

FIRST COMPLETE SKULLS OF *ELOMERYX CRISPUS* (GERVAIS, 1849)
AND OF *PROTACERATHERIUM ALBIGENSE* (ROMAN, 1912) FROM A NEW
OLIGOCENE LOCALITY NEAR MOISSAC (SW FRANCE)

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ABSTRACT—A new fossiliferous locality is reported from southwestern France (Moissac III) that yielded two skulls referred to the anthracotheriid *Elomeryx crispus* and the rhinocerotid *Protaceratherium albigense*, and an isolated rodent tooth. The anthracotheriid skull indicates a close relationship with *E. borbonicus* based on its cranial morphology. The rhinocerotid skull improves our knowledge concerning its anterior dentition, cranial morphology and proportions, and enables a more precise specific diagnosis. We suggest an early late Oligocene biochronological age (Mammal Paleogene European reference level MP25-26) for Moissac III, which is substantiated by the co-occurrence of *P. albigense* and of the theridomyid rodent *Issiodoromys cf. pauffiensis*. The European stratigraphic range of *E. crispus*, so far restricted to the late Eocene-early Oligocene interval (MP18-MP22), extends up to the MP25-26, which in turn supports an origination of 'Miocene bothriodontines' from a European ancestor.

INTRODUCTION

The Mid-Tertiary deposits in the Aquitaine basin (southwestern France) are well represented around the city of Moissac (Tarn-et-Garonne Department; Richard, 1948; Bonis, 1973; Hugué, 1997) and they correspond to lenticular accumulation due to fluvial activities. Before this find, two main localities were known in the vicinity: Moissac I is referred to the early Miocene Agenian European Land Mammal Age (ELMA; Bonis, 1973; Bruijn et al., 1992) equivalent to the Aquitanian standard age while Moissac II is referred to the late Oligocene Arvernian ELMA (Bonis, 1973; Schmidt-Kittler et al., 1997) equivalent to the Chattian standard age. We report here a new fossiliferous locality (Moissac III) at Malengane in the same area (Fig. 1) that yielded two well preserved specimens attributed to the small hornless rhinocerotid *Protaceratherium albigense* (Roman, 1912) and to the anthracotheriid *Elomeryx crispus* (Gervais, 1849). Those remains have been recovered by one of us (S. Rafay) and they constitute the first complete skull known for each species at this time. The description of this exceptional material will provide new characters to precisely diagnose the species and to propose accurate phylogenetic relationships. Moreover, the discovery of an upper molar of a theridomyid rodent in the same level allows us to discuss the stratigraphical range and position of this new locality in the local geological context.

GEOLOGICAL CONTEXT

The Agen area is composed of Mid-Tertiary deposits, most of them of fluvio-lacustrine origin. Early Oligocene molasses and

limestones are covered by thick molasse deposits ('Molasses de l'Agenais'), late Oligocene in age, which have yielded the vertebrate fauna of Moissac II (Bonis, 1973). Richard (1948) listed about 140 Oligocene mammalian localities in the Aquitaine Basin. Younger deposits of the Agen area are known as the 'Trilogie agenaise', referable as a whole to the early Miocene (Agenian ELMA; e.g., Duranthon et al., 1999). From bottom to top, it consists respectively of a basal white limestone, a clay and marl sequence in which the mammal assemblage of Moissac I occurs, and a grey limestone.

North East of Moissac at the locality of Malengane, an ancient marble mason yard displays an 18m thick section (Fig. 1). It allows us to observe the following stratigraphical succession. First, there is a layer of 12-15 meters of fine and compact sandstone with some lateral facies changing to sandy clay and marl. Then, we observe a 2.5-meter thick lenticular coarse sandstone with a grain size decrease toward the top where the vertebrate remains are concentrated. This layer includes a 12-centimeter thick lenticular fine sandy clay and an ochre heterogeneous sand (1.5 meters thick) that tops the section. The coarse sandstones display oblique lamina and correspond to a river channel, characterizing a high-energy deposit.

Methods—The anthracotheriid dental terminology follows Lihoreau and Ducrocq (2007:90, Fig. 7.1) and the taxonomy follows Hellmund (1991). The suprageneric systematics within Rhinocerotidae follows that proposed by Antoine et al. (2003b), based on a phylogenetic analysis. Rhinocerotid dental terminology follows Heissig (1969:11–12), Uhlig (1999:15–16), and Antoine (2002:122); osteological and dental features described for the rhinocerotid correspond basically to cladistic characters used and listed by Antoine (2002, 2003) and Antoine et al. (2003b). The biochronological framework is based on the European Land

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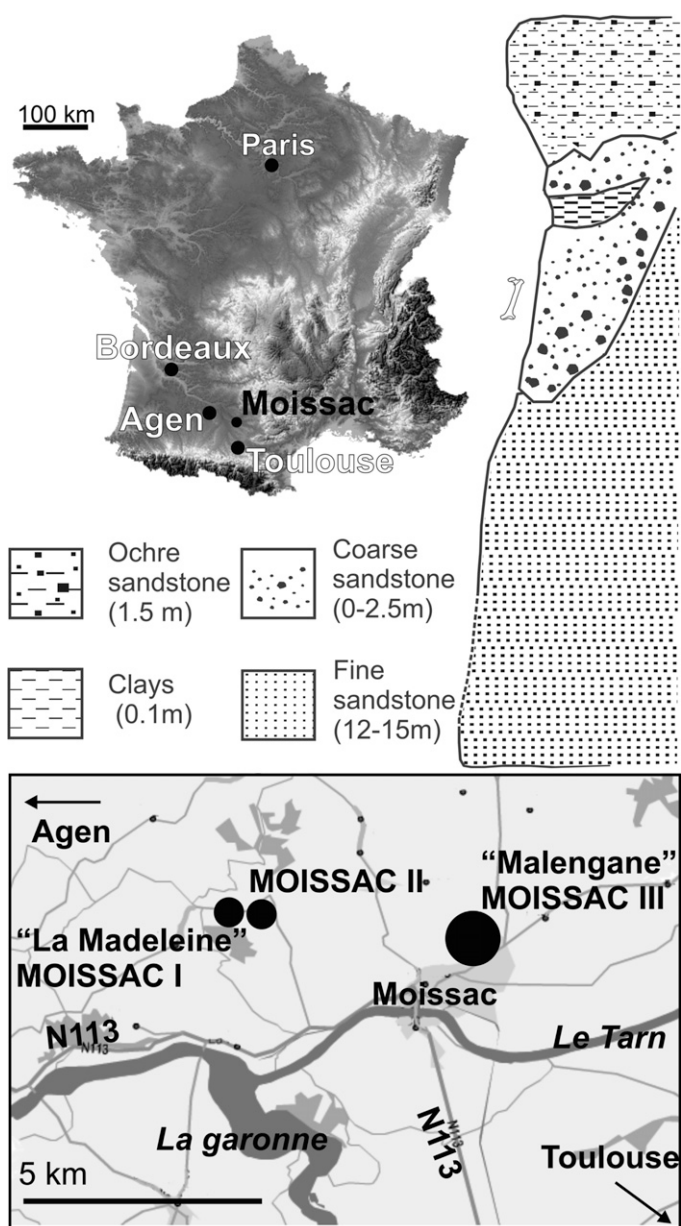


FIGURE 1. Location map of Moissac, SW France, and stratigraphic log of Moissac III locality.

Mammal Biochronological Scale defined by the succession of reference levels (MP; Schmidt-Kittler et al., 1987) and the Paleogene geological time scale (Luterbacher et al., 2004).

Institutional Abbreviations—MNHN, Muséum National d'Histoire Naturelle, Paris, France; MOI, Moissac III; AMNH, American Museum of Natural History, New York, USA; MHNT, Muséum d'Histoire Naturelle, Toulouse, France.

SYSTEMATIC PALEONTOLOGY

Order CETARTIODACTYLA Montgelard, Douzery, and Catezflis, 1997

Family ANTHRACOTHERIIDAE Leidy, 1869

Subfamily BOTHRIODONTINAE Scott, 1940

Genus *ELOMERYX* Marsh, 1894

Type Species—*Elomeryx armatus* Marsh, 1894 from the late Eocene to early-late Oligocene of North America.

