General palaeontology, systematics and evolution

A new late Early Oligocene vertebrate fauna from Moissac, South-West France

Une nouvelle faune de vertébrés de la fin de l'Oligocène inférieur à Moissac (Sud-Ouest de la France)

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ABSTRACT

The new vertebrate locality Moissac-IV, in SW France, yields the alligatoroid *Diplocynodon* sp., the turtle *Trionyx* sp., and a diversified mammal fauna. The mammal assemblage includes the rodent *Protechimys* cf. *lebratierensis*, the artiodactyls *Caenomeryx* sp., *Lophiomeryx chalaniati*, *Gelocus* sp., *Metriotherium* aff. *mirabile*, *Entelodon* sp., and *Anthracotherium* sp., the perissodactyls *Protaceratherium albigense* and *Eggysodon gaudryi*, the carnivore *Nimravus intermedius*, and the creodonts *Hyaenodon dubius* and *Hyaenodon*?*leptorhynchus*. The Moissac-IV fauna, referred to the MP24 reference level, is both totally distinct from those of Moissac-I (MN1, Earliest Miocene) and Moissac-II (MP29, Late Oligocene) and older than Moissac-III (MP26). It provides original data in a stratified context just prior the Early-Late Oligocene transition, i.e. a stratigraphical interval, which for SW France, was essentially documented by karstic fillings of the Phosphorites of Quercy so far.

RÉSUMÉ

La nouvelle localité Moissac-IV, dans le Sud-Ouest de la France, livre l'alligatoroïde *Diplocynodon* sp., la tortue aquatique *Trionyx* sp. et une faune diversifiée de mammifères. L'assemblage mammalien inclut le rongeur *Protechimys* cf. *lebratierensis*, les artiodactyles *Caenomeryx* sp., *Lophiomeryx chalaniati*, *Gelocus* sp., *Metriotherium* aff. *mirabile*, *Entelodon* sp. et *Anthracotherium* sp., les périssodactyles *Protaceratherium albigense* et *Eggysodon gaudryi*, le carnivore *Nimravus intermedius* et les créodontes *Hyaenodon dubius* et *Hyaenodon*?*leptorhynchus*. La faune de Moissac-IV, attribuée au niveau repère MP24, est à

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la fois totalement distincte de celles de Moissac-I (MN1, Miocène basal) et Moissac-II (MP29, Oligocène supérieur) et plus ancienne que Moissac-III (MP26). Elle fournit, en contexte stratifié, des données originales précédant immédiatement la transition Oligocène inférieur-supérieur, un intervalle stratigraphique jusqu'alors essentiellement documenté, dans le Sud-Ouest de la France, par les remplissages karstiques des Phosphorites du Quercy.

1. Introduction

The middle Garonne Basin, in Southwestern France (Fig. 1), yields hundreds of Cenozoic vertebrate localities often documented by a few – or a single – species (Richard, 1948). Oligocene land mammal assemblages are noticeably well documented in the karsts of the Phosphorites of Quercy area and in fluvio-lacustrine deposits of peripheral basins, Southeast and West to it (Fig. 1; BiochroM'97, 1997; Astruc et al., 2003; Lihoreau et al., 2009; Rémy et al., 1987).

From the vicinity of Moissac (Tarn & Garonne), (Cuvier, 1825) first reported fossil mammals, including the type of "*Rhinoceros minutus*" (i.e., *Protaceratherium minutum*). Later on, (Richard, 1948) considered this old collection was originating from sites located in the lower part of the so-called "*Molasse Stampienne*" (i.e., Late Oligocene in age), notably due to the co-occurrence of the large rhinocerotid "*Aceratherium filholi*" (i.e., *Ronzotherium filholi*) and of the anthracotheriid *Anthracotherium magnum*. Since 1973, three other mammal-bearing sites were described nearby Moissac, and precisely located: Moissac-I (MN1, earliest Miocene–with *P. minutum*; de Bonis, 1973; de Bruijn et al., 1992), Moissac-II (MP29, Late Oligocene; de Bonis, 1973; Schmidt-Kittler et al., 1997), and Moissac-III (MP26, early Late Oligocene; Lihoreau et al., 2009). In 2007, one of us (SR) discovered a new locality 4 km east of the city (i.e. between Moissac and Lafrançaise; Fig. 1), which was therefore named Moissac-IV. This new locality documents another stratigraphical level, still lower in the series than Moissac-III, and referable to the late Early Oligocene.

Moissac-IV consists of a lens of unconsolidated and massive grey fluvial sands, located at the very bottom of the surrounding hills, at 85 m above sea-level. This lens, ca. 1 m-thick and 30 m^2-wide, was excavated between 2007 and 2010; it yielded 166 identifiable specimens documenting twelve terrestrial mammal species, as well as aquatic vertebrates (alligatoroid: *Diplocynodon* sp., left dentary with 19 alveoli (287 mm-long), isolated teeth, and dermal plates; turtle: *Trionyx* sp., two neural plates and a fragmentary hypoplastron, with characteristic cupules). Even though some remains are eroded or fairly crushed, most specimens are complete and well-preserved.

The present article aims first to describe this original mammal assemblage, spanning five orders (rodents, cetartiodactyls, perissodactyls, carnivores, and creodonts) and documenting twelve species, second to enhance its biostratigraphical significance.

2. Material and methods

We use I/i, C/c, P/p, M/m, and D/d for upper/lower incisors, canines, premolars, molars, and deciduous molars, respectively. Dimensions are given in mm, except when mentioned.

Abbreviations: ant, anterior; ect, ectometaloph; est, estimated; FAD, first appearance datum; H, height; L, length; LAD, last appearance datum; max, maximum; post, posterior; S, synclinid; Sd, sinusid; W, width.

Institutional abbreviation: MNHN, Muséum National d'Histoire Naturelle, Paris.

