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Revising the species “*Mustela*” *ardea* Gervais, 1848–1852 (Mammalia, Mustelidae): *Martellictis* gen. nov. and the systematics of the fossil “Galictinae” of Eurasia

Révision de l'espèce « Mustela » ardea Gervais, 1848–1852 (Mammifères, Mustelidae) : Martellictis gen. nov. et systématique des « Galictinae » fossiles d'Eurasie

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ABSTRACT

A number of recent genetic and systematic reviews have changed our knowledge of the taxonomy of Mustelidae. In particular, the subfamily Galictinae Reig, 1956 has been recently grouped in the subfamily Ictonychinae Pocock, 1921. Among the Eurasian fossil taxa of this subfamily, the first to be described were *Enhydrictis* Major, 1901 and *Pannonictis* Kormos, 1931. The latter genus is well characterised from the Plio-Pleistocene deposits of central and southern Europe, whereas *Enhydrictis* is an endemic and enigmatic form, recovered from late Pleistocene localities of Sardinia. Other recent studies have revealed a more palaeo-diverse and complex taxonomic scenario than was previously thought. Based on various evidence, this review proposes a reinterpretation of the material of the galictini from early Pleistocene sites such as St. Vallier and Olivola, historically named “*Mustela*” *ardea* Gervais, 1848–1852, and its attribution to *Martellictis* gen. nov. The definition of *Martellictis ardea* reveals a more complex systematic panorama of western Eurasian Ictonychinae, and at the same time, this re-ascription stresses the importance of understanding the possible origin of the different morphological adaptations (such as those of *Enhydrictis*) and clarifying the phylogenetic relationships among these taxa.

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RÉSUMÉ

De nombreuses revues génétiques et systématiques récentes ont changé nos connaissances sur la taxonomie des Mustelidae. En particulier, la sous-famille des Galictinae Reig, 1956 a été récemment regroupée avec la sous-famille des Ictonychinae Pocock, 1921. Parmi les taxons fossiles eurasiens de cette sous-famille, les premiers à avoir été décrits ont été *Enhydrictis* Major, 1901 et *Pannonictis* Kormos, 1931. Ce dernier genre est bien caractérisé dans les dépôts pliocènes–pléistocènes de l'Europe centrale et méridionale,

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tandis qu'*Enhydrictis* est une forme endémique et énigmatique, récoltée dans des localités du Pléistocène sarde. D'autres études récentes ont révélé un scénario taxonomique plus paléodiversifié et complexe qu'on ne le pensait auparavant. Fondée sur des preuves variées, cette revue propose une réinterprétation du matériel de galictini de sites du Pléistocène inférieur, tels que Saint-Vallier et Olivola, historiquement dénommé « *Mustela* » *ardea* Gervais, 1848–1852 et attribué à *Martellictis* gen., nov. La définition de *Martellictis ardea* révèle un panorama systématique plus complexe d'Ictonychinae et, en même temps, la réattribution souligne l'importance d'une bonne compréhension de l'origine possible des adaptations morphologiques (telles celles d'*Enhydrictis*) et de la clarification des relations phylogénétiques parmi ces taxons.

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1. Introduction

The taxonomic status of the subfamily Galictinae Reig, 1956 of the Mustelidae has been highly debated in the scientific literature and researchers have not yet reached a unanimous agreement. The first to group these mustelids together was Pocock (1921), who grouped the neotropical greater and lesser grisons (*Grison* Oken, 1816) to establish the subfamily Grisoninae Pocock, 1921. Pilgrim (1932) included in this subfamily the genera *Eira* Smith, 1842, *Trochictis* Meyer, 1842, *Enhydrictis* Major, 1901, "Mustelidae gen. indet. sp. n." of Zdansky, 1927 and *Pannonictis* Kormos, 1931. *Eira* and *Trochictis* possess various dental features that led Schreuder (1935) to exclude them from the "Grisoninae". Recently, *Eira* has been related to other subfamilies of the Mustelidae (Mustelinae; see, among others, Presley, 2000; Guloninae; see Sato et al., 2012 and references therein). Hershkovitz (1949) considered the use of the genus *Grison* invalid and suggested using *Galictis* Bell, 1826; therefore, Reig (1956) erected the subfamily Galictinae.

In the last fifteen years, research has greatly improved our knowledge of these mustelids. From a palaeontological point of view, two new genera belonging to this subfamily have been described from the early and middle Pleistocene of Asia: *Eirictis* Qiu et al., 2004 from several Chinese localities and *Oriensictis* Ogino and Otsuka, 2008 from Kyushu Island (Japan). Baskin (1998, 2011) used the name Galictini Reig, 1956 to identify the tribe of Galictinae that includes the Old World fossil taxa (i.e. *Enhydrictis*, *Pannonictis*, *Oriensictis*, *Eirictis*) and the New World ones *Lutravus* Furlong, 1932, *Cernictis* Hall, 1935, *Trigonictis* Hibbard, 1941, *Stipanicia* Reig, 1956 and *Sminthosinus* Bjork, 1970, in addition to the extant *Galictis* and *Lyncodon*.

On the neontological side, molecular phylogenies (e.g., Fulton and Strobeck, 2006; Sato et al., 2012) have shown that the Galictinae represents a solid clade with extant species from South America (i.e. the genera *Galictis* and *Lyncodon* Gervais, 1844, the Patagonian weasel) and from the Old World (i.e. the genera *Ictonyx* Kaup, 1835, the striped polecat, *Poecilogale* Thomas, 1883, the African striped weasel, and *Vormela* Blasius, 1884, the marbled polecat). Wilson and Reeder (2005), by contrast, group *Galictis* and *Ictonyx* under the subfamily of Mustelinae, whereas a number of recent studies (Bornholdt et al., 2013; Nascimento, 2014; Puzachenko et al., 2017; Sato, 2016; Sato et al., 2012; Wolsan and Sato, 2010) suggest

using Ictonychinae Pocock, 1921, because Galictinae Reig, 1956 should be considered as a junior synonym for the former (International Commission on Zoological Nomenclature, 1999, Article 23). According to Sato et al. (2012), the Ictonychinae include two consistent clades: Ictonychini, with *Ictonyx*–*Poecilogale*–*Vormela*, and Lyncodontini, with *Galictis*–*Lyncodon*. In the present study, the nomenclature by Sato et al., 2012 is followed as far as the subfamilies are concerned, although Galictini Reig, 1956 (not Baskin, 1998; International Commission on Zoological Nomenclature, 1999 see Art. 50.3) was preferred on Lyncodontini Sato et al., 2012, taken into account the priority of the former on the latter. Therefore, the tribe Galictini comprises the taxa resumed in Baskin (2011).

Of the Eurasian taxa, *Pannonictis* is the best known and characterised (see, among others, Colombero et al., 2012; García and Howell, 2008). By contrast, the genus *Enhydrictis* requires a deep revision. It has been erected for the endemic mustelid recovered from the late Pleistocene deposits of the locality of Monte S. Giovanni (Sardinia) and has been described as *Enhydrictis galictoides* Forsyth Major, 1901. According to Forsyth Major (1901), the form had a strong affinity with the extant South American Ictonychinae *Galictis cuja* (Molina, 1782), *Galictis vittata* (Schreber, 1776) and *Eira barbara* (Linnaeus, 1758). Between the end of the 1800s and the beginning of the 1900s, a number of different Pliocene and early Pleistocene small mustelids have been described under different names (e.g., *Mustela ardea* Gervais, 1848–1852; *Proputorius olivolanus* Martelli, 1906) and Viret (1954) later included all of them in the taxon *Enhydrictis ardea* (Gervais, 1848–1852). The generic attribution of this species has been questioned by many authors (Fejfar et al., 2012; García and Howell, 2008; García et al., 2008; Rabeder, 1976; Spassov, 1999, 2000), who relate it to *Pannonictis*. In our opinion, since the genus *Enhydrictis*, as initially defined, is an endemic and highly specialised taxon of the late Pleistocene of Sardinia, its use for continental species is incorrect. In this study, the debated taxon "*Mustela*" *ardea* is revised from a morphological and phylogenetic point of view.

