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A revision of the late early Eocene mammal faunas from Mas de Gimel and Naples (Montpellier, Southern France) and the description of a new theridomorph rodent

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ABSTRACT

European terrestrial mammal sites dated from the late Ypresian are predominantly known from the Paris Basin. In Southern Europe (France and Spain), some localities are also known, but all have only yielded small faunas, composed by few taxa. An exception is the rich locality of Mas de Gimel (city of Montpellier, Hérault, France), which has long been considered the reference fauna of the late Ypresian in Southern Europe. Curiously however, only the rodents, artiodactyls and metatherians from this key locality have been studied in detail since the 1960s. Here, based on the original collection housed in the University of Montpellier, we revise the entire mammal taxa, which leads us to identify 38 species among 12 orders. We also study the close and co-eval localities of Naples and Naples 2, where we identify 23 species among 10 orders. Among the species identified from the three localities, we describe the new theridomorph rodent *Hartenbergeromys paillardensis* n. sp., characterized by numerous thin high extra ridges on upper and lower molars. Compared with the four standard MP (Mammal Paleogene) reference-levels for the European Early Eocene (MP7, MP8+9, MP10a, and the putative ‘MP10b’), the faunal assemblage from Mas de Gimel and Naples is attributed to the MP10a, representing a major European reference for this period. This study also supports the idea that, during the late Ypresian, the mammal faunas from North- and Southwestern Europe are quite homogeneous.

KEY WORDS

Mammalia,
Placentalia,
Metatheria,
Eocene,
Ypresian,
Europe,
France,
new species.

RÉSUMÉ

Révision des faunes de mammifères de la fin de l'Éocène inférieur de Mas de Gimel et de Naples (Montpellier, sud de la France) et description d'un nouveau rongeur théridomorphe.

Les sites européens ayant livré des mammifères terrestres datés de la fin de l'Yprésien sont principalement localisés dans le Bassin de Paris. En Europe méridionale (France et Espagne), quelques localités sont également connues, mais toutes n'ont livré que des faunes pauvres, composées de seulement quelques taxons, à l'exception de la localité de Mas de Gimel (ville de Montpellier, Hérault, France), longtemps considérée comme la faune de référence de la fin de l'Yprésien en Europe méridionale. Curieusement, seuls les rongeurs, les artiodactyles et les métathériens de cette localité-clé ont été étudiés en détail depuis les années 1960. Sur la base de la collection originale conservée à l'Université de Montpellier, nous révisons l'ensemble des taxons de mammifères, ce qui nous amène à identifier 38 espèces parmi 12 ordres. Nous étudions également les localités voisines et contemporaines de Naples et Naples 2, où nous identifions 23 espèces parmi 10 ordres. Parmi les espèces identifiées dans les trois localités, nous décrivons le nouveau rongeur théridomorphe *Hartenbergeromys paillardensis* n. sp., caractérisé par de nombreuses crêtes fines et hautes sur les molaires supérieures et inférieures. Comparé aux quatre niveaux de référence MP (Mammal Paleogene) pour l'Éocène inférieur européen (MP7, MP8+9, MP10a et le possible ‘MP10b’), l'assemblage faunique de Mas de Gimel et de Naples est attribué au MP10a, et représente une référence européenne majeure pour cette période. Ce travail renforce l'hypothèse de l'homogénéité des faunes mammaliennes du Nord- et du Sud-Ouest européen durant l'Yprésien récent.

MOTS CLÉS

Mammalia,
Placentalia,
Metatheria,
Éocène,
Yprésien,
Europe,
France,
espèce nouvelle.

INTRODUCTION

The Ypresian or early Eocene (56–47.8 Ma) corresponds to a key period of the mammalian radiation. At a worldwide scale, study of the fossil record gives evidence for the origin, radiation and dispersals of most extant mammalian orders during this time interval (e.g., Rose 2006). In western Europe, recent data has also shown that an intra-European provincialism affected mammals during this period, with the existence of two bioprovinces (North vs South) during the early-middle Ypresian (Marandat *et al.* 2012). It has been proposed that short-term climate changes, the

so-called Eocene Thermal Maxima (ETMs) triggered this provincialism whereas a subsequent long-term climate warming, the Early Eocene Climate Optimum (EECO) caused European faunal homogenization during the late Ypresian (Noiret *et al.* 2016). However, these apparent synchronicities between mammal evolution and climate changes are based on few data, whether they are mere coincidences or reflect causal relationships remain unknown.

The uncertainties are essentially due to: 1) the absence of available accurate dating of most European mammal faunas relative to ETMs and EECO; and to 2) the lack of a comprehensive paleontological dataset (e.g., only provisional

faunal lists are available for many localities). Regarding the time period of the apparent faunal homogenization, for instance, a more solid taxonomic framework is required for the few known localities from Southwestern France (Mas de Gimel, Naples, Mas de Piquet, and Azillanet) compared to the localities from Northern France (e.g., Prémontré, Grauves, Cuis, Monthelon, Mancy, Chavot, Saint-Agnan, and Venteuil). Among these localities, Mas de Gimel (city of Montpellier, Hérault) was frequently considered as the reference fauna of the late Ypresian in Southwestern France, and was correlated with the MP10 reference level (i.e., Grauves) of the mammalian biochronological scale for the European Paleogene (see Cappetta *et al.* 1968; Hartenberger *et al.* 1969; Hartenberger 1975; Escarguel 1999; Biochron 1997). However only rodents (Hartenberger 1971, 1975; Escarguel 1999; Vianey-Liaud & Marivaux 2021; Vianey-Liaud *et al.* 2022), artiodactyls (Sudre *et al.* 1983; Sudre & Lecomte 2000), and metatherians (Crochet 1979, 1980) have been studied in detail and the systematic assignment of the other mammals only lies on the original mention by Cappetta *et al.* (1968). Regarding the other vertebrate groups, only the characiform fishes have been studied (Cappetta *et al.* 1972; Monod & Gaudant 1998).

The main purpose of this study is therefore to provide a comprehensive and updated overview of the mammal fauna for Mas de Gimel, based on the original collection housed in the University of Montpellier. Our conclusions are also based on new specimens sorted from sediment samples conserved in the same institute since the 1960s. We also study the faunas from Naples and Naples 2, two localities which are coeval in age and geographically situated very close to Mas de Gimel. From Naples, only the artiodactyls (Sudre & Lecomte 2000) and rodents (Escarguel 1999; Vianey-Liaud & Marivaux 2021; Vianey-Liaud *et al.* 2022) have been studied; Naples 2 is a new unpublished locality. In this paper, we describe from Mas de Gimel and Naples a new theridomorph rodent and we propose new systematic assignments for mammals from Mas de Gimel, Naples, and Naples 2. Adding numerous taxa among Eulipotyphla, Pantolesta, Apatotheria, Primates, Chiroptera, Hyaenodonta, Perissodactyla and Artiodactyla, we strengthen correlations with the other European late Ypresian (MP10) localities. For ongoing and future paleobiogeographic and diversity analysis, we also establish for Europe the updated faunal lists for the middle Ypresian (MP8+9) to early Lutetian (MP11) time interval, with a peculiar focus on MP10 faunas. For this purpose, we follow Godinot *et al.* (2018) who proposed Rouzilhac as a potential reference-level for the latest Ypresian (here named 'MP10b', pending approval), implying that Grauves would be MP10a.

GEOLOGICAL AND HISTORICAL CONTEXT

Before the 1960s, the only known early Eocene locality near Montpellier was Mas de Piquet (Fig. 1), which yielded *Hyaenodictis blayaci* (Stehlin, 1926), *Lophiaspis occitanicus* Depéret,

1910, *Lophiodon* sp., and *Pachynolophus* aff. *duvali* Pomel, 1847 (Rouville & Delage 1896: 720; Roman & Gennevaux 1907; Depéret 1921; Stehlin 1926; Solé *et al.* 2018; Vautrin 2019). The precise location of this fossiliferous locus is unfortunately unknown but, in the same area, Hartenberger *et al.* (1969) mentioned the discovery of a second fossiliferous spot, Mas de Piquet 2, with *Pachynolophus* sp. Despite the low diversity of the fossil assemblages, both Mas de Piquet and Mas de Piquet 2 faunas are considered close to the MP10a (see discussion in Danilo *et al.* 2013). Fortunately, as early as the 1960's, geological and paleontological survey in the supposedly coeval late Ypresian levels around Montpellier led to the discovery of several more diversified new localities, providing more constrained ages (Cappetta *et al.* 1968; Hartenberger *et al.* 1969). These field discoveries benefited from important urban development works of Montpellier; the city was then in full expansion (construction of new districts and roads). In 1968, Mas de Gimel was thus discovered east of the *Lac des Garrigues* by the famous field and tectonic geologist Maurice Mattauer during the construction of the Paillade district (now called "quartier Mosson"). The fossiliferous levels were rapidly exploited by the paleontologists of the University of Montpellier during the short interval of these public works, but fossiliferous deposits were unfortunately quickly covered with the completion of the road works (Guilhem de Poitiers Avenue), making access them impossible today (Fig. 1). Twenty years later, in 1988, west of the Lake of Garrigues and nearly 300 m west from Mas de Gimel, the localities of Naples and Naples 2 were discovered during the digging of the foundations of the sports hall Pierre-de-Coubertin, Avenue of Naples.

Eocene levels of Mas de Gimel, Naples, and Naples 2 are south of the Montpellier Thrust, a major onshore compressional structure related to the Pyrenean orogeny (Fig. 1); noteworthy only few outcrops dated from the Eocene occur south of this thrust whereas the Eocene is very well exposed north of this structure. The fossiliferous beds of Mas de Gimel and Naples belong to the same lithostratigraphic unit consisting of brecciated levels underlying whitish to brownish marl with lignite bed. Specimens from Mas de Gimel come from four different thin and superimposed levels (Fig. 1; Cappetta *et al.* 1968). The numbering of the specimens in the original collection does not reflect the existence of several fossiliferous beds and only one level (Mas de Gimel) has been retained. Regarding Naples, two levels have yielded mammals, a dark brown marl, rich in organic matter (Naples) and a whitish marly limestone (Naples 2). Whereas Mas de Gimel and Naples levels essentially yielded micromammals represented by isolated teeth, Naples 2 yielded principally well-preserved remains of large mammals. The Ypresian levels of these localities are overlying Kimmeridgian marine limestone and are underlying Eocene lacustrine limestone poorly constrained in age; see Luccisano *et al.* (2020) for discussion about the age of the late Ypresian/early Lutetian lacustrine limestone of Aumelas, which is possibly coeval with that overlying the Ypresian levels of Mas de Gimel and Naples.

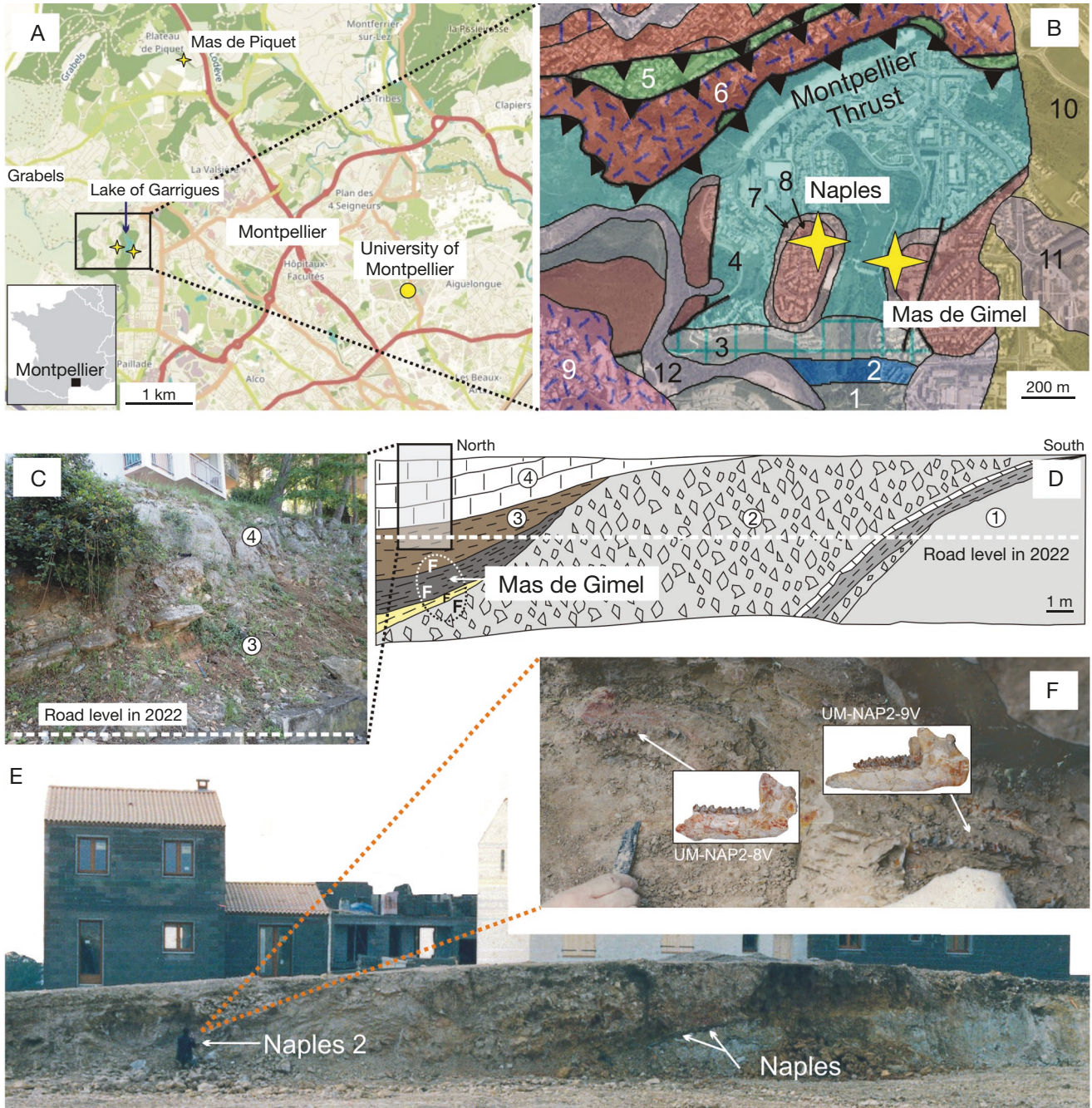


FIG. 1. — Geographic (A) and geological map (B) showing the location of Mas de Gimel, Naples, and Naples 2 (Montpellier, Hérault). Numbers: 1, Callovian; 2, lower Oxfordian; 3, upper Oxfordian; 4, lower Kimmeridgian; 5, Maastrichtian; 6, Paleocene ["Vitrollian"]; 7, late Ypresian; 8, Ypresian/Lutetian; 9, Oligocene; 10, Miocene; 11, Pliocene; 12, Holocene. Actual view (C) and schematic diagram in 1968 (D, modified from Cappetta *et al.* 1968) of Mas de Gimel outcrop, showing that fossiliferous deposits are now inaccessible (under the road level); Numbers: 1, lower Kimmeridgian; 2, late Ypresian brecciated limestone; 3, late Ypresian brownish marl; 4, late Ypresian/early Lutetian lacustrine limestone. View of Naples and Naples 2 localities in 1988 during urban development works (E) and detailed view of Naples 2 fossiliferous level, showing two mandibles of *Lophiodon* Cuvier, 1822 during excavations (F).

MATERIAL AND METHODS

DENTAL NOMENCLATURE

For Eulipotyphla, Apatotheria, Chiroptera, Pantolestia, Pleiadapiformes, Primates, Hyaenodonta, Carnivoraformes, and Perissodactyla, we follow the nomenclature of Van Valen (1966). For Metatheria, Rodentia and Artiodactyla, we fol-

low Muizon & Ladevèze (2022), Vianey-Liaud & Marivaux (2017) and Boisserie *et al.* (2010), respectively.

IMAGES AND MEASUREMENTS OF SPECIMENS

Small mammals are illustrated by X-ray μ CT surface reconstructions using EasyTom 150 microtomograph (MRI platform) and drawings (for the new rodent species only). Medium

(equoids) to large mammal teeth, coated with magnesium, are pictured, respectively, with a Leica M205C stereomicroscope using Leica LAS multifocus image fusion and a Nikon D750/micro-Nikkor 105 mm using Combine ZP for focus stacking. Measurements (in mm) have been made by Leica Application Suite (LAS) for small specimens and calliper for larger specimens.

ABBREVIATIONS

L	maximal mesio-distal length;
W	maximal labio-lingual width;
N	number of specimens;
MP	Mammal Paleogene reference level.

Institutional abbreviations

MNHN	Muséum national d'Histoire naturelle, Paris;
UM	University of Montpellier.

Collection abbreviations

MNHN.F	MNHN Palaeontological collection;
MNHN.FAL	collection "Agéén Lemoine";
MNHN.FGR	Grauves collection;
MNHN.FMT	Monthelon collection;
MNHN.FPRE	Prémontré collection;
MNHN.FSLP	Société laonnaise de Paléontologie collection;
MNHN.FSTA	Saint-Agnan collection;
UM-MGL	Mas de Gimel collection;
UM-NAP	Naples collection;
UM-NAP2	Naples 2 collection (regarding this locality, the suffix following the specimen number refers to the initial private collection, V: Dominique Vidalenc, L: Eric Lopez).

RESULTS

REVISION OF THE MAMMAL FAUNAS FROM MAS DE GIMEL AND NAPLES

Mas de Gimel

Metatheria. Among metatherians from Mas de Gimel (N = 101, including unpublished material), three herpetotheriid species are recognized by Crochet (1979, 1980): *Peratherium matronense* Crochet, 1979, *Peratherium monspeliense* Crochet, 1979, and *Amphiperatherium bourdellense* Crochet, 1979. Mas de Gimel is the type locality for *P. monspeliense*. Upper and lower molars of *P. matronense* and *P. monspeliense* from Mas de Gimel are highly similar in morphology, but those of *P. matronense* are smaller (e.g., UM-MGL-310, left m1, L = 1.60; W = 0.94, Fig. 2A). An ongoing revision of the systematics of European metatherians from the early Eocene will address the taxonomic status of those herpetotheriids. Pending further conclusions, the temporal extensions of *P. matronense* and *P. monspeliense* remain large. Indeed, *Peratherium matronense* is documented from localities in the MP7-MP8+9 interval (Rians and possibly Fournes; Godinot 1981, Marandat 1991), MP8+9 (Condé-en-Brie, the type-locality, Avenay, Sables de Brasles, Sézanne-Broyes and Evere; Crochet 1980, Smith & Russell 1992), MP10a (Coulondres; Crochet 1980) and ?MP10-11 (Vielase, Quercy; Legendre *et al.* 1992) to the middle Eocene locality of Santa Clara (Spain; Peláez-

Campomanes *et al.* 1989). *Peratherium monspeliense* is mostly restricted to MP10a faunas from southern France (Coulondres, Saint-Clement-de-Rivière and Azillanet; Crochet 1980, Marandat 1986) and is presumably present in Fournes and La Gasque (MP7-MP8+9 interval; Marandat 1991; Noiret *et al.* 2016), and Geiseltal (MP12-13; Storch & Haubold 1989).

Regarding *Amphiperatherium bourdellense*, it spans much of the Eocene (Crochet 1979: fig. 16), from MP8+9 localities of the Paris Basin (Condé-en-Brie, Avenay, Sables de Brasles and Sézanne-Broyes) to its type locality, Le Bretou (Quercy, MP16, late Eocene) (Crochet 1980). The only tooth from Mas de Gimel attributed by Crochet (1980) to this species is a worn left m1 with a fragmented talonid (UM-MGL-143, W = 0.95, Fig. 2B). The morphology of this molar is similar to that of *P. matronense* and *P. monspeliense* (Fig. 2A); it differs from the only m1 of *A. bourdellense* available from Le Bretou (UM-BRT-843, unpublished specimen) by a higher paraconid. An assignment to *P. matronense* or *P. monspeliense* is therefore more parsimonious for UM-MGL-143.

The poorly preserved lingual fragment of right M3 UM-MGL-309 exhibits two relatively huge conules and a large protocone, larger than all homologous dental remains from Mas de Gimel. Among the relatively large herpetotheriid species, this specimen is closer in size (as deduced from the length of the preproto- and postprotocristae and the size of the conules) to the holotype of *Amphiperatherium maximum* Crochet, 1979 (a species only known in Saint-Agnan and Grauves among French [-]MP10a localities; Crochet 1980; Louis & Laurain 1983), than to the slightly smaller *Amphiperatherium bastbergense* Crochet, 1979, the latter being probably present in Naples. However, the fragmentary nature of UM-MGL-309 and the weakly documented intraspecific variation of *A. maximum* M3 prevent its formal attribution; it is hereafter named Herpetotheriidae gen. and sp. indet.

We also identify two peradectid metatherians, the first known in Mas de Gimel. One of these taxa is documented by a small right labial fragment of M2 (UM-MGL-716, L = 1.48, Fig. 2C) displaying gracile and almost triangular paracone and metacone, a nearly straight centrocrista (only just labially curved, clearly distinct from the V-shaped centrocrista of herpetotheriids), a salient postmetacrasta forming a high distal wall on the stylar shelf, and labiolingually pinched stylar cusps distal to the deepest point of the ectoflexus, of which one is distally placed on the stylar shelf compared to the apex of the metacone. Up to now, the combination of these characters is only observable on *Peradectes* sp. from Azillanet (Marandat 1986: pl. 1, fig. 2) and Coulondres (Crochet 1980: fig. 28), limiting the attribution of UM-MGL-716 to cf. *Peradectes* sp. in Marandat (1986).

The right m4 UM-MGL-320 (Fig. 2D, L > 1.59 mm; W > 0.85 mm) is damaged on the whole labial margin and on the lingual part of the talonid. The trigonid is apparently longer than wide, with a distolingual metaconid relative to the protoconid. This morphology of the trigonid is not retrieved on herpetotheriid m4, but is distinctive of most peradectids. The size of the trigonid permits to compare it with lower molars referred to *Peradectes mutigniensis* Crochet, 1979 rather than those of the smaller *P. louisii* Crochet, 1979, and cf. *Peradectes* sp. in

Marandat (1986) from Mas de Gimel. UM-MGL-320 is thus attributed to *Peradectes* cf. *mutigniensis*. *Peradectes mutigniensis* is so far documented from MP8+9 localities of the Paris Basin (Mutigny, Avenay, Sables de Brasles and Condé-en-Brie) and the MP10a localities of Saint-Agnan (Louis & Laurain 1983), and possibly Vielase (Legendre *et al.* 1992).

Eulipotyphla. Eulipotyphlan mammals are represented by amphilemurids and nyctitheriids. The amphilemurid species *Macrocranion* cf. *nitens* (Matthew, 1918) (*sensu* Russell *et al.* 1975) is represented by two morphs, one of small size (morph A hereafter, N = 7; identical in size to the population of Avenay; e.g., right m3 UM-MGL-455; L = 1.67; W = 1.03) (Fig. 2F) and another of larger size (morph B hereafter, N = 14; identical in size to the population of Mutigny and Grauves; e.g., right m1 or m2 UM-MGL-426; L = 2.17; W = 1.64). The larger morph B cannot be attributed to *M. tenerum* (Tobien, 1962) from Messel (MP11) by the simplicity of the p4 without individualized entoconid and hypoconid (Fig. 2G); the upper molars are clearly more transversally elongated, they have more extended parastylar lobe and a more powerful labial shelf, and the ectoflexus is more accentuated (see Storch 1993) (see also the specimens from Naples; Fig. 2H-I). Interestingly, the existence of two morphs of *Macrocranion* cf. *nitens* in Mas de Gimel supports the assumption of Smith & Smith (1995) that at least two species are represented in the Paris Basin at the MP8+9 and MP10a. A revision of these taxa, based on the unpublished specimens from Condé-en-Brie (MP8+9) and Prémontré (MP10a) (Dégremont *et al.* 1985) appears necessary. Recently, *Macrocranion* cf. *nitens* has also been identified in Egem (Belgium, c. MP8+9) (Smith & Smith 2013).

