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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* « *Gallictinae* » *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 palaeodiverse 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.

Mots clés :
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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 Galictinae Reig, 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 gallictini 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.

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, *Stipanicicia* Reig, 1956 and *Sminthosinis* 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

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