Other Species Referred to the Genus—*Elomeryx cluai* (Depéret, 1906) from the late early Oligocene of Western Europe (Spain); *E. crispus* (Gervais, 1849) from the late Eocene to early-late Oligocene of Europe; and *E. borbonicus* (Geais, 1934) from the late Oligocene - early Miocene of Western Europe. Several remains from Asia need further review for accurate attribution (Ducrocq and Lihoreau, 2006).

ELOMERYX CRISPUS (Gervais, 1849) (Fig. 2A–D)

Synonymy—See Hellmund (1991:11–12) for recent synonymy list.

Holotype—Left D4–M1 (MNHN LDB 134) housed in the MNHN.

Locality and Type Horizon—La Débruge near Gargas, Vaucluse, France; late Eocene (MP 18).

Stratigraphical Range—Late Eocene to early late Oligocene, MP18–26, in Western and Southeastern Europe (Czech Republic, France, Germany, Greece, Isle of Wight in UK, Turkish Thrace).

New Material—MOI3.001, sub-complete adult skull with left and right P1–M3 series, lacking premaxillaries, occipitals, the right squamosal and parietal from Moissac III locality, SW France (early late Oligocene). Permanent repository of the original is at the University of Poitiers. Casts are available at the Muséum d'Histoire Naturelle in Toulouse (MHNT) and at the Musée d'Histoire Naturelle in Montauban.

Comparative Description

Skull—The skull is approximately 250 mm long (from the anterior end of the nasals to the occipital condyles) and the small-sized sockets for upper canines suggest that the specimen belongs to an adult female (Hellmund, 1991) (Fig. 2A–C). It is roughly the same dimensions as a female of *E. borbonicus* (Geais, 1934), whereas it is larger than *E. cluai* and smaller than *E. armatus*. The facial portion is much more developed than the brain case. The nasals are long and narrow. They run from above the canine level to the orbits where they project a V-shaped structure between the frontals. Two supraorbital foramina occur on the frontals on each side of the protruding nasal process. The snout is transversely constricted between the canine and the P3 area and it displays a rather short canine fossa that extends between the canine socket and the infra-orbital foramen. The lacrimal is long (its anterior rim reaches the level of the mesial wall of M1) and deep, and contacts with the nasal and the frontal processes. It is not observable on *E. borbonicus* or *E. cluai*, but in *E. armatus* the lacrimal is clearly separated from the nasal by a frontal process. Each lacrimal displays a groove on the anterior margin of the orbit, and the lacrimal foramen is absent (as in *E. armatus*). The infraorbital foramen opens low on the maxilla at the anterior end of the facial crest above the distal root of P3 as in *E. borbonicus* (Geais, 1934). In all of the specimens of *E. armatus* observed at the AMNH, it is above the distal root of P2. The anterior margin of the orbit is situated above the M3 as in all species of *Elomeryx*. The prominent facial crest (masseteric ridge) extends horizontally from the middle part of the jugal to the infra-orbital foramen. It displays a long insertion for the masseter muscle anterior to the orbit. This condition in *Elomeryx* can be regarded as plesiomorphic within Anthracotheriidae (Lihoreau et al., 2004). The upper margin of the orbits is situated slightly above the flat cranial roof. The orbits are widely open posteriorly and the brain case is globular and short. The zygomatic arch is somewhat ventrally depressed behind the orbit, whereas it is horizontal in *E. armatus* (Fig. 2A). The zygomatic process of the squamosal is anteriorly thin. It extends

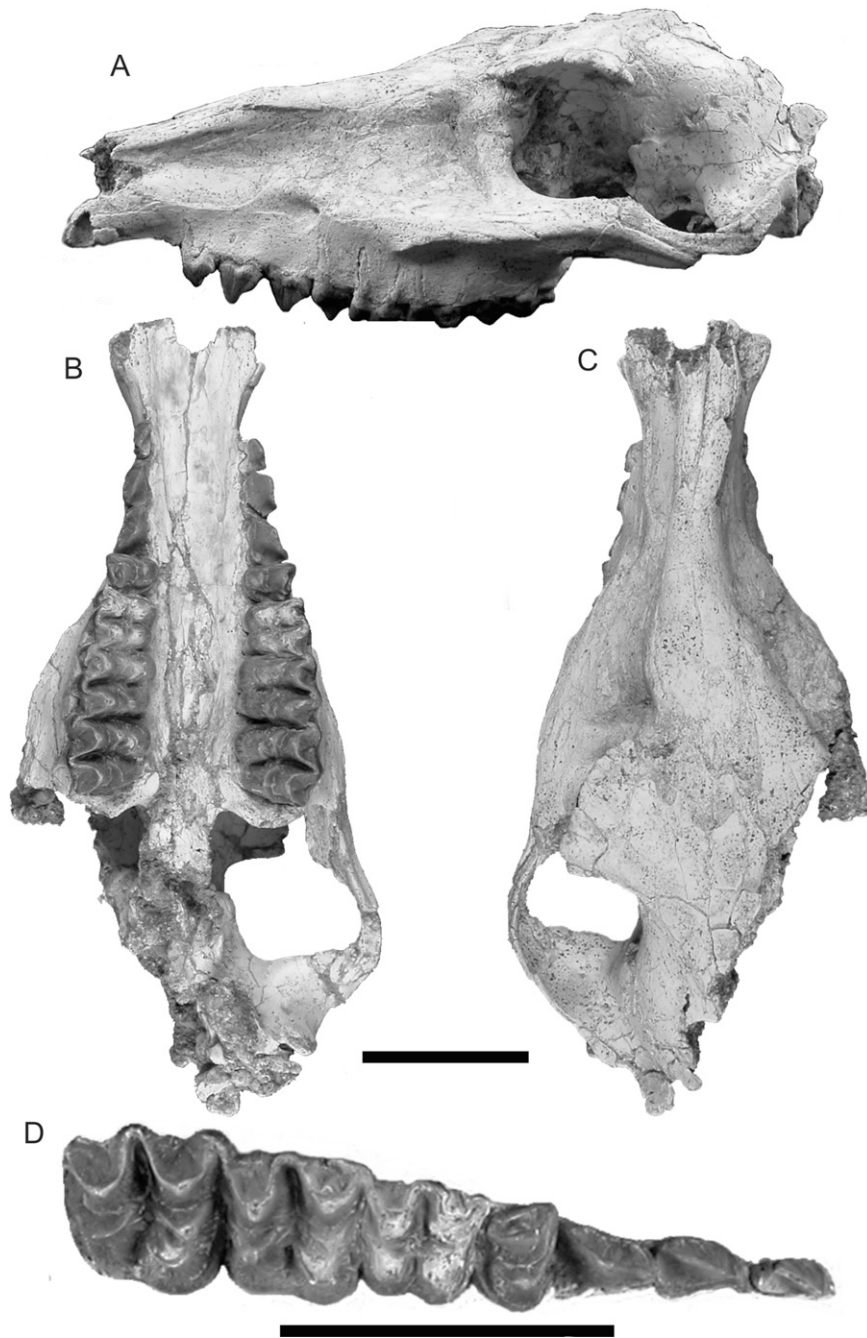


FIGURE 2. *Elomeryx crispus*, MOI3.001. Skull in lateral (A), ventral (B), and dorsal (C) views; right tooth row in occlusal view (D). Scale bars equal 50 mm.

backward and laterally over the auditory meatus where its posterior border raises and joins the temporal crest that separates the occipital from the parietal bones, as in *E. armatus*. The external auditory meatus opens dorso-laterally. It is horizontal and relatively short compared to that of advanced Bothriodontinae (Lihoreau et al., 2004).

In ventral view, both tooth rows are nearly straight and parallel. The main palatine foramina are situated at the level of the distal margin of P2 as in specimens of *E. borbonicus* (Geais, 1934), but they are at the level of the mesial margin of P4 in *E. armatus*. These foramina are anteriorly prolonged by straight grooves (sulci palatini) that reach the anterior end of the

maxillae. The latter markedly widen at the level of the canine sockets. The suture between the palatines and the maxillae are visible at the level of the anterior roots of M2. Although the palatine processes of the maxillae are partially broken away, it appears that internal choanae open well behind the M3 as in all other species of *Elomeryx*. This differs from the condition in the contemporaneous Bothriodontinae *Aepinacodon* and *Bothriodon* (MacDonald, 1956; Lihoreau, 2003). The anterior end of the facial crest is visible at M1 level and runs almost parallel to the tooth row before it widens at the jugal-squamosal junction. The preserved glenoid cavity is large, flat to slightly convex, and situated about 10 mm above the tooth row level.

