The Fossil Record of Viverrids (Mammalia: Carnivora: Viverridae) in Greece



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1 Introduction

The family Viverridae includes the genets, civets, and linsangs; its modern representatives consist of 15 genera and 35 species. The family is known from the Old World (Africa, Asia, and southern Europe) and some islands (Madagascar, Indonesia, Philippines). The viverrids are small-to-medium-sized animals with elongated and slender body and relatively short extremities with tetra- or pentadactyl feet. The feet are plantigrade or digitigrade and the claws semiretractile. Their body weight varies from <1 to 15 kg and their length, without the tail, ranges from 30 to 100 cm. The skull of viverrids is elongated, flattened and with elongated muzzle. The premolars are large and the carnassials well developed and trenchants. The P4 is short and broad with strong protocone. The m1 lacks longitudinal blade and has broad trigonid and long talonid. The upper molars are wider than long with three cuspids, and the lower molars have well-developed talonid. The majority of the modern viverrids are arboreal forms but few taxa are scansorial and can climb. They are mainly nocturnal predators and most are carnivorous, feeding on small invertebrates, insects and worms but some taxa include fruits or roots in their diet (Vaughan et al. 2015; Myers 2000; Orlov 1968). The Viverrids are scarce in Greece and known only from two localities; the family is also rare or unknown in the adjacent countries.

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Fig. 1 Map of Greece showing the geographic distribution of the localities with viverrid fossils. See Appendix for more information. Image exported from Google Earth Pro © 2019, map data from US Dept. of State Geographer, SIO, NOAA, U.S. Navy, NGA, GEBCO, image from Landsat/ Copernicus. Scale bar equals 8 km, North faces upward

2 Historical Overview

The Greek fossil record of the viverrids is poor, represented only by two species from the early–middle Miocene that belong to the subfamily Lophocyoninae (Fig. 1 and Appendix). The material is very poor and described by Schmidt-Kittler (1983) and Koufos et al. (1995). The scarcity of the viverrids is possibly due to the limited number of known early–middle Miocene fossiliferous sites. Also, during the late Miocene, the open and dry conditions did not favor the presence of the arboreal viverrids.

3 Phylogenetic Relationships

The family Viverridae *sensu lato* included, until recently, the families Herpestidae and Viverridae *sensu stricto*. Recent molecular studies indicated that the herpestids constitute a separate family, which is considered as the sister group of the family Hyaenidae, whereas Viverridae *sensu stricto* (containing the subfamilies Hemigalinae, Paradoxurinae, Genetinae, and Viverrinae) is considered monophyletic (Veron 2010 and references therein). Some African taxa (*Nandinia*) and oriental linsangs (*Prionodon*) are not real viverrids. The genus *Nandinia* belongs to the separate family Nandiniidae and it is referred as sister group of all modern Felidae (Flynn et al. 2005). The origin of Viverridae and Herpestidae is traced in the late Oligocene at ~25.0 Ma (Werdelin 1996). The early Miocene (>20.0 Ma) *Herpestides*

is the oldest known viverrid, traced in France and East Africa (Hunt 1991; Schmidt-Kittler 1987), which, for a long time, was considered as herpestid. During the Neogene/Quaternary the family is known from the tropical/subtropical regions of the Old World, but never moved to the north or migrated to the New World.

4 Systematic Paleontology

Viverridae Gray, 1821

Lophocyoninae Fejfar and Schimt-Kittler, 1987

Euboictis Fejfar and Schmidt-Kittler, 1984

Type Species Sivanasua aliverensis Schmidt-Kittler, 1983.

★ Euboictis aliverensis (Schmidt-Kittler, 1983)

Nomenclatural and Taxonomical History *Sivanasua aliverensis* in Schmidt-Kittler 1983 (new species); *Euboictis aliverensis* in Fejfar and Schmidt-Kittler 1984 (new combination, new genus).

Type Material LGPUT-ALI-AL-23 (holotype), right P4, housed in the Laboratory of Geology and Paleontology, Aristotle University of Thessaloniki and described and figured by Schmidt-Kittler (1983: p. 303, fig. 1; pl.1, fig. 6).

