et un protolophe connecté à l'ectolophe, protocône étranglé sur M3, p2 avec un paralophide non étranglé et une vallée postérieure ouverte lingualement, un atlas avec des facettes pour l'axis concaves transversalement, un magnum avec une tubérosité postérieure longue, un astragale avec une facette pour la fibula plus oblique et une expansion pour la facette Cc1 large et basse). Les spécimens en question, décrits et illustrés pour la première fois, permettent une nouvelle attribution taxonomique pour ce téléocératiné (*Prosantorhinus* aff. *douvillei*). Un calcanéum de Béon 2 est par ailleurs attribué à un représentant indéterminé de *Plesiaceratherium*. L'assemblage révisé de rhinocérotidés de Béon 2 consiste finalement en trois espèces: *Prosantorhinus* aff. *douvillei* (dominant), *Protaceratherium minutum* et *Plesiaceratherium* sp. (grande taille).

Mots-clés
Montréal-du-Gers, Orléanien, Teleoceratina, *Plesiaceratherium* sp., systématique, paléobiogéographie.

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1. INTRODUCTION

Two Early Miocene vertebrate localities are known near the place called Béon at Montréal-du-Gers, Gers, in Southwestern France (Fig. 1). The first one, named Béon 1 and discovered in 1987 in a limestone quarry, has yielded over 60 vertebrate species (e.g., Crouzel *et al.*, 1988; Duranthon *et al.*, 1995; Rage & Bailón, 2005; Orliac, 2006; Orliac *et al.*, 2006), including five distinct rhinocerotid species (Antoine, 1997, 2002; Antoine *et al.*, 1997, 2000a). In terms of biostratigraphical age, it is considered coeval to the Aérotrain locality in the Loire Basin [upper part of the MN4 zone following De Bruijn *et al.* (1992) and Mein (1999)], and intercalated between Pellecahus (older) and La Romieu (younger) in the Garonne Basin (Fig. 1A; Antoine *et al.*, 1997, 2000a, b). On the other hand, Béon 2 was incidentally discovered in 1994 in a remote sector of the quarry, ~150 m away from the main pit, and roughly at the same altitude (Fig. 1B). At first, the faunal assemblage was mistakenly amalgamated with that of Béon 1 and considered as strictly coeval to it (Antoine & Duranthon, 1997). Later on, taxonomic discrepancies between micromammal and megamammal components and geological observations showing a little dip between the two pits led to considering Béon 2 as biostratigraphically predating Béon 1 and being coeval to Artenay, in the Loire Basin (base of the MN4; Duranthon *et al.*, 1999; Antoine *et al.*, 2000a; Bulot *et al.*, 2009). In particular, the rhinocerotid assemblage of Béon 2 fully differed from that of Béon 1 in yielding only two rhinocerotid species, further undocumented in the latter locality. The small-sized and slender-limbed *Protaceratherium minutum* (Cuvier, 1822) has its Last Appearance Datum (LAD) in both Béon 2 and Artenay (Antoine *et al.*, 2000a). The concerned remains have been extensively described by Antoine & Duranthon (1997). The second species had been assigned to the medium-sized and short-limbed teleoceratine *Diaceratherium aurelianense* (Nouel, 1866), based on preliminary observation of unprepared cranio-dental and postcranial specimens (e.g., Antoine *et al.*, 2000a; Bulot *et al.*, 2009). In the present work we focus on the remains referable to this short-limbed rhinocerotid, comparing them with those of other Early Miocene teleoceratines from Eurasia, in order to constrain arguably its taxonomic assignment.