1.1. The intricate "*Mustela*" *ardea* issue in scientific literature

Since the first descriptions of the species, the generic attribution of species "*Mustela*" *ardea* has been strongly debated. Furthermore, even the acknowledgement of the

true authorship is still disputed. In scientific literature, the species is generally referred to Mr. Auguste Bravard (1828). The French architect was among the first to report the presence of a small mustelid from the locality of Côte de Ardé, near Issoire (Auvergne-Rhône-Alpes, central-southeastern France), in his work “*Monographie de la montagne de Perrier, près d’Issoire (Puy-de-Dôme), et de deux espèces fossiles du genre Felis, découvertes dans l’une de ses couches d’alluvion*” reporting it simply with the common name “marte” (Bravard, 1828: 8, 11, 111). As Peters and de Vos (2012) stated, no references to the genus *Mustela* Linnaeus, 1758 or to the specific name “*ardea*” can be found in Bravard’s work. Nevertheless, Jobert and Croizet (1828), already cited in Bravard (1828: 138–139), report a “martre” (Jobert and Croizet, 1828: 25). Even other works by Bravard, before his trip to South America around 1850 (Podgorny, 2001 for a deeper discussion of the biography of Auguste Bravard), do not report any description of this mustelid (Bravard, 1843, 1846). The first true description and illustration of the single specimen of the species collected by Bravard are contained in Gervais (1848–1852), who reports: “*Portion de maxillaire inférieur portant la molaire carnassière précédée de six alvéoles, indiquant trois avant-molaires, chacune à deux racines, et suivie d’une alvéole qui est celle de la dent tuberculeuse. Longueur de la carnassière 0,011 [m]. Son talon est un peu excavé. Cette pièce a été recueillie à Ardé, près Issoire, par M. Bravard, qui lui a donné le nom spécifique sous lequel nous la représentons.*” [Portion of the lower maxillary bone possessing the carnassial molar preceded by six alveoli, indicating three premolars, each of which with two roots, and followed by one alveolus of second molar. The length of the carnassial is 0.011 (m). Its talon is slightly furrowed. This specimen has been collected at Ardé near Issoire by Mr. Bravard, who has given it the specific name under which we cite it.]. Later on, Gervais (1859) suggested including the species in the invalid genus *Putorius* Cuvier, 1817, comparing the specimen to the extant polecat (Gervais, 1859: 252: “Plus robuste et plus grand que le Putois”). In the first half of the XIX century, museums of natural history across Europe started frequent cooperation with amateur naturalists, travellers, owners of private collections in order to expand their exhibition (Cohen, 1999; Secord, 1994). Mr. Bravard, along with other local naturalists, collaborated with the “Museum d’histoire naturelle de Paris” (MNHN, see section 2.3), especially with Georges Cuvier (Podgorny, 2001), collecting material in the region of Auvergne. In 1847, Bravard sold part of his collection to the “Muséum d’histoire naturelle” (Podgorny, 2001), which constitutes the “Bravard collection” still present in the MNHN. As in his works, Gervais referred to the authorship of the species to Bravard with the expression “*Coll.*” (Gervais, 1848–1852) and “*Coll. du Mus.*” (Gervais, 1859), it is likely that Bravard had labelled the specimen with the name “*Mustela ardea*” with no description or illustration in a paper or book. Therefore, *Mustela ardea* Bravard constitutes a *nomen nudum* (failing to satisfy the requirements of Art. 12, International Commission on Zoological Nomenclature, 1999) and should be cited as *M. ardea* Gervais, 1848–1852.

Schaub (1949) synonymised the “*M.*” *ardea* material together with the small mandible of *Proputorius olivolanus*

Martelli, 1906 from the Tuscan site of Olivola and suggested relating the taxon to the genus *Pannonictis* for its generalised affinity to *Pannonictis pliocaenica* Kormos, 1931 (the generic name *Proputorius* being not available, since it was established by Filhol in 1890 for a middle Miocene mephitid mustelid from Sansan). Viret (1950) studied the species *Mustela ardea* Gervais, 1848–1852: although he agreed with Schaub (1949) in considering the French and Italian specimens as a single species, he pointed out a stronger affinity with the genus *Enhydriactis*. A few years later, the same author (Viret, 1954) described the mustelid remains recovered from the early Pleistocene site of St. Vallier. He related these fossils to the mandibles of “*E.*” *ardea* in Viret (1950) (i.e. the type specimen described by Gervais, 1848–1852 and the one from Olivola), as the features of the latter were well adapted to the skull (e.g., the narrow width of the ascending ramus, and the narrow cranial region between glenoid fossa and M1). Given the similarity to *E. galictoides*, Viret (1954) proposed a close phylogenetic relationship between these two species. In the same paper, the author synonymised *Pannonictis pilgrimi* Kormos, 1933, based on the similarly small-sized mandible corpus, with “*E.*” *ardea*. Various scholars favoured this hypothesis (i.e. Fejfar et al., 2012; Kurtén, 1968; Rabeder, 1976; Willemssen, 1988), whereas others pointed out that *P. pilgrimi* from Villány has: a more convex dorsal profile of the cranium in lateral view; a proportionately longer muzzle; and a stouter ascendant ramus of the mandible (Ficcarelli and Torre, 1967; Rook, 1995). Some scholars shared the idea of Viret to assign the taxon “*M.*” *ardea* to *Enhydriactis*. For instance, Morlo and Kundrat (2001) reported the earliest sample of “*E.*” *ardea*, from the German site of Wölfersheim (MN 15, early Pliocene; Morlo and Kundrat, 2001). Nevertheless, these specimens possess several features that contrast both with the diagnostic characteristics of *Enhydriactis* and of “*Mustela*” *ardea* (see Discussion section).

Since Viret’s works, many different scholars (García and Howell, 2008; García et al., 2008; Rabeder, 1976; Spassov, 1999, 2000) have questioned the generic attribution of “*Mustela*” *ardea* to *Enhydriactis*, preferring *Pannonictis*. In particular, Fejfar et al. (2012) suggested ascribing “*E.*” *ardea* to *Pannonictis* on the basis of the morphology of the auditory region and of the tympanic bullae. These authors deemed a closer affinity in morphology to *P. pliocaenica*, rather than to *E. galictoides*. Here the use of a different generic name for the European continental species “*M.*” *ardea* is suggested and a differential diagnosis for the Eurasian Galictini genera (*Pannonictis*, *Martellictis*, *Eirictis*, *Enhydriactis* and *Oriensictis*) is therefore provided.

2. Materials and methods

2.1. Studied specimens and comparative sample

The present study is based on the revision of key diagnostic features of the problematic species “*Mustela*” *ardea* Gervais, 1848–1852 in comparison to other mustelids of the subfamily Ictonychinae of Eurasia, particularly of those of the tribe Galictini (sensu Baskin, 1998). The examined and described fossils are housed in the Museum of Natural History, Geological and Palaeontological section, the

University of Florence (IGF; see abbreviations below) and in the collections of the “Musée des Confluences”, in the collection of the “Université Claude-Bernard” (Lyon, France). As a comparative fossil sample, the collections of the IGF, “Museo Archeologico Nazionale”, Nuoro (Italy), “Museo di Geologia e Paleontologia” of the “Università degli Studi di Torino”, American Museum of Natural History (New York, United States of America) and Hungarian Museum of Natural History (Budapest Hungary) were studied, and all the relevant literature on the Plio-Pleistocene Ictonychinae was inspected (Colombero et al., 2012; Fejfar et al., 2012; Ficarelli and Torre, 1967; García and Howell, 2008; García et al., 2008; Geraads, 2016; Jin and Liu, 2009; Morlo and Kundrat, 2001; Ogino and Otsuka, 2008; Peters and de Vos, 2012; Qiu et al., 2004; Rook, 1995; Viret, 1954). Extant specimens from the “La Specola” Zoology section, Museum of Natural History, University of Florence (Italy) were also used for morphological and morphometric comparisons. Craniodental measurements were taken to the nearest 0.1 mm with a digital caliper, following Driesch von den (1976) also for anatomical nomenclature.

The fossil comparative sample includes specimens of *Pannonictis pliocaenica* Kormos, 1931 from Villany-Kalkberg; *Pannonictis pilgrimi* Kormos, 1933 from Villany and Beremend; *Pannonictis nestii* (Martelli, 1906) from Upper Valdarno and Pirro Nord; *Enhydriactis galictoides* Major, 1901 from Monte S. Giovanni; and *Pannonictis* sp. and *Enhydriactis* sp. from Monte Tuttavista. The extant comparative sample includes specimens of *Galictis cuja*, *G. vittata*, *Lutra lutra* (Linnaeus, 1758), *Lontra longicaudis* (von Olfers, 1818), *Lontra provocax* (Thomas, 1908), *Mustela putorius* Linnaeus, 1758, *Mustela nivalis* Linnaeus, 1758, and *Eira barbara* housed in the MZUF.

2.2. Cladistic analysis

A cladistic analysis was carried out based on fossil and extant genera of the Ictonychinae from Eurasia and the American continent. For this purpose, thirty cranial and dentognathic characters for nine genera were selected. The freeware software Mesquite version 3.31 (build 765) (Maddison and Maddison, 2017) was used to build the data matrix of these unpolarised, non-additive characters. The character descriptions and the resulting data matrix are provided in Appendix A and B of the Supplementary Material. The analysis used TNT version 1.5 (Golobov and Catalano, 2016) to provide a 50% major cutoff tree using the traditional search setting (2000 random addition sequences and the TBR algorithm). Subsequently, Mesquite 3.31 (build 765) was used to manage the tree resulting from the analysis and to export it in a graphic format.

