







A new lophocyonid, *Izmirictis cani* gen. et sp. nov. (Carnivora: Mammalia), from the lower Miocene of Turkey

Jorge Morales^a , Serdar Mayda^b , Alberto Valenciano^{c,d,*} , Daniel DeMiguel^{e,f}  and Tanju Kaya^g

^aDepartamento de Paleobiología, Museo Nacional de Ciencias Naturales, CSIC, C/ José Gutiérrez Abascal, 2. 28006, Madrid, Spain; ^bDepartment of Biology, Ege University, Bornova, 35100 Izmir, Turkey; ^cResearch and Exhibitions Department, Iziko Museums of South Africa, P.O. Box 61, Cape Town, South Africa; ^dDepartment of Biological Sciences, University of Cape Town, Palaeobiological Research Group, Private Bag X3, Rhodes Gift 7701, Cape Town, South Africa; ^eFundación ARAID/Universidad de Zaragoza, Departamento de Ciencias de la Tierra, Área de Paleontología, Pedro Cerbuna 12, 50009 Zaragoza, Spain; ^fInstitut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona. Edifici ICTA-ICP, C/ Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain; ^gNatural History Museum, Ege University, Bornova, 35100 Izmir, Turkey

(Received 31 May 2018; accepted 22 September 2018)

Lophocyonids are one of the more enigmatic groups of Carnivora in the European Miocene fossil record. Lophocyonids are clearly distinguished from other Feliformia by their peculiar lophodont dental morphology. For this reason, the systematic relationships of the family have been controversial. Here we describe and interpret dental remains from the early Miocene of Sabuncubeli, Turkey, which we attribute to a new genus and species: *Izmirictis cani*. The phylogenetic analysis allows us to include *Izmirictis* within a monophyletic group, Lophocyonidae new rank, characterized by the molarization of the anterior premolars (P3 and p4), the lophodont adaptation of the molar dentition and the complex morphology of the incisors. The phylogenetic analysis shows a close relationship between *Izmirictis* and primitive hyaenids (represented herein by *Protictitherium*). The divergence between Lophocyonidae and Hyaenidae is estimated by biochronological data to have occurred during the early Miocene (MN2). Dental microwear analysis, although limited by poor dental enamel preservation, indicates that the pronounced lophodonty in *Izmirictis cani* could be connected to a herbivorous feeding habit.

<http://zoobank.org/urn:lsid:zoobank.org:pub:8D75382D-6C22-41C1-A47F-BA3EAF766881>

Keywords: Lophocyonidae; Feliformia; systematics; Miocene; Europe; Turkey

Introduction

Lophocyoninae Fejfar, Schmidt-Kittler & Zacharov, 1987 is one of the most peculiar groups of terrestrial carnivorans in the fossil record due to its lophodont dentition, which is particularly advanced in the most derived members of the group. This subfamily includes the genus *Sivanasua* Pilgrim, 1932 with the species *S. viverroides* (Schlosser, 1916) and *S. moravica* Fejfar & Schmidt-Kittler, 1984; *Euboictis aliverensis* Schmidt-Kittler, 1983; the genus *Lophocyon* Fejfar *et al.*, 1987 with the species *L. carpathicus* Fejfar *et al.*, 1987 and *L. paraskevaidisi* Koufos *et al.*, 1995, all of which are from the early–middle Miocene of Europe. The first interpretations of the fossils by Schlosser (1916) related them to the extant red panda *Ailurus fulgens* Cuvier in Geoffroy Saint-Hilaire & Cuvier, 1825. Schlosser (1916) described the first species as ‘*Aeluravus viverroides*’ on the basis of fossils from the site of Attenfeld, MN4 (Bavaria, Germany). Pilgrim (1932) proposed for

this species the genus *Sivanasua* (*Aeluravus* was pre-occupied by a glirid) and included in it two new species, both of which were later classified as Adapidae by Gingerich & Sahni (1984). However, the genus name is valid, and is generally considered to be close to the coati-like procyonid carnivorans. After the study of Schmidt-Kittler (1983) they were considered to be primitive feliforms, classified in their own subfamily Lophocyoninae, within the Viverridae (Fejfar *et al.* 1987).

The aim of the present work is the description of a new form from the lower Miocene of Sabuncubeli (Turkey) (de Bruijn *et al.* 2006) tentatively attributed to this interesting group of carnivorans by Mayda (2004, 2010) and Hoek Ostende *et al.* (2015). The primitive morphology of its dentition, in comparison with the other representatives of the group, yields important clues about Lophocyoninae phylogenetic relationships. It is the first representative of the group to be found outside of continental Europe.