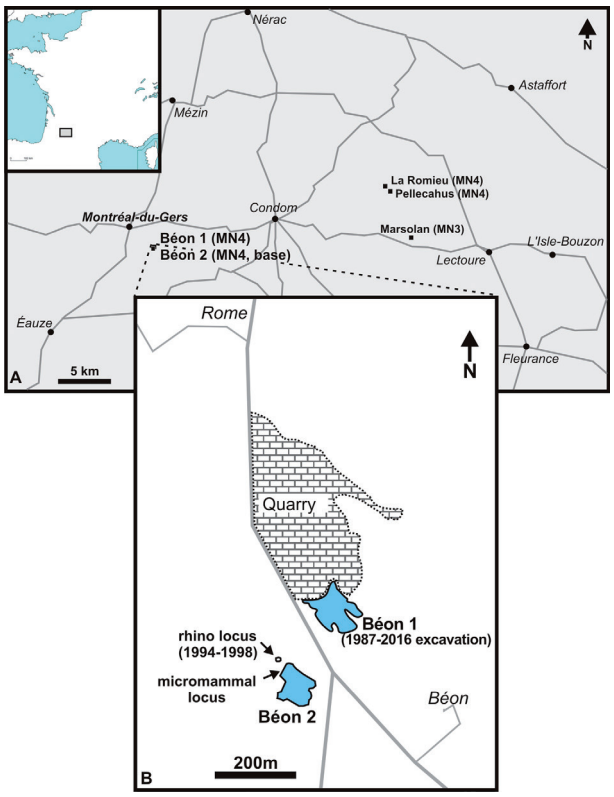

Fig. 1: A. Location map of Béon 2 locality, Montréal-du-Gers (base MN4; mid-Orleanian, late Early Miocene, SW France) and of other surrounding localities of interest. B. Detailed map of Béon 1 and Béon 2 localities. Modified from Bulot *et al.* (2009).

2. MATERIAL AND METHODS

Capital letters are used for upper teeth (D, P, M), and lower-case letters for lower teeth (i, d, p, m). Rhinocerotid dental terminology is that of Heissig (1972a: pl. 13) and Antoine (2002). Anatomical features described follow basically the same sequence as in Antoine (2002), and Antoine *et al.* (2010). Suprageneric systematics within Rhinocerotidae follows the arrangement proposed by Antoine *et al.* (2010) and Becker *et al.* (2013). Dimensions are given in mm.

Abbreviations: APD, antero-posterior diameter; Cc, Calcaneus; H, height; L, length; lat, lateral; max, maximum; med, medial; min, minimum; prox, proximal; TD, transverse diameter.

3. RESULTS

Systematic Paleontology

Order Perissodactyla Owen, 1848
Family Rhinocerotidae Gray, 1821
Subfamily Rhinocerotinae Gray, 1821
Tribe Rhinocerotini Gray, 1821
Subtribe Teleoceratina Hay, 1902
Genus *Prosantorhinus* Heissig, 1974

Prosantorhinus* aff. *douvillei
Figs 2-4

Described material: MNHT PAL.2015.0.1669, skull; MHNT PAL.2015.0.1518, nasal tip; MHNT PAL.2015.0.1532, edentulous right jaw fragment; MHNT PAL.2015.0.1517.1, right D1, eroded;

MHNT PAL.2015.0.1517.2, P4 fragment; MHNT PAL.2015.0.1517.3, left M1, ectoloph; MHNT PAL.2015.0.1517.4, left M2, antero-lingual fragment; MHNT PAL.2015.0.1517.5, unworn i1; MHNT PAL.2015.0.1517.6, right p2; MHNT PAL.2015.0.1670.1, axis; MHNT PAL.2015.0.1670.2, cervical vertebra; MHNT PAL.2015.0.1670.3, cervical vertebra; MHNT PAL.2015.0.1521, rib, proximal tip; MHNT PAL.2015.0.1515, rib fragments; MHNT PAL.2015.0.1539, left scapula, distal fragment; MHNT PAL.2015.0.1536, right humerus, diaphysis fragment; MHNT PAL.2015.0.1535, right radius, proximal tip; MHNT PAL.2015.0.1525, right magnum; MHNT PAL.2015.0.1523, right tibia, distal fragment; MHNT PAL.2015.0.1541, right patella; MHNT PAL.2015.0.1537, right astragalus; MHNT PAL.2015.0.1522, anterior part of a right ectocuneiform; MHNT PAL.2015.0.1524, right Mt4; MHNT PAL.2015.0.1526.1, second medial phalanx (right); MHNT PAL.2015.0.1526.2, second central phalanx (right); MHNT PAL.2015.0.1526.3, second lateral phalanx (right); MHNT PAL.2015.0.1520, second lateral phalanx. All these specimens originate from Béon 2 (base of the MN4, Montréal-du-Gers, Gers, SW France).

Description

Most specimens belong to the same adult individual, but there are evidences of at least a second adult individual (nasal tip MNHT PAL.2015.0.1518).

Skull (Fig. 2). The skull MNHT PAL.2015.0.1669 is almost complete, but the top of the cranial roof has been eroded in its distalmost part (braincase and occipital crest), after deposition. The right occipital condyle and the premaxillae are also lacking. The occipito-nasal length equals 620 mm, matching the average value for recent *Rhinoceros sondaicus*, following Guérin (1980: 48). The isolated nasal MNHT PAL.2015.0.1518 is laterally crushed and somewhat smaller than its counterpart from the complete skull (preserved L = 123; TD > 47).