3. Systematic palaeontology

Order RODENTIA Bowdich, 1821
Family THERIDOMYIDAE Alston, 1876
Genus **Protechimys** Schlosser, 1884
Protechimys cf. *lebratierensis* Vianey-Liaud, 1998
Fig. 2

This taxon is only documented by a damaged right mandibular fragment, bearing p4 (wear surface: L = 2.26; W = 1.66; labial H = 1.13; total crown L = 2.46; W = 2.05; Fig. 2.1) and a broken m1 (total crown L = 2.07; H = 1.10), and a well-preserved isolated right m1 (wear surface: L = 1.74; W = 1.28; labial H = 1.67; total crown L = 2.03; W = 1.84; Fig. 2.2). It has been compared directly to the type material, from Lébratières 14 (MP24, Quercy). The teeth display the primitive features of *Protechimys*. The mure is still separating the synclinid III from the sinusoid. There is a weaker difference in enamel thickness between the mesial and distal flanks of anticlinids than

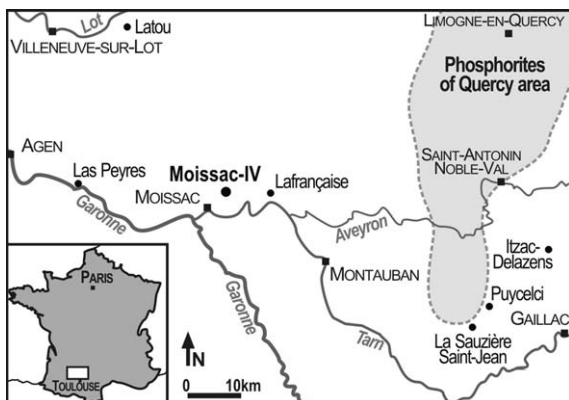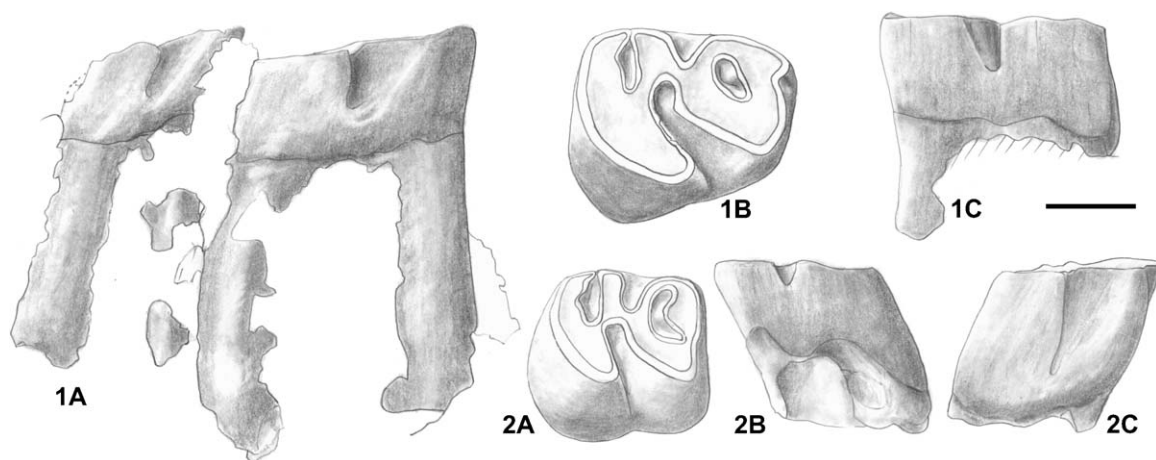**Fig. 1.** Location map of Moissac-IV (SW France) and main surrounding vertebrate localities referred to in the text.
Fig. 1. Localisation de Moissac-IV (SW France) et des principaux gisements de vertébrés avoisinants et mentionnés dans le texte.

Fig. 2. *Protechimys* cf. *lebratierensis*, from the late Early Oligocene of Moissac-IV, SW France., right mandible fragment with m1-p4 in labial view (**1A**), p4 in occlusal (**1B**) and in lingual views (**1C**); right m1 in occlusal (**2A**), lingual (**2B**), and labial views (**2C**). Scale bar = 1 mm.
Fig. 2. *Protechimys* cf. *lebratierensis*, Oligocène inférieur de Moissac-IV (SW France). fragment de mandibule droite avec m1-p4 en vues labiale (**1A**), occlusale (**1B**) et linguale (**1C**); m1 droite en vues occlusale (**2A**), linguale (**2B**) et labiale (**2C**). Barre d'échelle = 1 mm.

in *P. truci*, which is related to the crown weakly inclined mesio-distally (not inclined in *P. truci*). The wear surface is plane and the teeth are moderately worn. The synclinid I is not observed, but the shape of the synclinid II and the thickness of the anticlinids may indicate its occurrence on unworn teeth; the lingual wall of synclinids II and IV is closed; the ratio synclinid III/sinusid is comparable with that observed on equally worn specimens (Log H/L = 0.04) from Lébratières 14 (Log area Sd/SIII = 0.77; Log perimeter Sd/SIII = 0.49), and a little higher than in equally worn specimens of *P. truci* (Vianey-Liaud, 1998: 261–262). Morphological characters, occlusal dimensions, and height of the available teeth fit well with *P. lebratierensis*, but the material is too scarce to ascertain a formal specific synonymy with the latter taxon.

Order ARTIODACTYLA Owen, 1848
Family CAINOTHERIIDAE Camp & Van der Hoof, 1940
Genus ***Caenomeryx*** Hürzeler, 1936
Caenomeryx sp.

The material includes three fragmentary hemi-mandibles, morphologically very similar and comparable in size. They all belong to adult individuals. 27.07 is the most complete specimen, as it preserves left p3-m3; other specimens preserve left p3-m1 and m2-m3, respectively. Although these specimens show the diagnostic features of *Caenomeryx* in both their morphology (mandible massive and very wide beneath the molar area; p3 with an incipient talonid disto-lingually opened, p4 with a strong metaconid and paraconid) and their size, discriminating species on the basis of the sole lower dentition is quite hazardous. *Caenomeryx* is known by two species, *C. procommunis* and *C. filholi*, primarily documented in unallocated-undated localities from the Phosphorites of Quercy. The material from Moissac-IV is close in size and morphology to the newly dated material from several MP23-MP24 localities of Quercy (Blondel, 2005). Yet, the lack of upper dentition

that bear most diagnostic features of the two species referred to *Caenomeryx* leads us to leave these specimens as *Caenomeryx* sp.

Family LOPHIOMERYCIDAE Janis, 1987
Genus ***Lophiomeryx*** Pomel, 1854
Lophiomeryx chalaniati Pomel, 1854
Fig. 3.1–3

The material includes several fragmentary maxilla, lower jaws, and astragali. Interestingly, upper and lower decidual dentition is fairly well represented (e.g., 39-08 and 05-10, preserving D2-3, and D3-4 respectively), and adult specimens display a range from just erupted to heavily worn dentition.

The upper dentition is characteristic to *Lophiomeryx* (Fig. 3.1): P4 has strong and rounded styles, and the labial side of the labial cusp is almost flat; the upper molars are approximately square in occlusal outline, with four cusps; parastyle and mesostyle are labially salient; the labial rib of the paracone is poorly expressed, and the labial face of the metacone lacks such a rib so that it appears concave. The metaconule is variably reduced on M3; it is very small on 26-10, giving this molar a sub-triangular outline. This feature is sometimes thought as characteristic of *L. mouchelini*, a species known in MP22 (Brunet & Sudre, 1987).