Its anterior border is perpendicular to the longitudinal axis of the skull instead of being slightly oblique as in *E. armatus*. Its articular surface extends upon the front side of the postglenoid process. The latter is broad, ventrally short and projects backward. Only a small part of the left occipital condyle is preserved but it does not preserve the shape of the foramen magnum.

Dentition—The small canine alveoli suggest that the individual was a female, *Elomeryx* being known to display sexually dimorphic upper canines (Geais, 1934; Hellmund, 1991) (Fig. 2D). The diastema between C-P1 is short (25 mm on the right side, 30 mm on the left side). The premolars are arranged in a continuous row as in all species of *Elomeryx* except *E. borbonicus* where there is a short diastema between P1 and P2 (Geais, 1934). The first three premolars show the same simple occlusal pattern with a main laterally compressed triangular cusp from which two crests reach the mesial and distal margins of each tooth. The size (length and width) of premolars increases from P1 to P3 (Table 1). The P2 is a larger version of P1; both teeth have two roots and are mesiodistally elongated with the apex of the cusp above the mesial root. The P3 has a relatively enlarged distolingual occlusal basin and is three-rooted. The P4 shows the common bicuspidate occlusal pattern of anthracotheriids, both cusps being crescentic with a mesial and a distal crest. The distal crest of the lingual cusp does not reach the distal border of the tooth, as in all known species of *Elomeryx*. The three first premolars of MOI3.001 are markedly less massive than

those of *E. borbonicus* and *E. armatus* (Table 1) in having a less well-developed distolingual corner. They are less obliquely oriented in comparison with the longitudinal axis of the tooth row. The upper molars also increase in size from M1 to M3. They are typically pentacuspitate with a small paracone retained even in strongly worn teeth (Ducrocq and Lihoreau, 2006). The protocone is just slightly larger than the paracone (a plesiomorphic condition compared to derived bothriodontines in which the protocone is enlarged; Ducrocq and Lihoreau, 2006) and displays one mesial crest (preprotocrista) and two distal ones (postprotocristae). The preprotocrista is clearly distinct from the preparacristule (Fig. 3). The postparacristule reaches the transverse valley. The metacornules of M1-M3 display three crests, the mesiolingual one also being observed in *E. cluai* and *E. armatus* but never in *E. borbonicus* (Fig. 3; Hellmund, 1991). The mesiolabial crest of the metacornule reaches the more distal crest of the protocone and consequently hinders the transverse valley (Fig. 3). The condition seen in MOI3.001 is that of most species of *Elomeryx*, except in *E. borbonicus* where the transverse valley is continuous from the mesostyle to the lingual margin (Hellmund, 1991).

Discussion

MOI3.001 displays a combination of dental characters including a small protocone, a postparacristule that reaches the

TABLE 1. Dental measurements of the species of *Elomeryx* (in mm).

	Tooth	n	L	W
MOI3.001	P1	1	9.7;10	5.4;5.3
<i>E. borbonicus</i> (St André, Hellmund, 1991)		11	9.5-13.2	5.1-8.9
<i>E. armatus</i> (Big Badland, Mc Donald, 1956)		5	8.5-15.7	5.8-6.5
<i>E. cluai</i> (Tarrega, Hellmund, 1991)		4	6.8-11.2	3.8-7.5
MOI3.001	P2	1	14.5;13.2	8.6;9
<i>E. borbonicus</i> (St André, Hellmund, 1991)		7	14-15.7	9.1-12.1
<i>E. armatus</i> (Big Badland, Mc Donald, 1956)		9	13.3-17.4	9.5-12.1
<i>E. cluai</i> (Tarrega, Hellmund, 1991)		4	9.5-12.8	5.3-6.9
MOI3.001	P3	1	14.6;15	11/-
<i>E. crispus</i> (Detan)		1	11.2	10.6
<i>E. crispus</i> (Hampstead bed, NHM)		2	13.5-14.5	11.5-12.5
<i>E. borbonicus</i> (St André, Hellmund, 1991)		10	15.7-17.7	10.6-13.1
<i>E. armatus</i> (Big Badland, Mc Donald, 1956)		11	17.5-20.7	14.5-18.2
<i>E. cluai</i> (Tarrega, Hellmund, 1991)		5	11.8-13.8	8-9.6
MOI3.001	P4	1	13;11.5	16;15.9
<i>E. crispus</i> (Detan)		1	10.2	14
<i>E. crispus</i> (Möhren 13, Hellmund, 1991)		46	8.9-12.3	11.6-14.9
<i>E. crispus</i> (Hampstead bed, Hellmund, 1991)		7	9.4-11.4	12.9-15.8
<i>E. borbonicus</i> (St André, Hellmund, 1991)		19	11.2-15.1	14.9-17.7
<i>E. armatus</i> (Big Badland, Mc Donald, 1956)		11	12.9-15.5	17.3-22.5
<i>E. cluai</i> (Tarrega, Hellmund, 1991)		5	8.0-11.2	11.2-13.6
MOI3.001	M1	1	19.5;18	18;18.6
<i>E. crispus</i> (Detan)		1	13.3	14.6
<i>E. crispus</i> (Hampstead bed, NHM)		2	14.8-18	16.9-20
<i>E. borbonicus</i> (St André, Hellmund, 1991)		14	15.1-18.5	16.5-18.8
<i>E. armatus</i> (Big Badland, MacDonald, 1956)		10	17.4-21.4	20.1-24.8
<i>E. cluai</i> (Tarrega, Hellmund, 1991)		6	10.9-13.3	12.4-15.0
MOI3.001	M2	1	22;22.6	23.4;22.2
<i>E. crispus</i> (Detan)		1	15.7	18.5
<i>E. crispus</i> (Hampstead bed, NHM)		2	21	22-23.5
<i>E. borbonicus</i> (St André, Hellmund, 1991)		14	18.0-24.8	17.9-24.3
<i>E. armatus</i> (Big Badland, MacDonald, 1956)		12	23.8-28.3	25.7-29.2
<i>E. cluai</i> (Tarrega, Hellmund, 1991)		6	13.2-17.4	14.7-18.6
MOI3.001	M3	1	25.6;24.5	24.2;25.6
<i>E. crispus</i> (Detan)		1	17.2	20.4
<i>E. crispus</i> (Hampstead bed, NHM)		1	23.7	25.7
<i>E. borbonicus</i> (St André, Hellmund, 1991)		14	22.3-26.9	22.2-27.7
<i>E. armatus</i> (Big Badland, Mc Donald, 1956)		12	27.6-32.4	29.3-34.9
<i>E. cluai</i> (Tarrega, Hellmund, 1991)		3	14.1-15.7	15.5-17.2

Abbreviations: L, length; W, width; NHM, Natural History Museum, London. Measurements for MOI3.001 correspond to right and left teeth; for the others, given measurements are min-max values.