In lateral view, the nasals have a lateral apophysis on their ventral edge, close to their anterior tip (Fig. 2A, E). The infraorbital foramen is open above mid-P3. The nasal notch is quite short (~190 mm), ending above P2. There is no nasal septum. The nasal/lachrymal suture is not observable. The anterior border of the orbit is located above the P3-4. The processus lachrymalis is not observable; the processus postorbitalis is present on frontal bones. The anterior base of the processus zygomaticus maxillari is very low, only a few millimeters above the neck of jugal teeth. The zygomatic arch forms a thick and much elevated stripe, sigmoid in lateral view, with a concave dorsal border and a rounded dorso-distal tip. There is a very low processus postorbitalis on the zygomatic arch, located on the jugal. The jugal/squamosal suture is not observable. Although the top of the cranial roof has been eroded, the preserved part points to a concave dorsal profile for the skull. The foramina rotundum/sphenorbitale or ovale are not preserved. The temporal and nuchal crests are confluent and merged (no groove between them). The pseudo meatus acusticus externus is partly closed ventrally. The occipital side, merely lacking, was inclined antero-dorsally. The nuchal tubercle is not well developed. The back of the tooth row is located in the posterior half of the skull. The posterior margin of the pterygoid is nearly vertical. The occipital condyle and the skull follow the same axis.

In dorsal view, the skull is diamond-shaped, with a narrow nasal tip (PAL.2015.0.1669 and 1518) and broad zygomatic arches (Fig. 2B). The skull is wide and short (i.e., brachycephalic: nasal-occipital length = 620 mm; bizygomatic width ~420 mm). Nasal bones are long (naso-frontal suture not observable). They are totally separate on both specimens, with a sharp tip and nearly coalescent rugose bumps (insertion for a small and median nasal horn; Fig. 2C, D). There are no vascular imprints coinciding with the insertion of a frontal horn. Orbits are not laterally projected. Bizygomatic width widely exceeds frontal width (420/230). The fronto-parietal and occipital crests are not preserved. In palatine view (Fig. 2D), the processus zygomaticus maxillari follows the maxilla outline. There are five and four palatine foramina along the molar series, on the left and right sides, respectively. The palatine spine is located at the level of the M2-M3 transition. The vomer region is not observable. The articular tubercle of the squamosal is sharp-edged and somewhat concave transversely. The foramen postglenoideum is remote from the processus postglenoidalis. The latter processus is thick and forming a right dihedron in cross section. The foramen nervi hypoglossi is not observable. The basilar process has a sharp and elevated sagittal crest. A posterior groove hollows the processus zygomaticus of the squamosal. The well-developed processus posttympanicus and processus paraoccipitalis are distant. The foramen magnum is badly crushed. There is no medial ridge on the occipital condyle, the medial part of which shows no evidence of a truncation.

Mandible (Fig. 3B, C). The edentulous jaw fragment MHNT PAL.2015.0.1532 provides restricted information, as it only preserves a part of the corpus mandibulae and the alveoli of p4-m3 (adult individual). The shape of the symphysis and the position of the foramen mentale are unknown. A lingual groove (sulcus mylohyoideus) is present. The corpus is low, with a straight base. The foramen mandibulare is located below the teeth neck line.

Dental features (Fig. 3; Table 1). The left P2-M3 series is 245 mm long (P3-4 length = 75 [left] and 74 [right]; M1-3 length = 140 [left] and 139 [right]). The premolar/molar length ratio is high (100 * P3-4 length / M1-3 length = 53.4). There is no enamel folding or coronary cement. Enamel is wrinkled and corrugated. Teeth are low-crowned (brachydont). Roots are distinct,

Fig. 2: *Prosantorhinus* aff. *douvillei*, Béon 2, Montréal-du-Gers (base MN4; mid-Orleanian, late Early Miocene, SW France). Cranial material. A-D, skull MNHT PAL.2015.0.1669 in left lateral (A), dorsal (B), rostral (C), and palatine views (D); E-F, nasal tip of another horned individual (MHNT PAL.2015.0.1518) in left lateral (E) and dorsal views (F). Scale bar = 50 mm.

as shown by the alveoli of the right P2 (skull MHNT PAL.2015.0.1669) and the alveoli of p4-m3 (MHNT PAL.2015.0.1532). No anterior tooth is preserved, except for the i1 MHNT PAL.2015.0.1517.5.