*Corresponding author. Email: alb3rtovv@gmail.com

Fossil locality

The locality of Sabuncubeli is situated in the lower part of the Soma Formation (Fig. 1), along the forest road that leads from the main road between Manisa and Bornova to the village of Sarnic, 15 km NW of Izmir (de Bruijn *et al.* 2006; Kaya *et al.* 2007). The Sabuncubeli micromammal association is considered to be somewhat older than the one from Keseköy (Krijgsman *et al.* 1996) and it fits best into the lower part of MN 3. According to a preliminary identification (Mayda 2010) the carnivores found in the site are: an amphicyonid (*Cynelos* sp. nov.), a musteloid (*Stromeriella* sp.), a viverrid (*Semigenetta elegans*), a feliformia (*Palaegale* sp.) and an undetermined felid that cannot yet be formally attributed to a genus. Besides its diverse carnivore assemblage, Sabuncubeli has also yielded a new tragulid (*Dorcatherium* sp. nov.), an early cervid (*Procervulus* sp.) and a small rhino (*Protaceratherium* sp.), which are under study by SM.

Material and methods

Institutional abbreviations

EUNHM: Ege University Natural History Museum, Bornova, Izmir, Turkey; **IPS:** collection of the Institut Català de Paleontologia Miquel Crusafont (ICP), Universitat Autònoma de Barcelona, Spain; **MNCN:** Museo Nacional de Ciencias Naturales, Madrid, Spain; **MNHN:** Muséum national d'Histoire naturelle, Paris, France; **NHMUK:** Natural History Museum, London, UK.

Studied material

The fossil remains of *Izmirictis cani* gen. et sp. nov. are housed in EUNHM: PV-54000: right I3; PV-54001: left I2; PV-54003: right P3; PV-54004: left P4; PV-54005a: right M1; PV-54005b: fragment of right M1; PV-54006: left M2; PV-54007: right i2; PV-54008: left p1 or p2; PV-54009: right p4; PV-54010: left m1.

For comparison we used *Sivanasua viverroides* (Schlosser, 1916) from Rothenstein 1/13 described by Fejfar *et al.* (1997), including a cast of specimen 0030 stored at the MNCN, and the P4–P3 from Chêne de Navère, France, MN4, cast stored in the MNHN, figured by Ginsburg & Morales (1999), *Sivanasua antiqua* (Crusafont-Pairó, 1959) from Can Canals, Spain, lower Miocene, MN4, housed at the ICP; the holotype of *Euboictis aliverensis* Schmidt-Kittler (1983) from Aliveri, Greece, MN4 (Hoek Ostende *et al.* 2015), of which a cast is preserved at the MNCN; the holotype of *Lophocyon paraskevaidisi* Koufos *et al.* (1995) from