The lower dentition displays the diagnostic features of *L. chalaniati*: the paraconid is very faint or absent in p2; the transversal crests are poorly developed in p3, the metaconid is strong on p4, and just lingual to the proto-conid (Fig. 3.2B). However, the hypoconulid of m3 is linked to the second lobe of the molar through either a unique crest (21-07) or two crests (20-07 or 38-08). Again, (Brunet and Sudre, 1987) advocated that the way the third lobe of m3 is related to the second lobe, through one or two crests, was a feature differentiating *L. chalaniati* from *L. mouchelini*, respectively. Consequently, and despite the size range of the specimens that globally fits well with that of
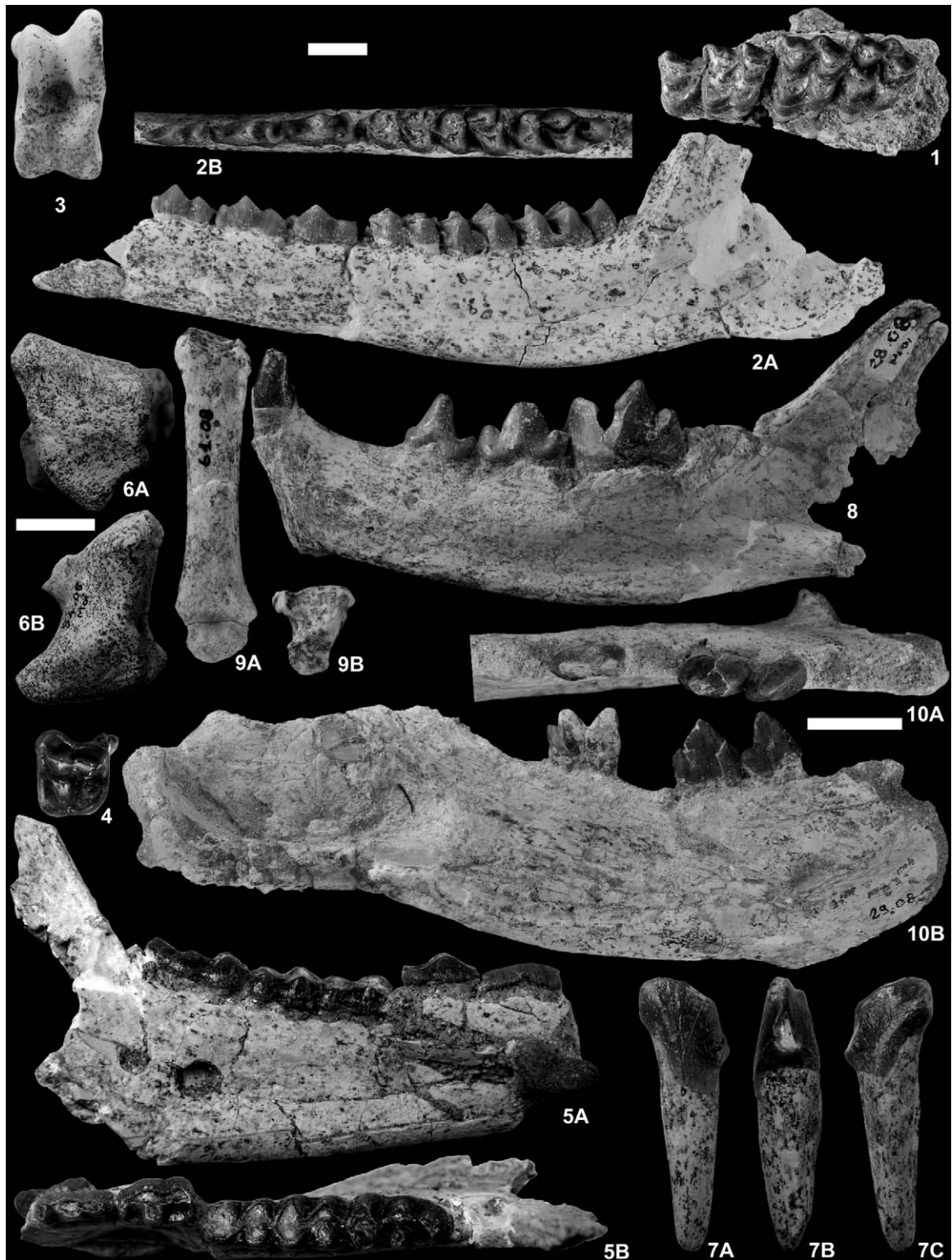
Fig. 3. Late Early Oligocene mammals of Moissac-IV, SW France. *Lophiomeryx chalaniati*. left maxilla with P4-M3 in occlusal view (**1**); 21-07, left hemi-mandible with p2-m3 in labial (**2A**) and occlusal views (**2B**); 57-08, left astragalus in antero-proximal view (**3**). *Metriotherium* aff. *mirabile*. 22.08, left M3 in occlusal view (**4**); right hemimandible with p3-m3 in labial (**5A**) and occlusal views (**5B**). *Entelodon* sp. 54-08, right lunatum in anterior view (**6A**) and proximal view (**6B**). *Anthracotherium* sp. 14-08, left i3 in labial (**7A**), distal (**7B**), and lingual views (**7C**). *Nimravus intermedius*. 28.08, left hemimandible in labial view (**8**); 61.08, right Mc III in anterior view (**9A**) and proximal view (**9B**). *Hyaenodon dubius*. 29.08, right mandible with p3, p4, and m2, in occlusal view (**10A**) and labial view (**10B**). Scale bars = 10 mm (1-5, 7-9) and 20 mm (6, 10).

L. chalaniati (especially the series from Le Garouillas, MP25), we cannot exclude that both *L. chalaniati* and *L. mouchelini* are represented among the material presently available from Moissac-IV.

The astragali are all fairly weathered and the sustentacular facet of 57-08 is damaged, but the crests delimiting articular surfaces are generally discernible. Characteristically, the proximal and distal trochleae are not aligned, the distal pulley being slightly rotated medially (Fig. 3.3). The medial ridge bordering the sustentacular facet is well marked, and the sustentacular surface occupies about two thirds of the total transversal width of the astragalus. The sustentacular facet is slightly concave, due to the presence of a longitudinal groove. The ridge separating the cuboid and the navicular articular surfaces is not visible on the distal trochlea as in some specimens of *Lophiomeryx chalaniati* from Quercy (Martinez and Sudre, 1995), but it may be due to post-mortem weathering. Astragali are morphologically similar and the observed range of the available material indicates that all belong to *L. chalaniati*.

Family GELOCIDAE Schlosser, 1886
Genus ***Gelocus*** Aymard, 1855
Gelocus sp.

47-08 is an upper molar (probably M1), morphologically distinct in showing very poorly developed styles; the postprotocrista is almost transversal, and it does reach the base of the pre-metaconule crista medially as in the upper molar of *Lophiomeryx*. The labial side of the paracone is strongly ribbed while labial ribs are poorly expressed in *Lophiomeryx*. These features of 47-08 are reminiscent to those of M1-2 s of *Gelocus*; size is comparable to that of *G. villebramarensis* (western Europe, MP22); *Gelocus* gets extinct at MP25 (Métais and Vislobokova, 2007).