Upper teeth. The paracone fold is increasingly thick and salient from P2 to M3 (Fig. 3A). Premolars are molariform (bilophodont; protocone and hypocone separate; lingual bridge at advanced wear stages). There is no labial cingulum or metaloph constriction on upper premolars. The crochet is short and usually multiple on P2-4. The lingual cingulum is present and continuous on P2-4. The postfossette is narrow and forming a deep pit on upper premolars. A smooth antecrochet is absent on P2 but present on P3. The D1 is persistent (one specimen is preserved and there is a wear facet on the mesial side of the left P2). Although eroded, the D1 MHNT PAL.2015.0.1517.1 is drop-shaped in occlusal view, with no protoloph but a thick and transverse metaloph (Fig. 3D). The ectoloph is convex (no parastylar groove or paracone fold), with no labial cingulum, but a sharp lingual cingulum closing the lingual valley. The protoloph is complete and joined to the ectoloph, the metaloph is transversely oriented, and the protocone and hypocone are equally developed on P2. There is no crista, pseudometaloph, or medifossette on P3-4. The protoloph is complete, sigmoid, and without a protocone constriction on P3-4 (skull MNHT PAL.2015.0.1669 and P4 MHNT PAL.2015.0.1517.2). The antecrochet is more developed on P4 than on P3. The metaloph is complete, without a constriction, on P3-4 and the hypocone is located distally with respect to the metacone. There is nor labial cingulum (except on the ectoloph of the M1 MHNT PAL.2015.0.1517.3), crista, cristella, or medifossette, but a strong antecrochet (never connecting the hypocone) on upper molars (in particular in the fragmentary M2 MHNT PAL.2015.0.1517.4, left M2). The crochet is simple, wide, short, and closely appressed to the ectoloph. A lingual cingulum is only observed at the entrance of the median valley on M3. A weak protocone constriction is always present on M1-2. The parastyle is short and smooth but there is a deep parastylar groove and a weak metacone fold on upper molars. The metastyle and the metaloph are long, and the distal part of the ectoloph is concave on M1-2. The posterior cingulum is complete and there is no anterior constriction isolating the hypocone on M1-2. The postfossette is deep and narrow on M1-2. The M2s have a weak mesostyle but no lingual groove on the hypocone. The M3s are triangular in occlusal view, with a convex ectometaloph (without a distolingual groove), a protoloph transversely oriented, and a constricted (trefoil-shaped) protocone.

Lower teeth. Only an i1 and a right p2 are preserved. The i1 MHNT PAL.2015.0.1517.5 has a single, long and straight root (Fig. 3E), oval and laterally compressed in cross section. The crown is unworn, globular and unicuspidate, with an acuminate mesial tip and a smooth and sagittal median ridge, but no cingulid. The right p2 MHNT PAL.2015.0.1517.6 has a simple paralophid and a strong hypolophid (Fig. 3F). Enamel is corrugated on the basal half of the ectolophid (Fig. 3G), but there are no strong rugosities. The paralophid is thick and short, simple and slighly curved mesiolingually (not spur-like). There is no trace of a wear facet due to the contact of d1/p1. The paraconid is the most prominent cuspid, associated with a labial ridge further isolated by a distal groove, restricted to the top of the crown. A low and oblique cingulid closes the entrance of a small and narrow mesio-lingual valley. The main lingual valley is open lingually, with no cingulid, and V-shaped in lingual view. There is no labial cingulid either. The hypolophid is straight and complete, with no constriction.

Postcranial elements (Fig. 4). Vertebrae are either unknown (atlas), unprepared (axis MHNT PAL.2015.0.1670.1), or partly crushed (cervical vertebrae MHNT PAL.2015.0.1670.2 and MHNT PAL.2015.0.1670.3). On the axis, the atlas-facets have a convex outline in dorsal view and the spine is long and thick.

Appendicular skeletal elements mostly consist of right limb bones. The left scapula MHNT PAL.2015.0.1539 only preserves the distal part (min APD ~89). In lateral view, the tuberculum supraglenoidale is well developed and hemispheric, with a rugose aspect. It is located well above the distal articulation. The incisura scapulae is not stretched. The spina scapulae is broken. The margo caudalis is concave, probably pointing to a spatulate outline for the scapula in lateral view. In distal view, the cavitas glenoidalis has a trapezoid outline (TD = 69; APD

Table 1: *Prosantorhinus* aff. *douvillei*, Béon 2, Montréal-du-Gers (base MN4; mid-Orleanian, late Early Miocene, SW France). Dental dimensions in mm. l, left; r, right; L, length; ant, anterior; post, posterior; H, height. Brackets denote estimated values. For M3s, postW value coincides with the ectometaloph length.