2.3. Site and institutional abbreviations

AMNH, American Museum of Natural History, New York, United States of America; **HMHN**, Hungarian Museum of Natural History, Budapest, Hungary; **IGF**, Museum of Natural History, Geological and Palaeontological section, the University of Florence (Italy); **MAN**, Museo Archeologico Nazionale, Nuoro (Italy); **MNHL**, Musée des Confluences, Lyon (France); **MZUF**, Museum of Natural

History, “La Specola” Zoology section, University of Florence (Italy).

3. Systematic palaeontology

Order **Carnivora** Bowdich, 1821.

Family **Mustelidae** Fischer, 1817

Subfamily **Ictonychinae** Pocock, 1921

Tribe **Galictini** Reig, 1956

Genus ***Martellictis*** gen. nov.

Generic diagnosis. This genus includes small-sized mustelids similar to or smaller than other fossil Eurasian Galictini mustelids. In general morphology, the cranium is rather short in comparison to those of *Enhydriactis* and *Pannonictis*. In lateral view, the cranium is not markedly flattened as in *Enhydriactis*, but possesses frontals that are rather elevated on the muzzle and have an arched dorsal profile, as in *Pannonictis*. The orbital fossa, mesial to the margin of the orbit, is shallower compared to that of *Enhydriactis*. The region of the postorbital constriction is elongated compared to *Pannonictis*, with a more marked constriction compared to the latter or to the Chinese *Eirictis*, but not to the extent seen in *Enhydriactis*. In dorsal view, the braincase has a globular shape unlike *Pannonictis*, *Enhydriactis*, *Galictis*, *Lyncodon* and *Stipanიცია*. In ventral view, the tympanic bullae are inflated only in their medial portions, and the embayment present in *Pannonictis* and *Galictis* is rather poorly developed. The palate of *Martellictis* is elongated, as testified to by the retention of the first upper premolars, in contrast with the rostrally large and very short palate of *Oriensictis*. In dental morphology, *Martellictis* differs from *Enhydriactis* by having a better developed protocone on the P4, by the oval morphology of P3 and p4 and by the stouter and shorter m1 with a round and buccolingually larger talonid. From *Pannonictis*, it differs by a reduction of the P4 hypocone and by the morphology and development of the cuspids on M1. The cup-like morphology of the protocone area, instead of a cone-shaped one and the retention of the P4 hypocone, even if reduced, testifies to the distinction from *Eirictis*. *Martellictis* differs greatly from *Oriensictis* in the lingual expansion of the P4 protocone, the prominent lutrine-like P4 hypocone, the development of the M1 protocone and the strongly buccolingually compressed m1. Some cranial morphologies (e.g., the elongated braincase), the extreme reduction of the upper and lower dentition and the teeth morphologies of *Lyncodon* and *Stipanიცია*, contrast evidently with the features of *Martellictis*. Compared to *Cernictis*, *Martellictis* possesses a slender m1 especially considering the talonid. From *Sminthosinis* it differs in the absence of a cone-shaped P4 protocone, in the morphology of the M1 cuspids and in the longer m1 paraconid. The mandible of *Martellictis* has a rather short horizontal ramus when compared to that of *Pannonictis*, *Oriensictis*, *Enhydriactis* and especially to *Eirictis*, and has a slenderer ascending ramus.

A summarising synthesis of the main characters of a generic diagnosis of the Eurasian genera *Martellictis*, *Enhydriactis*, *Eirictis*, *Oriensictis* and *Pannonictis* is provided in Table 1.

Table 1

Summary of the cranial and dentognathic differences of four fossil genera of Ictonychinae from Eurasia (i.e. *Pannonictis*, *Enhydriactis*, *Eirictis*, *Oriensictis* and *Martellictis*).

Tableau 1

Résumé des différences crâniennes et dentognathiques de quatre genres d'Ictonychidae fossiles d'Eurasie (c'est-à-dire, *Pannonictis*, *Enhydriactis*, *Eirictis*, *Oriensictis* et *Martellictis*).

	<i>Pannonictis</i> Kormos, 1931	<i>Martellictis</i> gen. nov.	<i>Enhydriactis</i> Major, 1901	<i>Eirictis</i> Qiu et al., 2004	<i>Oriensictis</i> Ogino and Otsuka, 2008	References
Cranium height, in lateral view	Cranium not so flattened	Cranium not flattened	Cranium consistently flattened	–	–	
Dorsal profile of the cranium, in lateral view	Arched	Arched, frontals rather elevated on the muzzle	Straight	Arched	–	
Cranium length	Long	Short	Long	–	–	
Muzzle	Long and robust	Long and robust	Short and robust	Long and very robust	–	
Temporal region	Developed	Shortened	Developed	Developed	–	Ficcarelli and Torre, 1967
Development of zygomatic arches	Long zygomatic arches	Short zygomatic arches	Long zygomatic arches	Long zygomatic arches	–	
Postorbital constriction	Slightly marked	Marked	Consistently marked	Slightly marked	–	Ficcarelli and Torre, 1967; modified this work
Frontals (posterior to postorbital processes)	Very short	Short	Long	Short	–	Ficcarelli and Torre, 1967
Infraorbital foramen	Small	Large	Large	Small	–	García and Howell, 2008
Orbital fossa	Shallow	Shallow	Deep	Shallow	–	
Anterior margin of the orbit	Not marked	Marked, crest-like	Prominent, crest-like	–	–	
Braincase	Generally elongated	Globular	Elongated (drop-shape)	–	–	
Tympanic bullae	Markedly inflated and protruding	Inflated only in medial portion	Flattened	–	–	
Tympanic bullae mesial embayment	Strong	Weak	Absent	–	–	
P3 and p4 shape	Oval	Oval	Rounded	Oval	Oval	Ficcarelli and Torre, 1967
P4 protocone area	Cup-like	Cup-like	Cup-like	Cone-shaped	Cup-like	Qiu et al., 2004
P4 protocone	Long (reaches ½ of p4).	Long (reaches 1/2 of p4).	Short (reaches 1/3 of p4).	Long (reaches 1/2 of p4)	Short (reaches 1/3 of p4)	García and Howell, 2008
P4 hypocone	Present	Reduced (cuspid-like cingulum)	Reduced (identified only as bulging of enamel)	Absent	Present	Qiu et al., 2004
Position of m1 metaconid	Posterior to protoconid.	Posterior to protoconid.	In line with protoconid	Posterior to protoconid	Posterior to protoconid	Ficcarelli and Torre, 1967
Robustness of mandible	Robust	Gracile	Robust	Very robust	Robust	Viret, 1954
Masseteric fossa	Very deep	Shallow	Deep	Very deep	Deep	
Ascending ramus	Robust	Slender	Robust	Robust	–	Ficcarelli and Torre, 1967

Derivatio nominis. After Prof. Alessandro Martelli (1876–1934; professor of Mineralogy and Geology in Florence's National Forestry Institute) who was the first to acknowledge the peculiarity of the mustelid material from Olivola, establishing *Proputorius olivolanus*.

Type species. *Mustela ardea* Gervais, 1848–1852 (monospecific).

***Martellictis ardea* (Gervais, 1848–1852)**

(Fig. 1)

1828 martre Jorbert and Croizer, p. 25

1828 marte Bravard, p. 8

1859 *Mustela ardea* Gervais, pl. XXVII, fig. 5

1906 *Proputorius olivolanus* Martelli, p. 603, pl. VIII, fig. 2a,b

1949 *Pannonictis ardea* Schaub, p. 500, fig. 5

1950 *Enhydriactis ardea* Viret, p. 166

1954 *Enhydriactis ardea* Viret, p. 83, pl. 4, figs. 1–2

1967 *Enhydriactis ardea* Ficcarelli and Torre, p. 140, figs. 1.f, 2.f, 3.d, 4.b, 5.h–i and m, 6.f–g, 7.e; pl. XXI, fig. 18