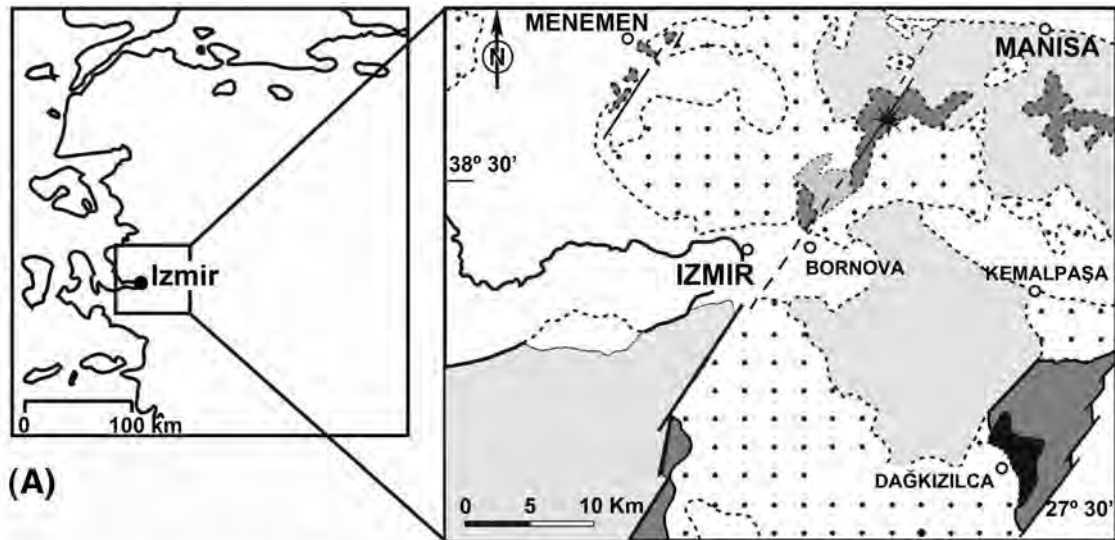
Thymiana-B, Chios Island, Greece, MN5 (Koufos 2011), of which a cast is kept at the MNHN; the holotype of *Kichechia zamanae* Savage (1965) from Rusinga, Kenya, lower–middle Miocene 17–15 Ma (Peppe *et al.* 2009) housed at the NHMUK; *Herpestides antiquus* (Blainville, 1842), from Saint-Gérard-le-Puy, France, MN2a, housed at the MNHN and described by Viret (1929) and Beaumont (1967); *Protictitherium crassum* (Depéret, 1892) from the Vallesian of Spain from the sites of Los Valles de Fuentidueña, MN9 and Cerro de los Batallones, MN10 (Fraile 2017). The taxa *Lophocyon carpathicus* Fejfar *et al.*, 1987 from Kosice-Bankov, Slovakia, MN5, *Legetetia nandii* Schmidt-Kittler (1987) from Legetet, Kenya, lower Miocene 19 Ma (Werdelin 2010), and *Protictis* spp. described in Flynn & Galiano (1982), Gingerich & Winkler (1985) and Meehan & Wilson (2002) from the middle Paleocene of North America were studied based on the original publications. The extant carnivores studied were the viverrids *Viverra tangalunga* Gray, 1832, and *Hemigalus derbyanus* (Gray, 1837) housed at MNCN and MNHN. Measurements in mm (L = length, W = width) were made with Mitutoyo Absolute digital callipers accurate to 0.1 mm. P4 = length mestastyle–parastyle, width parastyle–protocone. The photographs of the dentition of *I. cani* were made with a Scanning Electron Microscope Fei, model Quanta 200, at the MNCN.

Cladistic analysis

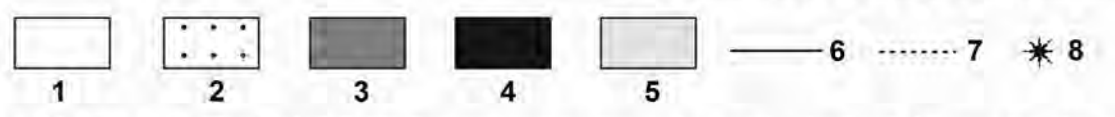
We performed a cladistic analysis to better assess the relationships of *Izmirictis* with other taxa possessing similar lophodont dentitions, such as *Sivanasua viverroides*, *Lophocyon* spp. (*L. paraskevaidisi* and *L. carpathicus*) and *Euboictis aliverensis*, together with the primitive hyaenid *Protictitherium crassum*, and lower–middle Miocene genera with uncertain relationships including *Herpestides antiquus*, *Kichechia zamanae* and *Legetetia nandii*, as well as the living viverrids *Viverra tangalunga* and *Hemigalus derbyanus*. The cladistic analysis includes 11 taxa and 67 equally weighted, unordered dental and cranial characters generated by us. The character list, data matrix and nexus files are available in the [Supplementary material](#). We selected *Protictis* spp. as the outgroup. The analysis was performed using PAUP*4.0b10 (Swofford 2002).