A second amphilemurid is represented by *Macrocranion* sp. (*sensu* Russell *et al.* 1975) (N = 14), a species which is rare in Avenay but more common in Condé-en Brie. This large *Macrocranion* species (e.g., right m3 UM-MGL-425; L = 2.96; W = 1.92) (Fig. 2J) was also reported at the MP10a in Saint-Agnan and Prémontré (Louis & Laurain 1983; Dégremont *et al.* 1985) and described during the ?MP10-MP11 interval in Amélas (Maitre *et al.* 2008). This species differs from *M. tupaion* Weitzel, 1949 from Messel (MP11) by lower and more swollen cusps, a shorter trigonid (the paracristid is more lingually oriented), and a more mesiodistally extended entoconid. Note that this amphilemurid is represented in Naples by upper molars (see below; Fig. 2K-L).

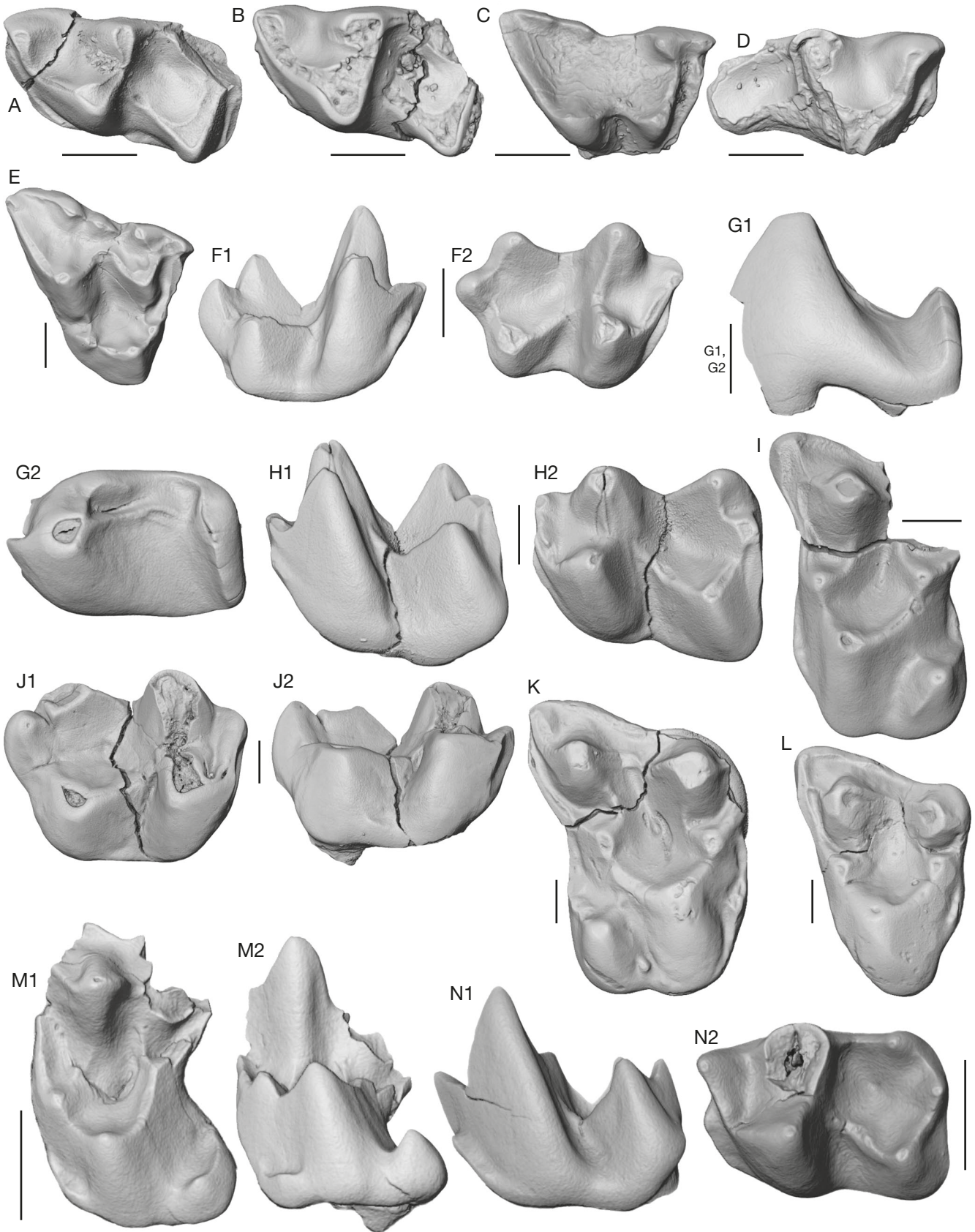
The nyctitheriid *Leptacodon* sp. (N = 5) is recognized by a complete left m1 or m2 (UM-MGL-802, L = 1.25; W = 0.89) (Fig. 2N) and fragmentary upper teeth. Distinctive characters of the family and genus are crestiform paraconid, subequal entoconid and hypoconid (a taller entoconid is diagnostic of *Plagioctenodon* Bown, 1979), cusps and median hypoconulid on lower molar, molariform P4 bearing a moderately high metacone (left P4 UM-MGL-459), gracile M1 or M2 with two conules, a developed postcingulum bearing a well-distinct

hypocone, and a distinct precingulum (Fig. 2M). This species is rather similar in size with *Leptacodon* sp. from Egem; they share also the lack of a postparaconule crista. Smith & Smith (2013) have however mentioned that the systematic value of this character is hard to estimate as it also occurs in *L. nascentoi* Estravis, 1996 from the ~MP7 of Silveirinha, Portugal. Pending a study of the unpublished dental specimens of *Leptacodon* from the MP8+9 (Avenay and Mutigny) and MP10a (Prémontré) (Dégremont *et al.* 1985; Smith & Smith 2013), the species from Mas de Gimel remains undetermined. We can keep in mind however that it clearly differs from *Leptacodon ceciliensis* Storch & Haubold, 1989 from the Geiseltal-Obere Mittelkohle (MP13) (Storch & Haubold 1989; Manz & Bloch 2015), by a more lingual cristid obliqua, deeper hypoflexid, cuspsate entoconid, and shorter talonid basin.

A second, larger, nyctitheriid species (N = 4) characterised by dilambdodont upper molars appears intermediate in morphology between *Wyoncteris* Gingerich, 1987 and *Pontifactor* West, 1974. This new nyctitheriid will be described in a separated paper; it is indeed documented by unpublished better-preserved specimens from Azillanet and La Rouyere (MP10a, Minervois, Southern France). It differs from *Wyoncteris* by smaller conules, absence of a pericone, and a more advanced dilambdodonty (duplicated mesostyle). It differs from *Pontifactor* (a monospecific genus from the middle Eocene of North America) by a less developed stylocone and more transverse upper molars. Interestingly, Dégremont *et al.* (1985) mentioned also *Pontifactor* sp. in Prémontré.

Apatotheria. An apatemyid mammal is documented by the left m2 UM-MGL-810 (L = 3.18; W = 2.00) (Fig. 3B). Typical characters of the family are a low trigonid with a reduced paraconid, the occurrence of a mesiolabial paralophid resulting in a quadrate trigonid, the absence of labial and lingual cingulids, and a rounded talonid. Apatemyids from the levels MP8+9 (Mutigny and Avenay) and MP10a (Grauves and Cuis) are all members of the genera *Apatemys* Marsh, 1872 and *Heterohyus* Gervais, 1848 (see Russell *et al.* 1979). Distinguishing these two genera on the basis of a lower molar is not easy. In comparison with *Apatemys*, the genus *Heterohyus* was proposed to have a more conical paraconid in mesial view (instead of crestiform), a more obtuse mesio-labial angle of the trigonid in occlusal view (but we note an important variation of this character) without any trace of a fourth trigonid cusp, and a smaller entoconid, more distant from the metaconid (Russell *et al.* 1979: 224). Moreover, following the measurements given by Russell *et al.* (1979), *Heterohyus* species are significantly larger than *Apatemys* ones. Considering all these data, UM-MGL-810 is tentatively attributed to *Heterohyus* sp. In size, this tooth is compatible with the large upper molars of *Heterohyus* sp. from Grauves and Cuis (Russell *et al.* 1979). A smaller *Heterohyus* species is documented in Avenay and Prémontré (Dégremont *et al.* 1985).

Fig. 2. — Metatheria and Eulipotyphla from Mas de Gimel and Naples: **A**, left m1 UM-MGL-310 of *Peratherium matronense* Crochet, 1979 in occlusal view; **B**, left m1 UM-MGL-143 of *Peratherium matronense* or *Peratherium monspeliense* Crochet, 1979 in occlusal view; **C**, labial fragment of right M2 UM-MGL-716 of cf. *Peradectes* sp. in Marandat (1986) in occlusal view; **D**, right m4 UM-MGL-320 of *Peradectes* cf. *mutigniensis* in occlusal view; **E**, right M1 UM-NAP-125 of cf. *Amphiperatherium bastbergense* Crochet, 1979 in occlusal view; **F-I**, Teeth of *Macrocranion* cf. *nitens*: right m3 UM-MGL-455 in labial (**F1**) and occlusal (**F2**) views



(small morph); left p4 UM-MGL-439 in labial (**G1**) and occlusal (**G2**) views, left m1 or m2 UM-NAP-2 in labial (**H1**) and occlusal (**H2**) views, left M2 UM-NAP-3 in occlusal view (**I**) (large morph); **J-L**, teeth of *Macrocranion* sp.: right m3 UM-MGL-425 in occlusal (**J1**) and labial (**J2**) views, right M2 UM-NAP-6 in occlusal view (**K**), left M3 UM-NAP-7 in occlusal view (**L**); **M, N**, teeth of *Leptacodon* sp.: left M1 or M2 UM-MGL-105 in occlusal (**M1**) and lingual (**M2**) views, left m1 or m2 UM-MGL-802 in labial (**N1**) and occlusal (**N2**) views. Scale bars: 0.5 mm.

Chiroptera. Bats are represented by three species. A minuscule Palaeochiropterygidae gen et sp. indet. is documented by a left m3 (UM-MGL-107, L = 1.23; W = 0.83) (Fig. 3C) and two poorly preserved upper molars (note that a sub-complete upper molar from Naples is attributed to this taxon, see below). Diagnostic characters of the family observed in the m3 are the very lingual direction of the cristid obliqua and the strong nyctalodonty associated with the lingual position of the hypoconulid distal to the entoconid (Hand & Sigé 2018). This m3 differs from that of *Palaeochiropteryx tupaiodon* Revilliod, 1917 and *P. spiegelii* Revilliod, 1917 by smaller size, less prominent and relatively lower cuspids; it further differs from *Matthesia* by the lack of bulbous cuspids; it is larger than *Microchiropteryx* Smith, Rana, Missiaen, Rose, Sahni, Singh & Singh, 2007 (Smith *et al.* 2007) and does not present the elongated and narrow crown that is characteristic of this genus; finally, relative to *Stehlinia* Revilliod, 1919, it differs from the oldest species *S. alia* Maitre, 2014 known from Aumelas (Maitre 2014) by smaller size and minor trigonid/talonid height difference. Further comparisons are possible thanks to the upper molar from Naples (see below; Fig. 3D).

A second palaeochiropterygid bat is represented by *Palaeochiropteryx* cf. *tupaiodon* (N = 2). The right m1-2 UM-MGL-449 (L = 1.45; W = 1) (Fig. 3F) is similar in morphology with *P. tupaiodon* from Messel but falls below the smallest individuals referred to this species. Interestingly, Russell *et al.* (1973) mentioned a similar small m1 from Grauves suggesting that the genus *Palaeochiropteryx* is represented as early as the MP10a by a species, smaller than *P. tupaiodon*.

A third bat, only documented by the small left P4 UM-MGL-456 (L = 1.28; W = 1.19) (Fig. 3E), is attributed to ?Icaronycteridae sp. indet. It differs from Palaeochiropterygidae and Archaeonycteridae by a slightly protruding parastyle and a short postparacrista. It resembles *Icaronycteris menui* Russell, Louis & Savage, 1973 from Avenay and Mutigny by a similar small size and the lack of hypocone. Note that a second, larger, Icaronycteridae species is present in Naples (see below; Fig. 3G-H).

Pantolestia. A pantolestid mammal, represented by the incomplete left M1 or M2 UM-MGL-424 (L > 3.45; W = 4.63) (Fig. 3I), probably documents a new taxon, significantly smaller than species attributed to the genera *Premontrelestes* Smith, 2001 and *Pantolestes* Cope, 1872 from Prémontré and to *Buxolestes* Jaeger, 1970 from Messel and Bouxwiller (Jaeger 1970; Koenigswald 1980; Smith 2001). This taxon also differs from any known pantolestid taxa from the early and middle Eocene of Europe by a moderate lingual expansion of the hypocone. Note that a second, larger, pantolestid species attributed to ?*Pantolestes sabatieri* is present in Naples (see below; Fig. 3J).

Plesiadapiformes. The paromyid *Arcius lapparenti* Russell, Louis & Savage, 1967 is represented by the right m2 UM-MGL-741 (L = 2.04; W = 1.62) (Fig. 3K). This assignment is supported by low crown with blunt cuspids, a tiny paraconid placed lingually, small difference in height between the trigonid and the talonid, a wide talonid basin, and a mesio-distally

compressed trigonid, not as mesially inclined relative to the level of the base of the talonid basin as in any other paromyid genus (Godinot 1984; López-Torres & Silcox 2018). Measurements of UM-MGL-741 match those of *Arcius lapparenti*, the largest *Arcius* species. Originally described from Avenay (Russell *et al.* 1967), *A. lapparenti* is also present in various MP10a localities from the Paris Basin (Grauves, Venteuil, Saint-Agnan, and Prémontré) and Southern France (Azillanet) (Aumont 2003; López-Torres & Silcox 2018).

Primates. They are confidently represented by three species. The most well-documented species is attributed to cf. *Protoadapis curvicspidens* (Lemoine, 1878) (N = 7), known from various MP10a localities of the Paris Basin (“Epernay” [for Lemoine’s specimens, including the holotype], Grauves, Monthelon, and Cuis) (Russell *et al.* 1967). The right p2 UM-MGL-739 is short, has two fused roots, and a single pointed cuspid (L = 2.88; W = 2.02). The left p4 UM-MGL-548 (L = 4.78; W = 3.05) (Fig. 4A) is a robust tooth with a well-defined metaconid and a small paraconid (as in MNHN.F.AL5180, a specimen which was described by Teilhard de Chardin [1922]). The left m2 UM-MGL-740 (L = 4.88; W = 3.6) (Fig. 4B) does not have an enlarged talonid basin and has a long subhorizontal paralophid with a residual paraconid; a very shallow groove separates the paraconid from the paralophid. The right M2 UM-MGL-542 (L = 4.27; W = 6.28) (Fig. 4C) is highly transverse (much more than in *Europolemur* Weigelt, 1933), rectangular in outline with rounded corners, and has lingually displaced paracone and metacone. The presence/absence of the metaconule is variable; it is absent on UM-MGL-542 but present on the fragmentary molars UM-MGL-486 and UM-MGL-547. As a whole, these characters support the attribution to *Protoadapis* rather than to *Europolemur*. Measurements match those of *P. curvicspidens* Lemoine, 1878. However, because of: 1) the massive hypocone and the enlarged mesiolingual cingulum observed in UM-MGL-542, which are convergent characters with species of *Periconodon*; and 2) the scarcity of published M2 of *P. curvicspidens* (MNHN.F.AL5191), we maintain the species from Mas de Gimel in open nomenclature pending a complete revision of the *Protoadapis-Europolemur* group (see Godinot 2015; Godinot *et al.* 2018, 2021).

A second primate is attributed to *Anchomomys* sp. This species is only represented by a fragmentary right lower molar (UM-MGL-551) characterised by an elongated talonid basin and a distolingually positioned entoconid relative to hypoconid. Note that a complete m1 (UM-NAP-31) of this anchomomyine species is present in Naples (see below; Fig. 4D).

The third primate is attributed to the microchoerid *Nannopithex zuccollae* Godinot, Russell & Louis, 1992 (N = 8), a species described from Prémontré and probably present, but extremely rare, in Grauves and Saint-Agnan (Godinot *et al.* 1992). The left p3 UM-MGL-408 is markedly smaller (L = 1.35; W = 0.89) (Fig. 4E) than the left p4 UM-MGL-413 (L = 1.7; W = 1.44) which is subrectangular and massive, with a high labial enamel wall (Fig. 4F2). Such an inflated p4 is diagnostic of *Nannopithex* Stehlin, 1916. Moreover, the p4 trigonid has a crestiform paraconid and a small low metaconid;

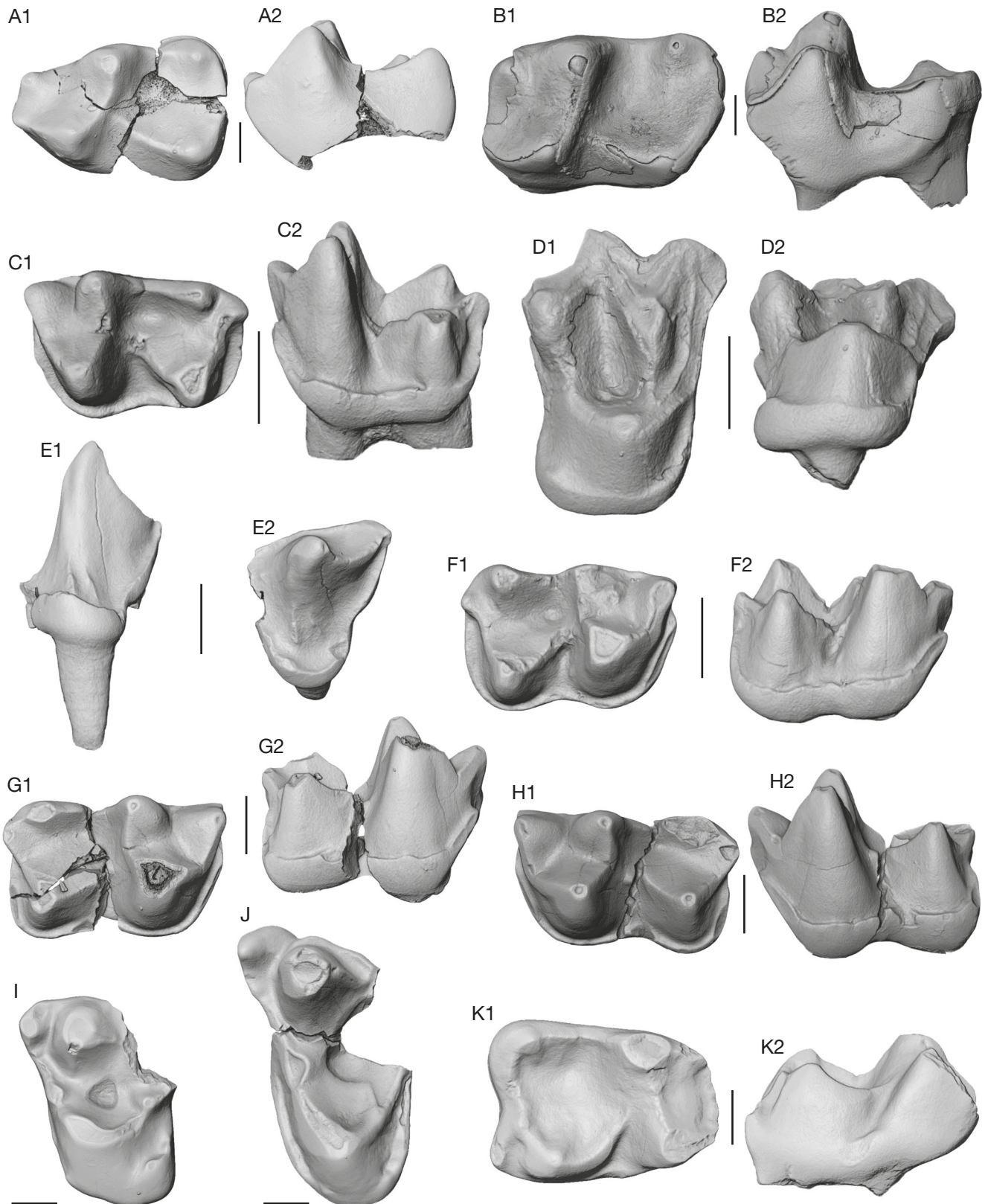


FIG. 3. — Apatotheria, Chiroptera, Pantolestia, and Plesiadapiformes from Mas de Gimel and Naples: **A, B**, molars of *Heterohyus* sp.: left m1 UM-NAP-16 in occlusal (**A1**) and labial (**A2**) views, left m2 UM-MGL-810 in occlusal (**B1**) and labial (**B2**) views; **C, D**, molars of Palaeochiropterygidae gen. et sp. indet.: left m3 UM-MGL-107 in occlusal (**C1**) and labial (**C2**) views, right M1 or M2 UM-NAP-19 in occlusal (**D1**) and lingual (**D2**) views; **E**, left P4 UM-MGL-456 of ?*Icaronycteris* sp. indet. in lingual (**E1**) and occlusal (**E2**) views; **F**, right m1-2 UM-MGL-449 of *Palaeochiropteryx* cf. *tupaiodon* Revilliod, 1917 in occlusal (**F1**) and labial (**F2**); **G, H**, molars of *Icaronycteris* sp.: right m1 or m2 UM-NAP-20 in occlusal (**G1**) and labial (**G2**) views, left UM-NAP-21 in occlusal (**H1**) and labial (**H2**) views; **I**, left M1 or M2 UM-MGL-424 of Pantolestidae gen. et sp. indet. in occlusal view; **J**, left M3 UM-NAP-1 of ?*Pantolestes sabatieri* Smith, 2001 in occlusal view; **K**, right m2 UM-MGL-741 of *Arcius lapparenti* in occlusal (**K1**) and labial (**K2**) views. Scale bars: A-H, K, 0.5 mm; I, J, 1 mm.