1976 *Pannonictis ardea* Rabeder, p. 39, pl. 5–7, figs. 12–15, 19

1988 *Enhydriactis ardea* Willemsen, p. 313, pl. 2–4

1995 *Enhydriactis ardea* Rook, p. 853

2000 *Pannonictis ardea* Spassov, p. 92

2002 *Enhydriactis ardea* Sotnikova et al., p. 380

2008 "*Enhydriactis*" *ardea* García and Howell, p. 2

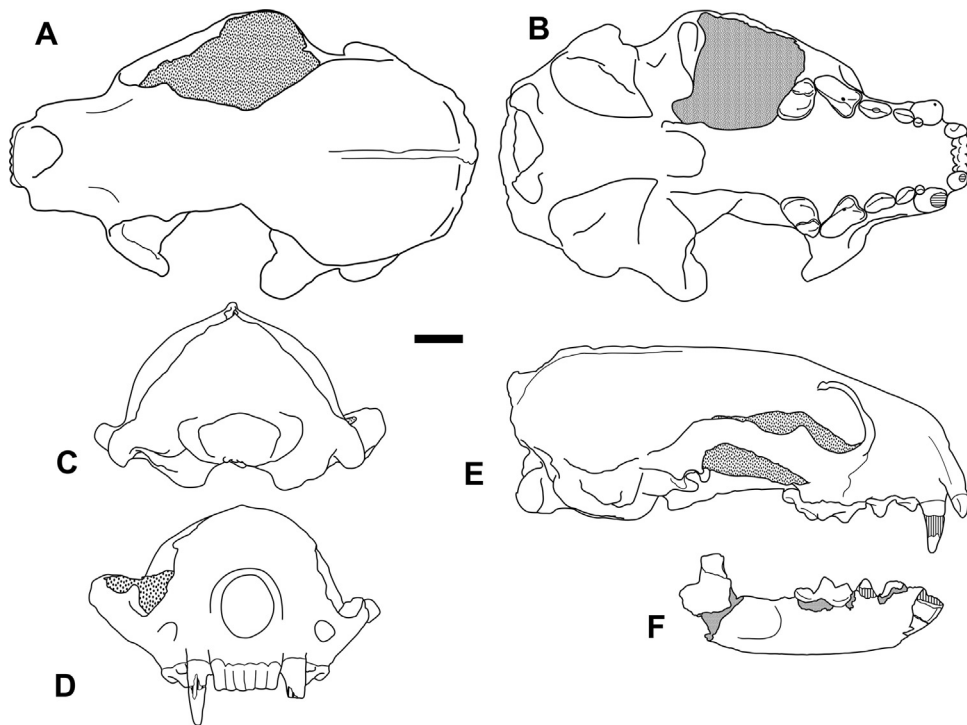


Fig. 1. *Martellictis ardea*, schematic outlines of MHNL 20161912 (QSV 150 in [Viret, 1954](#)), cranium. **A.** Dorsal view. **B.** Ventral view. **C.** Caudal view. **D.** Rostral view. **E.** Left lateral view. Schematic outline of IGF 4297, hemimandible. **F.** Buccal view. Scale bar = 1 cm.

Fig. 1. *Martellictis ardea*, contours schématiques de MHNL 20161912 (QSV 150 in [Viret, 1954](#)), crâne. **A.** Vue dorsale. **B.** Vue ventrale. **C.** Vue caudale. **D.** Vue rostrale. **E.** Vue latérale gauche. Coupe schématique de IGF 4297, hémimandibule. **F.** Vue buccale. Barre d'échelle = 1 cm.

2008 « *Enhydrictis* » *ardea* García et al., p. 3, fig. 2

2012 « *Enhydrictis* » *ardea* Colombero et al., p. 668

2012 *Pannonictis ardea* Fejfar et al., p. 99, fig. 3

Holotype. MNHN.F.PET2008, left hemimandible fragment with m1, recovered from Côte de Ardé (Perrier-Étouaires, Puy-de-Dôme, Auvergne-Rhône-Alpes, France).

Localities. Côte de Ardé, Olivola ([Martelli, 1906](#)), Saint-Vallier ([Viret, 1954](#)), Deutsch-Altenburg ([Rabeder, 1976](#)), Tegelen ([Willemsen, 1988](#)), Ivanovce ([Fejfar et al., 2012](#)).

3.1. Remarks

The species *Martellictis ardea* has been extensively described by other authors (among others, [Schaub, 1949](#); [Viret, 1954](#)). Here, we only provide a revised punctual comparison with other Plio-Pleistocene Eurasian species of the tribe Galictini. In size, *Martellictis ardea* is similar to *Pannonictis nestii* from Pietrafitta, *P. pilgrimi* from Villany and Beremend, *E. galictoides* from Monte San Giovanni and *Enhydrictis* sp. of Monte Tuttavista ([Abbazzi et al., 2004](#); [Ficcarelli and Torre, 1967](#); [García and Howell, 2008](#)). Compared to these latter species, the postorbital constriction of *M. ardea* is less marked, although more prominent than in *P. pliocaenica* from Villany-Kalkberg and *P. cf. nestii* from Atapuerca TE ([García and Howell, 2008](#)) or *Eirictis* ([Qiu et al., 2004](#)). The morphology of the tympanic bullae differs from the medial inflation of *P. pliocaenica* and *P. pilgrimi* from Hungary and especially from their sharp and marked notch on the mesial side the bullae of this species. It possesses a button-like P1 placed close to the C, as in *Eirictis robusta*

[Qiu et al., 2004](#) from Longdan and in some specimens of *P. pilgrimi* and *P. nestii* ([Rook, 1995](#)), whereas it is lacking in *Enhydrictis* spp. ([Ficcarelli and Torre, 1967](#)) and only rarely present in *P. pliocaenica* from Villany-Kalkberg. In contrast to *E. galictoides*, the mesial margin of P4 is lobed, as in some species of *Pannonictis* (e.g., *P. nestii*, *P. pilgrimi* or *P. pliocaenica*). The P4 protocone and the lingual cingulum that departs from it are reduced in comparison to those seen in *P. nestii* of Pirro Nord. Moreover, the protocone area is cup-shaped as that of *Enhydrictis*, *Oriensictis* and *Pannonictis*, unlike that of *Eirictis*, which possesses a prominent conical cusp. The P4 hypocone, although present, is not as developed as it is in *Oriensictis nipponica* [Ogino and Otsuka, 2008](#) from Matsugae cave ([Ogino and Otsuka, 2008](#)) or *P. pliocaenica* and *P. pilgrimi* from Hungary. It resembles more closely the condition visible in *E. galictoides* from Sardinia ([Ficcarelli and Torre, 1967](#)). The M1 shows an enlarged lobed talon, distally directed, unlike *P. pliocaenica* and similar to *P. nestii*, *P. pilgrimi* and *E. galictoides* to some extent, although less large than in the latter species. Unlike in *E. galictoides*, a narrowing occurs between the trigon cusps and the talon of M1, as can be found in *Pannonictis* species. Furthermore, the M1 in *Martellictis ardea* shows the buccal side that is smaller than the lingual one, in a condition similar to *P. nestii* from Pietrafitta and unlike *Enhydrictis* spp. or *P. pliocaenica*. The mandible corpus of *Martellictis ardea* from Olivola and St. Vallier is shallow, slender and it is rather shortened rostrocaudally if compared to other Galictini, e.g., most of all *Eirictis* spp. from China but also *P. pliocaenica* Villany-Kalkberg, *P. pilgrimi* from Beremend,

P. nestii Upper Valdarno and *Enhydrictis* spp. from Sardinia. The lower carnassial of *Martellictis ardea* possesses a short and enlarged paraconid and a large metaconid that ends posteriorly compared to the distal wall of the protoconid. The talonid has a large hypoconid, larger than that of *O. nipponica* from Matsugae cave, *E. robusta* from Longdan and *Eirictis variabilis* Jin and Liu, 2009 from Renzidong and *E. galictoides* from Monte San Giovanni. It is individualised by a low furrow from a distal accessory cuspid unlike *Eirictis*, *Enhydrictis* or *Oriensictis*. This distal accessory cuspid is followed lingually by a high distal cristid, which borders the distal and distolingual portion of the talonid. The distal cristid is not so elevated in *P. pliocaenica* from Villany-Kalkberg, but unworn specimens of *P. nestii* from Pirro Nord and Upper Valdarno and of *P. pilgrimi* from Beremend also show an accessory cuspid distal to the hypoconid.

4. Discussion

4.1. Taxonomic remarks on *Martellictis* gen. nov.

The analysis of the anatomical features of the highly disputed species “*Mustela*” *ardea* Gervais, 1848–1852 has revealed numerous cranial and dentognathic characteristics that, altogether, do not fit with the diagnosis of the Galictini genera (sensu Baskin, 2011) described in literature, namely in comparison to *Enhydrictis* Forsyth Major, 1901, *Eirictis* Qiu et al., 2004, *Oriensictis* Oginō and Otsuka, 2008, *Pannonictis* Kormos, 1931. Among these different morphologies there is the degree of embayment of the mesial side and the medial inflation of the tympanic bullae, the prominence of the postorbital constriction, morphology of the braincase, the cup-like P4 protocone, the P4 hypoconid; the development and morphology of the cuspids on M1 and the outline and cuspulids of m1 in occlusal view. From the morphological analysis, it is clear that some traits of *M. ardea* recall those of *Pannonictis* spp. but other those of *Enhydrictis* spp.: this is the reason why many scholars assigned the taxon to the former genus (Fejfar et al., 2012; Rabeder, 1976; Schaub, 1949) whereas others to the latter one (Ficcarelli and Torre, 1967; Rook, 1995; Viret, 1954). Nevertheless, neither attribution accords with the set of features possessed by *Martellictis ardea*. This is particularly true for the cranial ones, e.g., the morphology of the tympanic bullae, which in Carnivora is among the most systematically relevant characteristics (as noted by Fejfar et al., 2012).