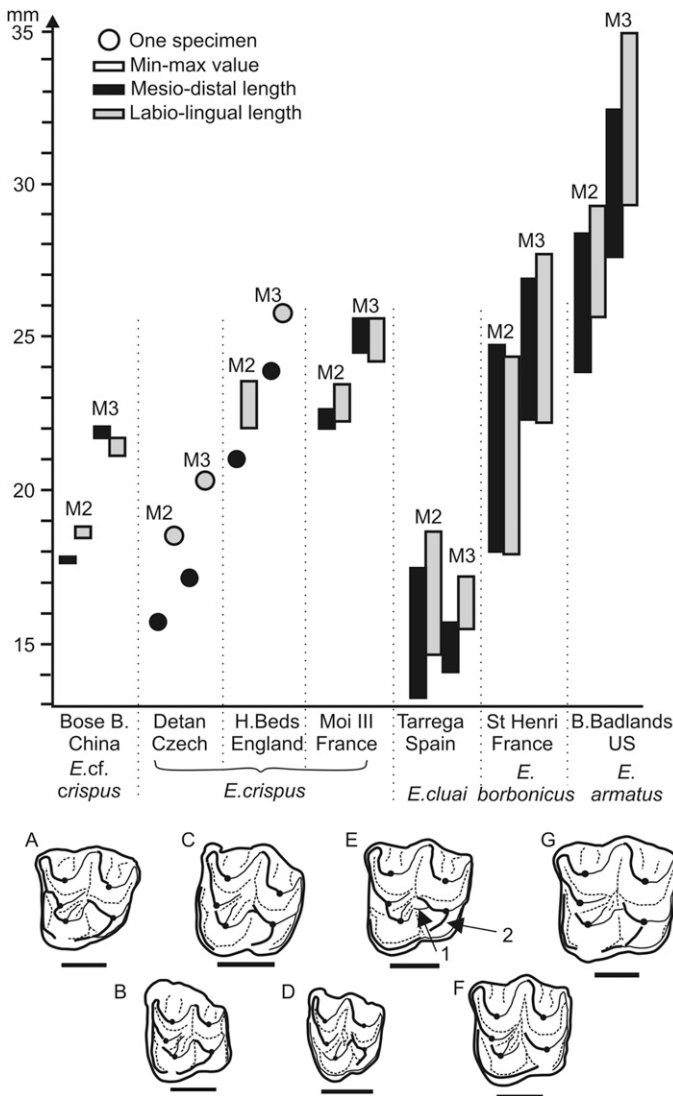


FIGURE 3. Biometrical and morphological comparisons between M2-3 of *Elomeryx* species. A–G, occlusal morphologies of left M2 of species of *Elomeryx*. A, *E. cf. crispus* from Bose basin, China. B, *E. crispus* from Detan Dverce, Czech Republic. C, *E. crispus* from Hampstead beds, England. D, *E. crispus* from Moissac, France. E, *E. cluiai* from Tarrega, Spain. F, *E. borbonicus* from Saint Henri, France. G, *E. armatus* from the Big Badland, USA. Scale bars equal 10 mm. Arrows indicate main differences between occlusal morphologies of *E. crispus* and *E. borbonicus*: 1—the lingual postprotocrista joins the premetacristule and blocks the transverse valley; 2—a marked crest on lingual border of metacristule. Measurements are from Table 1 except those from the Bose Basin (Ducrocq and Lihoreau, 2006).

transverse valley, and a preprotocrista distinct from the preparacristule, which is typical of the bothriodontine anthracotheriid *Elomeryx* from the late Eocene to early Miocene of Eurasia and North America (Ducrocq and Lihoreau, 2006).

The specimen from Moissac III is markedly smaller than *E. armatus* (Table 1; Fig. 3; early Oligocene, North America; MacDonald, 1956; Kron and Manning, 1998). Moreover, it differs from *E. armatus* by several cranial characters, such as nasal-lacrimal contact, the posterior position of the infraorbital foramen, the anterior position of the main palatine foramina, and the shape of the zygomatic arch. The size and skull anatomy of MOI3.001 are very close to those of *E. borbonicus*, notably for

the positions of infraorbital and palatine foramina. On the other hand, it can be distinguished from *E. borbonicus* (late Oligocene-early Miocene, Europe) by the presence of a mesiolingual crest on the upper molar metaconule and a closed transverse valley which never occurs in *E. borbonicus* (Geais, 1934; Hellmund, 1991:figs. 2D, 3). MOI3.001 displays teeth similar in size with those of both *E. crispus* from Hampstead Beds and *E. borbonicus*. The older *Elomeryx crispus* (La Débruge, France, MP 18; Bonis, 1964), Detan Dverce, Czech Republic (MP 21; Fejfar, 1987; Hellmund, 1991), and Bose basin, China (late Eocene; Ducrocq and Lihoreau, 2006) are slightly smaller than MOI3.001 (Fig. 3). Furthermore, the Chinese specimen also displays a hypopholid on lower molars that following Hellmund (1991) is primitive for the genus. Although the age of Detan Dverce is unclear either biochronologically dated from the base of the Oligocene (MP21) or radiometrically dated from ca. 37.7 Ma (late Eocene; K/Ar on biotite; Fejfar, 1987), *E. crispus* from the Czech Republic is older than *E. crispus* from the Hampstead Beds and Möhren 13 (MP22). This species might have been characterized by an increase in size through time. *Elomeryx cluiai* is a much smaller species known from the early Oligocene (MP23) of Northeastern Spain (Fig. 3; Agustí et al., 1987) that is considered as endemic of that area.

Since the *E. crispus* diagnosis is based on dental morphology, we can confidently refer the specimen of Moissac III to *E. crispus*. This corresponds to a large specimen, contemporaneous or younger than other known large *E. crispus* from the Hampstead Beds and Möhren 13 (MP22). The Eurasian *Elomeryx* differs from *E. armatus* by the foramina positions, lacrimal and glenoid morphologies. Therefore, the skull from Moissac III further supports closer phylogenetic relationships between both Eurasian species than between *E. crispus* and *E. armatus*.

Order PERISSODACTYLA Owen, 1848
Superfamily RHINOCEROTOIDEA Owen, 1845
Family RHINOCEROTIDAE Owen, 1845
Subfamily RHINOCEROTINAE Owen, 1845
Genus *PROTACERATHERIUM* Abel, 1910

Type Species—*Protaceratherium minutum* (Cuvier, 1822), early Miocene of Europe and central Asia (Kazakhstan).

Other Species Referred to the Genus—*P. albigense* (Roman, 1912), late early and late Oligocene of Europe.

PROTACERATHERIUM ALBIGENSE (Roman, 1912)
(Fig. 4A–D)

Rhinoceros minutus Duvernoy, 1853:90–91, plate 8, figs. 6, 7.
Acerotherium albigense nov. sp. Roman, 1912:27–36, 80, 83–84, figs. 6–8, pls. 3–4.

Aceratherium albigense Roman: Kretzoi, 1940:87–98.

Aceratherium albigense Roman: Richard, 1948:152, 175.

Aceratherium minutum (Duvernoy): Richard, 1948:163.

Protaceratherium albigense (Roman): Hugueney and Guérin, 1981:52–71.

Protaceratherium albigense (Roman): Prothero et al., 1989:327.

Protaceratherium albigense (Roman): Heissig, 1989:405–406, fig. 21.4.

Protaceratherium albigense (Roman): Hugueney, 1997:426, tab. 4.

Protaceratherium albigense (Roman): Uhlir, 1999:72–74, figs. 53, 54.

Protaceratherium albigense (Roman): Antoine et al. 2003a:fig.4.

Protaceratherium albigense (Roman): Astruc et al., 2003:640.

Aceratherium minutum (Duvernoy): Astruc et al., 2003:640.

Protaceratherium albigense (Roman): Saraç, 2003:509–517, figs. 2–5.

Holotype—Anterior part of an adult skull, with left and right P1–M3, stored in the Muséum Toulouse Lautrec (Albi, France)

and labelled as 'Caraven-Cachin collection, Lautier inventory n°2'. This specimen, supposedly lost (Uhlig, 1999:72) was recently recovered by Bernard Ménouret (B. Ménouret, pers. comm., 2005). In addition, a good cast of the holotype (FSL 9809), with the left P1–M3 series, is stored in the collections of the Université Claude-Bernard, Lyon-Villeurbanne, France.

Locality and Type Horizon—'Métairie Haute,' La Sauzière Saint-Jean, between Gaillac and Montauban, Tarn Department, SW France; early late Oligocene, most likely MP25–26 reference levels according to the local biostratigraphic context (Astruc et al., 2003).

New Material—MOI3.002, complete adult skull, slightly crushed, with left and right P1–M3 series and alveoli of both I1s and right ?DI2 from Moissac III locality, SW France (early late Oligocene). Permanent repository of the original is at the University of Poitiers. Casts are available at the Muséum d'Histoire

Naturelle in Toulouse (MHNT) and at the Musée d'Histoire Naturelle in Montauban.

Stratigraphy and Age—Late early Oligocene to middle late Oligocene, MP 24–28 reference levels (Antoine et al., 2003a; Astruc et al., 2003; Saraç, 2003) in Western and Southeastern Europe (mainly France, ?Spain, Hungary, and Turkish Thrace; Saraç, 2003).