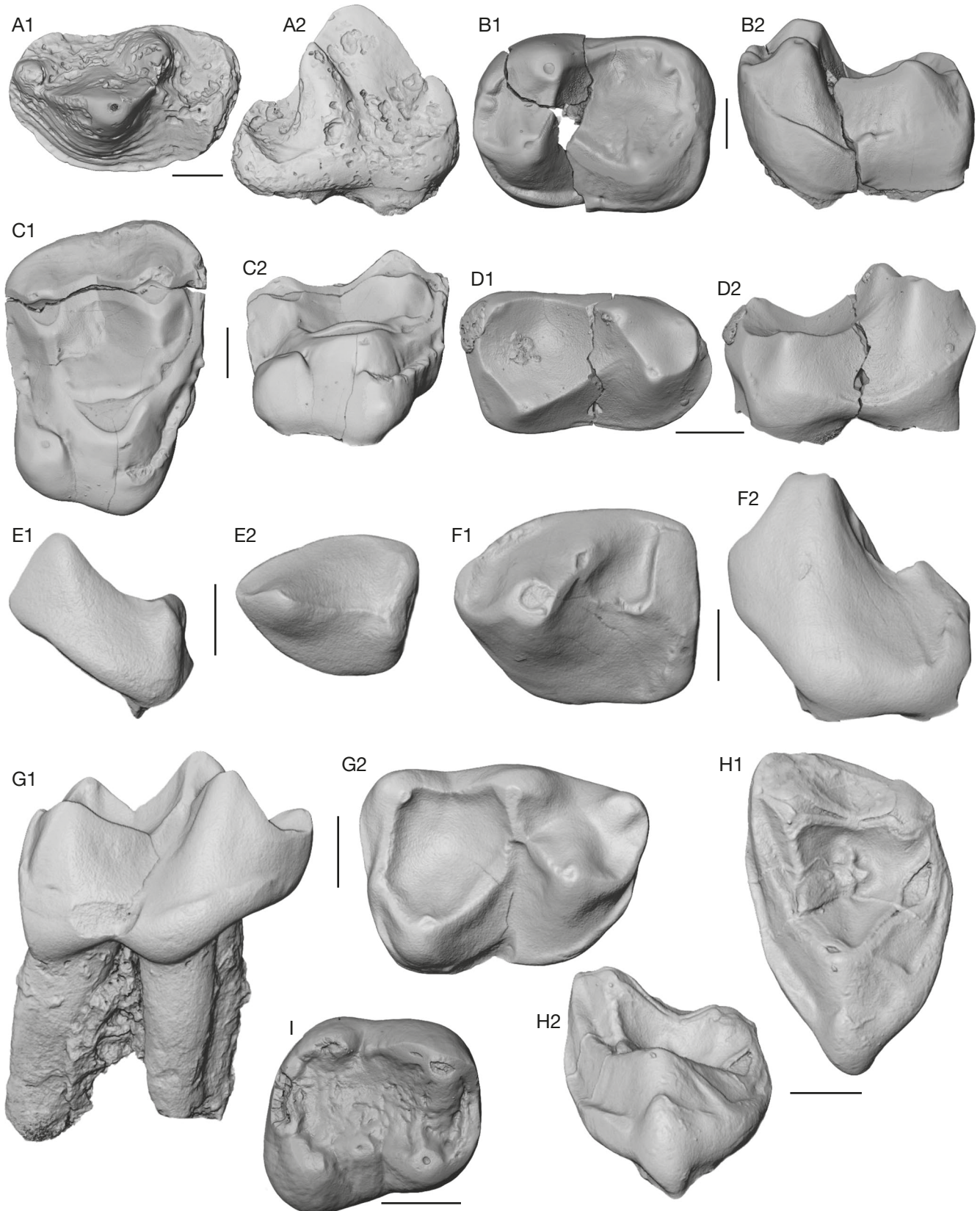


FIG. 4. — Primates and Rodentia from Mas de Gimel and Naples: **A-C**, teeth of cf. *Protoadapis curvicspidens* (Lemoine, 1878): **A**, left p4 UM-MGL-548 in occlusal (**A1**) and lingual (**A2**) views; **B**, left m2 UM-MGL-740 in occlusal (**B1**) and labial (**B2**) views; **C**, right M2 UM-MGL-542 in occlusal (**C1**) and lingual (**C2**) views; **D**, right m1 UM-NAP-31 of *Anchomomys* sp. in occlusal (**D1**) and labial (**D2**) views; **E-H**, teeth of *Nannopithecus zuccolae* Godinot, Russel & Louis, 1992: **E**, left p3 UM-MGL-408 in labial (**E1**) and occlusal (**E2**) views, left p4 UM-MGL-413 in labial (**F1**) and occlusal (**F2**) views, right m1 UM-MGL-401 in labial (**G1**) and occlusal (**G2**) views, left upper molar UM-MGL-743 in occlusal (**H1**) and lingual (**H2**) views; **I**, right m1 UM-MGL-219 of *Pseudoparamys* sp. indet. in occlusal view. Scale bars: A-D, I, 1 mm; E-H, 0.5 mm.

no real cuspid is developed on the talonid crest. The right m1 UM-MGL-401 (L = 1.97; W = 1.44) (Fig. 4G) has a strong and cusperate paraconid; the entoconid is considerably lower than the metaconid; the hypoconulid is weak. The left upper molar UM-MGL-743 (L = 1.48; W = 2.32) (Fig. 4H) has a short postprotocone-fold (= *Nannopithec*-fold), the hypocone is absent, and the conules are present.

Rodentia. Rodents from Mas de Gimel have been the subject of recent studies (Escarguel 1999; Vianey-Liaud *et al.* 2019, 2022; Vianey-Liaud & Marivaux 2021) but some specimens and taxa need some review considering recent advancement on the systematics of the group.

Among ischyromyoids, *Ailuravus* aff. *micchauxi* Hartenberger, 1975 (N = 5) is the largest rodent species from Mas de Gimel (see Escarguel 1999: 125, plate1). This ailuravid is known from various ~?MP8+9 (Pourcy, Rians) to MP10 (Grauves, Cuis, Prémontéré, Wittering Formation in the Sussex, and Naples, see below) localities.

A second ischyromyoid is *Eogiliravus wildi* Hartenberger, 1971 (N = 23); this species defined from Mas de Gimel is the smallest rodent from the locality. It was revised by Escarguel (1999: 240) and Vianey-Liaud *et al.* (2022: 757). This species, that interestingly represents the oldest known Gliridae, is exclusively documented from MP10a (Prémontéré, Azillanet, and Naples, see below) to ?MP10-11 (Cos and Vielase) localities. Noteworthy, Vianey-Liaud *et al.* (2022) suggested that the *Eogiliravus* species from Messel, attributed to *E. wildi* by Storch & Seiffert (2007), is more reminiscent of *E. hammeli* (Thaler, 1966) from Bouxwiller.

Among theridomorphs, two plesiarctomyid species are documented. *Pseudoparamys* sp. indet. is represented by the unique right m1 UM-MGL-219 (L = 2.31; W = 2.18) (Fig. 4I). Judging from unique specimen, the closest species is *P. lapicidinarum* (Escarguel, 1999) from Condé-en-Brie, which has been described on the basis of a few teeth (Escarguel 1999: 58-59), without any m1. The m1 from Mas de Gimel is narrow labiolingually and the talonid basin is not markedly deeper than that of the trigonid, whereas the difference of depth is much more marked on the m2 of *P. lapicidinarum*. The small bulged mesoconid bears low short mesolophid and ectomesolophid, but there is no trace of the ectolophid seen on the m2 from Condé-en-Brie. On the distal surface of the basin the entolophid is not distinct from a few low extra ridges, developed between a short low prehypocristid and the labial flank of the entoconid. The labial slopes, mainly that of the protocone, are thinly wrinkled.

The second plesiarctomyid, *Plesiarctomys* cf. *savagei* (Michaux, 1964), is documented by a left m2 (UM-MGL-663, Escarguel 1999: pl. 17F), a much worn right m1 (UM-MGL-662) and a damaged upper molar (UM-MGL-661). The size of the m2, the best-preserved specimen, is close to that of *P. savagei* from Prémontéré. A few differences can be found however. The lingual end of the metalophid I is not free (it connects the anterolophid); the crestulids are more numerous on the floor and the edges slopes of the talonid; and the crenulations are more pronounced on the outer slopes of the main cuspid.

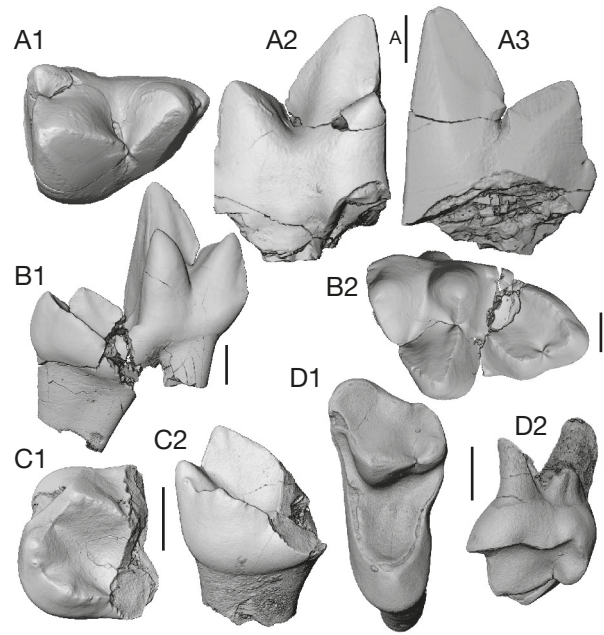


Fig. 5. — Hyaeodontidae and Carnivoraformes from Mas de Gimel: **A**, trigonid of right lower m1? of *Matthodon peignei* Solé, Marandat & Lihoreau, 2020 UM-MGL-70 in occlusal (**A1**) lingual (**A2**) and labial (**A3**) views; **B**, left m3 of *Leonhardtina meridianum* Solé, Marandat & Lihoreau, 2020 UM-MGL-707 in lingual (**B1**) and occlusal (**B2**) views; **C**, talonid of a left m1 of *Lesmesodon gunnelli* Solé, Morlo, Schaal & Lehmann, 2021 UM-MGL-36 in occlusal (**C1**) and lingual (**C2**) views; **D**, left M3 of *Uintacyon* cf. *hookeri* Solé, 2014 UM-MGL-108 in occlusal (**D1**) and labial (**D2**) views. Scale bars: A, 2 mm; B, C, 1 mm; D, 0.5 mm.

Another theridomorph is the massillamyid *Masillamyx mattaueri* Hartenberger, 1975, a species defined from Mas de Gimel. It is the most common rodent species in the locality (N = 85). This theridomorph has been recently revised by Vianey-Liaud *et al.* (2019: 461, 471-477) and represents a species less derived than *M. cosensis* Vianey-Liaud, Vidalenc, Orliac, Maugeoust, Lézin & Péliissié, 2022 from the ?MP10-11 locality of Cos (Vianey-Liaud *et al.* 2022).

The last rodent species belongs to the genus *Hartenbergeromys* Escarguel, 1999. Escarguel (1999) then Vianey-Liaud & Marivaux (2021) attributed this species to *Hartenbergeromys* aff. *hautefeuillei*. The material is revised in the second part of this section and attributed to a new species.

Hyaenodonta. Hyaenodonts are represented by three taxa of Hyaenodontidae. We recognized *Matthodon peignei* Solé, Marandat & Lihoreau, 2020 (Solé *et al.* 2020), a species known until now only from Aumelas. This large species is represented by a talonid of a right m1 (UM-MGL-31; W = c. 6.07) and a trigonid of lower m1? UM-MGL-70 (L = c. 7.87) (Fig. 5A).

We also recognized *Leonhardtina meridianum* Solé, Marandat & Lihoreau, 2020 (Solé *et al.* 2020), based on the left m3 UM-MGL-707 (L = ~5.9; W = 3.42) (Fig. 5B). The morphology of this tooth reminds the genera *Leonhardtina* Matthes, 1952 and *Lesmesodon* Morlo & Habersetzer, 1999 but its size is closer to that of *L. meridianum* also known from Aumelas and Rouzilhac (late Ypresian/early Lutetian) (Solé *et al.* 2020).

We finally recognized *Lesmesodon gunnelli* Solé, Morlo, Schaal & Lehmann, 2021 (Solé *et al.* 2021) on a talonid of

the left m1 UM-MGL-36 ($W = c. 2.34$) (Fig. 5C) clearly smaller than *Leonhardtina meridianum*. Its size and the strong labial cingulid better match with *Les. gunnelli* from Prémontré (Solé *et al.* 2021).

Carnivoraformes. The two upper molars UM-MGL-419 ($L = 1.37$; $W = 2.37$) and UM-MGL-108 ($L = 1.12$; $W = 2.25$) (Fig. 5D) with rectangular outline (protocone not twisted) display a rounded and not projected parastyle, lack a metastylar blade and metaconule, and show a weak metacone development compared to paracone. These traits indicate M3s of carnivoraformes. Among the Eocene European carnivoraformes that possess M3 (excluding *Quercygalie* Kretzoi, 1945 from the MP8+9 and MP10 and *Messelogale* Springhorn, 2000 from the MP11), this taxon differs from *Gracilocyon rundlei* (Hooker, 2010) (MP8+9, Abbey Wood, England; Hooker 2010) by its reduced to absent conules, and rather reminds the small genus *Uintacyon* Leidy, 1872 notably by its reduced stylar shelf. The M3s are smaller than those of *U. rudis* Matthew, 1915 (probably present in Abbey Wood [see Hooker 2010; Solé 2014]) and close to the unique M3 of *U. hookeri* Solé, 2014 known from Brasles ($L = 1.4$; $W = 3.33$; Solé 2014). However, they are less transversely elongated and their basin are larger with their crests joining the protocone to the conules being less internal than in *Uintacyon hookeri*. Considering the possible intraspecific variability, we refer the two specimens from Mas de Gimel to *Uintacyon cf. hookeri*. *Uintacyon hookeri* is known from Mutigny, Avenay, Condé-en-Brie, Brasles and Cuis extending during the MP8+9-MP10a interval (Solé 2014).

Artiodactyla. Five artiodactyl species are recognized at Mas de Gimel. Among them, *Protodichobune oweni* Lemoine, 1878 and *Cuisitherium lydekkeri* (Lemoine, 1891) have already been mentioned and illustrated in Sudre (1980), Sudre *et al.* (1983) and Sudre & Lecomte (2000). *Protodichobune oweni* is recognized in Mas de Gimel by four specimens. Three upper molars already published are bunodont with a triangular outline and marked mesostyle on the labial cingulum (Sudre *et al.* 1983): left M2 UM-MGL-27 ($L = 4.9$; $W = 6.3$, Fig. 6A), right M2 UM-MGL-6 ($L = 5.1$; $W = 7.4$) and right M3 UM-MGL-7 ($L = 4.5$; $W = 6.4$). The eroded broken m3 UM-MGL-812 ($L = 6.8$; $W = 4.0$) displays conical and enlarged cuspid with a slightly distally positioned entoconid as in the type specimen of *Protodichobune oweni* MNHN.F.AL5232. It falls within the range of m3 measurements from Cuis, Monthelon and Mancy ($L = 6.2-7$; $W = 3.6-5.3$ in Sudre *et al.* 1983). It differs from *Protodichobune hellmundi* Erfurt, 2018 from Rouzilhac (Godinot *et al.* 2018) by the smaller size of its lower molars and the presence of a paraconid.

Cuisitherium lydekkeri ($N = 5$) is recognized on the basis of a quadrangular molar with lingual displacement of the metaconule, and the paraconule very close to the protocone (UM-MGL-03, UM-MGL-28, UM-MGL-503). Initially described within the hypodigm of *Protodichobune lydekkeri* Lemoine, 1891 (see Sudre *et al.* 1983), this species shows slender lower molars with more selenodont pattern than those of *P. oweni* and with the entoconid more mesial than in *Diacodexis* Cope,

1882. The lower molars UM-MGL-495 ($L = 4.5$) and UM-MGL-510 ($L = 5.0$ $W = 4.0$) fit well with the size of the m1 of the holotype MNHN.F.AL5236, MNHN.F.STA577 and MNHN.F.STA561 from Saint-Agnan, MNHN.F.GR158L from Grauves and MNHN.F.MT9L from Monthelon. ($L = 5.0-5.4$; $W = 3.5-3.8$).

In addition to these two species, we recently found the right p4 UM-MGL-491 ($L = 6.7$; $W = 3.3$) (Fig. 6G) that is very close to the p4 attributed to *Eurodexis russelli* Sudre & Erfurt, 1996 from Prémontré (MNHN.F.PRE4-L, Sudre & Erfurt 1996). Both are very elongated with a small metaconid on the lingual flank of the protoconid, an accessory cusp on the preprotocristid, and a distal basin delimited by two cristids. It differs from *Cuisitherium* Sudre, Russell, Louis & Savage, 1983 (Sudre *et al.* 1983) lower premolar by the postcristids pattern and the absence of paraconid. *Eurodexis russelli* is also known from the MP10a localities of Saint-Agnan, Mancy, Cuis and Grauves (*E. cf. russelli* in Sudre & Erfurt 1996).

A trigonid of a left lower molar (UM-MGL-809; $W = 2.4$) and the right m2 UM-MGL-811 ($L = 4.3$; $W = 3.1$) (Fig. 6H) match in morphology with the lower molar of *Diacodexis cf. varleti* from Prémontré (e.g., the m1 MNHN.F.SLP29-PE-1412; Sudre & Erfurt 1996: fig. 10). The molar is slender and tiny, with no ectostylid, and with a very distal entoconid thus differing from the larger *Cuisitherium* and *Protodichobune* (Sudre *et al.* 1983). It falls within the range size of m2 of *D. varleti* Sudre, Russell, Louis & Savage, 1983 from Condé-en-Brie ($N = 8$; $L = 4-4.5$; $W = 2.9-3.4$; Sudre *et al.* 1983), Pourcy ($L = 4.6$; $W = 3.3$) and of the m2s of *D. cf. varleti* from Sézanne-Broye, Saint-Agnan, Cuis and Grauves ($N = 6$; $L = 3.7-4.5$; $W = 2.5-3.4$; Sudre *et al.* 1983) and Prémontré ($N = 6$; $L = 4.1-4.7$ $W = 2.9-3.2$; Sudre & Erfurt 1996). Slight differences between *D. varleti* and *D. cf. varleti* have been quoted for paraconid size and position, notched protolophid and development of the entoconid. These faint characteristics are not clearly observable in the molars from Mas de Gimel. We therefore consider these specimens as *Diacodexis cf. varleti*. This is the first mention of this taxon in Mas de Gimel as it was only known until now from the Paris Basin (MP8+9 and MP10a) and in the Site XIV of the Geiseltal (Unterkohle, MP11; Erfurt & Sudre 1996).

A large talonid of the left m3 UM-MGL-33 (Fig. 6J) can be attributed to an Artiodactyla on the basis of a crescentiform hypoconid, the development of the two cuspid of the talonid and the presence of a loop-like hypoconulid. The lack of entoconid cristid and the general bunoselenodont pattern remind us an haplobunodontid representative not so different from *Cuisitherium* (see Sudre & Lecomte 2000) nor *Lophiobunodon* Depéret, 1908 (see Luccisano *et al.* 2020). However, its large dimension ($W = 6.4$ mm) oversizes that of *Lophiobunodon minervoensis* Depéret, 1908 (mean $W = 3.9$ mm; Luccisano *et al.* 2020) and *Cuisitherium lydekkeri* ($W = 4.5$ mm in MNHN.F.AL5235). It also displays a faint hypolophid, a marked postectohypofossid and a continuous labial cingulid. The largest European Ypresian artiodactyls *Aumelasia* Sudre, 1980 and *Dichobune* Cuvier, 1822 (see Godinot *et al.* 2018; Luccisano *et al.* 2020) possess a small bulbous hypoconulid with a marked posthypocristulid that close the basin lingually

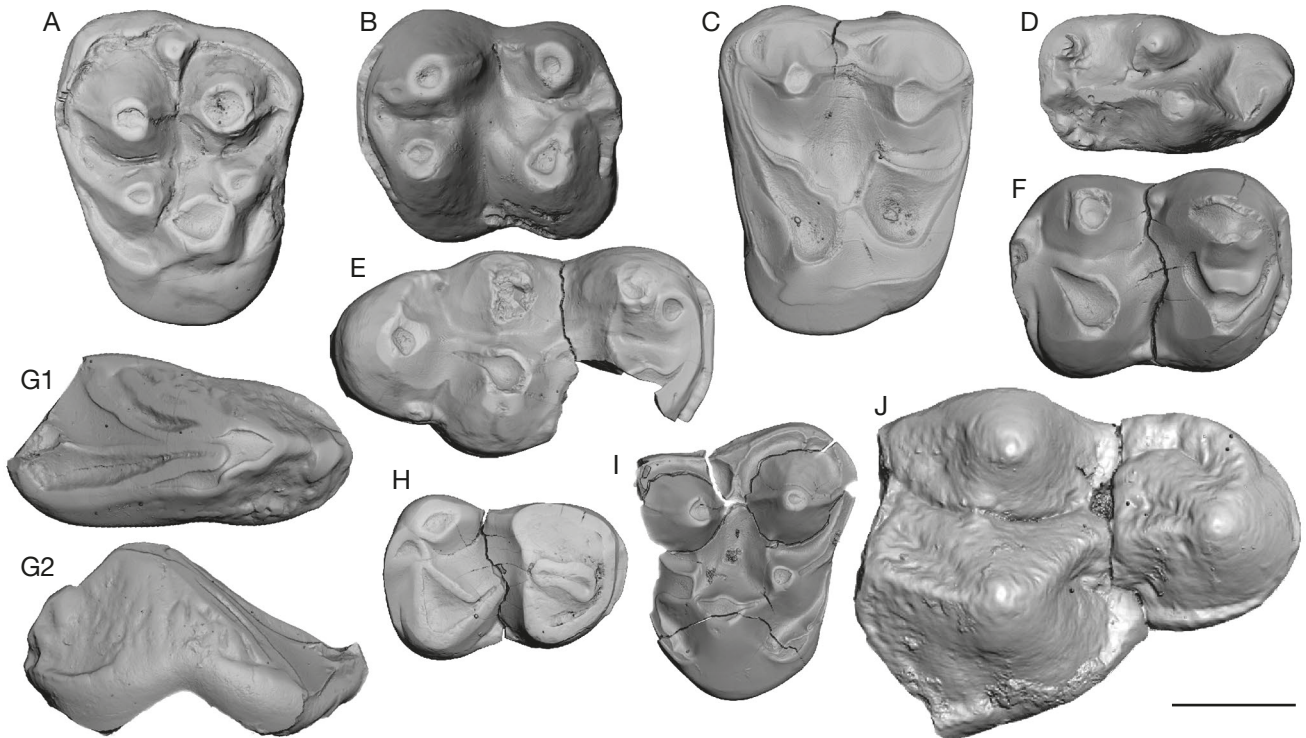


FIG. 6. — Artiodactyla from Mas de Gimel, Naples and Naples 2: **A, B**, molars of *Protodichobune oweni* Lemoine, 1878: right M3 UM-MGL-27 in occlusal view (**A**), left m1 UM-NAP-78 in occlusal view (**B**); **C-F**, teeth in occlusal view of *Cuisitherium lydekkeri* (Lemoine, 1891): left M1 UM-NAP-82 (**C**), right p4 UM-NAP2-73L (**D**), right m3 UM-NAP-76 (**E**) and right m1 UM-NAP-77 (**F**); **G**, right p4 of *Eurodexis cf. russelli* Sudre & Erfurt, 1996 UM-MGL-491 in occlusal (**G1**) and lingual (**G2**) views; **H, I**, molars of *Diacodexis cf. varleti* Sudre, Russel, Louis & Savage, 1983: right m2 UM-MGL-811 in occlusal view (**H**) and left M2 UM-NAP-84 in occlusal view (**I**); **J**, talonid of a left m3 UM-MGL-33 of cf. Haplobunodontidae indet. in occlusal view. Scale bar: 2 mm.

which is not the case in UM-MGL-33. The selenodont and loop-like pattern added to this size is original and could correspond to a new large early Haplobunodontidae, considered as cf. Haplobunodontidae indet. pending more material of this large artiodactyl.