Family DICHOBUNIDAE Turner, 1849
Genus ***Metriotherium*** Filhol, 1882
Metriotherium aff. *mirabile*
Fig. 3.4 and 5

The available material includes a left isolated M3 (22.08) and a right mandible with p3-m3 (24.08), which display diagnostic features of the late dichobunid *Metriotherium*. 22.08 has a reduced hypocone and no distal wear-facet on the distal side (all three features pointing to an M3). It is selenodont, with sharp and buccally shifted pre- and postcristae on buccal cusps, a strong mesiobuccal extension, a distally crested hypocone, and lingual roots forming a single lingual pillar; the hemimandible 24.08 is broken in front of the p3 and it preserves a small portion of the ascending ramus. p3 is a slender tooth with a wide

transversely extended mesiostylid and a strong cuspid distal to the protoconid, here considered as a hypoconid; the latter presents a sharp distal cristid running to the distal border of the tooth. There is no trace of distal cingulid. p4 has a strong mesiostylid (although smaller than in p3), a strong metaconid, and two distinct distal cuspids; the distal part of p4 is inflated and it exceeds the protoconid width. The lower molars are heavily worn so that their finest structures are not observable. However, they display closely apposed mesial cuspids and sharp pre- and postcristids on protoconid and hypoconid, observable by the crescentic wear pattern.

The buccal side of 24.08 presents two circular depressions (6.7 and 5.0 mm wide, respectively) below m3, which most probably correspond to predation marks, due to a large flesh-eater (carnivore or creodont?).

Metriotherium is far from being well-known, and M3 is only documented for *M. mirabile* so far (Sudre, 1995). 22.08 differs from the M3 of *M. mirabile* by a more buccal orientation of the postmetacrista, which confers to the crown a more rectangular outline. An isolated p3 from Le Garouillas (*M. mirabile*; Sudre, 1995) is morphologically similar to 24.08, but larger (16.7 *vs*. 13.8). The p4 from Moissac-IV resembles that of *M. mirabile*, but the distal part of the former is more inflated. The lower molars of 24.08 lack the strong labial indentation between the protoconid and the hypoconid as observed in *M. minutum* and *M. sarelense* (Astruc et al., 2003; Sudre, 1995) and there is no hypoconulid constriction either. The buccal cingulum is well developed on m1-2, which also occurs in some (larger) specimens of *M. mirabile* from Le Garouillas (Sudre, 1995). Overall dimensions of 24.08 (L m1–m3 = 43.0) compare well with those of the holotype of *M. mirabile* (Brunet and Sudre, 1980). Yet, the distinctive morphology of available material leads us to refer to the present specimens as *M.* aff. *mirabile*.

Family ENTELODONTIDAE Lydekker, 1883
Genus ***Entelodon*** Aymard, 1846
Entelodon sp.
Fig. 3.6

54.08 is a very large right lunatum (anteroposterior diameter = 47; proximo-distal height, mesial side = 46), which displays diagnostic features of Suina (Suoidea + Entelodontidae), such as the important mediolateral extension of the proximal articular facet, the presence of a deep notch for the anterolateral part of the scaphoideum, and the concavity of the anterior part of the magnum-facet. These characters differ from what is observed in other coeval large artiodactyls, i.e. Anthracotheriidae, the lunatum of which is mostly anteroposteriorly elongated, with a sub-straight medial edge

Fig. 3. Mammifères de l'Oligocène inférieur de Moissac-IV (Sud-Ouest de la France). *Lophiomeryx chalaniati*. Maxillaire gauche avec P4-M3 en vue occlusale (**1**); 21-07, hémimandibule gauche avec p2-m3 en vues labiale (**2A**) et occlusale (**2B**); 57-08, astragale gauche en vue antéro-proximale (**3**). *Metriotherium* aff. *mirabile*. 22.08, M3 gauche en vue occlusale (**4**); hémimandible droite avec p3-m3 en vues labiale (**5A**) et occlusale (**5B**). *Entelodon* sp. 54.08, semi-lunaire droit en vues antérieure (**6A**) et proximale (**6B**). *Anthracotherium* sp. 14-08, i3 gauche en vues labiale (**7A**), distale (**7B**) et linguale (**7C**). *Nimravus intermedius*. 28.08, hémimandibule gauche en vue labiale (**8**); 61.08, Mc III droit en vues antérieure (**9A**) et proximale (**9B**). *Hyaenodon dubius*. Moi 29.08, hémimandibule droite avec p3, p4 et m2, en vues occlusale (**10A**) et labiale (**10B**). Barres d'échelle = 10 mm (1-5, 7-9) et 20 mm (6, 10).

(Kowalewsky, 1874). The huge size of 54.08 does not coincide with any Paleogene suoid, but its size, proportions, and morphology fit those of the entelodontid *Entelodon*. 54.08 is slightly larger than the lunatum of *Entelodon magnum* described by (Kowalewsky, 1876), but its proximal side compares well with the corresponding articular facet, as observed and measured on a distal radius of *E. deguilhemi* from Villebramar (Brunet, 1979). Postcranial morphology of entelodontids is far from being well-known, so we consider 54.08 as documenting *Entelodon* sp.

Family ANTHRACOTHERIIDAE Leidy, 1869
Genus **Anthracotherium** Cuvier, 1822
Anthracotherium sp.
Fig. 3.7

The lower incisor 14.08 (mesio-distal crown L = 16.0) has a spatulated and highly asymmetrical crown, and a long and straight root (Fig. 3.7). In lingual view, the crown lacks an endocristid and the endosynclinid is deep and distally displaced. The lingual cingulid is restricted to the mesialmost and distalmost parts of the crown. Enamel is more extended ventrally on the labial side than on the lingual side, implying deep pre- and postanticlinids. The distal part of the cingulid slightly extends on the labial side of the crown. The crown is mesio-distally elongated, with an apical wear-facet due to I2 and a distal one, concave, due to I3. Referral to the Entelodontidae was discarded because entelodontids present simple conical lower incisors with a strong lingual cingulid and a wear pattern markedly different from what is observed in 14.08. Lower incisors of Anthracotheriidae are rarely described, thus making comparisons difficult. However, contrary to what is observed in Microbunodontinae and Bothriodontinae, this tooth lacks an endocristid. The general morphology and the enamel finely wrinkled of 14.08 recall both *Anthracotherium cuvieri* (MP26), with higher and slender proportions, a 25% smaller size, and a reduced lingual cingulid, and undescribed specimens referred to *A.* cf. *alsaticum* (Villebramar) and to *A. magnum* (pers. obs., MJO). This specimen is tentatively identified as a left i3 of *Anthracotherium* sp.