4.2. A review of the diversity of the Plio-Pleistocene Galictini

The genus *Pannonictis* is considerably widespread across Eurasia (Fig. 2), with a broad geographic range spanning from Spain (García and Howell, 2008; Madurell-Malapeira et al., 2014) to Great Britain (Stuart, 1982), southeastern Russia and Moldova (Sotnikova et al., 2002), China and Mongolia (Sotnikova, 1980). Fig. 2 resumes the most important and verified localities that record *Pannonictis* (as well as of the other palearctic genera *Eirictis*, *Enhydrictis*, *Oriensictis*). Its earliest record is most probably the one reported by Zdansky (1927) as Mustelidae gen.

indet. sp. indet. from the late Miocene *Hipparion* beds from China (as pointed out by numerous authors, e.g., García and Howell, 2008; Kormos, 1931; Pilgrim, 1932; Rook, 1995; Schreuder, 1935). Therefore, it could be possibly referred to as *Pannonictis* sp. indet. Zdansky (1927) (n.b. not as *P. pachygnatha* as García and Howell, 2008 suggested).

One of the most extensive records of Galictini of the Asian Pliocene is that the Yushe Basin (Teilhard De Chardin and Leroy, 1945) in China, that of Shamar in Mongolia (Sotnikova, 1980) and that of the early Pleistocene Nihe-wan Basin (Teilhard De Chardin and Piveteau, 1930). These fossils were ascribed to the large-sized species *Pannonictis pachygnatha*. Qiu et al. (2004) described the material from the early Pleistocene of Longdan (Dongxiang, Gansu, China) and erected a different genus, *Eirictis* Qiu et al., 2004, that included the “*P.*” *pachygnatha* of Nihe-wan and a new species from Longdan, *E. robusta*. García and Howell (2008) recognised the validity of the diagnostic features used by the authors to discriminate this new genus from *Pannonictis* (especially the absence of a hypocone on P4). More recently, Jin and Liu (2009) included the taxon from the early Pleistocene site Renzidong Cave (Eastern China) in this genus, ascribing the sample to a new species, *E. variabilis*. Another Asian taxon of Galictini comes from the middle Pleistocene Matsugae cave deposits (northern Kyushu) of West Japan, the genus *Oriensictis* with the species *O. nipponica* (Naora, 1968). These authors propose the inclusion of the species *Lutra melina* Pei, 1934 from Zhoukoudian 1 (middle Pleistocene, China) in the genus *Oriensictis*.

Of the numerous genera of Ictonychinae of North America, the one most probably related to *Pannonictis* is the early Pleistocene *Trigonictis* (Rook, 1995). Numerous authors have proposed synonymising these two genera (e.g., Kurtén and Anderson, 1980; Repenning, 1967), but the presence of primitive features and some characters (e.g., the morphology of the M1 and the development of its cusps), which cannot be found in either *Pannonictis* or in *Enhydrictis*, would suggest maintaining *Trigonictis* as a separate genus.

Among the earliest European representatives of *Pannonictis* is the record from the early Pliocene (MN 15) of Wölfersheim (Germany) (Fig. 2). From this site, Morlo and Kundrat (2001) described two dental specimens of *Pannonictis* sp. and few others of *E. ardea*. As the authors pointed out, the material is considerably old for the Eurasian Galictini record, probably the earliest record of *Pannonictis*-like mustelids in Europe. The partial right P4 (SMF 2000/212) and the right m2 (SMF 2000/213) seems reasonably ascribed to the genus *Pannonictis*, but the material of *Enhydrictis* possesses several features, which significantly contrast with the type specimen of the genus. The assumption of a primitive state of the taxon for its old age cannot compensate the “*lack of some typical features*” (Morlo and Kundrat, 2001: 170) or the prominence of other characters. This eventually casts doubts on the generic and specific attribution of the material, even if the specimens are close in size to *M. ardea* from St. Vallier. Among the most evident discrepancies, there is the high conical cuspid on the P4 protocone area, a feature absent in the majority of the Galictini of Eurasia, as they generally possess a cup-like concavity bounded by a swelling cingulum. Nevertheless,

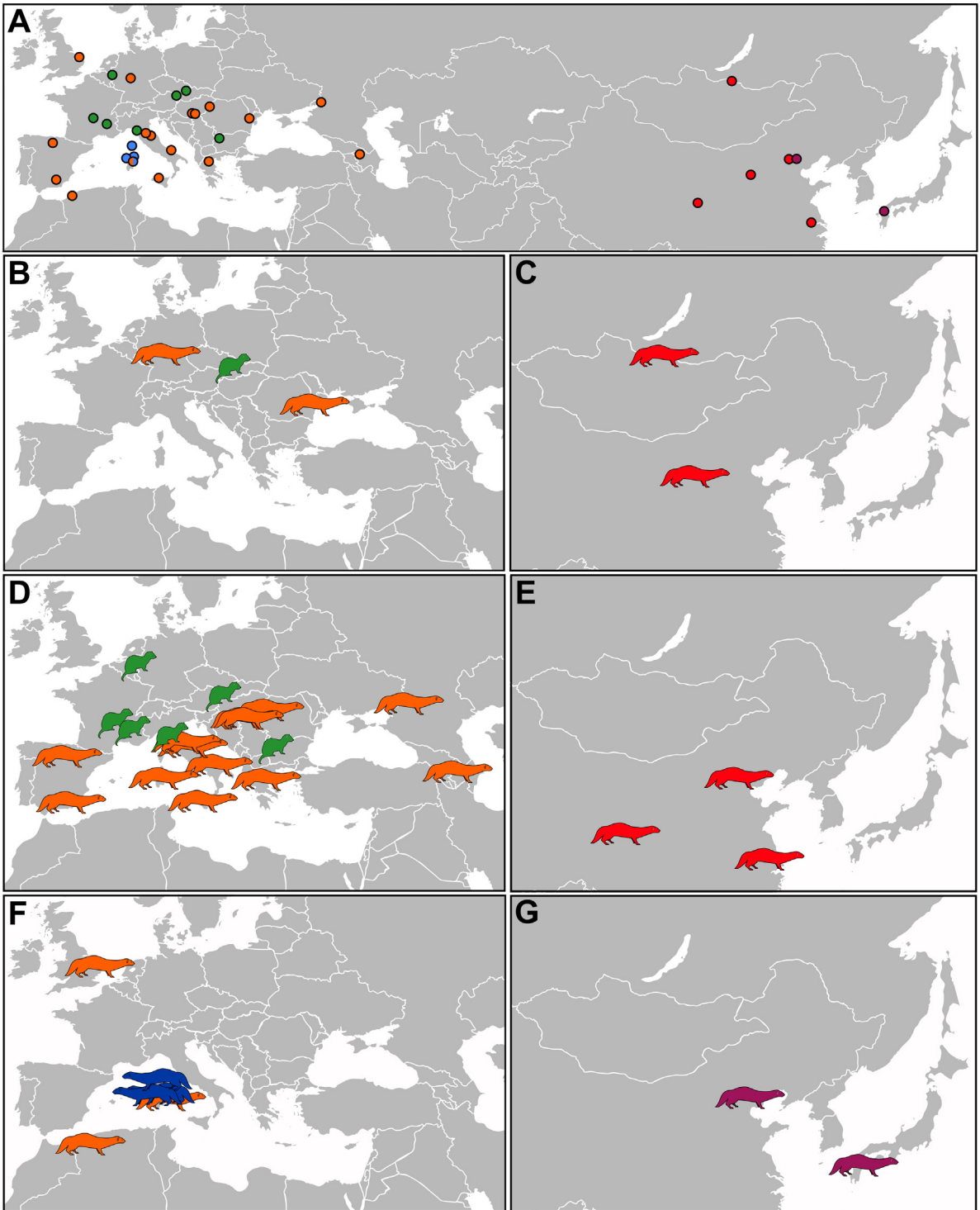


Fig 2. (Continued)