Perissodactyla. This order is represented by three distinct families and four distinct species. First, a small Rhinoceroidea Hyrachyidae, initially attributed to *Hyrachyus minimum* (Fischer, 1829) by Cappetta *et al.* (1968), is represented by nine remains: a fragment of the indeterminate lower molar UM-MGL-813, the m1 UM-MGL-514 (L = 13.9; W = 8.7), two m2s (UM-MGL-511 and UM-MGL-513; L = 15.3-16.2; W = 9.5-9.9) (Fig. 7C), the m3 UM-MGL-512 (L = 16.6; W = 10.6), the P3 UM-MGL-515 (L = 9.9; W = 12) (Fig. 7B), the incomplete M3 UM-MGL-815 (L = 15.6; W = 17.7), half of the dP4 UM-MGL-516 (W = 11.4) and the fragment of upper molar UM-MGL-814. These remains display the characteristic bilophodont jugal teeth, the m3 without hypoconulid, a labial prehypocristulid, lophids that are not parallel, non-molariform premolars with incomplete metaloph, and incipient hypocone, that were already described for *Hyrachyus* Leidy, 1871 (e.g., Savage *et al.* 1966). Contrary to Cappetta *et al.* (1968), all the specimens rather fit with the size of *H. stehlini* (Depéret, 1904) from Saint-Agnan (Louis & Laurain 1983), from the *Sables à Unio et Térédines* Formation (Cuis, Grauves, Monthelon, see Savage

et al. 1966), from Rouzilhac (Godinot *et al.* 2018) and from Bracklesham, Earnley Formation (Hooker 1996). The material from Mas de Gimel is always smaller than the mean of *H. minimum* from the Geiseltal (MP11-13, Hlawatsch & Erfurt 2007) and Argenton (MP11/12); moreover, it does not display the lingual cingula on upper molars and premolars, the labial cingula at metacone, and the M3 metacone shorter characteristic of this species (Radinsky 1967). It is not easy to establish the degree of molarization of premolars with the available material from Mas de Gimel. It should be notice that differentiation between the late Ypresian *H. stehlini* and the late Ypresian/early Lutetian *H. modestus* (Leidy, 1870) from North America is not clear (see Radinsky 1967), and that a review is needed (see Bai *et al.* 2017).

The family Lophiodontidae is well represented (N = 62) but only by isolated and fragmentary teeth. Initially interpreted as *Lophiodon tapirotherium* Desmaret, 1822 (see Cappetta *et al.* 1968; Hartenberger *et al.* 1969), the most complete teeth, such as the M2 UM-MGL-538 (L = 29.8; W = 29.6), show thin cingulum unlike in *L. tapirotherium* and are smaller (Vautrin 2019). A fainted paraconule is observable on the M2, which is sometimes the case in the populations of *L. leptorhynchum* Filhol, 1888 from Aumelas and La Livinière (Vautrin 2019). Three M3s (UM-MGL-535, UM-MGL-536, UM-MGL-537) display a triangular occlusal outline. These specimens are larger than *Eolophiodon laboriense* Robinet, Remy, Laurent, Danilo & Lihoreau, 2015 (Robinet *et al.* 2015) from Laborie (Vautrin

et al. 2019) and than *L. corsaensis* Checa Soler, 1997 and *L. baroensis* Checa Soler, 1997 from Spain. They are significantly smaller than *L. aff. eygalayense* from Rouzilhac (Godinot *et al.* 2018). The material from Mas de Gimel is approximately the size of *L. remense* Lemoine, 1878 and the lower limit of *L. leptorhynchum* (see Vautrin 2019). A revision of these two species is needed, notably to test a possible synonymy; but considering the well-known populations of *L. leptorhynchum* in Southern of France, we provisionally attribute this material to *L. cf. leptorhynchum*. Below, we describe from Naples 2 better preserved specimens of this taxon (Fig. 7D-F).

There are several specimens (N = 23) belonging to the family Palaeotheriidae. Discrimination between early representatives of this family is not easy due to the possible presence of several size equivalent species in the localities (Savage *et al.* 1965) and to some unclear definitions at generic level. This is true despite recent important revisions (Danilo *et al.* 2013; Remy 2017; Remy *et al.* 2019; Bronnert & Métais 2023). Two dP4s (UM-MGL-362; L = 8.9; W = 9.9; UM-MGL-360) are undoubtedly attributed to the genus *Propalaeotherium* Gervais, 1849 based on the presence of a marked mesostyle, their relative bunodonty (marked metaconule) and the short ectoloph with bulbous paracone rib and salient metacone rib. Measurements are congruent with small specimens described from the Ageian collection, Grauves, Cuis, Mancy, Monthelon, Chavot and attributed to *Propalaeotherium gaudryi* (Lemoine, 1878) (see Bronnert & Métais 2023) and slightly smaller than specimens published as *Pr. cf. gaudryi* from Aumelas (Remy *et al.* 2019). Noteworthy, Cappetta *et al.* (1968) and Hartenberger *et al.* (1969) indicated the presence of *Propalaeotherium* sp. and *Propachynolophus* sp. in the Mas de Gimel fauna but did not indicate specimen attributions. Recent revision of *Propachynolophus* Lemoine, 1891 by Remy (2017) supports that a weak development of the hypoconulid on m1-2 are unambiguous character appearing in the propalaeothere clade. In UM-MGL-77 (m1-m2: L = 10.8 and 12.2; W = 7.3 and 8.5 mm; Fig. 8A), the meta-stylid is very close to the entoconid unlike in *Pachynolophus* Pomel, 1847 where entoconid is distal and there is a small hypoconulid, suggesting that this specimen should be referred to *Propalaeotherium*. It is size-equivalent to the mean value of *Pr. gaudryi* from Paris basin (Bronnert & Métais 2023), *Pr. gaudryi* from Rouzilhac (Godinot *et al.* 2018) and *Pr. cf. gaudryi* from Aumelas (Remy *et al.* 2019). One other lower molar fit with this morphology (UM-MGL-365). We are also able to recognize two lower premolar morphologies among the Equoidea from Mas de Gimel. We attribute to *Propalaeotherium gaudryi* the two p4s UM-MGL-32 (L = 10.4; W = 6.7; Fig. 8E) and UM-MGL-26 (L = 11.6; W = 8.2; Fig. 8D) displaying size measurements equivalent to *Pr. gaudryi* from Paris Basin with prehypocristid mesiodistally oriented, open trigonid and large distal basin. The p4s are slightly molariform with the variable presence of an entoconid (e.g., on UM-MGL-26, Fig. 8D). We also attribute a p3 (UM-MGL-73, L = 7.9; W = 6; Fig. 8F) to *Pr. gaudryi* with a prehypocristid oriented toward the protoconid and a quite distal metaconid.

The broken M3 UM-MGL-361 (L = 11.4; W = 11.9) (Fig. 8G) and the M1 UM-MGL-15 (L = 10.4; W = 10.4) display quadrangular outlines, a long ectoloph without true mesostyle (i.e., not connected to the cingulum) and lack marked metaconule (continuous metaloph) and metacone rib. A large hypostyle is present on the M3 (Fig. 8G). This morphology resembles M3 of large *Pachynolophus*. These teeth are smaller than published specimens of *Pr. gaudryi* but size is congruent with *Pa. cesserasicus* (Gervais, 1849) (La Livinière; Savage *et al.* 1965) and *Pa. ruscasseriensis* Remy, Krasovec, Lopez, Marandat & Lihoreau, 2019 (Aumelas; Remy *et al.* 2019), which are both very similar in size and morphology. The m1 UM-MGL-13 (L = 8.8; W = 6.3) and the two m2s UM-MGL-368 (L = 10.1; W = 6.8) and UM-MGL-369 (L = 10.4; W = 6.9) (Fig. 8I) display large distostylid and important space between metaconid and entoconid due to reduction or absence of metastylid. They are smaller than the size variation of *P. gaudryi* from Paris Basin and Aumelas and fall within the range of *Pa. ruscasseriensis* (see Remy *et al.* 2019). Unfortunately, the holotype of *Pa. cesserasicus* has not been described in Savage *et al.* (1965). Its exact location is currently unknown and no other mandible had been attributed to this species. The elongated p3 UM-MGL-372 (L = 9; W = 4.8) (Fig. 8J) differs from those of *Pr. gaudryi* being slenderer with a prehypocristid oriented toward the metaconid. All of these specimens indicate the presence of a large *Pachynolophus* species. We consider them as belonging to *Pachynolophus cf. ruscasseriensis* waiting a thorough revision of *Pa. cesserasicus*.

Naples

Metatheria. Two herpetotheriid species are recognized in Naples through a limited number of specimens (N = 14). A first species, *P. matronense* or *P. monspeliense*, is documented by fragmentary upper and lower molars (N = 11) and a nearly complete right M4 (UM-NAP-11), which is characterized by a V-shaped centrocrista, a labiolingually pinched stylar cusp C bearing a long posterior crista, and a very thin paracingulum mesially to the paracone apex. This species is also documented in Naples 2 by two very fragmentary lower teeth.

The complete right M1 UM-NAP-125 (L = 2.12; W = 2.19; Fig. 2E) and a fragment of a right M1 (UM-NAP-128) are attributed to *cf. Amphiperatherium bastbergense*, of which the type series is from Bouxwiller (Crochet 1979). *Amphiperatherium bastbergense* is also known from other MP13-14 localities (Egerkingen, Le Pont, Laprade, and Cuzal; Crochet 1980; Crochet *et al.* 1997; Sudre *et al.* 1990; Marandat *et al.* 1993) and also from Aumelas (Crochet 1980). UM-NAP-125 is significantly larger and relatively longer than the M1 of *A. goethei* Crochet, 1979 (see Crochet 1980: fig. 89) and the conules are relatively larger and more individualized from the preproto- and postprotocristae. UM-NAP-125 is significantly smaller and has a more acute protocone than the M1 of *A. maximum* (see Crochet 1980: fig. 106). The taxon *cf. Amphiperatherium bastbergense* from Naples is possibly the oldest occurrence of the species.

Eulipotyphla. Amphilemurid eulipotyphlans are represented by two species. The large morph B of *Macrocranium* cf. *nitens* is documented by few (N = 7) but better-preserved specimens relative to Mas de Gimel, particularly the m1 or m2 UM-NAP-2 (L = 2.06; W = 1.57) (Fig. 2H) and the M2 UM-NAP-3 (L > 1.82; W = 2.7) (Fig. 2I), strengthening the systematic attribution.

The second amphilemurid is *Macrocranium* sp. (*sensu* Russell *et al.* 1975), also present in Mas de Gimel. This species is documented by the right M2 UM-NAP-6 (L = 2.72; W = 3.42) (Fig. 2K) and the left M3 UM-NAP-7 (L = 2.11; W = 2.77) (Fig. 2L) from Naples and by the two right m2s from Naples 2 UM-NAP2-74V (L = 2.64; W = 2.04) and UM-NAP2-75V (L = 2.68; W = 2.14). The M2 from Naples is similar to MNHN.FAV60-L from Avenay described by Russell *et al.* (1975) in the transverse development on the crown (the M2 of *M. tupaïdon* is more quadrate), the long postmetacrista bearing a robust metastyle (these two structures are tenuous in *M. tupaïdon*), and the distal cingulum does not ascend the metaconule, as it is the case in the species from Messel. *Macrocranium storchi* Maitre *et al.* 2008 from Arcambal (MP8+9, Quercy; Maitre *et al.* 2008), although similar in size with *Macrocranium* sp., presents a well-distinct M2 (holotype UM-ARC-03) having lower and more bulbous cusps (especially the protocone and hypocone), reduced metastyle, and thinner mesial and distal cingula. As for the new nyctitheriid (aff. *Pontifactor* sp.) mentioned in Mas de Gimel, only one specimen (UM-NAP-22, right M1 or M2) documents this taxon.

Apatotheria. The apatemyids are documented by only one specimen, a left m1 (UM-NAP-16; L = 2.85; W = 1.91) (Fig. 3A). This molar is attributed to the same species as that of Mas de Gimel (*Heterohyus* sp.). Again, we emphasize the large size of this species, in comparison to the taxa described from the Paris Basin.

Chiroptera. Bats are represented by two species. The minuscule Palaeochiropterygidae gen et sp. indet. from Mas de Gimel is documented by a right M1 or M2 (UM-NAP-19; W = 1.62) in Naples (Fig. 3D). This molar shares several important characters with palaeochiropterygids such as the metacone higher than the paracone as in *Palaeochiropteryx tupaïdon* and *P. spiegelii*, the ectoflexus between the parastyle and the mesostyle is narrow and mesially displaced, the centrocrista is long and joins the labial border, there is no paraconule, the metaconule is minute, the protocone is rather short, the lingual cingulum is thin, continuous but attenuated under the protocone (as in *P. spiegelii*), and there is a small hypocone. This upper molar, associated with the lower molar from Mas de Gimel, probably documents a new species, significantly smaller than all known palaeochiropterygids, including the small indeterminate species from Egem (Smith & Smith 2013).

The second bat is represented by an icaronycterid species, much larger than the species from Mas de Gimel. This species is documented by two m1s or m2s (UM-NAP-20; L =

1.98; W = 1.27 and UM-NAP-21; L = 2.02; W = 1.22) (Fig. 3G-H) well-characterized by a large paraconid, a necromantodont arrangement of talonid cusps with the hypoconulid rather lingual (not median as in the onychonycterids and the archaeonycterid *Xylonycteris* Hand & Sigé, 2018) and connected to the entoconid. This talonid arrangement corresponds to the subnyctalodonty of *Icaronycteris*. Moreover, the trigonid/talonid height difference is similar to that observed in *Icaronycteris* Jepsen, 1966. The species *I. index* Jepsen, 1966 (late early Eocene, Wa7, of North America) and *I. menui* (MP8+9 of Avenay) are ~20% smaller and have a lower paraconid. In that respect, more similarities are found with *I. sigei* from Vastan Lignite Mine, early Eocene of India (Smith *et al.* 2007) which differs however by a higher metaconid and a smaller hypoconulid. Pending new specimens (e.g. documenting the upper molar morphology), the icaronycterid from Naples is attributed to *Icaronycteris* sp.

Pantolestia. The pantolestids are represented by the left M3 UM-NAP-1 (L = 3.6; W = 6.42) (Fig. 3J). This molar is tentatively attributed to *Pantolestes sabatieri* Smith, 2001 from Prémontré (Smith 2001). Similarities concern an equal size, a transversally elongated crown, an oblique labial border of the crown in occlusal view, low and massive cusps, a huge and prominent parastyle, a bulbous paraconule, and the lack of hypocone.

Primates. Primates are documented by only two teeth belonging to species identified in Mas de Gimel. The right p3 UM-NAP-26 is attributed to *Nannopithecus zuccolae* based on similarities with UM-MGL-408. More interesting is the right m1 UM-NAP-31 (L = 3.86; W = 2.26) (Fig. 4D) which documents *Anchomomys* sp. This molar is typical of *Anchomomys* species in being elongated and narrow, in lacking a paraconid, and in having an entoconid distolingually positioned relative to hypoconid and an almost rectilinear mesial paralophid, which in occlusal and in mesial view, is at a roughly right angle with the strongly sloping preprotocristid. This species represents the oldest occurrence of the genus *Anchomomys* Stehlin, 1916 and documents an early unexpected large lineage (significantly larger than *A. gaillardi* Stehlin, 1916, *A. frontanyensis* Marigó, Minwer-Barakat, Moyà-Solà & Boyer, 2011, and *A. pygmaeus* Szalay, 1974). Interestingly also, the same new species is probably documented in Prémontré by more specimens (M. Godinot comm. pers. 2022).

Rodentia. Rodents are documented by the same assemblage as in Mas de Gimel, but with fewer specimens. All the specimens have been studied by Escarguel (1999) and part of them was subject of recent revisions (Vianey-Liaud *et al.* 2019, 2022; but see below for those here attributed to the new species *Hartenbergeromys paillardensis* n. sp.).

Ailuravus aff. *michauxi* (N = 3) is documented by a right DP4 (UM-NAP-65), a left dp4 (UM-NAP-67), and a talonid of a left m3 (UM-NAP-66) (see Escarguel 1999: 125). *Eoglivavus*

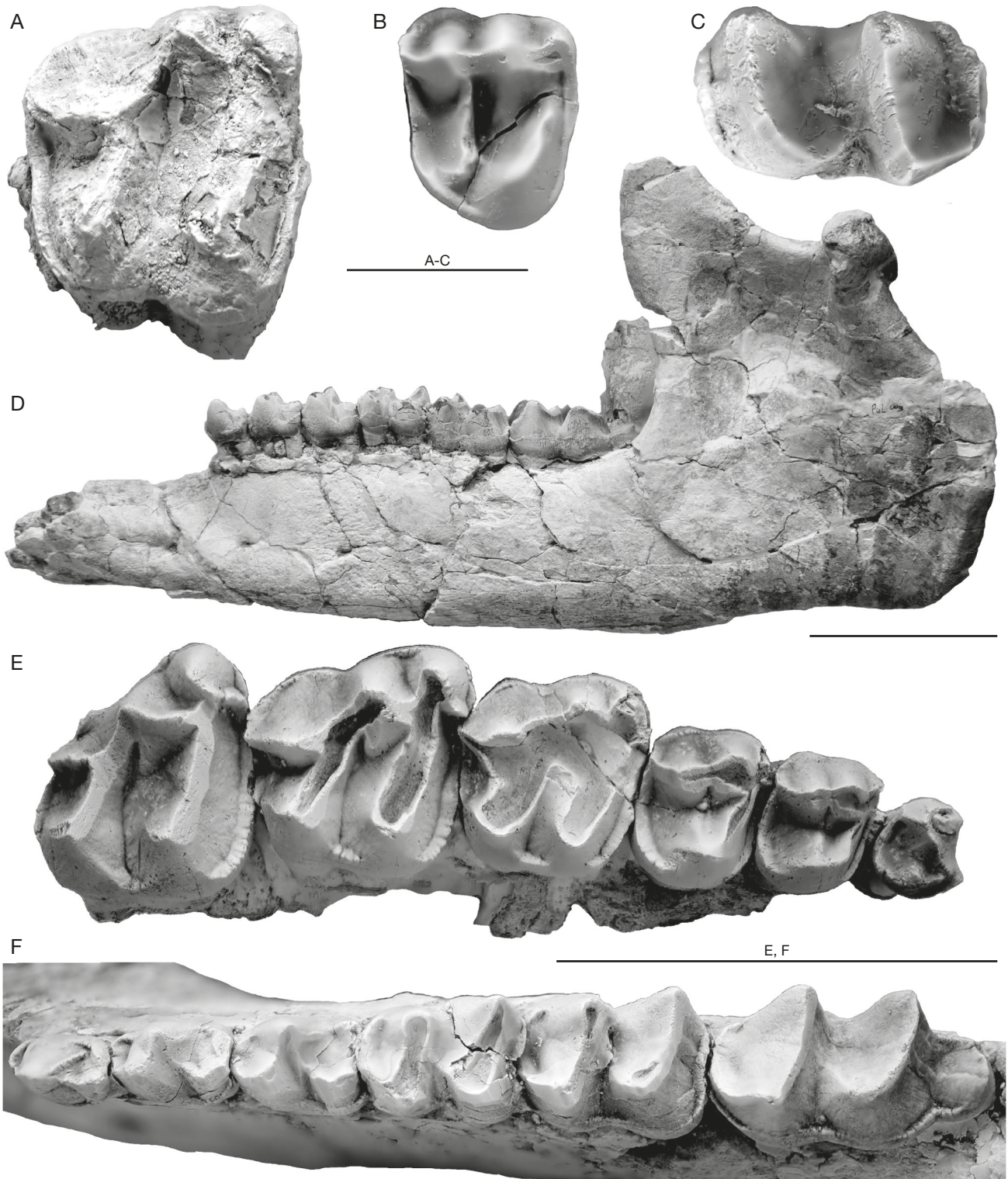


FIG. 7. — Large perissodactyl taxa from Mas de Gimel, Naples and Naples 2: **A-C**, teeth of *Hyrachyus stehlini* (Depéret, 1904) in occlusal view: right M1 UM-NAP-110 (**A**), right P3 UM-MGL-515 (**B**) and right m2 UM-MGL-513 (**C**); **D-F**, dental row of *Lophiodon cf. leptorhynchum* Filhol, 1888: mandible with right and left p2-m3 UM-NAP2-09 in lateral view (**D**) and occlusal focus on left side (**F**), right P2-M3 UM-NAP2-73 (**E**). Scale bars: A-C, 10 mm; D-F, 50 mm.

wildi (N = 7) is documented by four M1s (UM-NAP-69 to UM-NAP-72), a left p4 (UM-NAP-74), a left m1 (UM-NAP-73), and a right m2 (UM-NAP-75) (see Vianey-Liaud *et al.* 2022: 796). *Masillamys mattauei* (N = 5) is documented

by a right m1 (UM-NAP-60), a left m2 (UM-NAP-61), a right m3 (UM-NAP-59), a right M1 (UM-NAP-63), and a right M2 (UM-NAP-62) (see Escarguel 1999: 216; Vianey-Liaud *et al.* 2019: 471).

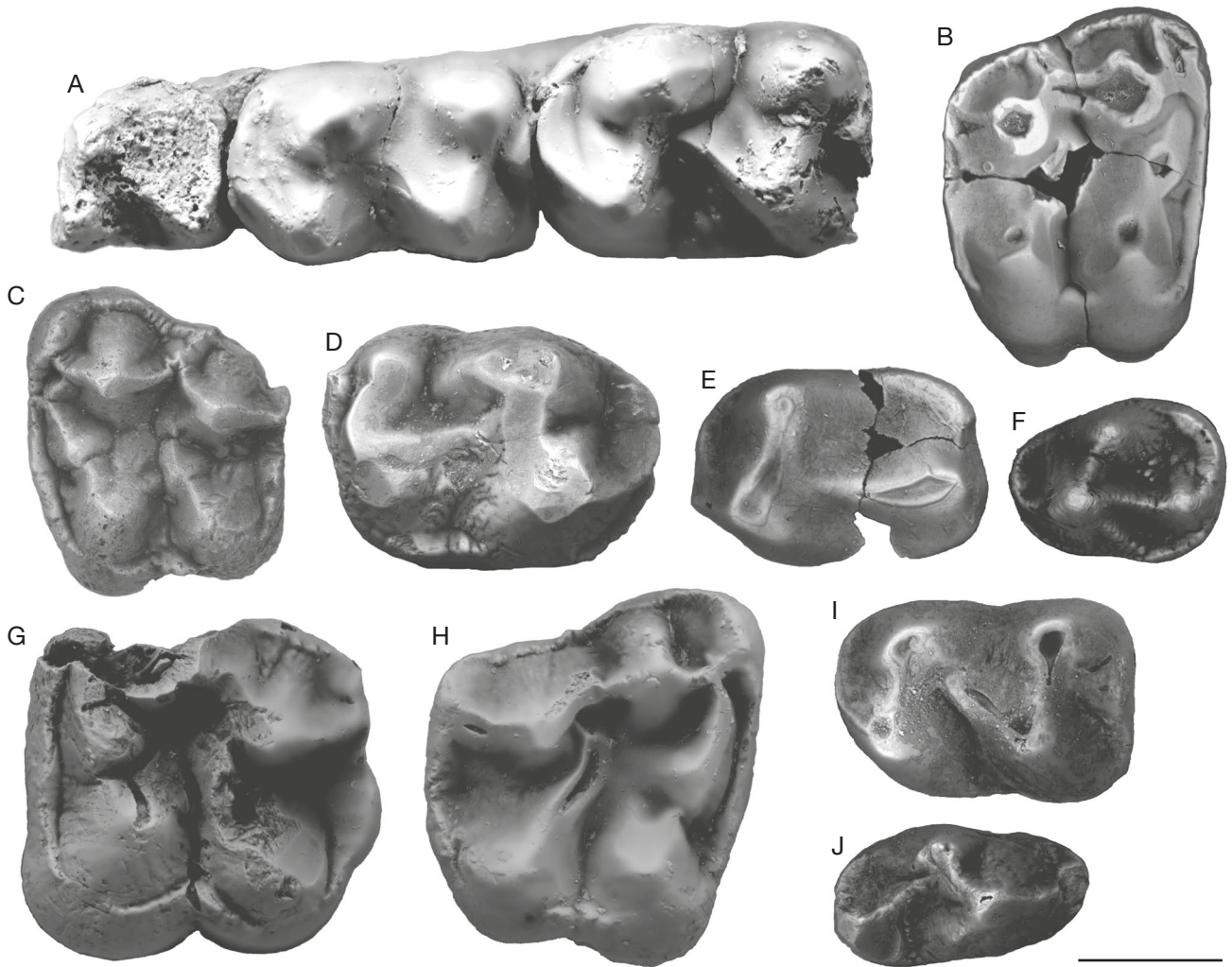


FIG. 8. — Equoidea from Mas de Gimel, Naples and Naples 2: **A-F**, teeth of *Propalaeotherium gaudryi* (Lemoine, 1878) in occlusal views: left m1-m2 UM-MGL-77 (**A**), right M1 UM-NAP-103 (**B**), left M1 UM-NAP2-72L (**C**), right p4 UM-MGL-26 (**D**), left p4 UM-MGL-32 (**E**) and left p3 UM-MGL-73 (**F**); **G-J**, teeth of *Pachynolophus* cf. *ruscasseriensis* Remy, Krasovec, Lopez, Marandat & Lihoreau, 2019 in occlusal views: broken left M3 UM-MGL-361 (**G**), right M3 UM-NAP-99 (**H**), left m2 UM-MGL-369 (**I**) and right p3 UM-MGL-372 (**J**). Scale bar: 5 mm.