Order PERISSODACTYLA Owen, 1848
Superfamily RHINOCEROTOIDEA Gray, 1825
Family RHINOCEROTIDAE Gray, 1821
Genus **Protaceratherium** Abel, 1910
Protaceratherium albigense Roman, 1912
Fig. 4.1–4.

The small and slender hornless rhinocerotid *Protaceratherium albigense* is documented by four mandibles and several isolated teeth. The left mandible 78-08 displays p3-m3 (estimated L for p2-m3 = 146), as well as the alveoli of i2 s (large, cylindrical, and procumbent) and of a biradiculate p2. The preserved part of the symphysis is slender, with a distal border located below the middle of p2, as is the foramen mentale. The ventral border of the corpus mandibulae is straight. The preserved part of

the ramus is vertical. The foramen mandibulare is located well below the "jugal teeth neck line". There is neither i3 nor c. Lower cheek teeth are brachydont and compressed labio-lingually, with a "m/w-shaped" occlusal pattern and no labial/lingual cingulids. Trigonids are angulous, forming an acute dihedron in occlusal view. Metaconids and entoconids are not constricted. Distal valleys are open lingually, deep and "V-shaped" in lingual view. The right mandible 018-07, from a younger individual, displays similar features. The juvenile mandible 02-10 is complete, with left and right procumbent i1 and di2, and functional d1-d4 and m1, but no di3/dc. The corpus displays a deep and wide *incisura vascularis* in its distal part. The ramus is low and developed sagittally. d2-d4 have no labial or lingual cingulids. d2 and d3 have a forked paralophid. The distal valley of d2 is almost closed lingually. On d3, the metaconid is deeply constricted but not the entoconid. On the right mandible 30-08, only d2-d4 are functional (L/Wd2 = 21/11; L/Wd4 = 28/16), which points to a young calf. The *incisura vascularis* is already marked at this ontogenetic stage. Dental features are consistent with those observed in 02-10. The I1 019-07 has an oval occlusal outline and a straight and prismatic root (total L = 48; crown H = 17; crown W = 10). The crown is bulbous, with a wear facet restricted to its distal side. The right P4 07-08 (L = 23; W = 29) is molariform, with a crista but neither crochet nor antecrochet. The paracone fold is attenuated. There is no metacone fold. The lingual and labial cingula are strong and continuous, with no inflection. The protocone is much thicker than the hypocone in occlusal view. The metaloph is constricted in its labialmost part.

The right M1 74-08 (L = 33; antW = 31.5; postW = 30.5) has a crochet, a strong antecrochet, and a constricted protocone. The lingual cingulum is restricted to a small median tubercle. The labial cingulum is low and continuous. The paracone fold is weak, but the paracone groove is deep, due to the parastyle lingually displaced. There is no metacone fold. The hypocone has an mesiolingual groove. The enamel is both wrinkled and corrugated. The left M3 10-07 (L = 27; antW = 29.5; ectL = 31.5) has a trapezoid occlusal outline. The ectoloph and metaloph are fused into an ectometaloph, but a vertical (vestigial) groove remains in the distal third of it. The mesostyle is developed distal to the strong paracone fold. The distal cingulum is low, oblique, and restricted to the distal half of the crown. The antecrochet is weak. There is neither crochet nor crista. The left D4 15-07 (L = 28.5; antW = 26; postW = 26) is low-crowned and square in occlusal view. The protoloph is bilobate, with an mesiolingual groove, and a strong antecrochet. The crista is thin, long and transversely oriented. The crochet is thin, bifid, sagittally oriented, and restricted to the top of the crown. The paracone fold is thick. There is no mesostyle. The metacone fold is thick and it widens nearby the neck. The lingual cingulum is almost continuous. There is no labial cingulum.

The concerned specimens are similar in size to the ones attributed to the hyracodontid *E. gaudryi*, but the presence of a deep *incisura vascularis*, of wrinkled and corrugated enamel, of a crochet on M1 and D4, of a distal groove on the ectometaloph and a low posterolingual cingulum on M3, of procumbent i1-di2, the absence of a metacone fold

on P4 and M1, of di3-dc (juvenile) and i3-c (adult), the bulbous shape of I1, and the distal valley of d2 almost closed lingually form a combination characteristic of the rhinocerotid *Protaceratherium albigense* (Roman, 1912). With the exception of a constricted metaloph on P4, a small crochet on M1, somewhat reduced and smooth cingulids on lower teeth, the concerned mandibles and teeth are undistinguishable from the hypodigm of this species (Lihoreau et al., 2009; Roman, 1912). On the other hand, these specimens are 20 to 50% smaller than the ones referred to other Oligocene European rhinocerotids such as *Epiaceratherium*, *Ronzotherium*, *Mesaceratherium*, and *Diaceratherium* (Brunet, 1979; Heissig, 1969; Uhlig, 1999).

Family HYRACODONTIDAE Cope, 1879
Genus ***Eggysodon*** Roman, 1910
Eggysodon gaudryi (Rames, 1886)
Fig. 4.5–9

The small hyracodontid *Eggysodon gaudryi*, exceptionally abundant in Moissac-IV, is documented by four skulls (three adults and one juvenile), eight maxillae (three adults and five juveniles), ten mandibles (seven adults and three juveniles), as well as isolated teeth (permanent and deciduous) and a dozen postcranial elements.

All cranial features are plesiomorphic (sensu Antoine, 2002), with the exception of several apomorphic traits shared by adults and juveniles: *processus zygomaticus maxillari* with a low base; *processus postorbitalis* located on the tip of the squamosal; external auditory pseudo-meatus closed; occipital side vertical; pterygoid with a distal margin dipping strongly; short nasal bones; sagittal crest present on the basilar process of the basioccipital; *processus posttympanicus* and *paraoccipitalis* distant one from another. Other apomorphies were observed only in adults (nuchal tubercle developed, high zygomatic/frontal width ratio, mesial tip of the *processus zygomaticus maxillari* projected laterally, *processus posttympanicus* little developed, and median ridge present on the occipital condyle).