	MNHT PAL.2015.0.1669											MNHT PAL.2015.0.1517			
	lP2	lP3	rP3	lP4	rP4	lM1	rM1	lM2	rM2	lM3	rM3	rD1	rP4	ri1	rp2
L	(31)	(36)	(37)	43	42	48	47	-	53	48	48	23	45	13	26.5
antW	39	(57)	53	(62)	61	(60)	62	(65)	63	-	60	15	-	6.5	18
postW	43	56	54	(58)	57	(61)	57	(55)	56	-	61	18	-	-	20
H	23	27	23	28	28	22	21	34	27	32	34	-	37	10	23

Fig. 3: *Prosantorhinus* aff. *douvillei*, Béon 2, Montréal-du-Gers (base MN4; mid-Orleanian, late Early Miocene, SW France). Mandibular and dental material. A, right dental series of the skull MNHT PAL.2015.0.1669 in occlusal view. B-C, edentulous right jaw fragment MHNT PAL.2015.0.1532, in labial (B) and occlusal views (C); D, right eroded D1 MHNT PAL.2015.0.1517.1, in occlusal view; E-F, right p2 MHNT PAL.2015.0.1517.6, in occlusal (E) and labial views (F); G, unworn i1 MHNT PAL.2015.0.1517.5, in lateral view (unidentified side). Scale bars = 50 mm (A-C) and 20 mm (D-G).

~87), with the straight medial and caudal sides forming a right angle (Fig. 4A) and the anterior and lateral sides forming an open angle (~135°).

The humeral diaphysis fragment MHNT PAL.2015.0.1536 has a strongly concave lateral border, indicating that this bone was short and robust, with a wide distal end. No other feature is observable.

The proximal tip of a right radius MHNT PAL.2015.0.1535 is partly caught in the limestone matrix. In proximal view, the anterior border is convex and the medial lip twice as wide as its lateral counterpart. The posterior side is straight medially and concave laterally. In anterior view, the proximal border forms a 135° dihedron, with a sharp ridge (egg-cup humerus articulation). The proximal end is much wider than the diaphysis (prox TD = 94; prox APD = 54). The insertion of the m. biceps brachii is

medially displaced and moderately hollowed (Fig. 4B). In posterior view, the ulna-facets seem to be connected. Other features are not visible.

The right magnum MHNT PAL.2015.0.1525 is low and robust (L = 89; max H = 57; TD = 49; ant H = 32). In proximal view, the bone forms a sagittally elongated isosceles triangle. The anterior side is wide and pentagonal, with a straight proximal border (Fig. 4C). In medial view, the proximal process is low, small, and acuminate (Fig. 4D). There is no medial indentation between the scaphoid- and the Mc2-facets. The latter facet forms a curved strip, straight sagittally and distally concave. The posterior tuberosity is long and straight. In distal view, the articular surface forms a sagittally elongated rectangle, with a concave posterior border.

MHNT PAL.2015.0.1523 is a distal fragment of a right tibia. It only preserves the posterior apophysis, high, sharp, and medially acuminated. The medio-distal gutter is shallow in the preserved part. Other features are not observable.

The right patella MHNT PAL.2015.0.1541 lacks it medial tip. It was most likely wider than high (H = 82; TD > 70; APD = 43.5), with a low antero-posterior diameter (compressed sagittally). Muscular insertions are smooth on the anterior side. On the articular side, the medial lip is wide, low, and moderately concave transversely, whereas the lateral lip is almost flat. The proximal border of the articular surface is damaged, but straight in its preserved part. The distal tip is smooth, with a shallow ridge delimiting the distal edge of the articular surface.

The astragalus MHNT PAL.2015.0.1537 is wide and low (TD = 89; TD trochlea = 65; med H = 70; min H = 52; lat H = 63; TD/H = 1.27; APD = 58; distal TD = 75; distal APD = 47), much lower medially than laterally (Fig. 4E). It is particularly robust in medial view (APD/H = 0.83). The fibula-facet forms a wide strip, transversely flat and oblique. The trochlea has no antero-distal notch. The collum tali is very high (H = 10), especially with respect to the general proportions of the astragalus. The medial tubercle is high, reaching 40% of the medial height of the bone, but rounded and moderately salient. In proximal view, the caudal border of the trochlea is partly broken. On the posterior side, the calcaneus-facet 1 is nearly flat, with a wide and short laterodistal expansion (Fig. 4F). The calcaneus-facets 2 (low oval) and 3 (low triangle) are not connected. In distal view, the axis of the trochlea is very oblique with respect to the distal articulation. The cuboid-facet forms a narrow and oblique triangle tapering posteromedially, lacking a posterior stop. The navicular-facet is lozengic, almost square.