Carnivoraformes. The broken right M3 UM-NAP-13 ($L = 1.27$; $W = 2.25$) which lacks labial cingulum and most of the distal border, presents the same morphology than specimens from Mas de Gimel attributed to *Uintacyon* cf. *hookeri*.

Artiodactyla. This order is represented in Naples by three distinct taxa also known in Mas de Gimel. Two specimens are interpreted as belonging to *Protodichobune oweni*: the left m1 UM-NAP-78 ($L = 5.4$; $W = 4.6$) (Fig. 6B) and the right m3 talonid UM-NAP-79 ($W = 3.7$). These specimens with bunodont morphology, distinct paraconid, a distal entocoid in regard to hypoconid position, and a reduced central hypoconulid, fit well with the material from the *Sables à Unios et Térédines* Formation (Sudre *et al.* 1983) and UM-MGL-812 in size and morphology.

The Haplobunodontidae *Cuisitherium lydekkeri*, already described from Naples in Sudre & Lecomte (2000), is the most represented artiodactyl taxon with at least 6 specimens: a right dP4 UM-NAP-86 ($W = 3.8$), a left M1 UM-NAP-82

($L = 4.7$; $W = 6.2$) (Fig. 6C), a left p3 UM-NAP-85 ($L = 5.3$; $W = 2.1$) with a reduced metaconid and narrow distal basin, a possible left p4 UM-NAP-91 which is very worn, a right m3 UM-NAP-76 ($L = 7$; $W = 3.8$) (Fig. 6E) and a right m1 UM-NAP-77 ($L = 5.3$; $W = 3.7$) (Fig. 6F). The new specimen UM-NAP2-73L ($L = 4.9$; $W = 2.6$) is described here from Naples 2 and corresponds to the first clearly established p4 of the species (Fig. 6D). Indeed, UM-NAP85 considered as a p4 in Sudre & Lecomte (2000) does not display a large independent metaconid as in UM-NAP2-73L and thus must correspond to a p3 of the same species. UM-NAP2-73L presents an elongated morphology with a long preprotocristid that forms a mesial hook toward a small parastylid, a large metaconid lingual to the protoconid and a postprotocristid that joins the distal cingulid forming a distostylid, and an entostylid is distinguishable on the distolingual corner of the cingulid. This morphology clearly differs from the simpler p4 of Diacodexidae (Boivin *et al.* 2018), *Protodichobune*, *Aumelasia* (Godinot

et al. 2018) and *Eurodexis* Erfurt & Sudre, 1996 (Fig. 6G). *Cuisitherium* is easily recognized as the metaconule of upper molars is very lingual and the lower molars are slender with an entoconid aligned with hypoconid. UM-NAP-82 is the size of the M1 MNHN.F.GR7464 (Sudre & Lecomte 2000) and UM-NAP-77 noted as a m2 in Sudre & Lecomte (2000) is the exact size of the m1 of MNHN.F.AL5236, the holotype from the *Sables à Unios et Térédines* Formation. All this material is attributed to *C. lydekkeri*.

There are three specimens that can be referred to *Diacodexidae*. The left M2 UM-NAP-84 (L > 4.3; W = 5.4) (Fig. 6I) is the size of the largest *Diacodexis* cf. *varleti* from Prémontéré (e.g., M2 MNHN.F.SLP29-PE-1084; L = 4.9 W = 5.5), Saint-Agnan and Sézannes-Broyes (Sudre *et al.* 1983); it corresponds to the median specimens of *Eurodexis russelli* (Sudre & Erfurt 1996). The presence of an ectoflexus unlike in *Protodichobune* (Sudre *et al.* 1983) and its linguo-mesial and linguo-distal cingula not bulged like in *Eurodexis russelli* permit to attribute this specimen to *Diacodexis*. Two small trigonids of lower molar, UM-NAP-80 (W = 2.8) and UM-NAP-81 (W = 3.1), with well distinguishable paraconid, which is size equivalent to metaconid, and elevated and acute cuspids are congruent with size and morphology of *Diacodexis* cf. *varleti*. Differences between *D. varleti* (Condé en Brie, Pourcy and Avenay) and *D. cf. varleti* (Saint-Agnan, Sézanne-Broye, Mancy, Grauves Cuis, Prémontéré, and site XIV Geiseltal) mainly deal with mean size and slight differences in paraconid position, entoconid development and accessory crests from conules on upper molar (Sudre *et al.* 1983, Sudre & Erfurt 1996; Erfurt & Sudre 1996). The premetacristule development on UM-NAP-84 makes us lean toward an attribution as in Mas de Gimel to the more progressive species *D. cf. varleti*.

Perissodactyla. The Perissodactyla discovered in Naples belongs to three distinct families. As in Mas de Gimel, a small Hyrachyidae is represented by the right P4 UM-NAP-111 (L = 10.4; W = 14.7) and the right M1 UM-NAP-110 (L = 15.1; W = 17) (Fig. 7A). They are the size of specimens of *Hyrachyus stehlini* already described from Mancy (P4 UM-MCY-51; noted M-62-63 in Savage *et al.* 1966) or Monthelon (MNHN.F.MT4-L; Savage *et al.* 1966). Despite a very small size difference with *H. minimum* for this dental locus, the thin lingual cingulum helps us to attribute this material to *H. stehlini*.

Two lophiodontid remains have been found in Naples with the right dP4 UM-NAP-109 (L = 14.1; W = 14.3) and a right M3 UM-NAP-108 (L = 26.2; W = 30.4). The M3 has a triangular occlusal outline, a light cingulum and is size-equivalent with those from Mas de Gimel suggesting the presence of *L. cf. leptorhynchum*.

The locality of Naples 2 has yielded numerous dental remains of lophiodontids (N = 67) which will help to make a clearer attribution notably due to well preserved material (Fig. 7D-F). Note that this important material will need a full description which is out the scope of this study. These specimens belong to the genus *Lophiodon* Cuvier,

1822 notably due to the absence of paraconule on most of the specimens or very small paraconule when present. The mandibular symphysis reaches the level of the p3-p4 whereas in *Lophiaspis* Depéret, 1910 and *Eolophiodon* it only reaches the p2 (Robinet *et al.* 2015, Vautrin *et al.* 2020). Size distribution of molars and premolars overlaps that of *L. remense*, *L. glandicus* Astre, 1960 and *L. leptorhynchum* (Vautrin 2019). The *Lophiodon* species from Naples 2 is far smaller than *L. tapirotherium* from Issel (Filhol 1888), *L. eygalayense* Labarrère & Montenat, 2011 from Eygalaye (see Labarrère & Montenat 2011) and *L. aff. eygalayense* from Rouzilhac (Godinot *et al.* 2018). It displays numerous morphological affinities with *L. leptorhynchum* such as the relatively thin cingulum (Fig. 7E-F; unlike in *L. tapirotherium*) and the long, narrow, and dorso-ventrally thin symphysis (Fig. 7D), which is the main diagnostic feature of *L. leptorhynchum* (Filhol 1888, Vautrin 2019). Moreover, the variable presence of a faint paraconule on upper molar is only known in the genus *Lophiodon* from *L. leptorhynchum* populations (Vautrin 2019). Finally, the specimens from Naples 2 correspond to the smallest specimens from La Livinière and Aumelas (Vautrin 2019) and thus we refer them to *L. cf. leptorhynchum* waiting the description of populations of *L. leptorhynchum* and discussion on a possible synonymisation with *L. remense*.

As with Mas de Gimel, we noted two morphs belonging to the family Palaeotheriidae. Two M1s from Naples UM-NAP-102 (L = 9; W = 10) and UM-NAP-103 (L = 9.4; W = 12.1) (Fig. 8B) and one M1 from Naples 2 UM-NAP2-72L (L = 9.1; W = 10.6) (Fig. 8C) can be attributed to *Propalaeotherium* based on the presence of a marked mesostyle, on their relative bunodonty and ectoloph morphology (see above, for Mas de Gimel). Measurements appear smaller than most of the specimens of *Pr. gaudryi* from the Paris Basin except some small specimens from the Aegean fauna and Grauves (Bronnert & Métais 2023) and, than all specimens of *Pr. cf. gaudryi* from Aumelas and *Pr. gaudryi* from Rouzilhac.

Four upper molars of *Pachynolophus* have been found in Naples: two M3s UM-NAP-99 (L = 12; W = 13.4) (Fig. 8H) and UM-NAP-100 (L = 12.1; W = 13.9), two M1s or M2s UM-NAP-101 (L = 10.6; W = 12.1) and UM-NAP-106 (L = 9.1; W = 10.6). They all display a long ectoloph without mesostyle or with a pseudo-mesostyle (just present at the cingulum; UM-NAP-100), no metacone rib and present a continuous metaloph. These teeth are the same size than that of *Pa. ruscasseriensis* (Aumelas; Remy *et al.* 2019) and *Pa. cesserasicus* from La Livinière (Savage *et al.* 1965). A small left p3 UM-NAP-107 (L = 7.6; W = 5.2) with a prehypocristid oriented toward the metaconid and a quite distal metaconid can also be confidently attributed to a large *Pachynolophus*. As for the material from Mas de Gimel, we consider that a thorough revision of *Pa. cesserasicus* is needed. Pending this revision and considering that *Pa. ruscasseriensis* is better represented and described than *Pa. cesserasicus* (see Remy *et al.* 2019), we attribute this material to *Pa. cf. ruscasseriensis*.

SYSTEMATIC PALAEOONTOLOGY

We here describe *Hartenbergeromys pailladensis* n. sp., a new rodent species from Mas de Gimel and Naples.

Order RODENTIA Griffith, 1827
Family indet.

Genus *Hartenbergeromys* Escarguel, 1999

[urn:lsid:zoobank.org:act:AD84FF9C-B208-40D1-A156-73F897FD298C](https://zoobank.org/act:AD84FF9C-B208-40D1-A156-73F897FD298C)

Hartenbergeromys Escarguel, 1999: 201.

TYPE SPECIES. — *Hartenbergeromys hautefeuillei* Escarguel, 1999 by original designation.

TYPE LOCALITY. — Prémontré (Aisne, late early Eocene, MP10).

OTHER SPECIES. — *Hartenbergeromys marandati* (Escarguel, 1999).

DIAGNOSIS. — See Vianey-Liaud & Marivaux 2021: 78.

Hartenbergeromys pailladensis n. sp.
(Figs 9; 10; Table 1)

[urn:lsid:zoobank.org:act:11CEEC60-37D4-4DF7-8092-A1B3923A8E32](https://zoobank.org/act:11CEEC60-37D4-4DF7-8092-A1B3923A8E32)

Hartenbergeromys aff. *hautefeuillei* – Escarguel 1999: 209-210.

HOLOTYPE. — UM-MGL-601: left M1.

TYPE LOCALITY. — Mas de Gimel (Hérault, France, late early Eocene, MP10).

OTHER LOCALITY. — Naples (Hérault).

DIAGNOSIS. — *Hartenbergeromys* with numerous thin high extra ridges on upper and lower molars. Crested cusps and complete pericingulum on upper molars. Metacone smaller than protocone and hypocone smaller than protocone on upper molars, anteroloph and posteroloph as high as the other lophs. Metaconid only slightly protruding in dp4 and p4. Protoconid stronger in molars than in dp4 and p4. Four main cuspids (proto-, meta-, ento- and hypoconid) crested, delimiting an incomplete pericingulid, due to the presence of the sinusid and of the narrow mesoflexid opening. Labial metalophulid I strong and generally short, never connected to a complete transverse lingual metalophulid I. Entolophid rarely complete, often connecting the mesoconid.

Differs from *H. hautefeuillei* and *H. marandati* by more crested cusps and cuspids, the development of the pericingulum, and the smaller metacone and hypocone on molars.

MATERIAL. — 24 specimens from Mas de Gimel and 27 from Naples (measurements in Table 1) are available in the collection.

REMARKS

Escarguel (1999: 200-210) described the type specimens of *Hartenbergeromys hautefeuillei* from the locality of Prémontré. In the same paper, he referred the specimens from Mas de Gimel and Naples as to *Hartenbergeromys* aff. *hautefeuillei*. Discussing the phylogeny of Theridomorpha, Vianey-Liaud & Marivaux (2017) followed the conclusions of Escarguel

TABLE 1. — Specimens and dental measurements (in mm) of *Hartenbergeromys pailladensis* n. sp. from Mas de Gimel (MGL) and Naples (NAP). Symbol *, fragmentary specimen.

upper teeth				
	Barcode	Side	L	W
DP4	MGL-647	right	1.35	1.60
	NAP-57	left	1.45	1.46
P4	NAP-58	left	1.62	2.01
	NAP-139	right	1.49	1.84
M1 or M2	MGL-601 (M1)	left	2.03	2.34
	MGL-772*	left	–	–
	MGL-790	right	1.75	1.88
	NAP-47	left	1.68	1.87
	NAP-48	left	1.65	1.78
	NAP-49 (M1)	left	1.84	1.82
	NAP-50 (M1)	left	1.83	1.90
	NAP-51*	left	–	–
	NAP-54	left	1.66	1.82
	NAP-55	left	1.59	1.77
M3	MGL-626	right	1.76	1.65
	NAP-52	right	1.48	1.48
	NAP-56	right	1.77	1.78
	NAP-64	left	1.74	1.73
lower teeth				
			L	W
dp4	MGL-649	left	1.65	1.28
	MGL-791	right	1.64	1.17
p4	MGL-616	right	1.66	1.30
	MGL-644	right	1.59	1.37
	MGL-768*	–	–	–
	MGL-786	right	1.56	1.15
	NAP-44	left	1.81	1.50
m1	NAP-53	right	1.63	1.37
	MGL-620	left	1.86	1.58
	MGL-637	right	1.77	1.66
	MGL-648	right	1.79	1.48
	MGL-652	left	1.81	1.60
m2	NAP-32	right	1.70	1.50
	NAP-39	left	1.77	1.57
	NAP-43	left	1.73	1.51
	MGL-618	left	1.82	1.74
	MGL-625	left	1.90	>1.58
	MGL-635	right	1.82	1.83
	MGL-653*	right	–	–
	MGL-750	left	1.90	1.56
MGL-751*	left	–	–	
m3	NAP-33	left	1.94	1.67
	NAP-34	right	1.69	1.54
	NAP-35	left	1.79	1.57
	NAP-40	right	1.75	1.67
	NAP-41	right	1.95	1.53
	MGL-617	right	1.82	1.60
	MGL-787	right	1.8	–
	MGL-749	left	1.86	1.54
NAP-36	right	1.80	1.56	
NAP-37	left	1.82	1.57	
NAP-38	right	1.92	1.60	
NAP-46	left	1.82	1.64	

(1999) using the diagnosis of *H. hautefeuillei* including the features of the specimens from Mas de Gimel and Naples in their phylogenetic analysis (*Hartenbergeromys* aff. *hautefeuillei* in Vianey-Liaud & Marivaux 2017: fig. 7). More recently, following a more detailed phylogenetic analysis including numerous early Eocene rodents (Vianey-Liaud & Marivaux

2021), we reconsidered the material of *Hartenbergeromys haute-feuillei* from Prémontré, and we can highlight differences in morphological characters between the Mas de Gimel/Naples populations and that of Prémontré.

DESCRIPTION

Upper teeth

The crown is not very high, the lingual flank is slightly higher than the labial one and sometimes weakly wrinkled.

DP4. There are two available specimens, a worn right DP4 from Mas de Gimel (UM-MGL-647) and an almost unworn left DP4 from Naples (UM-NAP-57) (Fig. 9A, B). The first has a long anteroflexus and anteroloph ending lingually with a worn stretched anterostyle. This style is weakly attached to the preprotocrista. The protocone is worn following a plane inclined posteromesially from the indistinct endoloph, towards the anterostyle. The hypocone is worn symmetrically, sloping backwards to its junction with the lingual end of the posteroloph. It is only slightly smaller than the protocone. The paracone is slightly stronger than the metacone, but of same height. The labial protoloph bears a swollen worn paraconule, which is aligned labiolingually with it. The paraconule connects the preprotocrista close to the protocone summit with a short lingual protoloph. The labial metaloph, transverse, is short and separates from the metaconule. The latter is strong and obliquely stretched distomesially, towards its attachment with the postprotocrista, close to the protocone summit. The posteroloph ends at the level of the base of the labial metaloph, making the posteroflexus open labially.

P4. There are two available P4s, both from Naples (UM-NAP-58 and 59). Although they show the same characteristic globular morphology (Escarguel 1999: 209), they differ by the morphology and nature of the mesial loph. On UM-NAP-58 (pl. 22, fig. n in Escarguel 1999; here: Fig. 9D) the anteroloph is absent; therefore, the anteriormost loph is made by the labial protoloph joining the preprotocrista. In UM-NAP-59 (Fig. 9C) instead the anteroloph is present and well distinct from the protoloph, which joins the preprotocrista closer to the protocone summit than on UM-NAP-58. A short mesoloph fills the labial part of the mesoflexus; it is separated from the mesostyle on UM-NAP-59, and linked to it on UM-NAP-58. On UM-NAP-59, it ends between the extremities of the extra ridges developed labially from the metaconule and distally from the labial part of the protoloph. A paraconule is present on UM-NAP-59 as developed as the metaconule. On both P4s, extra ridges descend from the conules and the protoloph to the mesoflexus. On UM-NAP-59, an anterolophule connects the paraconule to the anteroloph, and a posterolophule connects the metaconule to the posteroloph.

There is a pericingulum-like structure from the paracone-preparacrista, through the anteroloph, continuing to the preprotocrista, then the protocone-postprotocrista, turning distally at the level of a weak swelling, which resembles more a posterostyle than a hypocone, ending in the posteroloph up

to the metacone flank. On UM-NAP-59, the postprotocrista and premetacrista are linked to the mesiodistally stretched mesostyle continuing labially the pericingulum. This is less continuous on UM-NAP-58, on which there are furrows between the mesostyle and the two main cusps.

M1-2. There are eight complete M1-2s available (six from Naples, two from Mas de Gimel; Fig. 9A-E), among which it is difficult to separate M1 from M2, whereas it is relatively easy for *H. hautefeuillei* from Prémontré (Vianey-Liaud & Marivaux 2021: 81). In the latter «the paracone is more labial than the metacone, but this metacone is even more lingual on M2 than on M1. The parastyle is thicker and more elongated or curved labially on M1; the hypocone (and not the protocone as it was incorrectly indicated in the 2021 paper, p. 81) is more reduced and labial on M2, and the posteroloph is shorter». However, all the M1-2s from Naples and Mas de Gimel have a relatively short posteroloph, ending at the level of the labial part of the metaloph. Among them, the two upper molars from Mas de Gimel have a thickened and curved parastyle (M2: UM-MGL-606; M2: UM-MGL-790) and two of the molars from Naples (M1: UM-NAP-55; and M2: UM-NAP-47), whereas it is not distinct on the M1 UM-NAP-50 and the M1 or M2 UM-NAP-48. Protocone and hypocone are nearly at the same lingual level in all the M1-2s.