Differential Diagnosis—Differs from the type species including *P. tagicus* (Roman, 1907) and *P. betpakdalense* (Borissiak, 1938) by the short, acute, and triangular hornless nasal bones; the short nasal notch; the occipital face inclined backwards; the weakly developed nuchal tubercle and posttympanic process; the long premaxillae; the shape and relation of the frontoparietal crests; the wrinkled enamel; the roots separate and divergent; the constant presence of a labial cingulum on the upper cheek teeth; the narrow P1; the complete protoloph on P2;

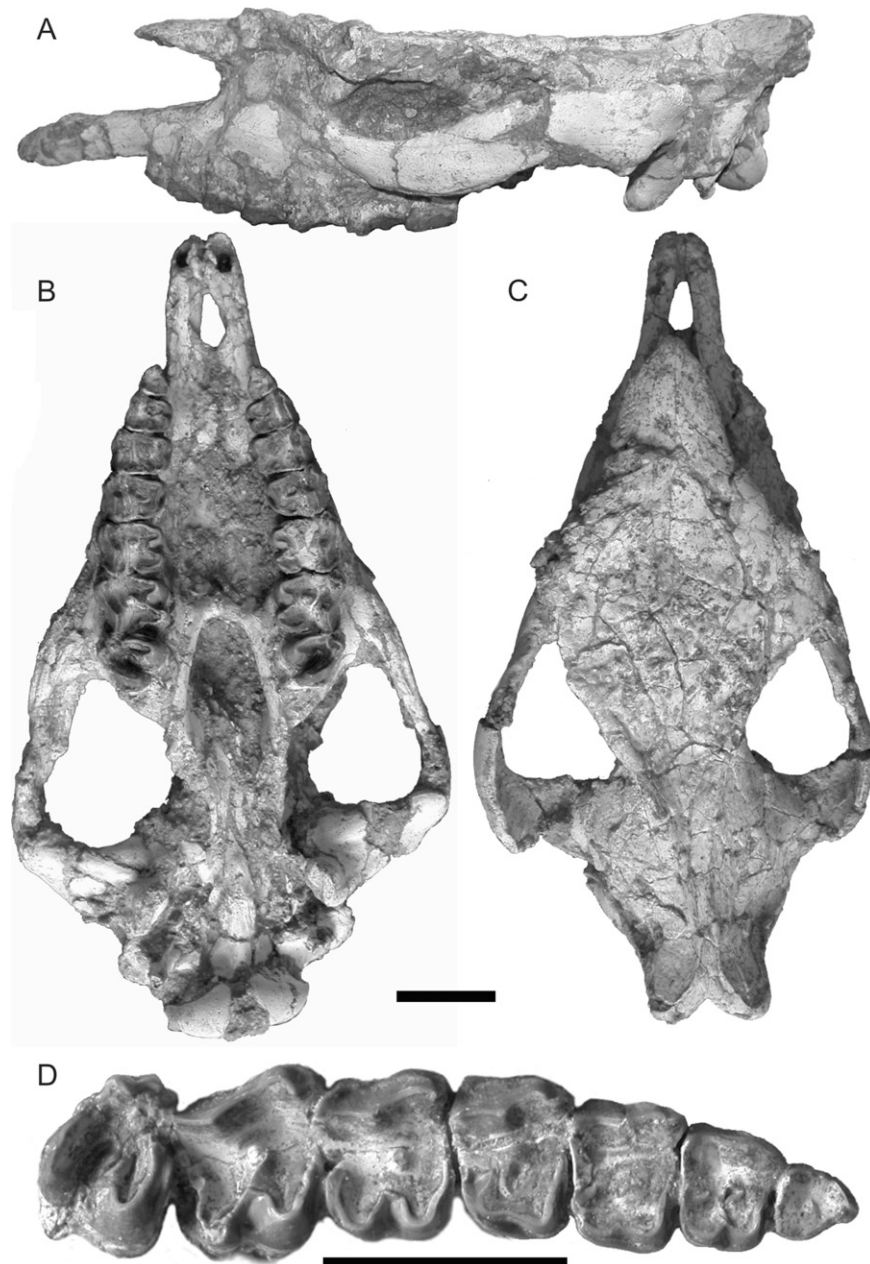


FIGURE 4. *Protaceratherium albigenae*, MOI3.002. Skull in lateral (A), ventral (B), and dorsal (C) views; right tooth row in occlusal view (D). Scale bars equal 50 mm.

the junction of the protocone and the hypocone forming a lingual bridge on P2; the P4 tapering backwards; the lack of an antecrochet on P4 and of a metacone fold on M1–2; the twisted ectoloph on M1–2 (oblique and concave distal part); the long metaloph on M2; the presence of a twinned distolabial cingulum, and a distolingual vertical groove on M3.

Description

Skull—MOI3.002 is a complete adult skull, slightly crushed (i.e., laterally twisted) (Fig. 4A–C, Table 2). It is small and brachycephalic (width/length ratio = 0.54). The premaxillae are complete and intact. They are long and narrow with respect to the size of the skull (length = 80 mm). The incisive foramina are long, narrow, and oval. The nasal bones are short and triangular, with a sharp and acute tip. They do not display any lateral apophysis on their ventral edge. The infraorbital foramen is open above the P2–P3 limit, whereas the short nasal notch ends above the posterior part of P3. The anterior border of the orbit is above the middle of M1. There is neither nasal septum ossification nor lateral projection of the orbit. The jugal/squamosal suture is sigmoid and smooth. The postorbital process area (on the frontal) and the lacrimal process area are badly damaged on both sides. The frontal bones are wide with respect to the zygomatic bones (zygomatic width/frontal width ratio = 1.43). The base of the zygomatic process of the maxilla is high: it begins several centimeters above the neck of M1–3. The zygomatic arch is high (nearly reaching the level of the cranial roof) and fairly developed. It forms a thin strip, with a small postorbital process on the squamosal. The dorsal profile of the skull is flat. The relations between the sphenorbital foramen and the foramen rotundum, i.e. distinct or fused (Antoine, 2002:87–88), are not observable. The temporal and nuchal crests are fused on their dorsal half; distally, the area between both crests is flat (Antoine, 2002:88). The external auditory pseudomeatus is partially closed. The occipital side is inclined backward: the occipital condyle is anterior to the tip of the occipital crest. The nuchal tubercle is well developed, which still deepens the large axial fossa lying just underneath the occipital crest. The tooth row does not reach the posterior half of the skull (Table 2; Antoine, 2002:91). On both sides, the pterygoid hamulus is broken. The nasal bones are straight and lacking any vascular print or domed structure indicating the presence of nasal horns. The nasal bones

are totally separate from one another by a shallow median groove. There is no evidence for any frontal horn either. The fronto-parietal crests are sharp and salient. They are joining in their posterior halves, only separated by a narrow groove (ca. 3 mm wide). The occipital crest is strongly concave, deeply forked, and very narrow (ca. 90 mm). The brain case and the occipital side are very small.

In palatine view, the anterior end of the zygomatic process of the maxilla progressively and widely diverges from the curvature of the tooth row. The palate is narrow (Table 2). The palatine fossa reaches mid-length of the M2 and the vomer is broken. The glenoid cavity is flat and it forms a smooth semi-cylinder in lateral view. The postglenoid process is short, thick and transversely narrow. The articular surface of the latter is sigmoid in cross section, with a convex anterior half. A sagittal crest runs all along the basilar process of the basioccipital. The posterior side of the zygomatic process of the squamosal is flat. It is about 45° from the sagittal axis. The posttympanic process is curved forward and very short, whereas the paroccipital process is long, straight, thin, and well developed; their bases are widely separated. The foramen magnum is filled with sediment, but it seems to have a subtriangular outline. A median transverse ridge runs all over the occipital condyle, but there is no axial truncation on the condyle.