Systematic palaeontology

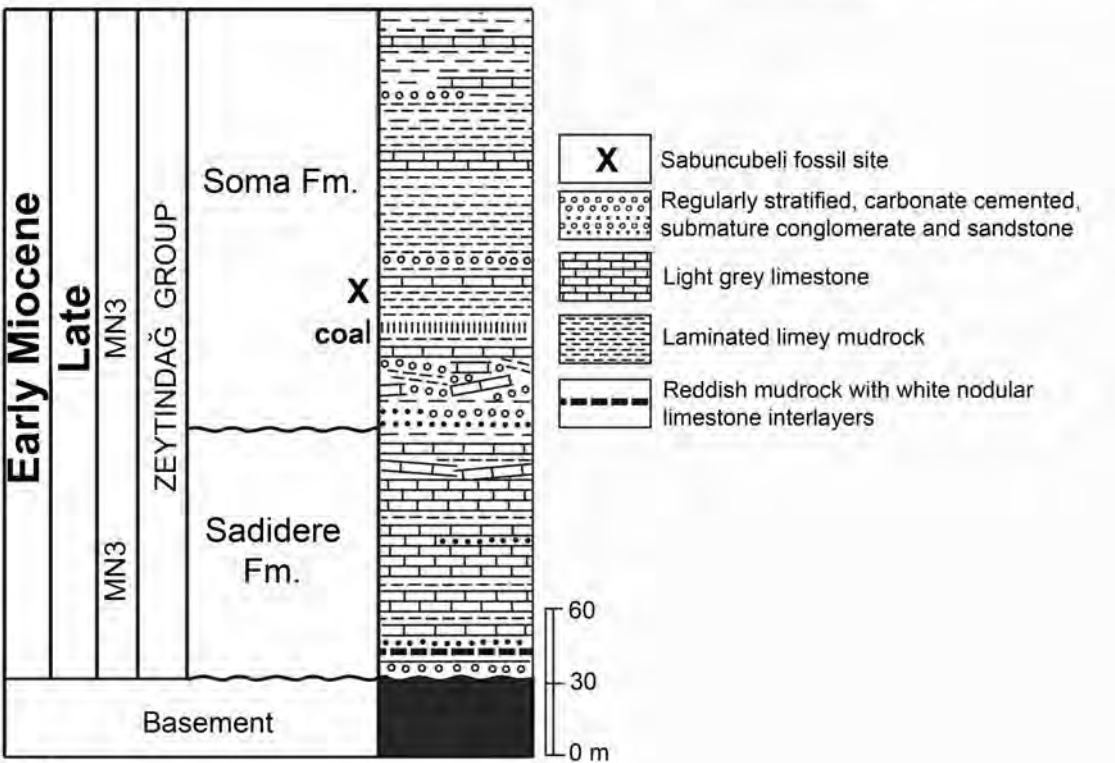
Order **Carnivora** Bowdich, 1821
 Suborder **Feliformia** Kretzoi, 1945
 Family **Lophocyonidae** Fejfar, Schmidt-Kittler & Zacharov, 1987 (new rank)



(A)



1. Alluvium; 2. Undifferentiated; 3. late Cenozoic sedimentary and volcanic units; 3 early Miocene lacustrine and fluvial deposits (Soma Fm); 4. Lacustrine paper shale; 5. Late Cretaceous to early Paleocene Ovacik Group; 6. Active faults; 7. Undifferentiated fault contacts; 8. 'Sabuncubeli' fossil locality



(B)

Figure 1. A, geological map of the Izmir area, Turkey, showing the location of the Sabuncubeli mammal fossil site. B, stratigraphy of the Zeytindağ Group (Saridere Formation and Soma Formation) showing the location of the fossil site in the section (figures modified from de Bruijn *et al.* 2006).