The mandibular symphysis is upraised and spindly, with a distal margin located below p2 (and d1). The foramen mentale is located below the middle of p2 (and d2). The *sulcus mylohyoideus* is present in juveniles and adults. The base of the corpus mandibulae is straight. The *incisura vascularis* is not marked. The ramus is inclined forward. The *processus coronoideus* is well-developed and the foramen mandibulare is located above the "jugal teeth neck line". The permanent dental formula is 3I/3i +C/c +4P/3p +3 M/3m. LP1-M3 ranges from 138 up to 148 (mean = 143.2). Lp2-m3 ranges from 123 up to 145 (mean = 136.5). The anterior dentition is sub-vertically oriented, with C and c being the largest anterior teeth, as in the hyracodontid *Eggysodon* (Uhlig, 1999), and contrary to what occurs in all Oligocene rhinocerotids (Brunet, 1979; Heissig, 1969; Ménouret and Guérin, 2009). P2 is quadratic, P2-M3 have a long parastyle, a wide and shallow paracone groove, and a weak paracone fold, and M1-3 always have an antecrochet, as in *E. gaudryi* and *E. pomeli*, but contrary to what is observed in *E. osborni* and *E. reichenaui* (de Bonis and Brunet, 1995; Roman, 1912; Uhlig, 1999). The labial

cingulum is always strong and continuous on P1-M1 and p2-m2, usually absent on M2-M3, and always absent on m3. According to (Uhlig, 1999), this condition distinguishes *E. gaudryi* and *E. reichenaui* from *E. osborni* and *E. pomeli*. All P3-4 are submolariform, and the paralophid of m1-m3 is short and low, contrary to *E. reichenaui* (Uhlig, 1999). On M1-3, the protocone is not constricted, contrary to what occurs in *E. pomeli* (Roman, 1912; Uhlig, 1999). The entoconid of p2 is part of a short and low hypolophid, while the paralophid is not bifid in p2 and p3. Both features are only observed in *E. gaudryi* (Uhlig, 1999).

To sum up, all the morphological traits observed in Moissac-IV are consistent with those of *E. gaudryi*, from the late Early to early Late Oligocene of France (MP24-28; Uhlig, 1999). The only discrepancy concerns the small dimensions of the present sample, which are 15 to 30% smaller than other series referred to this species (de Bonis and Brunet, 1995; Roman, 1912; Uhlig, 1999). These dimensions match the smallest representative of *Eggysodon*, *E. osborni*, from the Earliest Oligocene of western Europe (MP21-22; Uhlig, 1999).

To our knowledge, Moissac-IV yields not only the first comprehensive sample for *E. gaudryi* but also the only skulls referable to the hyracodontid *Eggysodon*. As a matter of fact, the current description is preliminary, as this material will necessitate further investigation.

Order CARNIVORA Bowdich, 1821
Family NIMRAVIDAE Cope, 1880
Genus ***Nimravus*** Cope, 1879
Nimravus intermedius (Filhol, 1872)
Fig. 3.8–9.

The material includes two left hemimandibles (28.08 and 28.10) that both preserve c, p3-m1 and lack the ventrodistal part of the dentary. The two specimens are morphologically very similar, 29.10 being from a larger and younger individual than 28.08. The dentary displays the diagnostic features of the genus, i.e. depth much greater below m1 than below p2, a ventral border narrow and somewhat pinched, no genial flange, although a small ventrally developed symphyseal apophysis is present, and a deep muscular fossa (for attachment of the digastric muscle) on the ventral side of the mesialmost part. The canine is small and bears two crests, one mesio-lingually and one, still preserving crenulations in 29.10, distally. The p1 is absent in both individuals. The p2 is absent in 28.08, which is quite unique in the species (only two specimens out of over 60 studied specimens); it was present in 29.09, although not preserved. The p3 and p4 are approximately the same height. Compared to p4, p3 is short, slender, and with a reduced (28.08) or vestigial (29.10) mesial cingular cuspid and a larger distal cingular cuspid. p4 is taller than the paraconid of m1; the mesial rim of the main cuspid is straight, while the distal rim is convex; the mesial cingular cuspid is larger than the distal one, which is diagnostic for the genus (Peigné, 2003). The m1 is typically trenchant and more elongated than in other nimravids; it lacks a metaconid and the talonid is short and more trenchant than in, e.g. *Eofelis*, *Dinailurictis* and *Quercylurus*. The m2

Fig. 4. Late Early Oligocene rhinocerotoids from Moissac-IV (SW France). *Protaceratherium albigense.* 16-07, left I2, lingual view (**1**); 74-08, right M1, occlusal view (**2**); 02-10, juvenile mandible, with right di2, d1-d4 and m1-2 in labial view (**3**); 30-08, right juvenile mandible with d2-4, occlusal view (**4**). *Eggysodon gaudryi.* 013-07, right juvenile maxilla with D1-D4, occlusal view (**5**); 06-08, skull in palatine (**6A**) and right lateral views (**6B**); 016-07, left C, lingual view (**7**); 01-08, right maxilla with P1-M3, occlusal view (**8**); 005-07, right hemimandible with c and p2-m3 in labial (**9A**) and occlusal views (**9B**). Scale bars: 20 mm (1, 2, 4, 5, 7, 8, 9B) and 50 mm (3, 6, 9A).

is not preserved but was present in both specimens. A right metacarpal is here assigned to the species on the basis of its size and felid-like morphology. Given the size of the species, this is a rather short bone (maxL = 57) compared to, e.g., felids similar or smaller in size such as *Pseudaelurus quadridentatus* (L = 59.3 for the Mc III MNHN Sa 634) and *Promegantereon ogygia* (mean = 67.65 for 35 specimens; Salesa, 2002). Compared to these felids, the distal part of the diaphysis of the Mc III of *Nimravus intermedius* is anteroposteriorly more compressed (but might partly result from post-mortem compaction); it also displays an articular facet for the Mc II that is both much less extended and less proximally developed, resulting in a much less concave facet for the magnum; the shelf forming the articulation with the Mc IV is less laterally developed.

Order CREODONTA Cope, 1875
Family HYAENODONTIDAE Leidy, 1869
Hyaenodon Laizer & Parieu, 1838
Hyaenodon dubius Filhol, 1873
Fig. 3.10.

H. dubius is documented by the right mandible 29.08, with p3-p4 and m2, and the roots of p2, m1, and m3. The mandible is deep (H = 35.2) and transversely compressed. The symphysis extends below p3. The masseteric fossa is deep, which implies the presence of a well-developed masseter muscle. The premolars are biradiculate and closely appressed: p3 and p4 are overlapped (brevirostric morphology). Based on the roots, p2 (estL = 13.2; estW = 6.7) was slightly shorter than p3 (L = 14.2; W = 8.0). p3 is shorter than p4 (L = 15.1; W = 8.7). The paraconid is not individualized and the talonid is short and narrow on the premolars. The only cusp present on the talonid is the hypoconid, transversely centred on it. No cingulid is present. The trigonid of m2 (L = 15.9; W = 7.0) is much worn labially, as usual in adult individuals of *Hyaenodon*. The paraconid is well shifted mesially. The paraconid and protoconid are of equal height. No metaconid is present. The talonid is very short and narrow. The only cusp present on the talonid is the hypoconid. The dimensions of m1 (L = 10.2; W = 7.0) and of m3 (L = 21.5; W = 7.4) are based on the roots.