Dentition—The upper dental formula is 1I–0C–4P–3M (Fig. 4D). Both premaxillae display a large but shallow rostral alveolus for an obligate I1 (length = 22 mm; width = 14 mm; depth = ca. 18 mm for the un-eroded left alveolus; the right one being fairly eroded, which impedes taking measurements). A smaller and shallower pit is visible along the sharp margin of the right premaxilla about 10 mm distally to the I1 alveolus. It may correspond to a supplemental alveolus for a tooth lost a long time prior to death, which makes us interpret it with some confidence as a DI2. The 4 cm-long diastema lacks any canine or alveolus for it. The premolar series is rather long when compared to the molar series (LP3–4/LM1–3 ratio = 0.53; Table 3). In Rhinocerotidae, values are comprised between 0.29 and 0.62 (Antoine, 2002:122, tab. 4). Most teeth are very worn, which somewhat precludes detailed observation. However, the dental structures are very simple and there are no secondary enamel folds or cement on the crowns. The enamel is thin and wrinkled. The crowns are low (brachydont teeth) and the roots are long, distinct and divergent (at least for the premolars).

The protoloph of the upper premolars lacks any antecrochet or anterior constriction, whereas both structures are present on the upper molars. The crochet, the crista, and the medifossette, absent at this late stage of wear, may have vanished due to wear; if present, they were restricted to the top of the crown. The paracone fold is constant and thick on P2–M3. The parastyle is sagittally oriented and the metacone fold is absent from the whole series.

The premolars are semi-molariform (sensu Heissig, 1969), with a lingual bridge. This bridge is narrow on P2 (probably appearing at late stages of wear) and wide on P3–4. There is a continuous labial cingulum on the whole premolar series, oblique with respect to the cervix (closer to the latter mesially). In lingual view, this cingulum is notched in its medial part on P2, while it is straight on P3–4. The lingual cingulum is always present: it is strong and continuous on P1–4. On P2–4 the remnant postfossette is small and triangular and lingually displaced. P1 is triangular in occlusal view, much narrower than P2, and much more worn; the mesiolingual valley is open, in spite of a thick lingual cingulum. The parastyle is well developed and curved inward. On P2, the protocone is less developed than the hypocone. The protoloph is thin but continuous and widely connected with the ectoloph. The hypocone is posterior to the metacone on P2–4. There is no pseudometaloph on P3 (sensu Antoine, 2002). The inner valley is small and triangular and the protoloph has no anterior constriction

TABLE 2. Cranial dimensions (in mm) of *Protaceratherium albigenae* (Roman, 1912), MOI3.002.

Measurements (mm)	MOI3.002
Length occipital crest/tip of nasals	(375)
Length occipital crest/tip of premaxilla	450
Length occipital crest/caudal end of M3	210
Length caudal end of M3/tip of premaxilla	240
Length occipital condyle/front of orbit	(247)
Length occipital condyle/tip of premaxilla	(423)
Length of nasal notch	(85) – 67*
Maximum zygomatic width	(243)
Maximum frontal width	(170)
Occipital crest width	(est. 90)
Occipital condyle width	80
Foramen magnum width	25
Palate width (at P1 level)	43
Palate width (at P4-M1 level)	56
Palate width (at M3 level)	59
Occipital face height	(101)

*The only measurement that can be compared with the type specimen of La Sauzière Saint-Jean is the length of the nasal notch (85 mm in MOI3.002; 67 mm in the type). Dimensions between brackets are estimated, due to distortion. Measurements follow the protocols of Guérin (1980) and Antoine (2002).

TABLE 3. Compared tooth row dimensions (in mm) of *Protaceratherium albigense* (Roman, 1912).

	Moissac (MOI3.002)	La Sauzière (FSL, cast of the type)	La Parisienne (FSL 9600)	Saint-Henri (FSL 8486)	Saint-Henri (FSL 8543)
Length of P1-M3	171/171	184	163	165/	—
Length of P1-P4	87/87	90	83	86/	—
Length of P3-P4	47/47	50.5	49	47/	48/
Length of M1-M3	90/(88)	94	87	87/92	91/
L _{P3-P4} /L _{M1-M3}	0.53	0.54	0.56	0.53	0.53

Right/left values when known. For comparison with other Rhinocerotidae, see Antoine (2002, tab. 4, p. 122).

on P2–4. P2 and P3 are quadrate, while the P4 tapers distally, with a metaloph shorter than the protoloph (Table 4).

There is a continuous labial cingulum on M1–2, running close to the cervix; by contrast, the labial cingulum is restricted to a small anterior spur, and to twinned distolabial tubercles on both M3. The lingual cingulum is restricted to small tubercles at the end of the median valley on M1–3. The metastyle of M1–2 is worn. The metaloph is long and the distal part of the ectoloph is concave on M1–2. The latter is much more oblique with respect to the dorso-ventral axis of the tooth than its anterior part. The metaloph is constricted on M1–2: there is a mesiolingual groove on the hypocone of M1–2. There is no cristella (sensu Antoine, 2002) and the distal cingulum is not observable on M1–2 due to wear. The central structures (crochet, crista) and the postfossette are totally worn on M1–2. There is no lingual groove on the protocone of M2. The mesostyle is absent on both M1 and M2, at least at this stage of wear. M3 has a trapezoidal occlusal outline, though the ectoloph and metaloph are fused. The protoloph is transverse and straight. There is a deep posterior groove on the ectometaloph, probably homologous to a vestigial metaloph (character 138 in Antoine, 2002).

Discussion

Numerous cranial and dental features of the skull MOI3.002 (lozenge-like dorsal outline of the skull; occipital side slanted backwards; obvious absence of I3–C; presence of an antecrochet on the upper molars; presence of a constricted protocone on M1–2; M3 with the ectoloph and the metaloph fused into an ectometaloph; Antoine et al., 2003b) point to Rhinocerotidae and impede referring this specimen to either Hyracodontidae (*Eggysodon*) or Amyndontidae (*Cadurcotherium*), which are also documented in the Oligocene of Europe.

Five rhinocerotid genera occur in the European Oligocene (Fig. 6; Uhlig, 1999; Antoine et al., 2003a, 2006): *Epiaceratherium* Abel, 1910, with *E. bolcense* Dal Piaz, 1930 and *E. magnum* Uhlig, 1999 (early Oligocene); *Ronzotherium* Aymard, 1854, with *R. velaunum* Aymard, 1854, *R. filholi* (Osborn, 1900), and *R. romani* Kretzoi, 1940 (Oligocene for the genus as a whole); *Protaceratherium* Abel, 1910, with *P. albigense* (Roman, 1912) (late early and late Oligocene); *Mesaceratherium* Heissig, 1969, with *M. paulhiacense* (Richard, 1937) (late Oligocene and early Miocene), and *Diaceratherium* Dietrich, 1931, with *D. lamilloquense* Michel, 1983 and *D. lemanense* (Pomel, 1853) (late Oligocene and earliest Miocene).

MOI3.002 differs from all of these taxa except *Protaceratherium albigense* by having short nasals, the external auditory pseudomeatus partially closed, the occipital wall inclined backward, a weakly developed nuchal tubercle, a deeply forked occipital crest, a subtriangular foramen magnum, and no I2. Additionally, MOI3.002 displays long premaxillae, wrinkled enamel and separate roots on the cheek teeth, a narrow P1, secondary folds (crochet, crista, and medifossette) absent or restricted to the upper part of the crown and a continuous labial cingulum on the upper premolars, a continuous protoloph on P2, a lingual bridge on P2–4, no antecrochet on the P4 which tapers backward,

a long metaloph and a constricted hypocone, but no metacone fold on M1–2, a constricted protocone, a twinned distolabial cingulum, and a posterior groove on the ectometaloph of M3. All of these characters appear in the type specimen of *P. albigense*, a fragmentary skull from La Sauzière Saint-Jean (SW France), and its hypodigm (Tables 3–4), either from Europe (Roman, 1912; Huguency and Guérin, 1981) or Turkish Thrace (Saraç, 2003:512, fig. 2), and make it distinct from *P. minutum* (early Miocene of Europe and central Asia; Antoine et al., 2000).

The only noticeable differences with the specimens of *P. albigense* described so far concern the protocone of P2 — as developed as the hypocone, whereas it is less developed in other P2 referred to *P. albigense* — and the smaller size of the P4 in MOI3.002 (Table 4). Therefore, this skull can be referred to *P. albigense* (Roman, 1912) with confidence.