Apart from this weak difference between M1 and M2, what is striking in the upper teeth of *H. paillardensis* n. sp. is the development of the pericingulum including the anteroloph and the “internal cingulum” (terminology used in Escarguel 1999, fig. 5) encompassing the preprotocrista, the protocone, the postprotocrista, the endoloph and the hypocone, all aligned in continuity and with a nearly indistinct lingual sinus. The hypocone, quite smaller than the protocone, connects the posteroloph through a marked angle; this posteroloph is relatively shorter and slightly higher than the anteroloph. A narrow furrow marks the junction of the posteroloph with the distal flank of the metacone. The metacone is quite smaller than the paracone. The mesostyle can be stretched mesiodistally into two elements connected to the postprotocrista and the robust premetacrista, the whole forming the outer part of the pericingulum. Most often, at least one short mesoloph arises lingually from the mesostyle towards the metaconule without fusing with it. The paraconule is most often crescent-shaped and directed mesiodistally towards the mesoflexus or/and the anteroflexus. Two to three low short ridges also descend from the protoloph towards the anteroflexus and mesoflexus, as well as from the protocone (protocrista). The ridge underlining the premetacrista-metacone-metaloph arch drops down to join the flank of the metaconule. The latter is crested with short ridges that are clearly visible on little worn teeth, one descending into the posteroflexus and attaching to the posterocingulum, the other, mediolabial, directed towards the mesoloph without joining it. On unworn teeth, like the holotype UM-MGL-601 (Fig. 9E), the pericingulum is overlying the flexi floor, and the four main cusps (paracone, metacone, protocone and hypocone), as well as the paraconule and metaconule are slightly protruding above the

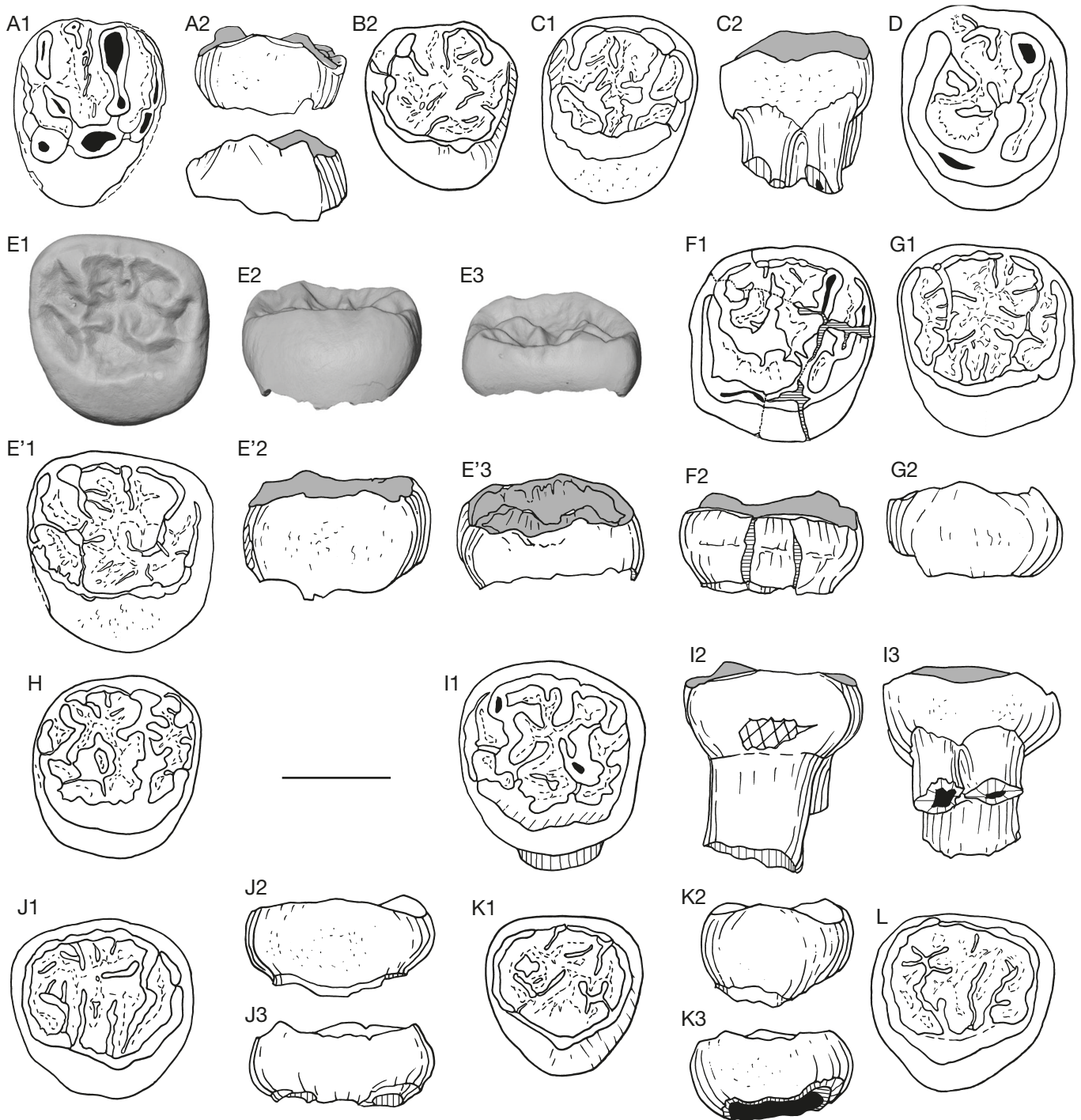


FIG. 9. — Upper deciduous (DP4), premolar (P4) and molars (M1-2-3) of *Hartenbergeromys paillardensis* n. sp. from the two closely related localities: MGL, Mas de Gimel (Hérault), and NAP, Naples (Hérault): **A**, UM-MGL-647, right DP4; **A1**, occlusal view; **A2**, lingual view; **B**, UM-NAP-57, enamel cover of a left DP4, unworn; **B1**, lingual view; **B2**, occlusal view; **C**, UM-NAP-59, left P4; **C1**, occlusal view; **C2**, labial view; **D**, UM-NAP-58, left P4, occlusal view; **E**, MicroCTScan of UM-MGL-601, holotype, unworn left M1: **E1**, occlusal view; **E2**, lingual view; **E3**, labial view; **E'**, same as **E** (UM-MGL-601), but drawings, to compare both figurations; **F**, UM-MGL-639, worn right M1: **F1**, occlusal view; **F2**, lingual view; **G**, UM-NAP-47, unworn left M1: **G1**, occlusal view; **G2**, lingual view; **H**, UM-NAP-55, right M1-2, moderately worn, roots partially preserved, occlusal view; **I**, UM-NAP-48, left M2, moderately worn, roots partially preserved: **I1**, occlusal view; **I2**, lingual view; **I3**, labial view; **J**, UM-NAP-56, left M3, weakly worn, roots broken; **J1**, occlusal view; **J2**, lingual view; **J3**, labial view; **K**, UM-NAP-52, right M3, nearly unworn; **K1**, occlusal view; **K2**, lingual view; **K3**, labial view; **L**, UM-NAP-64, right M3, nearly unworn, roots absent, occlusal view. Scale bar: 1 mm. The background of the profiles is greyed out. On Fig. F open cracks are filled with horizontal stripes.

pericingulum level, all being of same height. The paracone, metacone, protocone and hypocone, as well as the paraconule and metaconule, protrude. Then the wear affects primarily

the lingual half of the tooth, and highlights its labial half, the wear surface of the latter descending labiolingually from the labial cusps (UM-MGL-639, Fig. 9F).

M3. There are three M3s from Naples (UM-NAP-52, NAP-56, NAP-64), one from Mas de Gimel (UM-MGL-626) (Fig. 9J-L). On all these teeth, the tiny hypocone is more lingual than the protocone. The M3s differ from the M1-2s in their triangular shape due to the quite more reduced and more labial hypocone. They display a complete pericingulum without discontinuities either at the junction posteroloph-metacone-metaloph, or at the junction anteroloph-protocone. The mesostylar area is longer than on M1-2, bearing one (UM-NAP-52 Fig. 9K, UM-NAP-64, Fig. 9L) to three (UM-NAP-56) short labial mesolophs.

Lower teeth

The crown has its lingual flank nearly as high as the labial one and rarely thinly wrinkled. The ectoflexid (sinusid) is always marked and on the lingual profile, the mesoflexid opening is narrow.

dp4. There are two available dp4s from Mas de Gimel, a damaged left one (UM-MGL-649) and a well-preserved right one (UM-MGL-664). On the latter (Fig. 10A), the trigonid is shorter labiolingually than the talonid; it is closed with a low premetacristid-antерolophid and the metaconid is only slightly protruding. The protoconid is slightly more distal. Protoconid and metaconid connect with the metalophid I, which limits the anteroflexid distally. From there, a bifurcate mesiodistal ridge descends labially to the mesoflexid. The postprotocristid, whose distal part is indistinct from the mesial ectolophid, joins the ectolophid bearing the mesoconid. Then at the level of the junction between the distal ectolophid and the prehypocristid, the entolophid develops up to the base of the entoconid. There the entoconid appears isolated, separated also from the posterolophid. The hypoconid is followed with a strong posthypocristid, and then a strong distinct hypoconulid precedes the short posterolophid. An additional extra ridge lies in the posteroflexid, parallel to the entolophid.

p4. There are five available p4s, three, damaged, from Mas de Gimel (UM-MGL-616, MGL-644, and MGL-786), two better preserved from Naples (UM-NAP-44 and NAP-53). The two well-preserved long roots of UM-NAP-44 fuse below the crown along the $\frac{1}{3}$ to $\frac{1}{2}$ of their height (Fig. 10C). As on dp4, the metaconid is slightly protruding, but more than the protoconid. The latter is crested similarly as other cuspids of the crown. As formerly stated (Escarguel 1999: 210), the wrinkles are numerous along the distal slope of the trigonid and in the talonid, and one can recognize the metalophid I linking the protoconid and the metaconid, as well as the mesoconid and the ectolophid (UM-NAP-44; Fig. 10C), and elements of the entolophid connected to the prehypocristid and the posterior cingulum on both. On UM-NAP-53, the postmetacristid ends distally in a metastylid swelling, separated from the mesostylid, which closes the mesoflexid lingually (Fig. 10B).

m1 or m2. There are ten m1-2s from Mas de Gimel (m1s: UM-MGL-620, MGL-637, MGL-648, MGL-652; m2s:

UM-MGL-618, MGL-625, MGL-635, MGL-653, MGL-750, MGL-751) and eight from Naples (m1s: UM-NAP-32, NAP-39, NAP-43; m2s: UM-NAP-33, NAP-34, NAP-35, NAP-40, NAP-41) (Fig. 10D-K). The only difference between m1 and m2 is the narrower labiolingual width of the anterolophid-trigonid of m1 compare to m2.

As for dp4 and p4, the metaconid is only slightly protruding, but the protoconid is stronger than on these teeth. The four main cuspids (proto-, meta-, ento- and hypoconid) are crested, and their shape appears clearly on unworn teeth, delimiting an incomplete pericingulid, due to the presence of the sinusid and of the narrow mesoflexid opening.

The preprotocristid, attached to the mesial flank of the protoconid is either separated from the (labiolingual) premetacristid or joins it to make a complete transverse anterolophid. Distal to it, the protoconid bears a strong labial metalophulid I, which is generally short, never connected to a complete transverse lingual metalophulid I. The only case of a connection is the m1 UM-NAP-43 (Fig. 10E). Descending along the labiodistal flank of the metaconid, there is rather one short oblique ridge, sometimes joining the mesiodistal ridges developed distally from the anterolophid. There can be several (one to three) of these ridges, and another developed from the labial metalophid to the basin (Fig. 10G-K). The postmetacristid can show a metastylid-mesostylid thickening, and can be prolonged in a short lingual mesolophid (UM-MGL-618, MGL-648; UM-NAP-41; Fig. 10G, D, J). The protoconid is crested and stretched mesiodistally. It attaches to the mesial ectolophid through the postprotocristid. The mesoconid is aligned obliquely with the mesolophid. Distally, the mesoconid forms an angle with the distal ectolophid. The mesoconid makes another angle with the prehypocristid. The hypoconid is obliquely stretched to the posthypocristid.

The ridges are numerous in the basin, one of which derived from the mesoconid is a labial mesolophid. Another joins the distal ectolophid directly to the entoconid. This entolophid is either complete (UM-NAP-39, NAP-40 [Fig. 10F]) or broken in several elements (UM-NAP-35, NAP-41 [Fig. 10H, J]; UM-MGL-618 [Fig. 10G]). It connects to the posterolophid (UM-MGL-648 (Fig. 5A); UM-NAP-34) or to the distal ectolophid and the posterolophid (UM-MGL-618).

m3. There are four m3s from Naples (UM-NAP-36, NAP-37, NAP-38, NAP-46) and three from Mas de Gimel (UM-MGL-617, MGL-787, MGL-749) (Fig. 10L-O). The main difference between m3s and m1-2s is their narrower labiolingual width of the talonid.

The labial metalophulid I (named anterior arm of the protoconid in Escarguel 1999: 210) is rarely present, short and oblique mesiodistally (UM-MGL-617 and UM-NAP-38, Fig. 10L). On the two same specimens, the lingual metalophulid I is like on m1-2 as oblique ridges descending on the metaconid lingual flank, and directed to the basin. On the other m3s, the metalophulid I is absent and therefore, the anteroflexid is not individualized. The anterolophid and the premetacristid do not join on UM-NAP-38, NAP-46 (Fig. 10L-M) and UM-MGL-617, thus a mesiodistal furrow, bordered

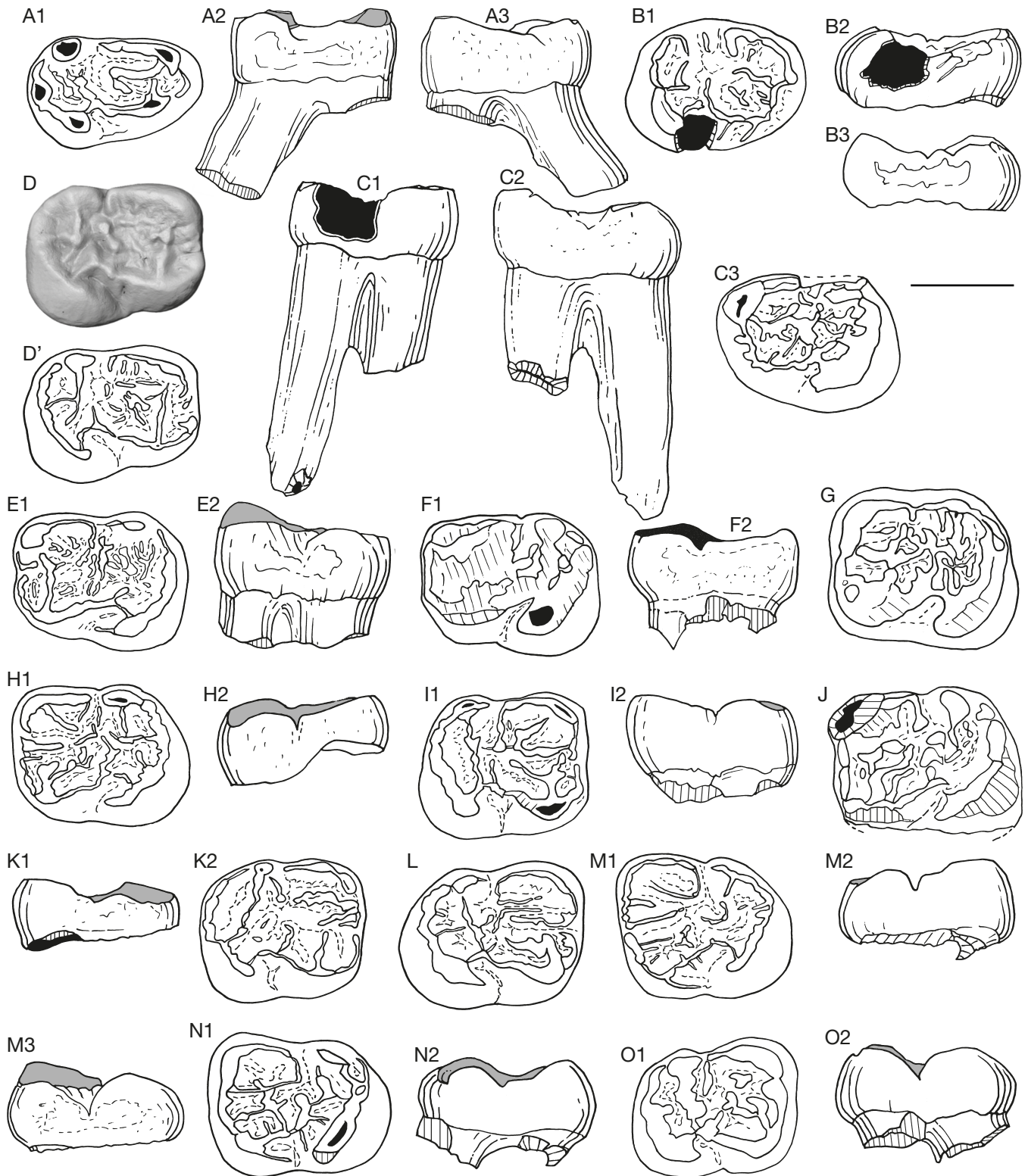


FIG. 10. — Lower deciduous (dp4), premolars (p4) and molars (m1-2-3) of *Hartenbergeromys pailladensis* n. sp. from the two closely related localities: MGL, Mas de Gimel (Hérault), and NAP, Naples (Hérault): **A**, UM-MGL-664, right dp4, showing the diverging roots: **A1**, occlusal view; **A2**, labial view; **A3**, lingual view; **B**, UM-NAP-53, right p4, nearly unworn: **B1**, occlusal view; **B2**, labial view, enamel cover partially erased, dentine blackened; **B3**, lingual view; **C**, UM-NAP-44, left p4: **C1**, occlusal view; **C2**, labial view; **C3**, lingual view, enamel cover partially erased, dentine blackened; two strong vertical roots, fused at their upper part; **D**, UM-MGL-648, right m1, nearly unworn, MicroCTscan, occlusal view; **D'**, same as **D**, drawings; **E**, UM-NAP-43, left m1, nearly unworn, incomplete roots: **E1**, occlusal view; **E2**, labial view; **F**, UM-NAP-39, left m1, weakly worn, incomplete roots: **F1**, occlusal view; **F2**, lingual view; **G**, UM-MGL-618, worn left m2, occlusal view; **H**, UM-NAP-35, unworn left m2: **H1**, occlusal view; **H2**, lingual view; **I**, UM-NAP-33, moderately worn right m2: **I1**, occlusal view; **I2**, lingual view; **J**, UM-NAP-41, worn m2 with labial side damaged, occlusal view; **K**, UM-NAP-34, unworn right m2: **K1**, occlusal view; **K2**, lingual view; **L**, UM-NAP-38, right m3, occlusal view; **M**, UM-NAP-46, left m3, unworn: **M1**, occlusal view; **M2**, lingual view; **M3**, labial view; **N**, UM-NAP-37, left m3, weakly worn, incomplete roots: **N1**, occlusal view; **N2**, lingual view; **O**, UM-NAP-36, right m3: **O1**, occlusal view; **O2**, labial view. Scale bar: 1 mm. The background of the profiles is greyed out on E2, F2, H2, M2.

with mesiodistal ridges, opens the trigonid mesially. Instead, they join on UM-NAP-36 and NAP-37 (Fig. 100, N). The postmetacristid shows a metastylid-mesostylid thickening, and is prolonged in a short lingual mesolophid (UM-NAP-36, NAP-37, NAP-46). A distolabial spur of the protoconid is present on UM-NAP-37, NAP-38, NAP-46 and UM-MGL-617.

The postprotocristid, ectolophid, mesoconid, distal ectolophid and prehypocristid are like in m1-2. Numerous ridges converge into the talonid basin. Likewise, numerous ridges converge from the posterolophid to the posteroflexid. The entolophid is either discontinuous or continuous (UM-NAP-36, NAP-38; UM-MGL-617) and the most often connects the entoconid to the mesoconid. On UM-NAP-37, it connects the base of the entoconid and twice the posterior cingulum. The external walls of the unworn UM-NAP-46 are very finely wrinkled.

COMPARISONS AND DISCUSSION

DP4 of *Hartenbergeromys paillardensis* n. sp. differs from that of *H. hautefeuillei* by less salient cusps above the grinding surface, less well-defined lophs on unworn tooth, and less lingual hypocone relative to the protocone. P4 differs mainly in its pericingulum and the less salient main cusps and more horizontal wear pattern. Moreover, the endoloph and hypocone are indistinct on UM-NAP-58, NAP-59 whereas they are well marked on some P4s of *H. hautefeuillei*. The main differences with upper molars of *H. hautefeuillei* and *H. marandati* are the more crestiform than bulging cusps, the metacone and hypocone respectively smaller relative to the paracone and protocone; the complete development of a relatively high pericingulum, as well as the different mode of wear and the size of teeth clearly lower for *H. paillardensis* n. sp. The three species of *Hartenbergeromys* are quite similar in size. Nevertheless, molars of *H. paillardensis* n. sp. appear intermediate in size between those of the larger *H. marandati* and the smaller *H. hautefeuillei*. Regarding lower molars only, the main differences with *H. hautefeuillei* and *H. marandati* are the more crestiform than pointed bulging cusps. In *H. paillardensis* n. sp., the entoconid is crested and displays pre- and posthypocristids, the crested hypoconid is prolonged to the posthypocristid; the crested protoconid and metaconid have pre- and postcristids.

Escarguel (1999) proposed that the specimens from Mas de Gimel and Naples he named *Hartenbergeromys* aff. *hautefeuillei* display a set of derived characters relative to *H. hautefeuillei* from Prémontré. He mentioned several characters, “making the population from Mas de Gimel and Naples even more derived than that of Prémontré” (very wrinkled enamel surface, anteroloph absent on P4, strongly developed lingual cingulum on upper molars, complete or almost complete hypolophid on m1-m3). These characters require some comments.

The absence of anteroloph on P4 is actually variable in *Hartenbergeromys paillardensis* n. sp., as well as in *H. marandati* and *H. hautefeuillei* (Escarguel 1999: 202; Vianey-Liaud & Marivaux: 80-82). The entolophid (= hypolophid) in *H. paillardensis* n. sp. is neither more nor less complete than in the two other *Hartenbergeromys* species. Teeth enamel surfaces of *H. paillardensis* n. sp. are not much more wrinkled

than *H. hautefeuillei* (see Vianey-Liaud & Marivaux 2021: 82-93). Finally, we agree with Escarguel (1999) regarding the strong development of crested cusps giving a pericingulum on upper teeth. This trait could be however related to a difference in eating habits with *H. hautefeuillei*, together with a chronological difference.

To conclude, *Hartenbergeromys paillardensis* n. sp. only occurs in Mas de Gimel and Naples whereas *H. hautefeuillei* occurs in Prémontré, Grauves, Saint-Agnan, and possibly Azillanet (pending new discoveries, the only two teeth from that locality are here attributed to *H. aff. hautefeuillei*).

DISCUSSION

FAUNAL COMPOSITION

The Mas de Gimel collection, known to be a reference fauna for the late Ypresian from southern European basin (Hartenberger *et al.* 1969), has in fact been the subject of few studies concerning its whole mammalian community. The first faunal list proposed the presence of 15 mammal species (Cappetta *et al.* 1968) whereas the most confident actualization by Vianey-Liaud *et al.* (2021) mentioned 23 species. The revision of the 1968' collection helps us to identify 36 taxa, completed by two others (cf. *Peradectes* sp. in Marandat [1986] and *Arcius lapparenti*) recently discovered from the unsorted sediment also sampled in 1968. Therefore, the 38 taxa recovered from Mas de Gimel permit nearly to double the species number previously identified. Among the mammalian remains (N = 574), 495 are identified at least at the order level. The important number of specimens in the collection allows us proposing percentage of abundance (Fig. 11A). Counting of NMI is not possible here considering that most of the fossils are isolated dental remains with very few locus repetitions. The ordinal or higher-level repartition of the specimens show an overrepresentation of Rodentia (25%, Fig. 11A). Then Perissodactyla and Metatheria display equivalent proportion (18%). Eulipothyphla are well represented (11%) and this is also the case for the Primates (7%). It worth notifying the weak proportion of Artiodactyla (4%) and Chiroptera (3%). The most represented species are *Masillamys mattaueri* (15% of the specimen abundance by species) and *Peratherium monspeliense* (14%). This is not surprising as both species were defined from this fossiliferous locality (Hartenberger 1975; Crochet 1979). These results are probably biased by the high number of indeterminate specimens. This is linked to the ancient established collection, in which a lot of too fragmentary specimens were numbered. It can also be noted that among the high number of perissodactyl specimens, an important number can be attributed at the generic level to *Lophiodon* but cannot be attributed confidently to the species *L. cf. leptorhynchum*. Therefore, based on the size of the tooth fragments and the enamel thickness, percentage of specimens of this species could reach 10% of the whole fauna instead of 4% (Fig. 11A). In the same way, the high proportion of unspecified specimens of Primates and Chiroptera corresponds to numerous anterior teeth or fragments of jugal teeth hardly attributable.