Fig. 2. Geographic and chronological distribution of Eurasian Galictini from the Early Pliocene to Late Pleistocene times. Colour legend; blue: *Enhydrictis* Major, 1901; green: *Martellictis* gen. nov.; orange: *Pannonictis* Kormos, 1931; purple: *Oriensictis* Ogino and Otsuka, 2008; red: *Eirictis* Qiu et al., 2004. **A.** Schematic representation of all the localities reporting specimens of Galictini references in the text. **B–C.** Pliocene European (B) and Asian (C) occurrences of Galictini–*Pannonictis*: Wölfersheim (Germany; Morlo and Kundrat, 2001); Etulia (Moldova, Sotnikova et al., 2002). *Martellictis*: Ivanovce (Slovakia, 1980; Fejfar et al., 2012). *Eirictis*: Shamar (Mongolia; Sotnikova et al., 2002), Nihewan Basin (China; Qiu et al., 2004). **D–E.** European (D) and Asian (E) localities of the early Pleistocene (partim, i.e. until the end of Late Villafranchian) – *Pannonictis*: Atapuerca TE (Spain; García and Howell, 2008); Barranco Leon 5, Fuente Nueva 3 (Spain, Madurell-Malapeira et al., 2014); Monte Tuttavista–VII Mustelide (Sardinia, Italy, Abbazzi et al., 2004); Upper Valdarno (Italy, Martelli, 1906); Pietrafitta (Italy, Rook, 1995); Pirro Nord (Italy, Colombero et al., 2012); Monte Pellegrino (Sicily, Italy, Burgio and Fiore, 1997); Villany (Hungary, Jánossy, 1986); Csarnota 1 (Hungary, Jánossy, 1986); Beremend (Hungary, Jánossy, 1986); Betfia 2–4/Püspököfúrdo (Romania, Jánossy, 1986); Livakkos (Greece, Koufos, 2014); Khapry (Russia, Sotnikova et al., 2002); Palan-Tyukan (Azerbaijan). *Eirictis*: Longdan (China, Qiu et al., 2004); Renzidong (China, Jin and Liu, 2009); Yushe (China, Teilhard De Chardin and Leroy, 1945); *Martellictis*, Perrier-Étouaires (France, Schaub, 1949); Saint-Vallier (France, Viret, 1954); Tegelen (The Netherlands, Willemsen, 1988); Olivola (Italy, Martelli, 1906); Deutsch-Altenburg 2 (Austria, Rabeder, 1976); Varshets (Bulgaria, Spassov, 2000). **F–G.** late early Pleistocene (Epivillafranchian) – late Pleistocene localities of Europe (F) and Asia (G) – *Pannonictis*: West Runton (Great Britain, Stuart, 1982); Tighennif/Ternifine (Algeria, Geraads, 2016); Monte Tuttavista–X-3-Uccelli (Sardinia, Italy, Abbazzi et al., 2004). *Enhydrictis*: Monte Tuttavista–numerous younger fissures (Sardinia, Italy, Abbazzi et al., 2004); Monte San Giovanni (Sardinia, Italy, Major, 1901), Grotta della Dragonara (Sardinia, Italy, Masseti, 1995); Oletta cave (Corsica, France, Ferrandini and Salotti, 1995). *Oriensictis*: Zhoukoudian (China, Pei, 1934); Matsugae Cave (Japan, Ogino and Otsuka, 2008).

Fig. 2. Distribution géographique et chronologique de Galictini eurasiens du Pliocène inférieur au Pléistocène supérieur. Légende des couleurs ; bleue : *Enhydrictis* Major, 1901 ; verte : *Martellictis* gen. nov. ; orange : *Pannonictis* Kormos, 1931 ; pourpre : *Oriensictis* Ogino et Otsuka, 2008 ; rouge : *Eirictis* Qiu et al., 2004. **A.** Représentation schématique de toutes les localités renvoyant aux spécimens de Galictini référencés dans le texte. **B–C.** Occurrences pliocènes européennes (B) et asiatiques (C) de Galictini. **D–E.** Localités européennes (D) et asiatiques (E) du Pléistocène inférieur. **F–G.** Localités fin du Pléistocène inférieur–Pléistocène supérieur d'Europe (F) et d'Asie (G).

a similar condition is found in *Eirictis*, which, according to Qiu et al. (2004), possesses a conical cusp in the protocone area. Furthermore, the lack of a hypocone on the lingual side of the P4 as in the Wölfersheim specimen is another diagnostic feature of *Eirictis* (García and Howell, 2008; Qiu et al., 2004). The morphology of the right M1 SFM2000/217 from Wölfersheim differs from that of other Galictini taxa, as it is proportionately shortened buccolingually, with an enlarged buccal cingulum, expanded buccally and undivided between the paracone and the metacone. In contrast, the species of *Pannonictis*, *Enhydrictis*, *Martellictis*, *Eirictis* and *Oriensictis* have the cingulum divided into two lobes, a larger one for the paracone and the smaller for the metacone (Abbazzi et al., 2004; Ficarelli and Torre, 1967; García and Howell, 2008; Ogino and Otsuka, 2008; Qiu et al., 2004). As in *Enhydrictis* from Monte San Giovanni and Monte Tuttavista, the M1 is not so curved distally, in occlusal view. Nevertheless, when compared closely to the M1 of *Enhydrictis* spp., the M1 metacone of SMF 2000/217 is more developed than that in the Sardinian taxa. The development of the cusp is more similar to that of some *Pannonictis* species (e.g., *P. pilgrimi* and *P. pliocaenica* from Hungarian localities) or to *M. ardea* from St. Vallier. Furthermore, the hypocone is missing or greatly reduced in the German specimen, whereas it is generally enlarged in *Pannonictis* and *Eirictis*. The area of the hypocone lobe differs greatly even from *M. ardea* from St. Vallier as the latter shows a prominent distal extension of the M1, giving the tooth a peculiar morphology in occlusal view. The upper and lower canines (respectively, SMF 2000/214 and SMF 2000/215) are short mesiodistally. The left m1 SMF 2000/218, and particularly its paraconid, is shorter mesiodistally compared to that of *Enhydrictis* from Monte San Giovanni and Monte Tuttavista (Ficarelli and Torre, 1967) and *Eirictis robusta* from Longdan (Qiu et al., 2004), but similar to the m1 of the holotype of *M. ardea* from Côte de Ardé. In occlusal view, the metaconid is more developed and stouter than in *Enhydrictis* and *Eirictis* spp. but not as individualized as in *Pannonictis* and *Martellictis*. Proportionately, the metaconid is more developed than in *Eirictis* from Longdan (Qiu et al., 2004). Among the Galictini of Eurasia, *Oriensictis* has the

largest and the most individualised m1 metaconid (Ogino and Otsuka, 2008). In occlusal view, the m1 talonid of SMF 2000/218 shows a round outline of the cristid starting from the hypoconid and reaching the correspondent point on the lingual side, similar to some species of *Pannonictis* (e.g., *P. nestii* from the Upper Valdarno and Pirro Nord) or *Oriensictis* from Matsugae Cave (Ogino and Otsuka, 2008). *Enhydrictis*, *Eirictis* and *Martellictis* have more elongated m1 talonids. Considering all these features, the attribution to the genus *Enhydrictis* or the species *M. ardea* are rather unlikely. Some features are suggestive of an affinity with the genus *Eirictis* (e.g., the P4 protocone, the absence of a P4 hypocone) even if the specimens are considerably smaller and thinner than the average *Eirictis* individuals are. Morlo and Kundrat (2001) also point out some similarities with the taxon *Martes wenzensis* Stach, 1959 (e.g., in the “crenulation” of the enamel of the hypocone lobe of the m1). In conclusion, the record from Wölfersheim reports possibly the earliest European specimens of a member of the genus *Pannonictis* and a few other specimens of an undetermined taxon not related to the genus *Enhydrictis* nor with the species *M. ardea*. Future revision and additional cranial and dentognathic material could help clear out these doubts on *Eirictis* sp. indet.

Next to the record from Wölfersheim, the early Pleistocene species *P. nestii*, from the Upper Valdarno in Tuscany (Martelli, 1906) and the younger site of Pietrafitta in Umbria (Rook, 1995) is among the first *Pannonictis* species to be described. Several specimens from Sima del Elefante (Sierra de Atapuerca) have been referred to *Pannonictis* cf. *nestii* by García and Howell (2008). García et al. (2008) grouped *P. nestii* with “*E.* *ardea*”, with no discussion of the morphological grounds for this placement. On this matter, other scholars disagree (see, among others, Ficarelli and Torre, 1967; Rook, 1995; Sotnikova et al., 2002; Viret, 1954). Another record is that of *P. pliocaenica* from the complex of cavities of Villany-Kalkberg, Hungary. In particular, two of the richest localities for Galictini remains are Villany 3 and 5, which span between 2 and 1.5 Ma (Jánossy, 1986; Spassov, 2000). From these localities, Kormos (1933) re-described some small specimens