BIOSTRATIGRAPHICAL IMPLICATIONS

A right upper molar of a theridomyid rodent (MOI3.003) referred to *Issiodoromys* has also been recovered from the lens at Moissac III. The specimen has been damaged during excavation and the crown is incomplete (Fig. 5A–C). However, the thickening of the root and the length of the sinus associated with the remnant of a syncline II (Fig. 5A, B) illustrate the advanced stage of wear of an adult. The crown height is nearly equivalent to the tooth length, and comparisons with specimens of the same stage of wear show that MOI3.003 displays a crown height and a wear occlusal pattern equivalent with those of *I. pauffiensis* Vianey-Liaud, 1976 (cf. MPF13 from Mas de Pauffié; Fig. 5F, G). The crown height of *I. minor* (Schlosser, 1884) is shallower (cf. GAR877 from Garouillas; Fig. 5D, E). *Issiodoromys minor* from Garouillas and *I. pauffiensis* from Mas de Pauffié are respectively known in Europe in MP25 and in MP26 (Vianey-Liaud, 1976; Schmidt-Kittler and Vianey-Liaud, 1987). Until more material is collected and taking into account that MOI3.003 is badly damaged, we consider that this upper molar can be attributed to *I. cf. pauffiensis*. The biochronological age of Moissac III likely corresponds to the MP25–26 reference levels, which also matches the stratigraphic occurrence of *P. albigense* (Fig. 6). These reference levels correspond to the beginning of the late Oligocene (Luterbacher et al. 2004).

Until this discovery, *Elomeryx crispus* was known from La Débruge (MP18) up to Möhren 13 (MP22), while the endemic Spanish species *E. cluai* is restricted to the MP23 locality of Tarrega (Hellmund, 1991). The more derived species *E. borbonicus* FAD (First Appearance Datum) is known from St. Henri (MP26; Astruc et al., 2003) up to Pyrimont-Challonges (MN1; Hellmund, 1991). Even though the *Elomeryx* fossil record is virtually unknown between MP22 and MP26, with the notable exception of *E. cluai* (MP23), *Elomeryx borbonicus* is supposed to have originated from a stock of *E. crispus* (Hellmund, 1991; Lihoreau, 2003; Lihoreau and Ducrocq, 2007). The age of Moissac III is constrained near MP25–26 by the *Issiodoromys* tooth (Fig. 6). *Elomeryx crispus* from Moissac III is therefore the youngest and the most complete specimen known for the species. The remains described here fill a part of the MP22–MP26

TABLE 4. Dental measurements (in mm) of the teeth of *Protaceratherium albigense* (Roman, 1912) from its main localities.

	Tooth	n	L	Mes. W	Dist. W	H
MOI3.002 (r/l)	P1	1	19.0/20.0	12.5/13.5	15.5/16.5	5.5/5.0
La Sauzière (FSL)		1	17.5	10.0	—	—
La Parisienne (FSL)		1	18.0	—	—	—
Saint-Henri (FSL)		1	17.0	—	14.0	—
Saint-Menoux (MNHL)		1	19.0	14.5	16.5	8.0
MOI3.002	P2	1	22.5/22.5	24.5/25.0	26/26	11.0/12.0
La Sauzière (FSL)		2	25.0	27.0	28.0	19.0
La Parisienne (FSL)		1	21.0	—	—	—
Saint-Henri (FSL)		4	22.9 [21-26]	25.9 [22-28]	26.5 [23-28]	16.0
Saint-Menoux (MNHL)		1	24.0	27.0	26.0	17.0
Dohlan (Saraç, 2003)		1	19.0	23.0	—	—
MOI3.002 (r/l)	P3		24.5/24.0	31.0/31.5	30.5/30.5	12.0/12.5
La Sauzière (FSL)		2	25.8 [25.5-26]	33 [32.5-33.5]	32.5	18.5 [15-22]
La Parisienne (FSL 9600)		1	23.5	29.0	26.0	—
Saint-Henri (FSL)		5	25 [22-27.5]	32 [27-34]	31.5 [27-33]	21.5 [17-26]
Saint-Menoux (MNHL)		1	28.0	33.0	30.5	18.0
Dohlan (Saraç, 2003)		1	22.0	—	—	—
MOI3.002 (r/l)	P4		25.5/25.5	33.0/32.0	31.5/30.5	14.0/15.0
La Sauzière (FSL)		2	27.8 [27.5-28]	35.3 [35-35.5]	35.5 [35-36]	20.5 [17-24]
La Parisienne (FSL)		1	26.0	32.5	(28.0)	—
Saint-Henri (FSL)		2	26.0	37.0	34.0	—
Saint-Menoux (MNHL)		1	29.5	34.0	32.0	20.0
Dohlan (Saraç, 2003)		1	23.0	—	—	—
Laspeyres (MHNT)		2	25.3 [24.5-26]	32.5	29 [28.5-29.5]	16.5 [15-18]
MOI3.002 (r/l)	M1	1	(29.0)/31.0	36.0/37.5	33.5/34.0	11.0/11.0
La Sauzière (FSL)		2	35.3 [34-36.5]	35.5	34.5	17 [14-20]
La Parisienne (FSL)		1	33.0	(32.0)	28.0	—
Saint-Henri (FSL)		3	30.3 [28-32]	35.5 [31-38]	33.2 [30-35]	—
Saint-Menoux (MNHL)		1	—	35.0	—	15.0
Dohlan (Saraç, 2003)		1	23.0	32.0	—	—
MOI3.002 (r/l)	M2	1	(31.5)/34.5	38.0/38.0	32.5/32.5	15.5/14.5
La Sauzière (FSL)		1	(32.0)	40.0	(39.0)	28.0
La Parisienne (FSL)		1	35.0	34.0	28.0	—
Saint-Henri (FSL)		5	34 [32-35.5]	38.2 [33-41]	33 [29-35]	8 [4-12]
Dohlan (Saraç, 2003)		1	33.0	34.5	—	—
Laspeyres (MHNT)		1	35.5	35.0	—	24.0
MOI3.002 (r/l)	M3	1	28.5/28.0	34.5/33.5	36.0/35.0	18.5/17.5
La Sauzière (FSL)		1	32.0	37.0	40.0	—
La Parisienne (FSL)		1	27.0	(31.0)	34.0	—
Saint-Henri (FSL)		5	30.2 [28-32]	35.1 [33-37]	38.4 [37.5-40]	16.0
Dohlan (Saraç, 2003)		1	30.5	34.0	—	—
Laspeyres (MHNT)		2	33.3 [33-33.5]	37.8 [37.5-38]	40.3 [39.5-41]	21 [16-26]

Abbreviations: L, length; Mes. W, mesial width; Dist. W, distal width; H, crown height; (r/l), right and left teeth; (), estimation; [], range value. FSL, Université Lyon-Villeurbanne; MNHL, Muséum d'Histoire Naturelle, Lyon; MHNT, Muséum d'Histoire Naturelle, Toulouse.

gap between *E. crispus* and *E. borbonicus* (Ducrocq and Lihoreau, 2006; Lihoreau and Ducrocq, 2007). MOI3-001, the first known complete skull of *E. crispus*, allows us to determine evolutionary trends on the skull of *Elomeryx* between the late Eocene and the early late Oligocene. However, the morphology of the skull is similar in size and proportions (position of foramina) with a female of *E. borbonicus* from MP26. Differences between the specimen from Moissac III and those from Saint Henri are only the small crest development of the molar occlusal pattern. Therefore, MOI3-01 supports the hypothesis that *E. borbonicus* originated from a stock of European *E. crispus* and that it dispersed at the end of the Oligocene towards the Indian sub-continent to give rise to the 'Miocene bothriodontines' (Lihoreau 2003).

The occurrence of *Elomeryx* at Moissac III might be a key to understanding the faunal exchanges between Europe and Asia at the end of the Eocene and during the Oligocene. This genus is rare in Europe and it is absent in many rich localities. It dispersed towards Europe before the Eocene-Oligocene boundary, which was a main dispersal event in Europe implying an important faunal turnover (Stehlin's (1909) 'Grande Coupure'). *Elomeryx crispus* displays a long temporal distribution from the

late Eocene up to the end of the early Oligocene but its occurrence was interrupted several times in the European fossil record (Fig. 6). Further investigations are needed to determinate whether *Elomeryx* entered once in Europe and still remained scarce in the fossil record or if it entered several times and therefore corresponds to several lineages.