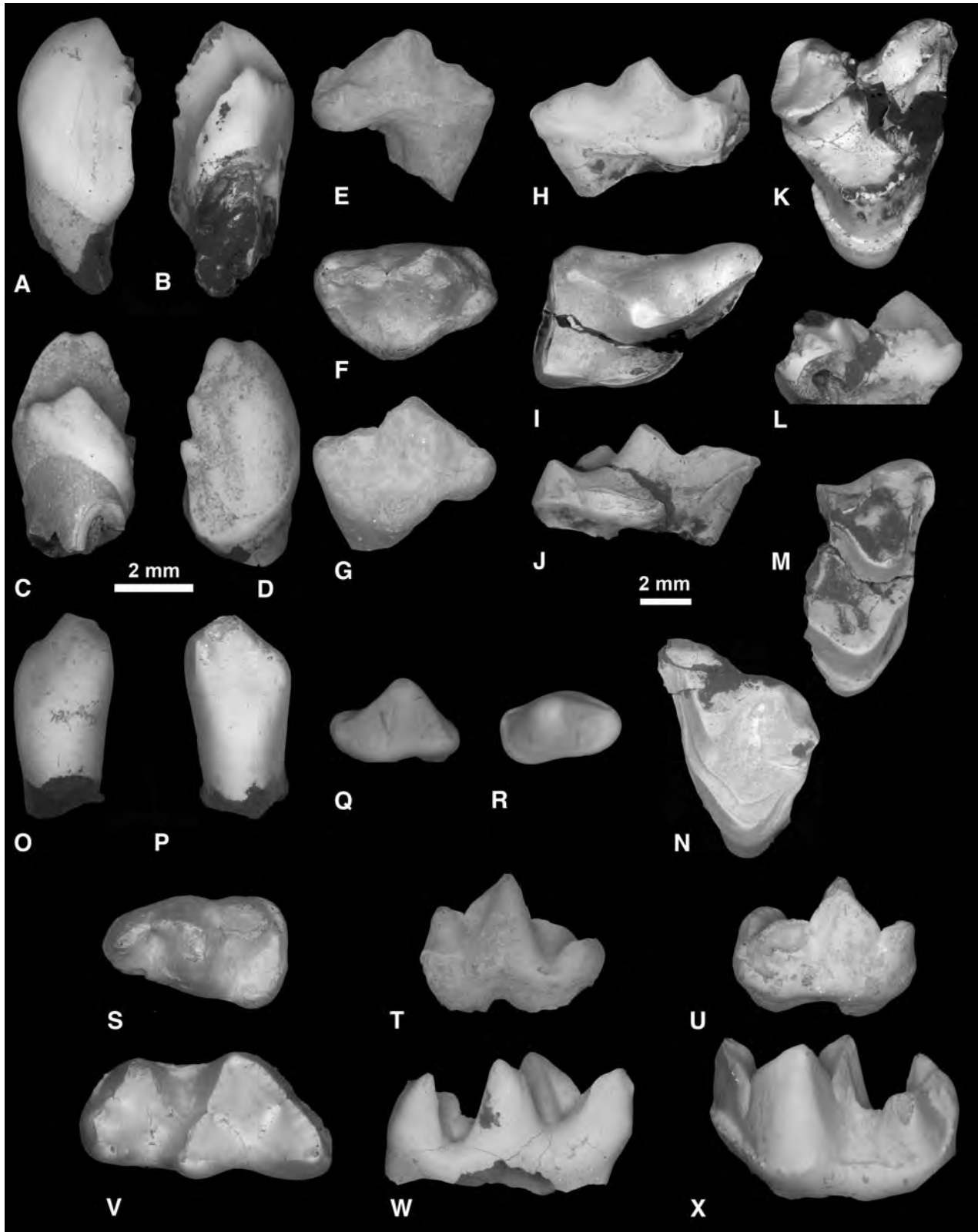


Figure 2. *Izmirictis cani* gen. et sp. nov. from Izmir, Turkey, Scanning Electron Microscope (SEM) photographs. **A, B**, PV-54000, right I3. **A**, buccal view, **B**, lingual view; **C, D**, PV-54001, left I2. **C**, buccal view, **D**, lingual view; **E–G**, PV-54003, right P3. **E**, buccal view, **F**, occlusal view, **G**, lingual view; **H–J**, PV-54004, left P4 (paratype). **H**, buccal view, **I**, occlusal view, **J**, lingual view; **K, L**, PV-54005a, right M1. **K**, occlusal view, **L**, buccal view; **M**, PV-54005b, fragment of right M1, occlusal view; **N**, PV-54006, left M2, occlusal view; **O, P**, PV-54007, right i2. **O**, buccal view, **P**, lingual view; **Q, R**, PV-54008, left p1 or p2. **Q**, lingual view. **R**, occlusal view; **S–U**, PV-54009, right p4. **S**, occlusal view, **T**, lingual view, **U**, buccal view; **V–X**, PV-54010, left m1 (holotype). **V**, occlusal view, **W**, lingual view, **X**, buccal view. Figures **A–D**, and **O–P** (incisives) left scale, other teeth right scale.

Type genus. *Lophocyon* Fejfar Schmidt-Kittler, & Zacharov, 1987.

Included genera. *Sivanasua* Pilgrim, 1932, *Euboictis* Fejfar & Schmidt-Kittler, 1984 and *Izmirictis* gen. nov.

Stratigraphical range. Early Miocene (MN3 biozone) to middle Miocene (MN7/8 biozone).

Geographical range. Eurasia and Anatolia (Turkey).

Diagnosis. Feliformia with dental formula (permanent teeth) 3142/3142. Large molars, the upper molars exhibiting dilambdodont morphology, lower molars lophodont with height of the talonid as well developed as that of the trigonid. Molarized premolars, incipient in primitive forms, p4 always with metaconid and P3 with metacone. In the most derived forms the dentition is hypsodont and the molarization affects all of the anterior premolars.

Genus *Izmirictis* gen. nov.