The important reduction of the metaconid and talonid on molars permits to refer 29.08 either to the hyaenodontine *Hyaenodon* or to the hyaenaelurine *Pterodon*. Both genera are distinguished mostly based on cranial features (Polly, 1996). Yet, in 29.08, the teeth are less robust and the talonid is more reduced on m2 than in *Pterodon*, thus pointing to *Hyaenodon*. This long-lasting genus is known by eleven European species (Lange-Badré, 1979). Among the early Oligocene representatives of *Hyaenodon*, 29-08 compares well to *H. leptorhynchus* and *H. dubius* (MP21-MP23; BiochroM'97, 1997). Dental dimensions match those of

H. dubius from Villebramar (MP22), and the robust and very appressed premolars are much similar to the specimens of *H. dubius* from Itardies (MP23; Lange-Badré, 1979).

Hyaenodon? *leptorhynchus* Filhol, 1873

Due to the presence of a disto-lingually oriented wear facet, 20.08 is interpreted as a left inferior canine. Most of the base of the crown has been worn out. The tooth is oval in occlusal view and no developed crest is visible. 20.08 has smaller dimensions (L = 9.1; W = 5.9) than the canines of *H. dubius* from Itardies (MP23). Such a size matches the specimens of *H. leptorhynchus* (Phosphorites of Quercy, old collections, MNHN). As a consequence and pending new discoveries, we tentatively refer 20.08 as to *H.?leptorhynchus*.

4. Biostratigraphical implications

The present assemblage documents eleven distinct mammalian families: a theridomyid (rodent); a cainotheriid, a lophiomerycid, a gelocid, a dichobunid, an entelodontid, and an anthracotheriid (artiodactyls); a rhinocerotid and a hyracodontid (perissodactyls); a nimravid (carnivore); two hyaenodontids (creodonts). In terms of specific diversity, artiodactyls dominate, with six species out of 12 for the complete fauna, while the hyracodontid *Eggysodon gaudryi*, the lophiomerycid *Lophiomeryx chalaniati* and, to a lesser extent, the rhinocerotid *Protaceratherium albigense*, widely exceed all other taxa in terms of specimen abundance.

The Moissac-IV fauna is totally distinct from those of Moissac-I (MN1, Earliest Miocene) and Moissac-II (MP29, Late Oligocene), at species and/or genus level (Fig. 5; de Bonis, 1973; de Bruijn et al., 1992; Schmidt-Kittler et al., 1997; Lihoreau et al., 2009). On the other hand, Moissac-III (MP26) and Moissac-IV have one species in common (the rhinocerotid *Protaceratherium albigense*), while theridomyid rodents and anthracotheriids are distinct, with *Protechimys* cf. *lebratierensis* and *Anthracotherium* sp. in Moissac-IV and *Issiodoromys* cf. *pauffiensis* and *Elomeryx crispus* in Moissac-III (Lihoreau et al., 2009), respectively.

The Moissac-IV assemblage compares well with other Early Oligocene faunas of the Phosphorites of Quercy, such as Cavalé for creodonts (MP22: *Hyaenodon dubius* + *H. leptorhynchus*; Vianey-Liaud & Schmid, 2009), Itardies for Ferae (MP23: *Nimravus intermedius* + *Hyaenodon dubius*; BiochroM'97, 1997), Lébratières 14 for the theridomyid rodent (MP24: *Protechimys lebratierensis*; Vianey-Liaud, 1998), and Le Garouillas, for most macromammals (MP25: *Metriotherium mirabile*, *Plesiomeryx*, *Lophiomeryx chalaniati*, *Eggysodon gaudryi*, and *Nimravus intermedius*; BiochroM'97, 1997). The "Middle" Oligocene locality of Las

Fig. 4. Rhinocérotoïdes de l'Oligocène inférieur de Moissac-IV (SW France). *Protaceratherium albigense*. 16-07, C gauche, vue linguale (**1**); 74-08, M1 droite, vue occlusale (**2**); 02-10, mandibule juvénile, avec di2, d1-d4 et m1-2 droites en vue labiale (**3**); 30-08, mandibule juvénile droite avec d2-4, vue occlusale (**4**). *Eggysodon gaudryi*. 013-07, maxillaire droit juvénile avec D1-D4, vue occlusale (**5**); 06-08, crâne en vues palatine (**6A**) et latérale droite (**6B**); 016-07, C gauche, vue linguale (**7**); 01-08, maxillaire droit avec P1-M3, vue occlusale (**8**); 005-07, hémimandibule droite avec c et p2-m3 en vues labiale (**9A**) et occlusale (**9B**). Barres d'échelle: 20 mm (1, 2, 4, 5, 7, 8, 9B) et 50 mm (3, 6, 9A).
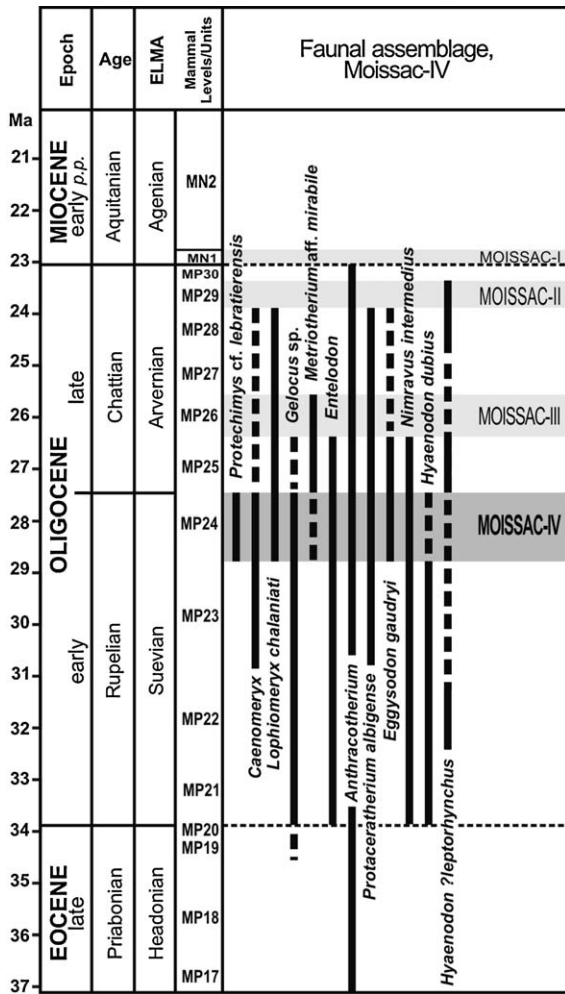
Fig. 5. Stratigraphical range of mammals from Moissac-IV (late Early Oligocene, SW France). Age comparison with other vertebrate localities from Moissac. After BiochroM'97, 1997; Astruc et al., 2003; Erfurt and Métais, 2007; Hugueney, 1997; Lihoreau et al., 2009; Métais and Vislobokova, 2007; Uhlig, 1999 and Vianey-Liaud and Schmid, 2009. The age of the Rupelian/Chattian transition is that proposed by Van Simayes and Vandenberghe, 2006.

