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Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea) ☆

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ABSTRACT

We analyzed a concatenated (8492 bp) nuclear–mitochondrial DNA data set from 44 musteloids (including the first genetic data for *Lyncodon patagonicus*) with parsimony, maximum likelihood, and Bayesian methods of phylogenetic and biogeographic inference and two Bayesian methods of chronological inference. Here we show that Musteloidea emerged approximately 32.4–30.9 million years ago (MYA) in Asia, shortly after the greenhouse–icehouse global climate shift at the Eocene–Oligocene transition. During their Oligocene radiation, which proceeded wholly or mostly in Asia, musteloids diversified into four primary divisions: the Mephitidae lineage separated first, succeeded by Ailuridae and the divergence of the Procyonidae and Mustelidae lineages. Mustelidae arose approximately 16.1 MYA within the Mid-Miocene Climatic Optimum, and extensively diversified in the Miocene, mostly in Asia. The early offshoots of this radiation largely evolved into badger and marten ecological niches (Taxidiinae, Melinae, Mellivorinae, Guloninae, and Helictidinae), whereas the later divergences have adapted to other niches including those of weasels, polecats, minks, and otters (Mustelinae, Ictonychinae, and Lutrinae). Notably, and contrary to traditional beliefs, the morphological adaptations of badgers, martens, weasels, polecats, and minks each evolved independently more than once within Mustelidae. Ictonychinae (which is most closely related to Lutrinae) arose approximately 9.5–8.9 MYA, most likely in Asia, where it diverged into the Old World Ictonychini (*Vormela*, *Poecilictis*, *Ictonyx*, and *Poecilogale*) and New World Lyncodontini (*Lyncodon* and *Galictis*) lineages. Ictonychini presumably entered Africa during the Messinian Salinity Crisis (at the Miocene–Pliocene transition), which interposed the origins of this clade (approximately 6.5–6.0 MYA) and its African *Poecilictis–Ictonyx–Poecilogale* subclade (approximately 4.8–4.5 MYA). Lyncodontini originated approximately 2.9–2.6 MYA at the Pliocene–Pleistocene transition in South America, slightly after the emergence of the Panamanian land bridge that provided for the Great American Biotic Interchange. As the genera *Martes* and *Ictonyx* (as currently circumscribed) are paraphyletic with respect to the genera *Gulo* and *Poecilogale*, respectively, we propose that *Pekania* and *Poecilictis* be treated as valid genera and that "*Martes*" *pennanti* and "*Ictonyx*" *libyca*, respectively, be assigned to these genera.

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1. Introduction

The weasel-like carnivorans (Musteloidea) include weasels, otters, martens, badgers, and relatives (Mustelidae); raccoons and their kin (Procyonidae); the red panda (Ailuridae); and skunks and stink badgers (Mephitidae; e.g., Delisle and Strobeck, 2005; Flynn et al., 2005; Fulton and Strobeck, 2006, 2007; Sato et al., 2006, 2009; Árnason et al., 2007; Yonezawa et al., 2007). With its 84 living species classified into 33 genera (Wozencraft, 2005; the Japanese otter, *Lutra nippon*, is considered extinct—Sasaki, 2009), Musteloidea encompasses ~30% of the extant carnivoran species diversity, which makes this clade the most species-rich superfamily within the order Carnivora. Musteloids are widespread in Eurasia, Africa, and the Americas, and also occur in New Zealand

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following human-mediated introductions in the late nineteenth century. Musteloids have adapted to a variety of climatic and biotic conditions, being found today in a broad and diverse spectrum of habitats spanning from tropical rainforest to arctic tundra, and from desert to inland waterways and coastal sea waters. They exhibit diverse locomotor and dietary habits, with not only terrestrial forms but also largely arboreal, fossorial, and aquatic specialists, with diets ranging from strictly carnivorous to vegetarian (see Macdonald, 2006). All this renders Musteloidea a fascinating and challenging taxon for evolutionary and biogeographic investigations.

The most species-rich, ecomorphologically diverse, and widely distributed musteloid family is Mustelidae (e.g., Wolsan, in press), which makes this family particularly well-suited for addressing evolutionary and biogeographic questions. Within Mustelidae, recent multilocus DNA studies (Koepfli and Wayne, 2003; Fulton and Strobeck, 2006; Koepfli et al., 2008; Wolsan and Sato, 2010) have provided sound evidence for a close phylogenetic relationship between some Old World (mostly African) polecats and weasels (*Ictonyx*, *Poecilogale*, and *Vormela*) and the New World (South and southern North American) grisons (*Galictis*). Given the large distance separating the current distributions of these two groups of mustelids, their evolutionary and biogeographic history is especially intriguing. A conspicuous feature shared by these mustelids is a contrastingly colored pelage. For most of these species, defensive behaviors with threat displays and excretion of pungent musk from anal glands have been reported, suggesting that the primary adaptive value of their striking coloration lies in warning potential predators (Pocock, 1909; Koepfli et al., 2008). To refer to a clade uniting both groups, Fulton and Strobeck (2006; followed by Koepfli et al., 2008) adopted the subfamilial name Galictinae Reig, 1956, whereas Wolsan and Sato (2010) applied Ictonychinae Pocock, 1922 because it has nomenclatural priority (International Commission on Zoological Nomenclature, 1999, Article 23). The latter name is therefore used here.