Type species. *Izmirictis cani* sp. nov.

Diagnosis. Lophocyoniid with moderately lophodont lower molars, m1 talonid cuspids high and well differentiated. M1 with paracone and metacone in buccal position and strong lingual cingulum. P4 with conservative carnassial morphology. Anterior premolars (P3 and p4) robust and moderately molarized.

Etymology. From Izmir, Turkey, the province and city where the locality of Sabuncubeli is located. Izmir was known as Smyrna in the Classical Age; plus *-ictis*, the Latin name for small carnivores.

Izmirictis cani sp. nov.

(Figs 2, 3)

Diagnosis. As for the genus.

Holotype. EUNHM PV-54010, left m1.

Paratype. EUNHM PV-54004, left P4.

Type locality. Sabuncubeli, Turkey.

Age. Early Miocene (MN3 biozone).

Etymology. This species is named after Can Mayda, son of Serdar Mayda, co-author of this work.

Description.

Upper dentition. PV-54000, I3 right (L = 3.4; W = 3.6) (Fig. 2A, B) is tall and large in relation to the jugal dentition. It has a strong and individualized cingulum on the lingual surface, which decreases abruptly towards the anterior edge of the tooth.

PV-54001, I2 left (L = 3.3; W = 3.1) (Fig. 2C, D), shows that it is smaller than the I3. Its morphology is close to that of the I3, although on the lingual surface the edge shows strong irregular crenulations. The lingual

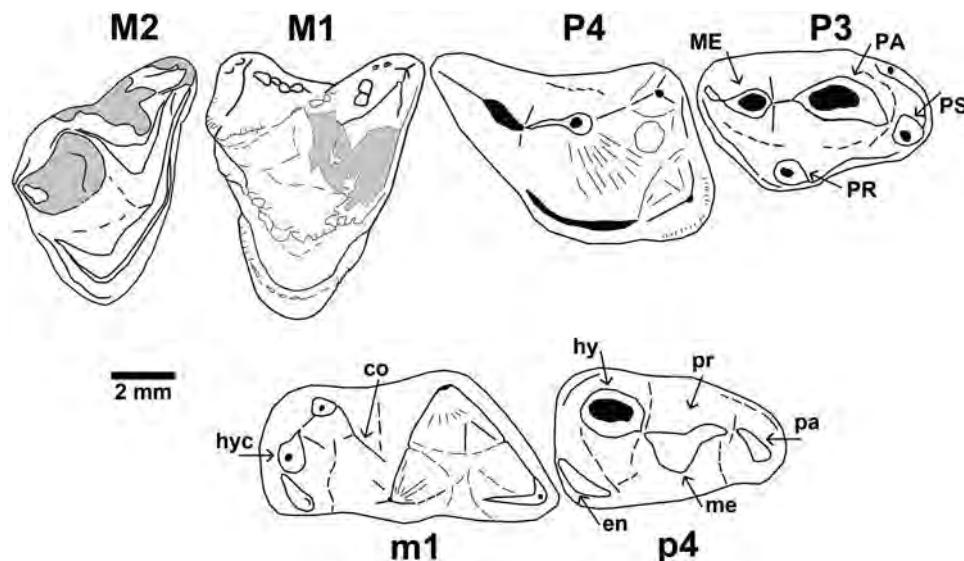


Figure 3. Drawings of dentition in occlusal view of *Izmirictis cani* gen. et sp. nov., from Izmir, Turkey. The M2, P4 and p4 drawings are mirrored. Abbreviations: co, cristid obliqua; en, entoconid; hy, hypoconid; me, metaconid; ME, metastyle; PA, paracone; pa, paraconid; PR, protocone; pr, protoconid; PS, parastyle.