as *P. pilgrimi*. In the scientific literature, various synonyms have been provided for this taxon: in addition to those reported above regarding the disputed synonymy to “*E. ardea*” (Viret, 1954), Ficarelli and Torre (1967) suggested uniting this species with *P. nestii* rather than with “*E. ardea*”. By contrast, García and Howell (2008) proposed the inclusion of *P. pilgrimi* within *P. pliocaenica*, addressing the issue of the large size difference as a strong sexual dimorphism (where *P. pliocaenica* would represent the larger male individuals, whereas *P. pilgrimi* would represent the smaller females). The genus *Pannonictis* has also been recovered from Mediterranean islands: *Pannonictis arzilla* (De Gregorio, 1886) from Sicily, in the endemic fauna of the Monte Pellegrino, a taxon probably close to *P. nestii* (Burgio and Fiore, 1997; Rook, 1995); and *Pannonictis* sp. from the early-middle Pleistocene levels of Monte Tuttavista (Nuoro, Sardinia; Abbazzi et al., 2004). Recently, Peters and de Vos (2012) described some dentognathic remains from the Dutch locality of Langenboom (Noord-Brabant) attributing them to “*Pannonictis*” *ardea*. The specimens show several peculiarities worth noting, as described by Peters and de Vos (2012). For instance in the upper teeth, the presence of a cusp surrounded by a marked cingulum in the protocone area on the P4, the P4 hypocone absent or greatly reduced, the buccolingually large and slightly distally curved M1 in the talon area, the expanded and continuous buccal cingulum on the M1 paracone and metacone, the large M1 protocone and protoconule but no metaconule and absence of the M1 hypocone. On the lower teeth, the p3 and p4 are strongly elongated mesiodistally in occlusal view, the p4 possesses a prominent distal accessory cuspid, visible in buccal, lingual, and occlusal views. Furthermore, the m1 has a mesiodistally elongated paraconid, it possesses an enlarged and strongly individualized metaconid and a round talonid. Many of these features are similar to those of the fossils from Wölfersheim (Morlo and Kundrat, 2001; discussed above), although in size the specimens from Langenboom are larger compared to those from the German sample. As for the German sample, the attribution to the genus *Pannonictis* and to the species *M. ardea* seems unlikely. As the Langenboom fauna resembles that of St. Vallier and Tegelen (Peters and de Vos, 2012), the affinity between the German and the Dutch finds would suggest the occurrence of a previously unknown form of mustelid, possibly related to *Eirictis*, in the Pliocene-earliest Pleistocene of central-western Europe.

The most peculiar taxon within the European record of Galictini is *Enhydrictis galictoides*, described by Forsyth Major (1901) from the late Pleistocene Sardinian locality of Monte San Giovanni (Ficarelli and Torre, 1967) (Fig. 2). In the fossil record, the genus *Enhydrictis* is more elusive than *Pannonictis* and, apart from *E. galictoides*, is only known from few other Sardinian and Corsican localities (e.g., the older *Enhydrictis* sp., from the fissure filling of Monte Tuttavista, Abbazzi et al., 2004). The peculiar features that typify this genus (e.g., strong postorbital constriction, shorter muzzle, etc.) have been regarded by many authors as adaptations to an aquatic lifestyle (Ficarelli and Torre, 1967; Forsyth Major, 1901; Pilgrim, 1932).

The first fossils of a taxon of the tribe Galictini from northern Africa were recently reported by Geraads (2016).

The author described the sample from Tighennif (or Ternifine, Algeria; Fig. 2) and ascribed the scarce sample to the new species *Enhydrictis hoffstetteri* Geraads, 2016. This discovery greatly expands our knowledge and the areal of Plio-Pleistocene Galictini, up to then unknown in the African continent. Unfortunately, no complete cranial or mandibular specimens have been found other than these three, so it is difficult to precisely ascribe the material to a species because the major diagnostic characters are missing (e.g., the postorbital constriction, the height of the cranium, the shape of the braincase, the presence and/or the development of hypocone on the P4 and features of the m1 talonid; Table 1). Nevertheless, there are several features displayed by the holotype and the referred specimens (Fig. 1 in Geraads, 2016: page 447) that cast doubts on the attribution of the Algerian material to the genus *Enhydrictis*. Among these, we can briefly discuss here the morphology of M1 that tends to be distally curved and stretched and possesses a thick talon, enlarged compared to the trigon cusps. In *Enhydrictis*, the M1 is not curved distally in occlusal view. Moreover, the M1 metacone of *E. hoffstetteri* is smaller than the paracone but still prominent and it is evidently bounded by a large and round cingulum especially on the distal side, unlike the specimens of *Enhydrictis* from Monte S. Giovanni or Monte Tuttavista in which the metacone is greatly reduced and does not possess a prominent cingulum around it (Abbazzi et al., 2004; Ficarelli and Torre, 1967). The positions of the enlarged M1 protocone and protoconule differ from the condition visible in *Enhydrictis* spp. because in the specimens from Tighennif they lie in the centre of the tooth, whereas in latter taxa they are displaced towards the lingual side of the M1, very close to the hypocone. The talon tends to narrow towards the hypocone area, unlike the condition seen in *M. ardea*. The features of the M1 of Tighennif taxon are similar to those retained by some species of *Pannonictis* (e.g., *P. pliocaenica* from Villany). The considerable height and breadth of the mandible corpus of TER-2008 contrast with the slender and shallow mandibles of *M. ardea* and resemble those of robust forms like *Pannonictis pliocaenica* or even *Eirictis*, even though it is hard to say as the author did not include a table of measurements of the specimen with mandibular measures. In the lower teeth, the prominent and high wrinkled pattern of the basal cingulid of the canine is similar to that shown by some species of *Pannonictis* (e.g., *P. pliocaenica* from Villany or *P. cf. nestii* from Atapuerca, García and Howell, 2008). Furthermore, the stout and shortened m1, especially considering the talonid, and the enlarged metaconid extended lingually differ from the principal features evident in specimens of *Enhydrictis* spp. (e.g., large metaconid but close to the protoconid). By contrast, *M. ardea* possesses a buccolingually wider m1, with a shorter and stouter paraconid, compared to that of TER-2008. Altogether, these morphologies are suggestive of a closer affinity between the taxon from Tighennif (Ternifine) and the genus *Pannonictis* rather than to *Enhydrictis*. Probably the species “*E. hoffstetteri*” should be referred to as *Pannonictis hoffstetteri*. The misinterpretation might have arisen as a consequence of the underestimation of the diversity of Plio-Pleistocene Galictini of Eurasia as the Geraads (2016) suggests to include

the cluster of all the genera in *Enhydriactis* sensu lato, which seems cumbersome considering the numerous differences between these taxa (for further discussion on the variability of Galictini see also [Colombero et al., 2012](#) and [García and Howell, 2008](#)).

As shown in [Table 1](#), the peculiar morphological pattern of the cranial and dentognathic features of *M. ardea* differ quite prominently from those of other Eurasian taxa of Galictini, thereby supporting the recognition of a new genus. Furthermore, this has important implications in the complex taxonomic dispute as it forces a reconsideration of the Plio-Pleistocene palaeodiversity of Galictini and their morphological affinities and relationships.

4.3. Cladistic analysis and the phylogenetic implications

The cladistic analysis was carried out based on the character matrix for fossil and extant genera of Eurasian and American Galictini, as described in the [Appendix B of the Supplementary material](#). The genera analysed were selected among the holarctic fossil members of the tribe Galictini based on the completeness of their fossil record and the number of characters effectively recognizable in the type specimens of these taxa. According to recent molecular phylogenies (e.g., [Sato, 2016](#); [Sato et al., 2012](#)) the two closest subfamilies to Ictonychinae are Lutrinae and Mustelinae. As the members of the former subfamily possess several marked adaptations to an aquatic lifestyle, the genus chosen as outgroup in the performed cladistic analysis is *Mustela* [Linnaeus, 1758](#).

The analysis used TNT ver. 1.5 to provide a 50% major cutoff tree ([Fig. 3](#)) based on the six shortest trees ([Appendix C of the Supplementary material](#)). This first attempt to investigate the phylogeny of fossil Eurasian Galictini at a generic level, produced relatively well resolved tree, with a consistency index of 0.645 and a retention one of 0.352. As is visible in [Fig. 3](#), there are different degrees of possible affinities previously underestimated in scientific literature. *Lyncodon* and *Oriensictis* equally differ from the two clustered groups, i.e. *Pannonictis*-*Eirictis* and *Enhydriactis*-*Trigonictis*. The displayed arrangement – with the marked distinction of the Eurasian “pannonictine” group (i.e. *Pannonictis*-*Eirictis*) from *Martellictis*, on the one side, and from *Enhydriactis* and the American *Trigonictis*, on the other – indeed testifies to previously unnoticed relationships in the tribe Galictini. The resulting tree emphasizes the peculiarly of the set of morphological features of *Martellictis* for the position of this genus in the phylogenetic tree ([Fig. 3](#)): together with the South American *Galictis*, it is the sister taxon of all the other Eurasian genera of Galictini and the American *Lyncodon* and *Trigonictis*. In this configuration, the affinity of *Martellictis* to *Pannonictis* or to *Enhydriactis* is not as close as expected from literature (sections [1.1](#) and [4.2](#)) and *Martellictis* possesses a set of features suggestive of a probably more primitive state among Galictini. This supports the distinction of these taxa into different genera. [Fig. 3](#) also points out the difference between the endemic genus *Enhydriactis* and the European taxa of Galictini, suggesting that its evolution was limited to the insular context of Sardinia and Corsica ([Fig. 2](#)) from mainland ancestors like *Martellictis* or *Pannonictis* (the lat-