MHNT PAL.2015.0.1522 is a right ectocuneiform lacking its posterior tip (TD = 49; H = 25). In proximal view, the anterior edge is convex; the medial and lateral sides get closer posteriorly (at a 50° angle). In anterior view, the proximal border is sigmoid, convex medially and concave laterally (Fig. 4G). The distal border is convex, pointing to an Mt3 with a concave proximal border. The anterior side has strong and salient muscular insertions, especially on the medial edge. In medial view, the anterior Mt2-facet is wide semicircular. In lateral view, the antero-distal facet is damaged.

The Mt4 MHNT PAL.2015.0.1524 is short and robust (Fig. 4H; brachypod pattern; L = 95.5), with thick ends and a sagittally compressed diaphysis (Fig. 4I). In proximal view, the proximal end is lozengic (Fig. 4J), with obtuse postero-medial and antero-lateral angles (TD = 40, APD = 43.5). The articular side is sub-triangular. The posterior border is notched in its median part, with a bumpy and isolated postero-lateral tuberosity. On the medial side, the Mt3 facets are vertical, flat, and almost connected. They form a ~160° angle. The anterior facet is semicircular and the posterior facet is almond-shaped and sagittally elongated. Its posterior end does not reach the posterior tip of the bone. In anterior view, the medial length of the bone widely exceeds its lateral length. The diaphysis is concave laterally, with parallel medial and lateral sides, and a strong medial inflection at the proximal third of the shaft (distal end of the insertion for the m. interossei). The diaphysis is wide and compressed sagittally (TD = 37, APD = 22). There are strong medial and lateral tubercles above the distal articulation. The distal end is also particularly developed sagittally (TD = 41, APD = 44), with a sub-circular outline in medial view. It is flat transversely in its medial part and concave in its lateral part, with a low and smooth intermediate relief. In distal view, the distal end forms a quarter-circle, with a postero-medial right angle (Fig. 4K).

Phalanges are wide and low, with salient muscular insertions. The second lateral phalanx MHNT PAL.2015.0.1520 is damaged (H = 21; TD = 39; APD = 38). The second central phalanx MHNT PAL.2015.0.1526.2 has a kidney-like symmetrical outline in proximal view (H = 26; TD = 54; APD = 35). The second medial phalanx (MHNT PAL.2015.0.1526.1; H = 30; TD = 42; APD = 37) and the second lateral phalanx (MHNT PAL.2015.0.1526.3; H = 32; TD = 42; APD = 32) have strong and salient anterior tubercles at the abaxial angle. Their distal facet is flat.

Systematic discussion

The large and robust-limbed rhinocerotid from Béon 2 can be unambiguously referred to as a teleoceratine due to the small nuchal tubercle, the corpus mandibulae low and straight-based, the protocone less developed than the hypocone on P2, the fused proximal radius-ulna facets, the presence of a nearly flat Cc1-facet on the astragalus, the short insertions for the musculi interossei on lateral metapodials, and its brachypod pattern (shortened limb extremities with thick muscular tubercles).

Among Teleoceratina, the previous referral to *Diaceratherium aurelianense* can be discarded as the Béon 2 rhinocerotid has a shorter nasal notch, a latero-ventral expansion on the nasals, a high and sigmoid zygomatic

Fig. 4: *Prosantorhinus* aff. *douvillei*, Béon 2, Montréal-du-Gers (base MN4; mid-Orleanian, late Early Miocene, SW France). Selected postcranial material. A, distal fragment of a left scapula (MHNT PAL.2015.0.1539) in distal view; B, proximal tip of a right radius (MHNT PAL.2015.0.1535) in anterior view; C-D, right magnum MHNT PAL.2015.0.1525, in anterior (C) and medial views (D); E-F, right astragalus MHNT PAL.2015.0.1537, in anterior (E) and posterior views (F); G, anterior part of a right ectocuneiform MHNT PAL.2015.0.1522, in anterior view; H-K, right Mt4 MHNT PAL.2015.0.1524, in anterior (H), medial (I), proximal (J), and distal views (K). *Plesiaceratherium* sp., Béon 2, Montréal-du-Gers (base MN4; mid-Orleanian, late early Miocene, SW France). Left calcaneus MHNT PAL.2015.0.1540, in lateral (L) and antero-distal views (M). Scale bar = 20 mm.