Type Locality Aliveri, Euboea Island, Greece, early Miocene, MN4.

Distribution It is only known from its type locality.

Remarks The known sample from Aliveri includes a few isolated teeth found during washing sediments for micromammals (Fig. 2a, b). The teeth originally were described as a new species of *Sivanasua*, but soon they were transferred to the new genus *Euboictis*. The species is characterized by a single-rooted and tricuspid P1, a slightly molarized P2 and P3, a paracone-metastyle blade in the P2 and P3 like that of the P4, a short metastyle in the P4, a W-shaped paracone and metacone in the M1 and M2, a continued lingual cingulum in the protocone of the M1 and M2, the absence of conules in the M1 and M2, a relatively molarized p1, the presence of trigonid and short-broad talonid in the lower premolars, an m1 shorter than the m2 with very low trigonid, an m2 talonid longer than trigonid, and an equal-sized hypoconid and hypoconulid in the m2 (Schmidt-Kittler 1983; Fefjar and Schmidt-Kittler 1984).

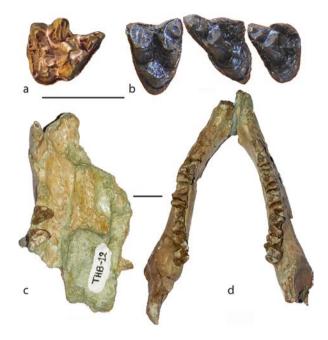


Fig. 2 Selected fossils of Viverridae from Greece. (**a**, **b**) *Euboictis aliverensis* from the Early Miocene (MN3) of Aliveri, Euboea Island, (**a**) right P4 (holotype) in occlusal view (the tooth has been gilded), (**b**) upper composite dentition (casts) in occlusal view, (**c**, **d**) *Lophocyon paraskevaidisi*, from the Middle Miocene (MN5) of Thymiana-B, Chios Island, (**c**) right maxilla with P4–M1 in occlusal view, (**d**) mandible (holotype) with the tooth rows in occlusal view. Scale bars equal 1 cm

Lophocyon Fejfar et al., 1987

Type Species Lophocyon carpathicus Fejfar et al., 1987.

★Lophocyon paraskevaidisi Koufos, de Bonis, Sen, 1995

Type Material LGPUT-THB-1 (holotype), mandible with both tooth rows, housed in the Laboratory of Geology and Paleontology, Aristotle University of Thessaloniki (Koufos et al. 1995: 512, fig. 3; pl. 67, fig. 2).

Type Locality Thymiana-B (THB), Chios Island, Greece, middle Miocene, MN5.

Distribution It is only known from its type locality.

Remarks *Lophocyon paraskevaidisi* was found in the middle fossiliferous horizon of Thymiana (Thymiana-B, THB) in Chios Island and includes some maxillary and mandibular remains (Fig. 2c, d) collected at the beginning of the 1990s. However, the locality Thymiana was found in the 1940s with a quite rich mammal fauna (Paraskevaidis 1940). The molarized P3 and P4, the strongly projected metastyle

and shallow groove between it and the parastyle on the P3 and P4, the high-crowned lower teeth, the molarized premolars with broad talonid, and the strong hypoconulid in the m2, are the main characters of *L. paraskevaidisi*. This species differs from *L. carpathicus* in having a shorter size, a higher degree of molarization, and a weaker basal cingulum in the teeth (Koufos et al. 1995).

Appendix

List of the Greek localities containing viverrid fossils. Type localities are marked with bold. Locality numbers refer to the collection numbers of the PaleoBiology Database (PBDB)

Localities ^{PBDB No}	Age (MN; GPTS)	Taxon
Thymiana B ²⁰²⁷²⁸	Middle Miocene (MN5; ~15.5 Ma)	Lophocyon paraskevaidisi ¹
Aliveri ⁶⁸⁰³²	Early Miocene (MN4)	Euboictis aliverensis ²

MN Mammal Neogene, *GPTS* Geomagnetic Polarity Time Scale ¹Koufos et al. (1995), ²Schmidt-Kittler (1983)

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