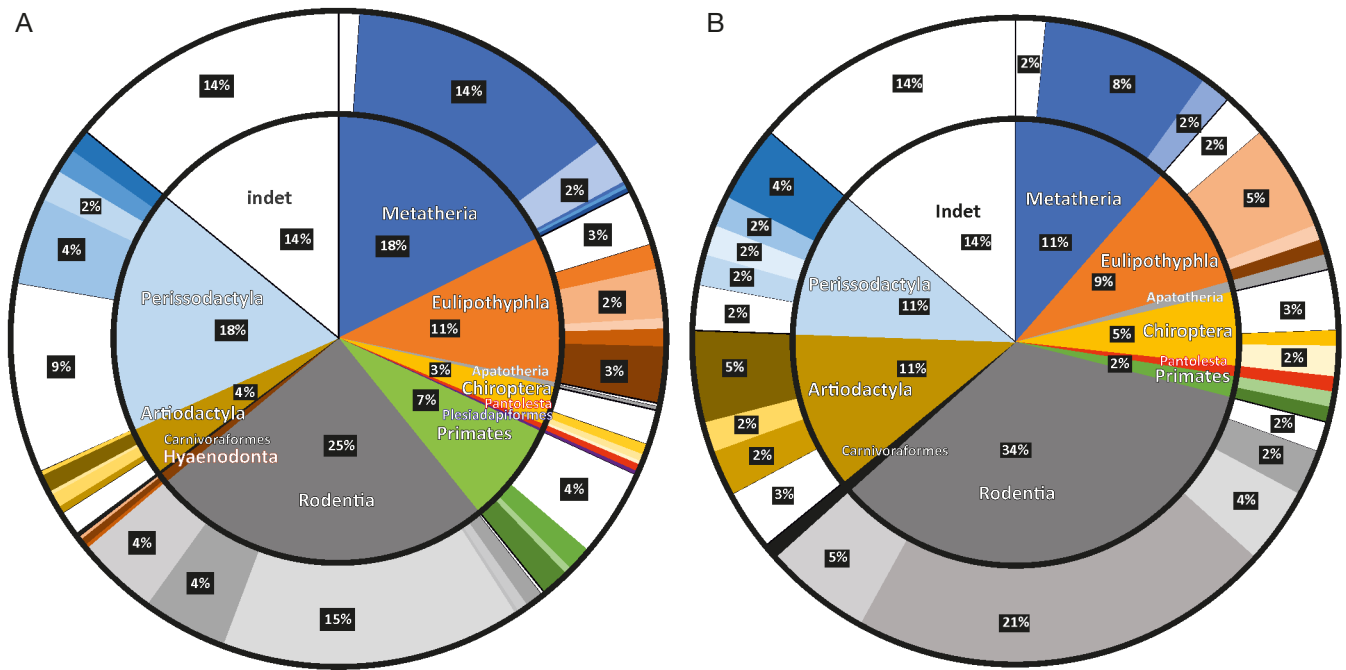


FIG. 11. — Distribution in percent of specimens by order and species from Mas de Gimel and Naples elaborated from data of Tables 2 and 3: **A**, color pie chart of Mas de Gimel collection; **B**, color pie chart of Naples collection. White sections correspond to specimens of indeterminate order or, within an order, of indeterminate specific attribution. Each identified species presents a color variation of the order color section. Percentage number are indicated when superior to one.

The locality of Naples has never been the subject of a faunal survey. Discovered in 1988, this locality was just punctually mentioned within specific taxonomical work mainly on rodents and artiodactyls (Escarguel 1999; Sudre & Lecomte 2000; Vianey-Liaud *et al.* 2019, 2022). Compared to Mas de Gimel, the number of specimens is weaker (131 mammalian specimens) and the observed mammal diversity is lower (23 recognized species instead of 38). The ordinal or higher rank repartition of specimen is however very similar to that observed for Mas de Gimel with a high representation of Rodentia (34%) followed by two equally distributed taxa: Perissodactyla and Metatheria (11%) (Fig. 11B). Noteworthy, the Artiodactyla appear proportionally more numerous in Naples fauna (11%, as much as Perissodactyla) despite a weaker specific diversity (3 species vs 5). Primates are not abundant in Naples with only 2% instead of 7% in Mas de Gimel. Moreover, Plesiadapiformes are not retrieved from Naples. Finally, Eulipothyphla (9%) and Chiroptera (5%) present the same relative importance than in Mas de Gimel. The most abundant species from Naples is the newly described rodent *Hartenbergeromys paillardensis* n. sp. (21%). It is just followed by the Metatheria *Peratherium* sp. (8%) that potentially includes *P. monspeliense* and *P. matronense*, for which a revision is needed.

Both faunas of Mas de Gimel and Naples are much diversified and display representatives of small, medium and large mammals, without any apparent fossilization bias. Moreover, the species repartition within each order follows a similar pattern in the two fossiliferous localities (Fig. 11). Conversely, the fauna discovered in Naples 2 is evidently biased in favour of large mammals (1 haplobunodontid, 1 palaeotheriid, and 67 *Lophiodon* remains, including numerous dentar rows and

not only isolated teeth). This is due to the different nature of the lithologies (marl rich in organic matter for Mas de Gimel and Naples, and marly limestone for Naples 2) and the low sieving effort (15 kg) for Naples 2. The five taxa from Naples 2 are nevertheless also known in Naples and Mas de Gimel (*P. monspeliense* or *P. matronense*, *Macrocranion* sp., *Hartenbergeromys paillardensis* n. sp., *Cuisitherium lydekkeri*, *Lophiodon* cf. *leptorhynchum*, and *Propalaeotherium gaudryi*).

Despite numerous similarities in both faunas from Mas de Gimel and Naples, we notice 16 taxa known from Mas de Gimel but not found in Naples (Tables 2; 3): the two peradectids, the small eulipothyphlans (*Macrocranion* cf. *nitens* morph A and *Leptacodon* sp.), two chiropterans (*P.* cf. *tupaiodon* and ?*Icaronycteridae* indet.), a small indeterminate pantolestid, a paromomyid (*Arcius lapparenti*), a large notharctid (cf. *Protoadapis curvicspidens*), two rodents (*Plesiartctomys* cf. *savagei* and *Pseudoparamys* sp.), hyaenodontids (*Lesmesodon* cf. *gunelli*, *Matthodon peignei*, and *Leonhardtina meridianum*) and two artiodactyls (*Eurodaxis russelli* and an original large haplobunodontid). On the other hand, some taxa from Naples are not known in Mas de Gimel such as the chiropteran *Icaronycteris* sp., the pantolestid *Pantolestes sabatieri*, and the metatherian cf. *Amphiperatherium bastbergense*. In any way, these three taxa are always weakly represented (by one or two specimens), which suggests that they are uncommon taxa, hardly recovered from these fossiliferous localities. In fact, in both cases, the taxonomic disparity is correlated with uncommon taxa (one to three specimens; Tables 2; 3) with the exception of the small *Macrocranion* cf. *nitens* morph A, *Leptacodon* sp. and the larger cf. *Protoadapis curvicspidens* that are quite well represented in Mas de Gimel (5 to 7 specimens).

TABLE 2. — New faunal list of Mas de Gimel based on 574 mammalian specimens (495 defined at least at order level), established after first description (Cappetta *et al.* 1968 and Hartenberger *et al.* 1969), subsequent targeted reviews (Hartenberger 1971; Crochet 1980; Sudre *et al.* 1983; Sudre & Lecomte 2000; Escarguel 1999) and according to this study (the main changes are in bold police).

Order or higher rank	N	Family	N	Species	N
Metatheria	101	Herpetotheriidae	99	<i>Peratherium monspeliense</i> Crochet, 1979	79
				<i>Peratherium matronense</i> Crochet, 1979	13
				Herpetotheriidae gen. et sp. indet.	1
Eulipotyphla	61	Peradectidae	2	cf. Peradectes sp. in Marandat (1986)	1
				Peradectes cf. mutigniensis Crochet, 1979	1
				Macrocraion cf. nitens (Matthew, 1918) morph A	7
Apatotheria	2	Apatemyidae	2	Macrocraion cf. nitens morph B	14
				Macrocraion sp. (sensu Russell et al. 1975)	3
				Leptacodon sp.	5
Chiroptera	16	Palaeochiropterygidae	5	aff. Pontifactor sp.	16
				Heterohyus sp.	1
				Palaeochiropterygidae gen. et sp. indet.	3
Pantolestia	2	Pantolestidae	2	Palaeochiropteryx cf. tupaiodon Revilliod, 1917	2
				?Icaronycteridae sp. indet.	1
				Pantolestidae gen. et sp. indet.	2
Plesiadapiformes	1	Paromomyidae	1	Arcius lapparenti (Russell, Louis & Savage, 1967)	1
Primates	42	Notharctidae	16	cf. Protoadapis curvicaudatus (Lemoine, 1878)	7
				Anchomomys sp.	2
				Nannopithecus zuccolae Godinot, Russel & Louis, 1992	8
Rodentia	142	Microchoeridae	13	Ailuravus aff. michauxi Hartenberger, 1975	5
				Plesiarctomys cf. savagei (Michaux, 1964)	3
				Pseudoparamys sp.	1
Rodentia	142	Ailuravidae	5	Masillamys mattaueri Hartenberger, 1975	85
				Hartenbergeromys paillardensis n. sp.	24
				Eogilravus wildi Hartenberger, 1971	23
Rodentia	142	Plesiarctomyidae	4	Uintacyon cf. hookeri Solé, 2014	2
				Lesmesodon cf. gunelli Solé, Morlo, Schaal & Lehmann, 2021	1
				Matthodon peignei Solé, Marandat & Lihoreau, 2020	2
Rodentia	142	Masilamyidae	85	Leonhardtina meridianum Solé, Marandat & Lihoreau, 2020	1
				Diacodexis cf. varleti Sudre, 1983	2
				Protodichobune oweni Lemoine, 1878	4
Rodentia	142	Rodentia indet	24	Eurodexis russelli Sudre & Erfurt, 1996	1
				Cuisitherium lydekkeri (Lemoine, 1891)	5
				cf. Haplobunodontidae indet.	1
Rodentia	142	Gliridae	23	Lophiodon cf. leptorhynchum Filhol, 1888	25
				Hyrachyus stehlini (Depéret, 1904)	9
				Propalaeotherium gaudryi (Lemoine, 1878)	7
Carnivoraformes	4	"Miacidae"	2	Pachynolophus cf. ruscasseriensis Remy, Krasovec, Lopez, Marandat & Lihoreau, 2019	6
				Hyaenodontidae	4
				Hyaenodontidae	4
Hyaenodonta	4	Hyaenodontidae	4	Diacodexis cf. varleti Sudre, 1983	2
				Protodichobune oweni Lemoine, 1878	4
				Eurodexis russelli Sudre & Erfurt, 1996	1
Artiodactyla	21	Diacodexidae	2	Cuisitherium lydekkeri (Lemoine, 1891)	5
				cf. Haplobunodontidae indet.	1
				Lophiodon cf. leptorhynchum Filhol, 1888	25
Artiodactyla	21	Dichobunidae	5	Hyrachyus stehlini (Depéret, 1904)	9
				Propalaeotherium gaudryi (Lemoine, 1878)	7
				Pachynolophus cf. ruscasseriensis Remy, Krasovec, Lopez, Marandat & Lihoreau, 2019	6
Artiodactyla	21	Haplobunodontidae	6	Lophiodon cf. leptorhynchum Filhol, 1888	25
				Hyrachyus stehlini (Depéret, 1904)	9
				Propalaeotherium gaudryi (Lemoine, 1878)	7
Perissodactyla	101	Lophiodontidae	62	Pachynolophus cf. ruscasseriensis Remy, Krasovec, Lopez, Marandat & Lihoreau, 2019	6
				Hyrachyidae	9
				Palaeotheriidae	27

Mas de Gimel and Naples belong to the same stratigraphic unit with similar sedimentological facies and are only separated one to the other by around 300 m. The only noticeable differences are basically on the representativeness of uncommon taxa. The two mammalian paleocommunity structures do not evocate ecological nor chronological differences. In addition, and depending on some taxonomic interpretations (see Results), twenty to twenty-two species are common to both localities. Following these arguments, we confidently propose to assemble these two contemporaneous faunas in one fossiliferous unit MGL/NAP rich of 41 species. This faunal assemblage is thus comparable in term of specific richness with the main reference faunas listed in Table 4 (Mutigny = 48 sp., Avenay = 55 sp., Saint-Agnan = 37 sp., Grauves and all contemporaneous localities near Epernay = 47 sp., Prémontré = 37 sp.). MGL/NAP, with 41 species, gathers with the most diverse faunas of the Ypresian with quasi-equivalent diversity than the well-known Lutetian locality of Messel (44 species). Such a result strengthens the longstanding conclusion

proposed by Hartenberger *et al.* (1969) that MGL/NAP is a key European Ypresian reference fauna, very informative for biochronological and paleobiogeographical purposes.

BIOCHRONOLOGY AND PALEOBIOGEOGRAPHY

Biochronological questions inferred from the rich mammal assemblage from MGL/NAP require detailed faunal comparisons with European localities encompassing the MP8+9 to MP11 reference-levels (Table 4). With Avenay (reference-level for the MP8+9), MGL/NAP shares the herpetotheriid *Peratherium matronense* (note however that this species is the subject of a current taxonomic revision), possibly *Peradectes mutigniensis*, and the two amphilemurid species *Macrocraion cf. nitens* (morphs A and B) and *Macrocraion sp.* With Mutigny (commonly considered as older than Avenay), MGL/NAP shares also these two amphilemurids and possibly *Peradectes mutigniensis*. More similarities are found with the locality of Saint-Agnan, which is commonly attributed to the MP10a but considered intermediate in age between Avenay and the

TABLE 3. — Faunal list of Naples and Naples 2 based on 130 and 78 mammalian specimens, respectively.

Order or higher rank	N	Family	N	Species Naples	N	Species Naples 2	N	
Metatheria	15/2	Herpetotheriidae	14/2	<i>Peratherium monspeliense</i> Crochet, 1979 or <i>P. matronense</i> Crochet, 1979 cf. <i>Amphiperatherium bastenbergense</i> Crochet, 1979	11	<i>Peratherium monspeliense</i> or <i>P. matronense</i>	2	
Eulipotyphla	12/2	Amphilemuridae	10/2	<i>Macrocranion</i> cf. <i>nitens</i> (Matthew, 1918) morph B	7	–	–	
				<i>Macrocranion</i> sp. (sensu Russell <i>et al.</i> 1975)	1	<i>Macrocranion</i> sp. (sensu Russell <i>et al.</i> 1975)	2	
		Nyctitheriidae	1	aff. <i>Pontifactor</i> sp.	1	–	–	
Apatotheria	1	Apatemyidae	1	<i>Heterohyus</i> sp.	1	–	–	
Chiroptera	7	Palaeochiropterygidae Icaronycteridae	1	Palaeochiropterygidae gen. et sp. indet.	1	–	–	
				2	<i>Icaronycteris</i> sp. indet.	2	–	–
Pantolesta	1	Pantolestidae	1	? <i>Pantolestes sabatieri</i> Smith, 2001	1	–	–	
Primates	2	Notharctidae	1	<i>Anchomomys</i> sp.	1	–	–	
		Microchoeridae	1	<i>Nannopithex zuccolae</i> Godinot, Russell & Louis <i>et al.</i> , 1992	1	–	–	
Rodentia	45	Ailuravidae Masillamyidae indet Gliridae	3	<i>Ailuravus</i> aff. <i>michauxi</i>	3	–	–	
				5	<i>Masillamys mattaueri</i> Hartenberger, 1975	5	–	–
				28	<i>Hartenbergeromys pailladensis</i> n. sp.	28	–	2
				7	<i>Eoglravus wildi</i> Hartenberger, 1971	7	–	–
Carnivoramorph	1	“Miacidae”	1	<i>Uintacyon</i> cf. <i>hookeri</i>	1	–	–	
Artiodactyla	15/1	Diacodexidae Dichobunidae Haplobunodontidae	3	<i>Diacodexis</i> cf. <i>varleti</i> Sudre, 1983	3	–	–	
				2	<i>Protodichobune oweni</i> Lemoine, 1878	2	–	–
				6/1	<i>Cuisitherium lydekkeri</i> (Lemoine, 1891)	6	<i>Cuisitherium lydekkeri</i>	1
Perissodactyla	14/68	Lophiodontidae Hyrachyidae Palaeotheriidae	2/67	<i>Lophiodon</i> cf. <i>leptorhynchum</i> Filhol, 1888	2	<i>Lophiodon</i> cf. <i>leptorhynchum</i>	67	
				2/2	<i>Hyrachyus stehlini</i> (Depéret, 1904)	2	–	–
				9/1	<i>Propalaeotherium gaudryi</i> (Lemoine, 1878) <i>Pachynolophus</i> cf. <i>ruscasseriensis</i> Remy, Krasovec, Lopez, Marandat & Lihoreau, 2019	2	<i>Propalaeotherium gaudryi</i>	1
				5	–	–		

MP10a reference localities from the *Sables à Unios et Térédines* Formation (see below) (Louis & Laurain 1983; Lecomte 1994; Escarguel 1999). MGL/NAP shares with Saint-Agnan the ten following species: *Macrocranion* cf. *nitens*, *Macrocranion* sp., *Masillamys mattaueri*, *Nannopithex zuccolae*, *Propalaeotherium gaudryi*, *Hyrachyus stehlini*, *Diacodexis* cf. *varleti*, *Protodichobune oweni*, *Eurodexis russelli*, and *Cuisitherium lydekkeri*; plus the following four species in open nomenclature: *Peradectes* cf. *mutigniensis*, *Ailuravus* aff. *michauxi*, *Plesiarctomys* cf. *savagei*, and cf. *Protoadapis curvicauspiciens*. Among these species, only *Peradectes* cf. *mutigniensis* evokes the level MP8+9; the other are typical of the level MP10a.

Comparisons with Grauves (reference-level of the MP10a) and other localities from the *Sables à Unios et Térédines* Formation (Cuis, Mancy, Monthelon, Mont Bernon, Venteuil, and Chavot) indicate that MGL/NAP shares with one or more of these localities the following twelve species: *Heterohyus* sp.3, *Macrocranion* sp., *Macrocranion* cf. *nitens*, *Masillamys mattaueri*, *Arcius lapparenti*, *Nannopithex zuccolae*, *Lesmesodon gunnelli*, *Propalaeotherium gaudryi*, *Hyrachyus stehlini*, *Diacodexis* cf. *varleti*, *Protodichobune oweni*, and *Cuisitherium lydekkeri*; plus the species in open nomenclature *Palaeochiropteryx* cf. *tupaiondon*, *Ailuravus* aff. *michauxi*, *Plesiarctomys* cf. *savagei*, cf.

Protoadapis curvicauspiciens, and *Eurodexis russelli* (note that this species is identified as *E. cf. russelli* at Grauves, Saint-Agnan, Mancy, and Cuis).

Among the localities from the Paris Basin attributed to the MP10a, Prémontré has the particularity of having a well-constrained dating using nannoplankton and dinoflagellate biostratigraphy. The locality is estimated to postdate the onset of both NP13 and Chron C22r, at about 50.4 to 50.3 Ma (Steurbaut *et al.* 2016). MGL/NAP shares with this locality the species *Macrocranion* sp., *Pantolestes sabatieri*, *Arcius lapparenti*, *Nannopithex zuccolae*, *Eoglravus wildi*, *Diacodexis* cf. *varleti*, *Eurodexis russelli*, and *Lesmesodon gunnelli*. Interestingly, among these taxa, the three species *Pantolestes sabatieri*, *Eoglravus wildi*, and *Lesmesodon gunnelli* are not documented elsewhere in the Paris Basin from MP10a localities, suggesting that MGL/NAP and Prémontré could be coeval. This hypothesis is however uncertain because most of the pantolestids from the MP10a localities are still unpublished and the rodent *E. wildi* also occurs in localities from the MP10-MP11 interval (Cos and Vielase, Southern France, Quercy) (Vianey-Liaud *et al.* 2022). Finally, also from Southern France, the locality of Azillanet, attributed to the MP10a, requires a mention as it shares significant taxa with MGL/NAP: *Peradectes* sp.

TABLE 4. — Faunal list of Mas de Gimel/Naples compared to those of other European localities dated from MP8+9 to MP11 reference-levels (data compiled from Bronnert & Métais 2023; Crochet 1979, 1980; Dégremont *et al.* 1985; Erfurt & Sudre 1996; Escarguel 1999; Fischer 1977; Franzen 1988; Franzen & Haubold 1986; Franzen & Habersetzer 2017; Franzen *et al.* 2009; Gingerich 1976; Gingerich 1977; Godinot 1998; Godinot *et al.* 1992, 2018; Haubold 1989; Hand & Sigé 2018; Hellmund 2013; Hlawatsch & Erfurt 2007; Hooker 1996, 2010; Kurtz 2005; Lange-Badré & Haubold 1990; López-Torres & Silcox 2018; Louis & Laurain 1983; Marandat 1986; Morlo *et al.* 2004, 2010; Russell *et al.* 1967, 1973, 1975, 1979, 1982; Savage *et al.* 1965; Sigé 1976; Smith 2001; Smith *et al.* 2012; Solé 2014; Solé *et al.* 2015, 2018, 2019, 2020, 2021; Sudre *et al.* 1983; Sudre & Erfurt 1996; Sudre & Lecomte 2000; Theodor *et al.* 2007; Thewissen 1990; Vautrin *et al.* 2020; Vianey-Liaud & Marivaux 2021; Vianey-Liaud *et al.* 2022). Abbreviations: **MUT**, Mutigny; **AVE**, Avenay; **STA**, Saint-Agnan; **MGL**, Mas de Gimel; **NAP**, Naples; **GRA**, Grauves, Cuis, Mancy, Monthelon, Mont Beron, Venteuil, and Chavot; **PRE**, Prémontré; **AZI**, Azillanet; **ROU**, Rouzilhac; **GEI**, Geiseltal Unterkohle (United Kingdom), **MES**, Messel.