arch with a low rostral base of the processus zygomaticus maxillari, the temporal and nuchal crests determining a flat triangular area, a sharp and carinate articular tubercle on the squamosal, a metaloph transversely oriented on P2, no protocone constriction on P3-4, no p1 or persistent d1, no labial cingulid on lower premolars, and no medial indentation on the magnum (contrary to what occurs at Chilleurs-aux-Bois; Cerdeño, 1996). It is in particular distinct from *Diaceratherium aurelianense* as documented at Beaulieu (late MN3; Aguilar *et al.*, 2003; Ginsburg, 2005). The astragali have equal heights and transverse diameters (70 x 89 mm, respectively), but MHNT PAL.2015.0.1537 from Béon 2 is more robust antero-posteriorly (58 vs. 52 mm), with a medial tubercle higher and less salient, a navicular-facet more horizontally oriented, and a higher lateral trochlear lip (Aguilar *et al.*, 2003, fig. 7D). Moreover, the Mt4 is 20% shorter at Béon 2 than at Beaulieu (L=95 vs. 119; Ginsburg, 2005), with a more robust diaphysis, which is a general discrepancy between representatives of *Prosantorhinus* and *Diaceratherium*.

It does not belong to *Brachypotherium* either (presence of a latero-ventral expansion on the nasals, high zygomatic arch with a low rostral base of the processus zygomaticus maxillari, presence of a median nasal horn, cheek teeth with distinct [unfused] roots, crochet multiple on P2-4, metaloph transversely oriented on P2, P4 with an antecrochet, lingual cingulum usually absent on upper molars, mesostyle present on M2, p2 with a thick and developed paraconid, axis with atlas-facets transversely concave, posterior tuberosity straight on the magnum, posterior apophysis sharp on the tibia, Cc2 and Cc3 facets independent).

In contrast, it shares several features with *Prosantorhinus* (lateral apophyses on the nasals, high and sigmoid zygomatic arch with a smooth processus postorbitalis, posterior groove on the processus zygomaticus, presence of a median nasal horn, processus paraoccipitalis well developed, proximal radius-ulna facets fused, and posterior tibial apophysis sharp; Wang, 1929; Heissig, 1972b; Cerdeño, 1996; Antoine, 2002; Peter, 2002; Heissig & Fejfar, 2007) and, to a lesser extent, with *Teleoceras fossiger* (Miocene of North America; high zygomatic arch, transversal profile of the articular tubercle concave on the squamosal, and metaloph transverse on P2).

Within *Prosantorhinus*, it differs from the type species *P. germanicus* (Wang, 1929; Heissig, 1972b; Peter, 2002; Heissig & Fejfar, 2007) in being much larger-sized (between 20-25% for tooth length, patella, astragalus, and Mt4, up to 50% larger for tooth width, radius, and magnum), in having longer and stronger nasal bones, a longer premolar series (with respect to the molar series), a crochet and a lingual cingulum always present on P2-4, an antecrochet usually present on P2-3, protocone and hypocone equally developed on P2, no labial cingulum on upper molars, no anterior groove on the metaloph of M1-2, a lingual cingulid, no labial cingulid, and a lingually open posterior valley on p2, but also a more robust astragalus regarding APD. It further differs from *Prosantorhinus laubei* Heissig & Fejfar, 2007 from Tuchořice (early MN3, Czech Republic; Heissig & Fejfar, 2007) in being also much larger-sized (15-50%) except for the patella and the Mt4 (same dimensions; Heissig & Fejfar, 2007), in possessing a crochet usually multiple and a continuous cingulum on P2-4, protocone and hypocone equally developed on P2, almost no labial cingulum on upper molars, M3s with a strictly triangular occlusal outline and a constricted protocone, a curved paralophid and a posterior valley lingually open on p2, and in having a much higher collum tali and a wide and low expansion of the Cc1 facet on the astragalus. The hypodigm of *P. shahbazi* (Pilgrim, 1910) from the early Miocene of Balochistan, Pakistan is quite restricted (Pilgrim, 1912; Antoine *et al.*, 2010, 2013), but direct comparison show that both taxa can anyway be distinguished by their contrasting size (much larger at Béon 2, as for teeth and the astragalus), by the absence of a labial cingulum and the usual absence of a lingual cingulum on upper molars, the presence of a metacone fold and of a mesostyle on M1-2, and both the oblique orientation of the fibula-facet and the wide and low expansion of the Cc1 facet on the astragalus at Béon 2.