The FAD of Rhinocerotidae in Western Europe corresponds to the beginning of the Oligocene (MP21 reference level; Brunet, 1979; Antoine et al., 2003a). *Protaceratherium albigense* (Roman, 1912) is known from the late early Oligocene up to the early late Oligocene in Western Europe (MP 24-28; Ginsburg, 1969; Huguency and Guérin, 1981; Ginsburg and Huguency, 1987; Russell et al., 1982; BiochroM'97, 1997; Huguency, 1997; Ühlig, 1999; Antoine et al., 2003a; Astruc et al., 2003) and from the early late Oligocene of Turkish Thrace (Saraç, 2003). *P. sp.*, cf. *P. albigense* was also recently described in the late Oligocene of north central Anatolia (Antoine et al., 2008).

As mentioned above, the surroundings of Moissac (Fig. 1) have yielded several mammal localities, either referable to the early Miocene (La Madeleine, Saint-Laurent, and Moissac I-Lespinasse, MN 1; Richard, 1948; Bonis, 1973; Bruijn et al., 1992) or to the late Oligocene (Moissac II, MP29; Bonis, 1973;

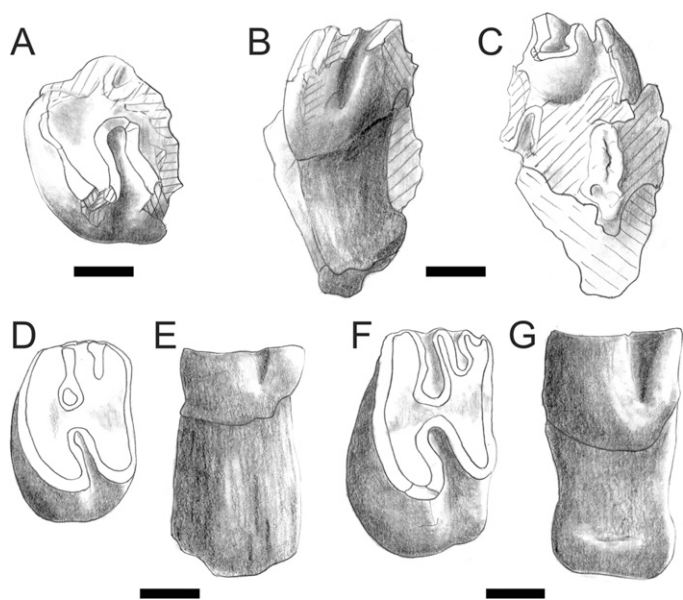


FIGURE 5. *Issidoromys* cf. *pauffiensis*, MOI3.003. Drawing of a broken right upper molar in occlusal (A), lingual (B) and labial (C) views. MOI3.003 is compared at nearly the same stage of wear with: a left reversed upper molar of *Issidoromys minor* from Garouillas (GAR877) in occlusal (D) and lingual (E) views, and a left reversed upper molar of *Issidoromys pauffiensis* from Mas de Pauffié (MPF13) in occlusal (F) and lingual (G) views. Scale bars equal 1 mm.

Schmidt-Kittler et al., 1997). La Madeleine is the type locality of *P. minutum* (Cuvier, 1822). The co-occurrence of *Issidoromys* cf. *pauffiensis* and *P. albigenae* in Moissac III therefore extends the stratigraphic range of this region back to the early late Oligocene.

CONCLUSIONS

Moissac III is a new Oligocene mammal locality in the Aquitaine Basin, southwestern France, that lays stratigraphically under both Moissac I (MN1, Agenian, early Miocene) and Moissac II (MP29, Arvernian, late Oligocene) localities (Bonis, 1973; Bruijn et al., 1992). Two nearly complete and very well preserved skulls have been discovered there, which are referred to the anthracotheriid *Elomeryx crispus* and the rhinocerotid *Protaceratherium albigenae*. These ungulate remains are associated with an upper molar of a theridomyid rodent, *Issidoromys* cf. *pauffiensis*. The latter and *P. albigenae* indicate an early late Oligocene age (MP25–26) for the mammal assemblage of Moissac III, whereas *Elomeryx crispus* was so far restricted to the late Eocene-early Oligocene period (MP18–22; Hellmund, 1991). As a consequence, the anthracothere specimen from Moissac III extends the stratigraphic range of the species and it moreover represents its youngest representative as suggested by its dental dimensions. It is the first complete skull known of the species and it allows us to differentiate a European lineage, distinct from the North American one. This succession of European species is probably at the origin of the ‘Miocene bothriodontines’ notably on the Indian sub-continent.

Although the fossil record of Moissac III is scarce, the exceptional state of preservation of both skulls is promising and we can expect further discoveries that might lead to a better knowledge of the ungulate evolutionary history in southwestern Europe during the Oligocene epoch.

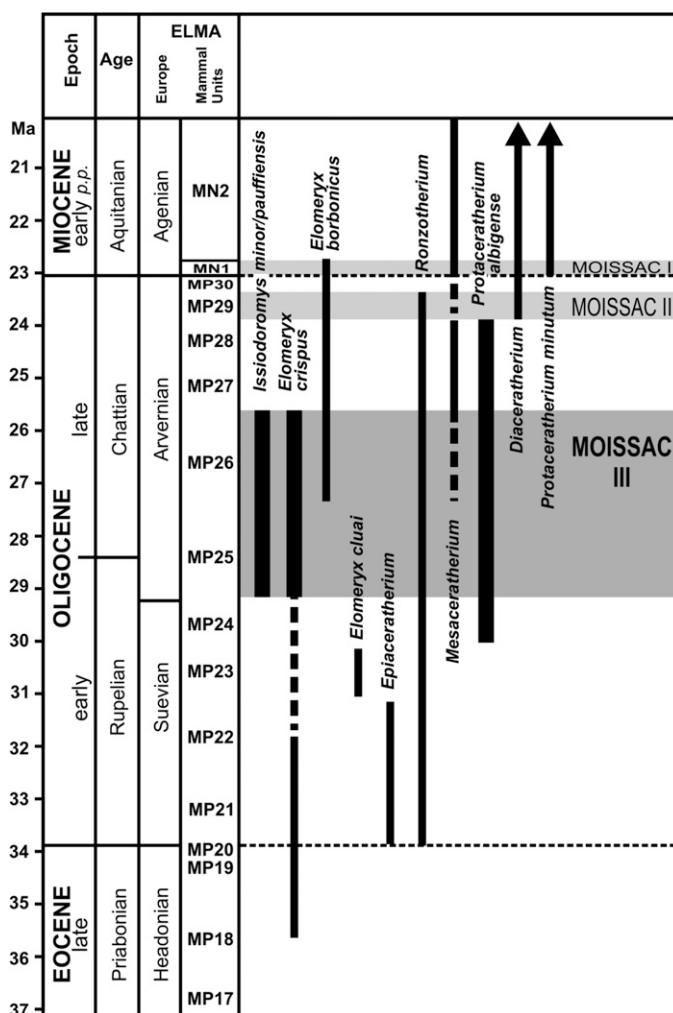


FIGURE 6. Biostratigraphic ranges of the theridomyid rodent *Issidoromys pauffiensis* and *I. minor*, of the anthracotheriids *Elomeryx crispus*, *E. borbonicus*, and *E. cluai*, of the rhinocerotids *Epiaceratherium*, *Ronzotherium*, *Mesaceratherium*, *Protaceratherium albigenae*, *Diaceratherium*, and *Protaceratherium minutum*, and inferred age for the Moissac III locality (MP25–26 European reference level). Ages of Moissac I and Moissac II localities are also given (MN1 and MP29, respectively). After Bonis (1973), Brunet et al. (1987), Schmidt-Kittler and Vianey-Liaud (1987), Hellmund (1991), Bruijn et al. (1992), Schmidt-Kittler et al. (1997), Antoine et al. (2000, 2003a, 2006), Astruc et al. (2003), Lihoreau (2003), Saraç (2003), Luterbacher et al. (2004), and Ducrocq and Lihoreau (2006).

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