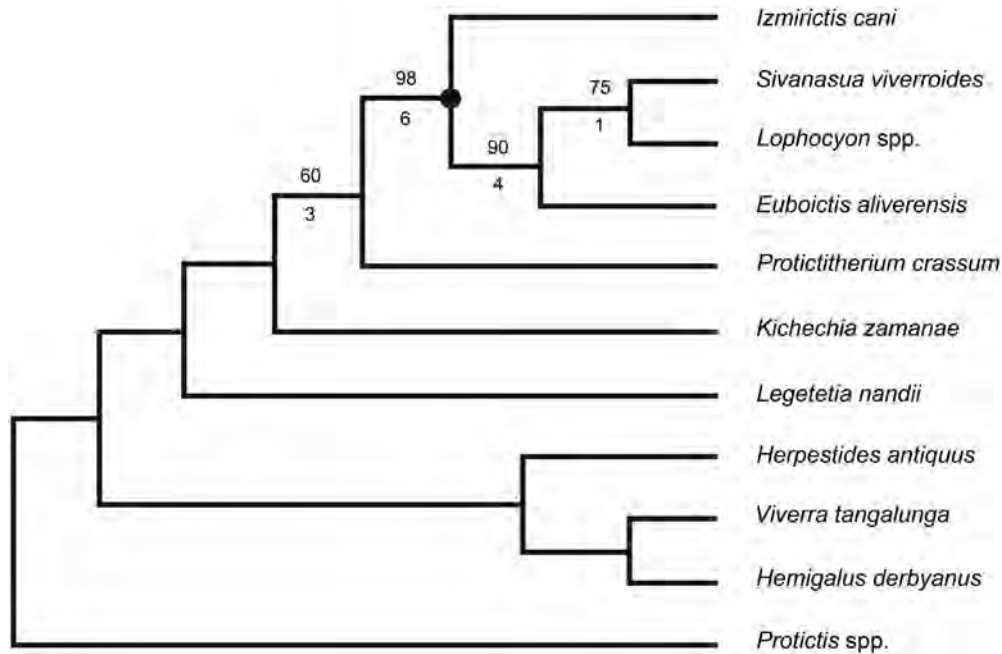


Figure 4. Phylogenetic relationship of *Izmirictis cani* gen. et sp. nov., within Lophocyonidae (node with a filling circle), and of some extinct Neogene feliform carnivorans and living viverrids (*Viverra tangalunga* and *Hemigalus derbyanus*). *Protictis* spp. is the outgroup. Searches were performed by means of the branch and bound and a bootstrap analysis through 1000 replicates. A single tree is obtained (length 119 steps, consistency index (CI)=0.5072, retention index (RI)=0.4963). The numbers below nodes are Bremer indices, and the numbers above nodes are bootstrap support percentages (only shown if ≥ 50).

cingulum is well developed and it is slightly subdivided in the posterior area.

In PV-54003, P3 right (L = 7.2; W = 4.5) (Fig. 2E–G), the main cusp paracone is robust and of moderate height. There is a small parastyle and a small but strong postero-buccal cingulum. The metacone is well developed and possesses a sharp posterior cusp, the metastyle. The lingual cingulum is strong. The tooth shows a lingual expansion at the base of the crown, in which a remarkably small protocone is present.

PV-54004, P4 left (L = 7.8; W = 5.5) (Fig. 2H–J) has a well-developed conical parastyle attached to the anterior crest of the paracone. The paracone is massive and is separated from the metastyle by the carnassial notch. Lingually the metastyle is vertical and sharp, but buccally it is globose. The protocone is pyramidal and well developed, located in front of the parastyle. There is a wide platform with a broad valley between the protocone and the buccal surface, which ends in the lingual cingulum of the metastyle. There is a smooth cingulum developed anteriorly between the base of the parastyle and protocone. Additionally, there is a conspicuous worn area between the paracone and the parastyle.

PV-54005a, M1 right (L = 6.4; W = 8.6) (Fig. 2K, L). This tooth is triangular in occlusal view. The

paracone is partially broken. This cusp is similar to the metacone and both cusps are lingually displaced. The paracone, metacone and dune shaped with a concave buccal wall (ectoflexus) and the lingual one convex. There is a flattened cusp between the buccal wall of the paracone and metacone; a second cusp is located in the base of the paracone. The parastyle is well developed. There are several styler cusps on the buccal wall, but without developing a real cingulum. The posterior crista of the metacone is strong and somewhat thickened, showing a vertical groove in the buccal wall. There is a well-developed basal cusp, accompanied by smaller ones. The protocone is high and possesses strong and sharp cristae. The anterior one reaches the anterobuccal corner of the tooth, while the posterior one extends to the posterior base of the metacone. It has a strong lingual cingulum enclosing the entire protocone. The trigon valley (basin) is deep.

PV-54005b, a fragment of M1 (Fig. 2M) is interpreted to be from the right side; consequently, it comprises the anterior half of the molar. It has a deeply worn dune-shaped paracone, similar in shape to the metacone of the other M1. However, its anterior crista is smoother than the crista of the metacone.