The teleoceratine from Béon 2 has the closest affinities with *P. douvillei* from Orleanian localities of France (e.g., Osborn, 1900; Cerdeño, 1996; Wermelinger, 1998; Antoine *et al.*, 2000a, 2002; Antoine, 2002) in sharing most craniodental and postcranial features (including shape and proportions), in being much larger than other species referred to *Prosantorhinus*, and in having a continuous lingual cingulum on P2-4 but almost no lingual cingulum on upper molars. Nevertheless, the teleoceratine from Béon 2 shows several discrepancies with the hypodigm of *P. douvillei sensu stricto* (see Cerdeño, 1996; Antoine, 2002), such as the absence of a median ridge on the occipital condyle, the presence of a lingual groove (sulcus mylohyoideus) on the corpus mandibulae, of a developed crown on i1 (vestigial in *P. douvillei*), the shape of P2 (molariform instead of having lingual cusps usually connected by a lingual bridge, with a protocone more developed, and a protoloph joining the ectoloph), the presence of a constricted protocone on M3, of an unconstricted paralophid and of a lingually open posterior valley on p2, the transversally concave axis-facets on the atlas, the long posterior tuberosity on the magnum, the fibula-facet more oblique and the wide and low expansion of the Cc1 facet on the astragalus. The size of Béon 2 specimens equals or slightly exceeds that of the largest remains assigned to *P. douvillei* from Neuville-aux-Bois (MN3), Beaugency and Pontlevoy (MN5, Loire Basin) as synthesized by Cerdeño (1996: tables 2-4, 6). Accordingly, we prefer to consider these remains as documenting an unusually large-sized ally of *P. douvillei*, under the name *Prosantorhinus* aff. *douvillei*, following the recommendations of Bengtson (1988).

4. GENERAL DISCUSSION

The Béon 2 locality unambiguously yields a larger-sized relative of the teleoceratine *Prosantorhinus douvillei* (Osborn, 1900), well known in Orleanian deposits of Western Europe (e.g., Cerdeño, 1996; Antoine *et al.*, 2000b). As mentioned by Antoine *et al.* (2000b), *Prosantorhinus* cf. *douvillei* was recognized at Marsolan, Gers. The concerned remains are undescribed so far, but they most likely document the same morphotype as in Béon 2 (pers. obs. by POA). Marsolan, geographically close to Béon 2, slighly predates it, as it is assigned to the top of the MN3 zone (Ginsburg, 2005; Hugueney & Bulot, 2011). In particular, Marsolan testifies to one of the earliest proboscidean occurrences at the Western European scale (*Zygolophodon turicensis*; Bulot & Ginsburg 1993; Ginsburg & Bulot, 2000). Interestingly, Béon 2 yields another stem elephantoid (*Gomphotherium sylvaticum*; Antoine *et al.*, 2000b).

Moreover, a left calcaneus (MHNT PAL.2015.0.1540), robust and compact (H = 123; TD sustentaculum = 66; H tuberosity > 55), was originally gathered with the teleoceratine remains from Béon 2. Nevertheless, the processus calcanei is long (50% of the total length), with a wide and low tuber calcanei, partly eroded medially (Fig. 4L-M). The beak is high, with a sagittally convex astragalus-facet, unambiguously discarding its referral to teleoceratines. There is a small tibia-facet, but no fibula-facet. The trochlea fibularis is not marked, contrary to what occurs in teleoceratines. The sustentaculum tali is distinctively narrow with respect to what is observed in teleoceratines. The astragalus-facets 2 and 3 are independent. In lateral view, the distal and caudal sides form an obtuse dihedron (~120°). In distal view, the cuboid-facet is bulb-like and biconcave. All these features (shape, dimensions, and proportions) allow for assigning this calcaneus to a large-sized *Plesiaceratherium*, probably close to *P. mirallesi* from Montréal-du-Gers (Béon 1) and Pellecahus (see Antoine *et al.*, 2000a). We provisionally refer to it as *Plesiaceratherium* sp., pending new discoveries.

As a consequence, the rhinocerotid assemblage at Béon 2 finally consists of three species: an unusually large-sized and one-horned representative of *Prosantorhinus* (*Prosantorhinus* aff. *douvillei*, dominant; this work), a very small *Protaceratherium minutum* (three dental and postcranial remains; Antoine & Duranthon, 1997), and a large *Plesiaceratherium* (*Plesiaceratherium* sp., one calcaneus; this work). In documenting at the same time a late *Protaceratherium* (MN1–base MN4) and early large-sized *Prosantorhinus* and *Plesiaceratherium* (base MN4–MN5), this assemblage unexpectedly differs from that of Artenay (*Diaceratherium aurelianense* + *Protaceratherium minutum*; see Antoine *et al.*, 2000b).

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