Fig. 5. Extension stratigraphique des mammifères de Moissac-IV (fin de l'Oligocène inférieur, SW France). Comparaison avec l'âge des gisements classiques de Moissac. D'après BiochroM'97, 1997 ; Astruc et al., 2003 ; Erfurt et Métais, 2007 ; Hugueney, 1997 ; Lihoreau et al., 2009 ; Métais et Vislobokova, 2007 ; Uhlig, 1999 et Vianey-Liaud et Schmid, 2009. L'âge de la limite Rupélien/Chattien est celui proposé par Van Simayes et Vandenberghe, 2006.

Peyres yields the same rhinocerotoid fauna (Fig. 1; Lihoreau et al., 2009).

As a whole, the concerned assemblage most probably documents the MP24 reference level, as synthesized for all recognized mammals in Fig. 5. The theridomyid *Protechimys lebratierensis* has been originally described on the basis of a rich assemblage (282 teeth) from the fissure filling Lébratières 14 (Phosphorites of Quercy; Vianey-Liaud, 1998). This locality also yields the issiodoromyine rodent *Issiodoromys minor* (grade 1), the evolutionary stage of which allows the concerned site to be correlated with

MP24, as well are some poorer localities, such as Itzac-Delazens (Fig. 1; Vianey-Liaud, 1998). In our opinion, (Astruc et al., 2003) do not provide reliable arguments to push Itzac-Delazens up to MP25 and in turn, to extend the stratigraphical range of *P. lebratierensis* (Vianey-Liaud and Schmid, 2009). We consider *P.* cf. *lebratierensis* as a strong argument for Moissac-IV to be referred to MP24.

So far, the middle-sized creodont *Hyaenodon dubius* had a MP21-MP23 range (Ronzon, Villebramar, Cavalé, Itardies, and Montalbán; Lange-Badré, 1979). Together with the ramus transversely compressed, the robustness and the overlapping of the available premolars represent a derived condition for *H. dubius* (Lange-Badré, 1979), which would make sense with a referral to MP24 for Moissac-IV. The lophiomerycid *Lophiomeryx chalaniati* may have its FAD in Moissac-IV (MP24-28; Métais and Vislobokova, 2007). The dichobunid *Metriotherium* is documented in Early to early Late Oligocene localities from Southern France, ranging from MP22 (*M. minutum*, Villebramar) up to MP27 (*M. sarelense*; Sudre, 1995; Astruc et al., 2003). The specimens from Moissac-IV display close affinities with *M. mirabile*. In Moissac area, Le Garouillas (MP25) yields *M. mirabile* and Puycelci (MP26; Fig. 1) *M.* cf. *sarelense*, respectively (Astruc et al., 2003). To date, the stratigraphical range of *M. mirabile* was MP25-MP26 (Astruc et al., 2003), but the small dimensions of p3 among the present specimens referred to as *M.* aff. *mirabile* would be consistent with an older age for Moissac-IV (i.e., MP24). The hyracodontid *Eggysodon gaudryi* spans the MP24-26 interval with certainty, and it perhaps extends up to MP28 (Hugueney, 1997; Ménouret and Guérin, 2009; Uhlig, 1999). At a regional scale, *E. gaudryi* is mentioned in Latou, Las Peyres, and in various loci from the Phosphorites of Quercy (Fig. 1; Roman, 1912; de Bonis and Brunet, 1995; Uhlig, 1999). Given the size increase observed both for this species and this genus throughout their stratigraphical range (Uhlig, 1999), the small dimensions of *E. gaudryi* in Moissac-IV would point to an age close to its FAD (Fig. 5). The entelodontid *Entelodon* spans the Early Oligocene in France, from Soumailles (MP21: *E. antiquus*), up to Saint-Martin-de-Casselvi (MP25: *E. deguilhemi*; Brunet, 1979; Astruc et al., 2003). The cainotheriid *Caenomeryx* ranges from the middle Early to the Late Oligocene (MP23-?28; Erfurt and Métais, 2007). The rhinocerotid *Protaceratherium albigense* is well known throughout the middle Early-Early late Oligocene interval in southwestern Europe and Turkish Thrace (MP23-28; for review, Lihoreau et al., 2009). *P. albigense*, first defined in La Sauzière Saint-Jean (Fig. 1), was also recognized in Las Peyres, Lafrançaise and Moissac-III, all of them being referred to the MP25-26 interval (Fig. 1; Astruc et al., 2003; Lihoreau et al., 2009; Roman, 1912). In Europe, *Nimravus intermedius* is known from a large sample from the old and undated collections of the Phosphorites of Quercy (Rémy et al., 1987). However, recently found and well-dated material comes from Early Oligocene sites: MP21 (Liptingen 1A, Germany; Scherzinger et al., 2005), MP22 (Mas-de-Got, La Plante 2, and Villebramar in France, Grafenmühle 10 and Möhren 13 in Germany), MP23 (Pech Crabit and Itardies, France) and MP25 (Rigal-Jouet, France). Outside Europe, the species is mentioned from a couple Late Eocene-Early Oligocene Asian sites (Peigné,

2003), but the classification of this material needs to be refined. The specimens from Moissac (e.g., L m1 ranges from 21 to 23.6) have greater dental dimensions than the holotype of *N. intermedius* (MNHN QU 9541; Peigné, 2003: Fig. 5). Considering only the material from well-dated sites, dental measurements (especially p3, p4 and m1) of Moissac specimens, which are distinctly greater than those of specimens from MP21 and MP22 sites, support an age ranging from MP23 to MP25 for that locality. The anthracotheriid *Anthracotherium* ranges from the late Middle Eocene up to the Late Oligocene in Asia and Europe (Lihoreau and Ducrocq, 2007). Its recognition in Moissac-IV is of no biostratigraphical use in the local context. Similarly, and according to Lange-Badré, 1979, Hugueney, 1997, and Astruc et al., 2003, the long-lasting creodont *Hyaenodon leptorhynchus* spans the Oligocene in France (MP22: Mas-de-Got, Villebramar; MP25: Saint-Martin-de-Casselvi; MP28: Pech-du-Fraysse, Cournon; MP29: La Milloque and Dieupentale) and Germany (MP22: Möhren 13; MP29: Gunzenheim). The tentative recognition of this species in Moissac-IV does not further constrain the stratigraphical age of it.

The new diversified meso- and macro-mammal assemblage from Moissac-IV is the oldest vertebrate fauna recognized in the Moissac area. It provides original data just prior the Early-Late Oligocene transition in the middle Garonne basin, a stratigraphical interval which was essentially documented by karstic fillings of the Phosphorites of Quercy so far.

Acknowledgements

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