Extensive research during recent decades (Schmidt-Kittler, 1981; Wolsan, 1993; Ledje and Árnason, 1996; Dragoo and Honeycutt, 1997; Flynn and Nedbal, 1998; Bininda-Emonds et al., 1999; Flynn et al., 2000, 2005; Koepfli and Wayne, 2003; Sato et al., 2003, 2004, 2006, 2009; Fulton and Strobeck, 2006, 2007; Árnason et al., 2007; Koepfli et al., 2007, 2008; Yonezawa et al., 2007; Harding and Smith, 2009; Eizirik et al., 2010; Wolsan and Sato, 2010; and others) has considerably extended and refined knowledge on the evolutionary history of Musteloidea. The monophyly of this taxon has been demonstrated conclusively and many internal phylogenetic relationships have likewise been convincingly resolved. The degree of consensus among published estimates of divergence times for particular lineages has also improved recently. Nevertheless, there are important aspects of musteloid phylogeny and its chronology that still await clarification, such as the pattern and timing of early mustelid diversification and the phylogenetic placement of the Patagonian weasel (*Lyncodon patagonicus*).

In contrast to the evolutionary history, the biogeographic history of Musteloidea has not been extensively investigated and is not well understood. A comprehensive study of Mustelidae (Koepfli et al., 2008) provided insight into this family's historical biogeography, but the power of inference in that study was limited by the fact that the method used for ancestral-area reconstruction did not allow polymorphous characters, and therefore species distributed on two or more continents were assigned to one of them on potentially arbitrary grounds.

To shed more light on the pattern and timing of the evolutionary and biogeographic diversification of Musteloidea, we first prepared a dataset of concatenated nuclear DNA (nDNA) and mitochondrial DNA (mtDNA) sequences from 44 musteloids and two outgroup species, each 8492 bp in aligned length. We then applied parsimony, maximum likelihood (ML), and Bayesian methods of phylogenetic and biogeographic inference and two different Bayesian methods of chronological inference. Special consideration has been given to the initial radiation of Musteloidea and the diversification of Mustelidae with particular reference to Ictonychinae. Specifically, we report the first genetic data for *Lyncodon patagonicus* and show that this species is an ictonychine. In addition, we provide the first rigorous analytical ancestral-area reconstruction of Musteloidea and a complete species-level reconstruction of the evolutionary and biogeographic history of the extant Ictonychinae.

2. Material and methods

2.1. Sampling

The nucleotide sequences obtained were from 12 protein-coding exons and four noncoding introns of nine nDNA genes and from a protein-coding mtDNA gene (Table 1). The sequence data were either newly obtained (DDBJ/EMBL/GenBank accessions AB285330–AB285332, AB305635, and AB564020–AB564112) or derived from previous studies (Supplementary Tables S1 and S2). Altogether, 45 wild species and one domestic form (*Mustela furo*) of the arctoid Carnivora were sampled; the sampling included 44 members of the ingroup Musteloidea plus a pinniped (*Phoca largha*) and an ursid (*Melursus ursinus*) as a collective outgroup (Supplementary Table S1). Selection of this outgroup was based on multiple lines of evidence indicating that Pinnipedia (seals, sea lions, walrus) and Ursidae (bears) are the closest extant relatives of Musteloidea (e.g., Wolsan, 1993; Wyss and Flynn, 1993; Delisle and Strobeck, 2005; Flynn et al., 2005; Fulton and Strobeck, 2006; Sato et al., 2006, 2009; Árnason et al., 2007; Rybczynski et al., 2009; Schröder et al., 2009; Eizirik et al., 2010).

2.2. Laboratory techniques

Total genomic DNA was extracted from tissue samples using a standard phenol–chloroform procedure (Sambrook and Russell, 2001). The PCR amplification of DNA from *Mellivora capensis* was preceded by whole-genome amplification with the illustra GenomiPhi V2 DNA Amplification Kit (GE Healthcare, Little Chalfont, UK). All PCR reactions were conducted in an automated thermal cycler (model PC 808, Astec, Fukuoka, Japan) with the following conditions: a 3-min denaturation period at 94 °C followed by 30 cycles of denaturation at 94 °C for 30 s, annealing at 50 °C for 30 s, and extension at 72 °C for 90 s; this was followed by an extension period at 72 °C for 10 min. Each 50-μl reaction mixture contained 10× Ex Taq buffer, 2 mM $MgCl_2$, 0.2 mM dNTP mix, 1.25 U of Ex Taq (Hot Start version) polymerase (Takara, Shiga, Japan), 0.8 μM of each primer, and 0.1–0.5 μg of genomic DNA. Amplification was performed through nonnested (for *CHRNA1*, *FES*, *GHR*, and *RHO*) or nested (for *APOB*, *BRCA1*, *MT-CYB*, *RAG1*, *RBP3*, and *VWF*) PCR reactions, using two new (vWF-F281-mustelids [5′-TGGTGCCCCCCACGGAAGGC-3′] and vWF-R1432-mustelids [5′-TCTCCAGCTCCTGCGGGTCGG-3′]) and 37 published primers (Supplementary Table S3). A 1-μl aliquot of each reaction mixture after the first nested PCR was used as a template for the second nested PCR. Sequencing was carried out with the Big Dye Terminator (version 3.1) Cycle Sequencing Kit (Applied Biosystems, Tokyo, Japan). The raw sequence data were generated on an ABI3130 automated sequencer (Applied Biosystems, Tokyo, Japan).

2.3. Phylogenetic analyses

2.3.1. Sequence alignment and supermatrix assembly

Sequences were aligned via multiple alignment in DNASIS Pro version 2.6 (Hitachi Software Engineering, Tokyo, Japan) following

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