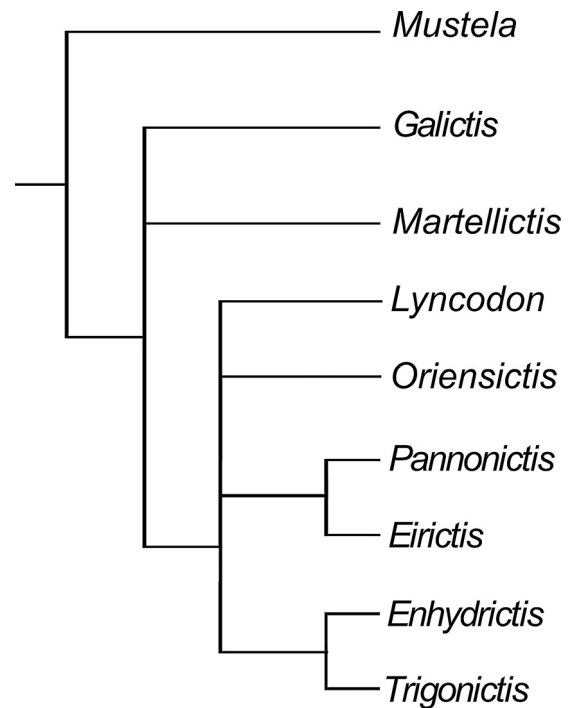


Fig. 3. The 50% major cutoff cladogram of selected Eurasian and American Galictini mustelids produced with a cladistic analysis in TNT, based on 30 craniodental characters ([Supplementary Material, Appendices A–C](#)).

Fig. 3. Cladogramme majeur coupé à 50%, de mustélidés Galictini eurasiens et américains sélectionnés, produit par analyse cladistique en TNT, basée sur 30 caractères craniodentaires ([matériel supplémentaire, annexes A–C](#)).

ter is notably present in the record of Sardinia, i.e. Monte Tuttavista see [Abbazzi et al., 2004](#)). The schematic representation in [Fig. 4](#), relates the phylogenetic relationship between the Galictini genera considered in the cladistics analysis here performed and the fossil and extant distribution of these taxa.

5. Conclusions

The taxonomic scenario of the Plio-Pleistocene tribe Galictini of Eurasia is intricate and has been debated since the beginning of the last century. The dispute arose mainly due to the scantiness and the sparse nature of their fossil record. Before the 1950s, few and pivotal studies were done on these taxa but, since then, only few authors have worked on their systematics. In recent years, the tribe of Galictini has regained the interest of scholars (e.g., [García et al., 2008](#)). Among the most discussed species of this group the is “*Mustela*” *ardea*: its generic attribution, either assigned to *Pannonictis* ([Fejfar et al., 2012](#); [Rabeder, 1976](#); [Schaub, 1949](#)) or to *Enhydriactis* ([Ficcarelli and Torre, 1967](#); [Rook, 1995](#); [Viret, 1954](#)) and even its correct authorship ([Peters and de Vos, 2012](#)), have all been matter of harsh debate.

Thanks to a deep bibliographic and morphological revision of the Eurasian and American material, the present work demonstrates the need of the use of a different generic name for the peculiar Galictini sample coming from sites like Perrier-Étouaires, St. Vallier and Olivola. This pro-

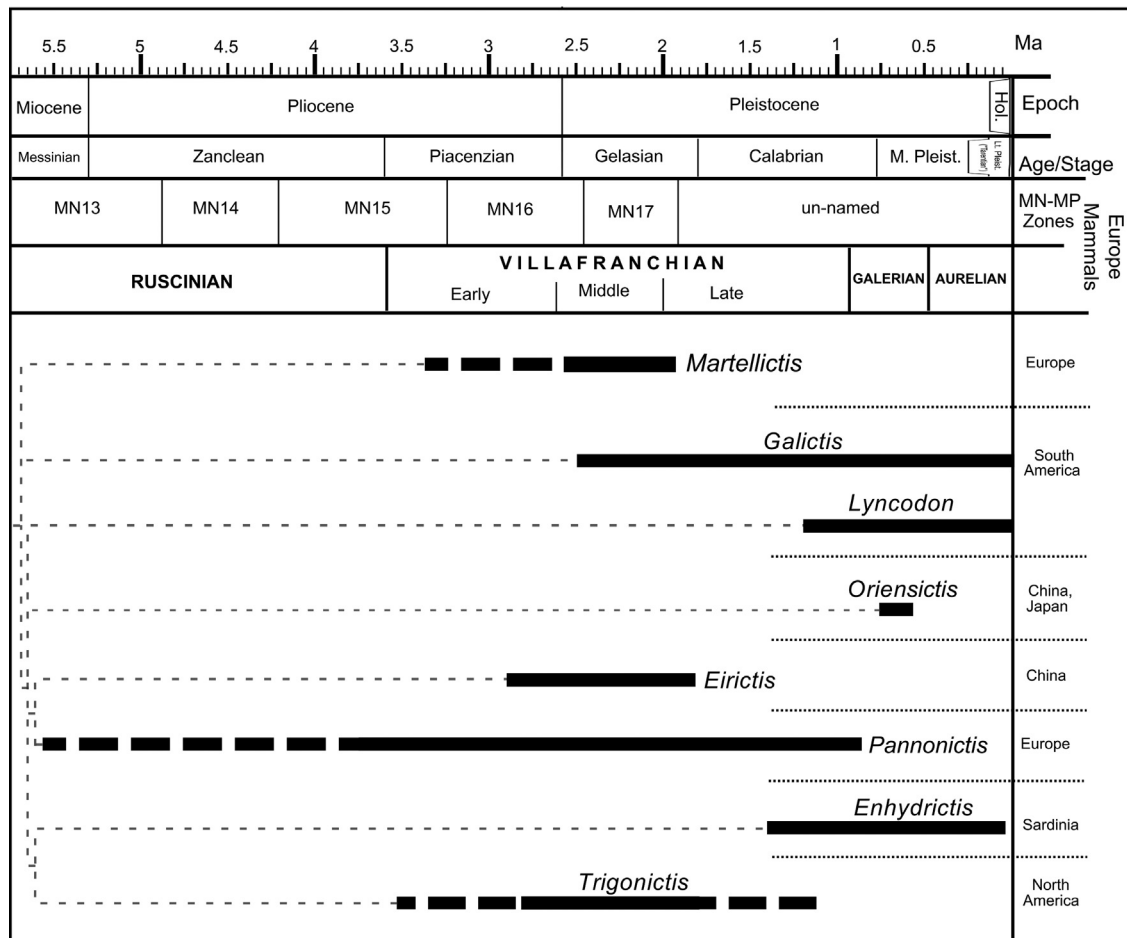


Fig. 4. Stratigraphic ranges and postulated phyletic relationships for genera of the tribe Galictini discussed in this report. The relationship is largely based on the cladogram in Fig. 3. Based on the following references: Bjork, 1970; Yensen and Tarifa, 2003; Abbazzi et al., 2004; Qiu et al., 2004; García et al., 2008; Ogino and Otsuka, 2008; Rodrigues et al., 2015.

Fig. 4. Gammes stratigraphiques et relations phylétiques postulées pour les genres de la tribu des Galictini discutés dans l'article. La relation est basée de façon importante sur le cladogramme de la Fig. 3. D'après les références suivantes : Bjork, 1970; Yensen et Tarifa, 2003; Abbazzi et al., 2004; Qiu et al., 2004; García et al., 2008; Ogino et Otsuka, 2008; Rodrigues et al., 2015.

posal provides a clearer taxonomic scenario and is based on evident morphological features of the specimens from these and other localities (Fig. 2), which differ markedly from other fossil taxa of the same subfamily (Table 1). Furthermore, it is supported by a cladistics analysis – the first for these taxa – based on thirty characters of nine genera of Eurasian and American Galictini that acknowledges both these differences and the distinction of *Martellictis* gen. nov., especially in comparison to *Enhydriictis* and *Pannonictis* (Figs. 3 and 4 and Supplementary material).

In view of all this, *Martellictis ardea* becomes an important and widespread element within this highly complex systematic debate, particularly as it reveals a palaeodiversity of the Eurasian Plio-Pleistocene Mustelidae that is greater than was assumed in the last century. Even though a different generic attribution for the species *M. ardea* poses new problems regarding the origin of this group of mustelids in western Eurasia and of their dispersion from or into the American continent, it also could help resolving part of the debate on these taxa. For instance, the

presence of a primitive-like *Martellictis ardea* in Pliocene-earliest Pleistocene continental sites allows us to infer that the genus *Enhydriictis*, which shows several derived cranial and postcranial features, represents a distinct and fully endemic genus exclusive of the insular context of the late early to the late Pleistocene of Sardinia and Corsica. In the light of this new taxonomic arrangement, a revision of the collections of European fossil mustelid is urgent and desirable in order to acknowledge the previously underestimated diversity of fossil Galictini.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.crpv.2018.02.003>.

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