			MUT	AVE (MP8+9)	STA	MGL	NAP	GRA (MP10a)	PRE	AZI	ROU (MP10b)	GEI (MP11)	MES	
Multituberculata	Neoplagiaulacidae	<i>Ectypodus</i> sp.	x	x	-	-	-	-	-	-	-	-	-	
		<i>Parectypodus</i> sp.	x	x	-	-	-	-	-	-	-	-	-	
		<i>Neoplagiaulax sylvani</i>	aff.	-	-	-	-	-	-	-	-	-	-	
	Family indet.	gen. et sp. indet.	-	-	-	-	-	x	-	-	-	-		
Metatheria	Peradectidae	<i>Peradectes lousi</i>	x	x	-	-	-	x	-	-	-	-	-	
		<i>Peradectes mutigniensis</i>	x	x	x	cf.	-	-	-	-	-	-	-	
		<i>Peradectes</i> sp. (Crochet 1980)	x	x	-	-	-	-	-	-	-	-	-	
		<i>Peradectes russelli</i>	-	x	-	-	-	-	-	-	-	-	-	
		<i>Peradectes</i> sp. (Marandat 1986)	-	-	-	cf.	-	-	-	x	-	-	-	
			"Peradectes" (?Peradectidae)	-	-	-	-	-	-	-	-	-	x	
	Herpetotheriidae		<i>Peratherium constans</i>	x	-	-	-	-	-	-	-	-	-	-
			<i>Peratherium matronense</i>	-	x	-	x	?	-	-	-	-	-	-
			<i>Peratherium monspeliense</i>	-	-	-	x	?	-	-	x	-	-	-
			<i>Peratherium</i> sp. 1 (Crochet 1980)	-	-	-	-	-	-	-	cf.	-	-	-
			"Amphiperatherium brabantense"	x	-	-	-	-	-	-	-	-	-	-
			<i>Amphiperatherium maximum</i>	x	x	x	-	-	x	-	-	-	-	cf.
			<i>Amphiperatherium bourdellense</i>	-	x	-	-	-	-	x	-	-	-	-
			<i>Amphiperatherium goethei</i>	-	x	-	-	-	x	x	-	-	-	x
			<i>Amphiperatherium</i> sp. 1 (Crochet 1980)	-	x	-	-	-	x	-	-	-	-	-
			<i>Amphiperatherium</i> sp. 2 (Crochet 1980)	x	x	-	-	-	-	-	-	-	-	-
			<i>Amphiperatherium bastbergense</i>	-	-	-	-	cf.	-	-	-	-	-	-
			gen. et sp. indet. (this study)	-	-	-	x	-	-	-	-	-	-	-
			<i>Amphiperatherium</i> sp. (Marandat 1986)	-	-	-	-	-	-	-	x	-	-	-
gen. et sp. indet.			-	-	-	-	-	-	-	-	-	-	x	
Pantolestia	Pantolestidae	<i>Palaeosinopa</i> sp.	x	x	-	-	-	-	x	-	-	-	-	
		<i>Pantolestes sabatieri</i>	-	-	-	-	x	-	x	-	-	-	-	
		<i>Pantolestes</i> sp.	-	-	-	-	-	-	-	cf.	-	-	-	
		<i>Premontrelestes duchaussoisi</i>	-	-	-	-	-	-	-	x	-	-	-	
		<i>Premontrelestes</i> sp.	-	-	-	-	-	-	-	cf.	-	-	-	
		gen. et sp. indet.	-	-	-	x	-	-	x	-	-	-	-	
		<i>Buxolestes</i> sp.	-	-	x	-	-	x	-	-	-	-	-	
		<i>Buxolestes piscator</i>	-	-	-	-	-	-	-	-	-	-	x	
		<i>Buxolestes minor</i>	-	-	-	-	-	-	-	-	-	-	x	
		Paxoxyclaenidae		<i>Fratrodon tresvauxi</i>	x	x	-	-	-	-	-	-	-	-
				<i>Sororodon tresvauxae</i>	x	x	-	-	-	-	-	-	-	-
				<i>Paraspaniella gunnelli</i>	-	-	-	-	-	x	x	-	-	-
				<i>Kopidodon macrognathus</i>	-	-	-	-	-	-	-	-	-	-
<i>Paroxyclaenus</i> sp.	-			-	-	-	-	-	-	-	-	-	x	
Apatotheria	Apatemyidae	<i>Apatemys mutinacus</i>	x	x	x	-	-	-	-	-	-	-		
		<i>Apatemys sigogneai</i>	x	x	-	-	-	-	-	-	-	-		
		<i>Heterohyus</i> sp. 1 (Russell <i>et al.</i> 1979)	x	-	x	-	-	-	-	-	-	-		
		<i>Heterohyus</i> sp. 2 (Russell <i>et al.</i> 1979)	-	x	x	-	-	-	-	-	-	-		
		<i>Heterohyus</i> sp. 3 (Russell <i>et al.</i> 1979)	-	-	-	x	x	x	-	-	-	-		
Eulipotyphla	Amphilemuridae	<i>Neomatronella luciannae</i>	x	x	x	-	-	-	-	-	-	-		
		<i>Macrocranion</i> cf. <i>nitens</i> morph A	x	x	x	x	x	x	-	-	-	-		
		<i>Macrocranion</i> cf. <i>nitens</i> morph B	x	x	x	x	x	x	-	-	-	-		
		<i>Macrocranion</i> sp. (Russell <i>et al.</i> 1979)	x	x	x	x	x	x	x	-	-	-		
		<i>Macrocranion tenerum</i>	-	-	-	-	-	-	-	-	-	-	x	
		<i>Macrocranion tupaidon</i>	-	-	-	-	-	-	-	-	-	-	x	
		<i>Pholidocercus hassiacus</i>	-	-	-	-	-	-	-	-	-	-	x	
	Nyctitheriidae		<i>Leptacodon</i> sp.	x	x	-	x	-	-	cf.	-	-	-	
			<i>Placentidens lotus</i>	x	x	-	-	-	-	-	-	-	-	
			<i>Pontifactor</i> sp.	-	-	-	aff.	aff.	-	x	x	-	-	
	Talpidae	gen. et sp. indet.	-	-	-	-	-	-	-	x	-	-		

Table 4. — Continuation.

			MUT	AVE (MP8+9)	STA	MGL	NAP	GRA (MP10a)	PRE	AZI	ROU (MP10b)	GEI (MP11)	MES	
Order indet.	Pseudorhyncocyonidae	<i>Leptictidium tobieni</i>	-	-	-	-	-	-	-	-	-	-	×	
		<i>Leptictidium nasutum</i>	-	-	-	-	-	-	-	-	-	-	-	×
		<i>Leptictidium auderiense</i>	-	-	-	-	-	-	-	-	-	-	-	×
Chiroptera	Icaronycteridae	<i>Icaronycteris menui</i>	×	×	-	-	-	-	-	cf.	-	-	-	
		<i>Icaronycteris</i> sp.	-	-	?	-	×	-	-	-	-	-	-	
		gen. et sp. indet.	-	-	-	?	-	-	-	-	-	-	-	-
		<i>Xylonycteris stenodon</i>	-	-	-	-	-	-	×	-	-	-	-	-
	Archaeonycteridae	<i>Archaeonycteris brailloni</i>	×	×	-	-	-	-	-	-	-	-	-	-
		<i>Archaeonycteris</i> sp.	-	-	-	-	-	-	-	cf.	-	-	-	-
		<i>Archaeonycteris trigonodon</i>	-	-	-	-	-	-	-	-	-	-	-	×
		<i>Archaeonycteris pollex</i>	-	-	-	-	-	-	-	-	-	-	-	×
	Onychonycteridae	<i>Ageina tobieni</i>	×	-	-	-	-	-	-	-	-	-	-	-
		cf. <i>Ageina</i> sp.	-	×	-	-	-	-	-	-	-	-	-	-
	Palaeochiropterygidae	<i>Palaeochiropteryx</i> sp.	-	-	?	-	-	?	-	-	-	-	-	-
		<i>Palaeochiropteryx tupaiodon</i>	-	-	-	cf.	-	cf.	-	-	-	-	-	×
		<i>Palaeochiropteryx spiegelii</i>	-	-	-	-	-	-	-	-	-	-	-	×
		gen. et sp. indet.	-	-	-	×	×	-	-	-	-	-	-	-
	Hassianycteridae	<i>Hassianycteris messelensis</i>	-	-	-	-	-	-	-	-	-	-	-	×
		<i>Hassianycteris magna</i>	-	-	-	-	-	-	-	-	-	-	-	×
		<i>Hassianycteris revilliodi</i>	-	-	-	-	-	-	-	-	-	-	-	×
	Family indet.	gen. et sp. indet.	-	-	×	-	-	-	-	-	-	-	-	-
	Vespertilionidae	<i>Premonycteris vesper</i>	-	-	-	-	-	-	×	-	-	-	-	-
Emballonuridae	<i>Tachypteron franzeni</i>	-	-	-	-	-	-	-	-	-	-	-	×	
Rodentia	Gliridae	<i>Eogiliravus wildi</i>	-	-	-	×	×	-	×	×	-	-	-	
		<i>Eogiliravus hammeli</i>	-	-	-	-	-	-	-	-	-	-	-	cf.
	Ischyromyidae	<i>Ailuravus michauxi</i>	-	-	aff.	aff.	aff.	×	×	×	aff.	-	-	-
		<i>Ailuravus inexpectatus</i>	-	-	×	-	-	-	×	×	-	-	-	-
	Euromyidae	<i>Meldimys lousi</i>	×	×	×	-	-	-	-	-	-	-	-	-
		<i>Euromys thaleri</i>	×	×	-	-	-	-	-	-	-	-	-	-
		<i>Euromys woodi</i>	×	×	×	-	-	-	×	-	-	-	-	-
	Pleisarctomyidae	<i>Pseudoparamys teilhardi</i>	×	×	×	-	-	-	-	-	-	-	-	-
		<i>Pseudoparamys</i> sp.	-	-	-	×	-	-	-	-	-	-	-	-
		<i>Plesiarctomys savagei</i>	-	-	×	cf.	-	×	×	-	-	-	-	-
	Family indet.	<i>Sparnacomys chandoni</i>	×	×	-	-	-	-	-	-	-	-	-	-
		<i>Pantrogna russelli</i>	×	×	×	-	-	-	-	-	-	-	-	-
		<i>Reinomys rhomboides</i>	-	×	-	-	-	-	-	-	-	-	-	-
	Theridomyoidea	<i>Hartenbergeromys hautefeuillei</i>	-	-	×	-	-	×	×	×	-	-	-	-
		<i>Hartenbergeromys pailladensis</i> n. sp.	-	-	-	×	×	-	-	-	-	-	-	-
		<i>Hartenbergeromys marandati</i>	-	-	-	-	-	-	×	-	-	-	-	-
		<i>Masillamys mattaui</i>	-	-	×	×	-	×	×	-	-	-	-	-
		<i>Masillamys parvus</i>	-	-	-	-	-	-	?	-	-	-	-	×
		<i>Masillamys beegeri</i>	-	-	-	-	-	-	-	-	-	-	-	×
<i>Masillamys krugi</i>	-	-	-	-	-	-	-	-	-	-	-	×		
Plesiadapiformes	Paromomyidae	<i>Arcius fuscus</i>	×	×	×	-	-	-	-	-	-	-	-	
		<i>Arcius lapparenti</i>	×	×	-	×	-	×	×	×	-	-	-	
	Plesiadapidae	<i>Platychoerops daubrei</i>	×	×	×	-	-	×	-	-	-	-	-	
		<i>Platychoerops ?richardsoni</i>	-	-	-	-	-	×	-	-	-	-	-	
	Toliapinidae	<i>Toliapina lawsoni</i>	×	-	-	-	-	-	-	-	-	-	-	-
		<i>Toliapina vinealis</i>	-	×	-	-	-	-	-	-	-	-	-	-
<i>Avenius amatorum</i>	×	×	-	-	-	-	-	-	-	-	-	-		
Primates	Notharctidae	<i>Cantius savagei</i>	×	×	×	-	-	×	-	-	-	-	-	
		<i>Cantius</i> sp.	-	-	-	-	-	-	×	-	-	-	-	-
		<i>Donrussellia gallica</i>	-	×	×	-	-	-	-	-	-	-	-	-
		? <i>Donrussellia russelli</i>	-	×	-	-	-	-	-	-	-	-	-	-
		? <i>Donrussellia lousi</i>	-	×	-	-	-	-	-	-	-	-	-	-
		<i>Protoadapis curvicaudens</i>	-	-	×	cf.	-	×	aff.	-	-	-	-	-

Table 4. — Continuation.

			MUT	AVE (MP8+9)	STA	MGL	NAP	GRA (MP10a)	PRE	AZI	ROU (MP10b)	GEI (MP11)	MES	
Primates (cont.)	Notharctidae (cont.)	<i>?Protoadapis recticuspidens</i>	-	-	-	-	-	×	-	-	-	-	-	
		<i>Protoadapis</i> sp.	-	-	-	-	-	-	×	-	-	-	-	-
		<i>?Periconodon lemoinei</i>	-	-	-	-	-	-	×	-	-	-	-	-
		cf. <i>Periconodon</i> sp.	-	-	-	-	-	-	-	×	-	-	-	-
		gen. et sp. indet. (Louis & Laurain 1983)	-	-	×	-	-	-	×	-	-	-	-	-
		<i>Anchomomys</i> sp.	-	-	-	×	×	-	-	×	-	-	-	-
		<i>Agerinia</i> cf. <i>rosselli</i>	-	-	-	-	-	-	-	-	×	-	-	-
		<i>Rouzilemur pulcher</i>	-	-	-	-	-	-	-	-	-	×	-	-
		<i>Europolemur midiensis</i>	-	-	-	-	-	-	-	-	-	×	-	-
		<i>Europolemur koenigswaldi</i>	-	-	-	-	-	-	-	-	-	-	-	×
		<i>Europolemur kelleri</i>	-	-	-	-	-	-	-	-	-	-	-	×
		<i>Europolemur</i> sp.	-	-	-	-	-	-	-	-	-	-	-	×
		<i>Darwinius masillae</i>	-	-	-	-	-	-	-	-	-	-	-	×
		<i>Nannopithecus zuccolae</i>	-	-	×	×	×	×	×	×	-	-	-	-
		Didelphodonta	Cimolestidae	“cf. <i>Didelphodus</i> ”	×	×	-	-	-	-	-	-	-	-
Pholidota		<i>Eurotamandua joresi</i>	-	-	-	-	-	-	-	-	-	×	×	
		<i>Eomanis waldi</i>	-	-	-	-	-	-	-	-	-	-	×	
		<i>Eomanis krebsi</i>	-	-	-	-	-	-	-	-	-	-	×	
Hyaenodonta	Hyaenodontoidea	<i>Minimovellentodon russelli</i>	×	-	-	-	-	-	-	-	-	-	-	
		<i>Morlodon vellerei</i>	-	×	×	-	-	-	-	-	-	-	-	-
		cf. <i>Preregidens langebadrae</i>	-	×	-	-	-	-	-	-	-	-	-	-
		<i>Oxyaenoides lindgreni</i>	-	-	-	-	-	-	×	-	-	-	-	-
		<i>Oxyaenoides bicuspidens</i>	-	-	-	-	-	-	-	-	-	×	×	-
		<i>Matthodon peignei</i>	-	-	-	×	-	-	-	-	-	-	-	-
		<i>Matthodon menui</i>	-	-	-	-	-	-	×	-	-	-	-	-
		<i>Matthodon tritens</i>	-	-	-	-	-	-	-	-	-	-	×	-
		<i>Protoproviverra palaeonictides</i>	-	-	-	-	-	-	×	-	-	-	-	-
		<i>Leonhardtina meridianum</i>	-	-	-	×	-	-	-	-	-	×	-	-
		<i>Leonhardtina godinoti</i>	-	-	-	-	-	-	×	-	-	-	-	-
		<i>Lesmesodon gunnelli</i>	-	-	-	×	-	-	×	×	-	-	-	-
		<i>Lesmesodon edingeri</i>	-	-	-	-	-	-	-	-	-	-	-	×
		<i>Lesmesodon behnkeae</i>	-	-	-	-	-	-	-	-	-	-	-	×
		<i>Cynohyaenodon smithae</i>	-	-	-	-	-	-	-	×	-	-	-	-
		<i>Eurotherium mapplethorpei</i>	-	-	-	-	-	-	-	×	-	-	-	-
<i>Eurotherium matthesi</i>	-	-	-	-	-	-	-	-	-	-	×	-		
Carnivoramorpha		<i>Uintacyon hookeri</i>	×	×	-	cf.	cf.	×	-	-	-	-	-	
		<i>Quercygalie smithi</i>	×	-	-	-	-	×	-	-	-	-	-	
		<i>Quercygalie helvetica</i>	-	-	-	-	-	-	-	-	-	×	-	
		<i>Messelogale kessleri</i>	-	-	-	-	-	-	-	-	-	-	×	
		<i>Paroodectes feisti</i>	-	-	-	-	-	-	-	-	-	-	×	
Mesonychia	Mesonychidae	<i>Hyaenodictis filholi</i>	-	-	-	-	-	×	-	-	-	-		
Tillodontia		<i>Plesiesthonyx minimus</i>	×	×	-	-	-	×	-	-	-	-	-	
		<i>Plesiesthonyx munieri</i>	×	?	×	-	-	×	-	-	-	-	-	
		<i>Franchaius luciae</i> (= <i>P. minimus</i> ?)	-	×	-	-	-	-	-	-	-	-	-	
		<i>Esthonyx tardus</i>	-	-	-	-	-	-	-	-	-	×	-	
Condylarthra		<i>Phenacodus lemoinei</i>	×	×	-	-	-	×	-	-	-	-		
Perissodactyla	Equoidea	<i>Hyracotherium leporinum</i>	×	×	-	-	-	-	×	-	-	-	-	
		<i>Hallensia louisi</i>	×	×	-	-	-	×	-	-	-	-	-	
		<i>Hallensia parisiensis</i>	-	-	×	-	-	×	-	-	-	-	-	
		<i>Hallensia matthesi</i>	-	-	-	-	-	-	-	-	-	×	×	
	Palaeotheriidae	<i>Orolophus maldani</i>	-	-	×	-	-	-	×	×	-	×	-	-
		<i>Propalaeotherium gaudryi</i>	-	-	×	×	×	×	-	-	-	×	-	-
		<i>Propalaeotherium voighti</i>	-	-	-	-	-	-	-	-	-	-	×	-
		<i>Propalaeotherium hassiacum</i>	-	-	-	-	-	-	-	-	-	-	×	×
		<i>Propalaeotherium argentonicum</i>	-	-	-	-	-	-	-	-	-	-	×	-
		<i>Eurohippus messelensis</i>	-	-	-	-	-	-	-	-	-	-	-	×
<i>Eurohippus parvulum</i>	-	-	-	-	-	-	-	-	-	-	×	-		
<i>Pachynolophus livinierensis</i>	-	-	?	×	-	-	?	×	-	×	-	-		
<i>Pachynolophus</i> cf. <i>ruscasseriensis</i>	-	-	-	×	×	-	-	-	-	-	-	-		

Table 4. — Continuation.

			MUT	AVE (MP8+9)	STA	MGL	NAP	GRA (MP10a)	PRE	AZI	ROU (MP10b)	GEI (MP11)	MES	
Perissodactyla (continuation)	Hyrachyidae	<i>Hyrachyus stehlini</i>	-	-	x	x	x	x	-	-	x	-	-	
		<i>Hyrachyus minimus</i>	-	-	-	-	-	-	-	-	-	x	x	
	Lophiodontidae	cf. <i>Lophiaspis maurettei</i>	x	-	-	-	-	-	-	-	-	-	-	-
		<i>Lophiodon</i> cf. <i>leptorhynchum</i>	-	-	-	x	x	-	-	-	-	-	-	-
		<i>Lophiodon remense</i>	-	-	-	-	-	x	-	-	-	-	x	-
		<i>Lophiodon</i> aff. <i>eygalayense</i>	-	-	-	-	-	-	-	-	-	x	-	-
	<i>Lophiodon</i> sp.	-	-	-	-	-	-	-	-	-	-	x		
Artiodactyla	Diacodexidae	<i>Diacodexis varleti</i>	x	x	cf.	cf.	cf.	cf.	cf.	-	-	cf.	-	
		<i>Bunophorus cappetai</i>	x	x	-	-	-	-	-	-	-	-	-	
	Dichobunidae	<i>Protodichobune oweni</i>	-	-	x	x	x	x	-	-	-	-	cf.	-
		<i>Protodichobune hellmundi</i>	-	-	-	-	-	-	-	-	-	x	-	-
		<i>Eurodexis russelli</i>	-	-	cf.	x	-	cf.	x	-	-	-	-	sp.
		<i>Aumelasia menieli</i>	-	-	-	-	-	x	-	-	-	-	-	-
		<i>Aumelasia sudrei</i>	-	-	-	-	-	-	-	-	-	x	-	-
		<i>Aumelasia</i> cf. <i>gabineaudi</i>	-	-	-	-	-	-	-	-	-	-	-	x
		<i>Messelobunodon schaeferi</i>	-	-	-	-	-	-	-	-	-	-	aff.	x
		<i>Buxobune</i> aff. <i>daubreei</i>	-	-	-	-	-	-	-	-	-	-	x	-
	Haplobunodontidae	<i>Cuisitherium lydekkeri</i>	-	sp.	x	x	x	x	-	-	-	-	-	-
		large haplobunodontid	-	-	-	x	-	-	-	-	-	-	-	-
		<i>Lophiobunodon hookeri</i>	-	-	-	-	-	-	-	-	-	x	-	-
		<i>Masillabune martini</i>	-	-	-	-	-	-	-	-	-	-	-	x

(probably the same species), *Peratherium monspeliense* (a species unknown in the Paris Basin), *Eoglyiravus wildi*, *Masillamys mattaueri*, the new yet unnamed *Pontifactor*-like nyctitheriid, and *Arcius lapparenti*. The absence of medium to large mammals at Azillanet, however, limits the comparisons with MGL/NAP. Regarding the potential reference-level 'MP10b' Rouzilhac, only three species are recorded at MGL/NAP: *Propalaeotherium gaudryi*, *Hyrachyus stehlini*, and *Leonhardtina meridianum*. Another similarity is *Ailuravus* aff. *michauxi*; but this species, like *Propalaeotherium gaudryi* and *Hyrachyus stehlini*, is known since the MP10a. The same is true when drawing comparison with MP11 localities (Geiseltal Unterkohle and Messel), as common species with MGL/NAP are *Palaeochiropteryx* cf. *tupaiondon*, *Diacodexis* cf. *varleti* and *Protodichobune oweni*.

To conclude, all the combined data exposed above strongly favour to attribute MGL/NAP to the level MP10a. Such a result also supports the idea that, during the late Ypresian, the West European mammal faunas are quite homogeneous. A situation which is different from what we observe during early to middle Ypresian, a period instead characterized by a faunal North/South provincialism in Europe (Marandat 1997; Marandat *et al.* 2012; Solé *et al.* 2011, 2013, 2018). The homogeneity of West European late Ypresian mammal faunas is however far from being global. For instance, we note some prominent differences among North/South distribution of metatherian and perissodactyl species. Ongoing revision and phylogenetic studies of metatherians will determine if the still existing North/South disparities are factual or not. Likewise, further studies on lophiodontid and palaeotheriid perissodactyls appear necessary, because we suspect that some

North/South disparities are the possible consequence of old inaccurate taxonomic attribution. We suspect, for instance, that *Lophiodon leptorhynchum* (known from MP10a localities from Southern France) and *L. remense* (known from MP10a localities from Paris Basin) could be synonym. It is worth mentioning that *L. leptorhynchum* only differs from *L. remense* by a long and dorso-ventrally narrow mandibular symphysis and by a mesio-distal alignment of the lower incisors. The variability of these traits has never been clearly discussed. Similarly, regarding the palaeotheriid perissodactyls, the presence/absence of the genus *Pachynolophus* in Northern localities deserves to be discussed in further studies. For instance, the recent mentions of *P. livinierensis* (a classical species from Southern France; Savage *et al.* 1965; Godinot *et al.* 2018) in several MP10a localities from Northern France is not fully established due to lack of figure and description (Franzen in Godinot *et al.* 2018: 267). A recent review of equoids from Northern France did not address this question (Bronnert & Métais 2023). We cannot exclude that among specimens from the Paris Basin currently attributed to the highly variable species *Propalaeotherium gaudryi*, some of them having no mesostyle, document in fact a large *Pachynolophus* species, such as *Pa. ruscasseriensis* or *Pa. cesserasicus*. On the other hand, the homogeneity we conclude among West European late Ypresian mammal faunas at the MP10a could be weakened for few species, among them the amphilemurid *Macrocranion* cf. *nitens* and *Macrocranion* sp. (*sensu* Russell *et al.* 1975), which probably document several species during the MP8+9-MP10a interval (see also Smith & Smith 1995; Smith 1997).

CONCLUSION

Rich of 41 identified species, the mammal assemblage from the localities of Mas de Gimel and Naples constitutes a European reference for the late early Eocene; this fauna is attributed to the MP10a (reference-level Grauves, Paris Basin). Some biochemostratigraphic studies have interestingly demonstrated that the MP10a level corresponds to a part of the EECO (Noiret *et al.* 2016, Steurbaut *et al.* 2016). However, the EECO is a long-term warming event (*c.* 53 to 49 Ma) and several short-term hyperthermal events are surimposed to the EECO, complicating our interpretation of the climate context during this period (Westerhold *et al.* 2018). These hyperthermals have never been clearly identified in the Paris Basin, notably due to the absence of long and continuous stratigraphic sections. It is obvious however that the various localities in the Paris Basin, attributed to the MP10a, represent a substantial period of time during the late Ypresian (e.g., from Saint-Agnan to Prémontré, via Grauves). In Southern France, the stratigraphic context, with the presence of long and continuous fossiliferous sections, appears more promising to characterise both the EECO and the associated hyperthermals, and to examine the impact of these warming events on mammal evolution. From this point of view, the EECO interestingly coincides in North America with a period of mammal diversification and major faunal turnover (Woodburne *et al.* 2009). Such results have been made possible by obtaining a solid chronological context (bio-magneto-chemostratigraphy) along a series of mammal assemblages. At Mas de Gimel and Naples, such approach is not possible due to the disappearance of outcrops; but current research in well-exposed sections in the same area could provide decisive results, linking mammal evolution to Ypresian climate change.

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