PV-54006, M2 left (L = 5.6; W = 8) (Fig. 2N): This tooth is heavily worn and the metacone is partly broken. The occlusal outline is subtriangular with a well-developed parastylar area. The paracone is pyramidal. Its anterior crista is long and smooth and it runs towards the complete parastylar area. The posterior crista is smooth and it ends at the base of the metacone. The metacone is broken; however, it would have been similar in size to the paracone, in relation to the area that it occupies. The protocone is large and triangular, and occupies the entire lingual part of the molar. The anterior crest is well developed as in the M1, and it reaches the anterobuccal base of the paracone. The posterior crest is comparatively short, not being in contact with the metacone. There is a smooth posterolingual cingulum at the base of the protocone.

Lower dentition. PV-54007, i2 right (L = 2.65; W = 3.92) (Fig. 2O, P). This is a robust tooth, which is buccolingually widened. The lingual cingulum is tall and smooth. The buccal wall shows an asymmetrical subdivision as in the i2 of *Viverra*. The buccal wall has a wear facet.

PV-54008, p1 or p2 left (L = 4.29; W = 2.5) (Fig. 2Q, R). A simple unicuspid premolar, with weak cristids.

PV-54009, p4 right (L = 9.47; W = 4.87) (Fig. 2S–U). An elongated premolar, with a tall main cusp (protoconid). Its anterior cristid is sharp, very individualized and separated by a notch from the anterior cuspid (paraconid), which is well developed and has a cutting blade morphology. The posterior cristid is short but clearly individualized. Lingually the protoconid is expanded and comprises a well-defined but weakly individualized metaconid. The talonid is highly developed. It has a well-developed buccal cuspid (hypoconid) with a beveled cuspid in a posterolingual position. There is a posterobuccal cingulum at the base of the hypoconid.

PV-54010, m1 left (L = 10.32; W = 7.12) (Fig. 2V–X). The trigonid is more developed than the talonid. The cusps of the trigonid are arranged in an equilateral triangle, in which the metaconid occupies a very posterior position, being almost as developed as the paraconid. The cristids of the trigonid are thickened; thus, they are clearly individualized from the conids. The lingual cristid of the metaconid is high and contacts the lingual one of the protoconid, establishing a high wall that is oblique to the anteroposterior axis of the tooth, which abruptly divides the trigonid from the talonid. A strong cingulum is developed at the base of the paraconid. The trigonid valley (basin) is deep. The talonid is elevated with a massive pyramidal hypoconid. The entoconid is also high and is attached to the hypoconulid. The hypoconid, hypoconulid and entoconid are united by elevated

cristids, establishing a continuous wall. The oblique cristid is well developed and reaches the base of the metaconid, leaving a buccal valley which is delimited by a high and robust cingulum. Anteriorly the entoconid ends abruptly, so that the separation of the latter from the metaconid is neat, leaving the trigonid valley open lingually.

Discussion

Izmirictis cani can be considered a genuine ‘missing link’ between Lophocyonidae and basal Feliformia. *Izmirictis*, along with the lophocyonine genera *Sivanasua*, *Euboictis* and *Lophocyon*, shares the basic herbivorous adaptations that characterize the group, such as the dilambdodont morphology of the upper molars (M1–M2), m1 with a talonid that is enlarged and close in size to the trigonid, and a clear lophodont tendency, the robust P4, the incipient molarization of P3 with a strong metacone, which is close in size to the paracone, and a p4 with an incipient trigonid and an enlarged talonid. In *Izmirictis* the known incisors show a strong development of the cingulum and a general increase in complexity, similar to that described by Schmidt-Kittler (1983) for *Euboictis aliverensis*.

However, *Izmirictis* differs from *Euboictis* in retaining several manifestly primitive morphological features in the dentition, such as M1 with a more buccal position of the paracone-metacone, deep ectoflexus, and the presence of a more developed lingual cingulum. The P4 preserves an elongated cutting blade aligned with the anteroposterior mandibular axis, and the same is observed in the P3 buccal cuspid. In the lower dentition, the p4 is more elongated, with an open trigonid, a weak metaconid and a larger talonid with a small entoconid. *Izmirictis* differs from *Sivanasua viverroides* from the Rothstein 1/13 locality (Fejfar *et al.* 1997) in the same characters of M1 and P4 already indicated for *Euboictis*, but the differences from the P3 are minor, because both taxa possess the same disposition of the paracone-metacone, although the other cuspid and cingula are better developed in *Sivanasua*. The m1 and p4 of *Izmirictis* are less robust, and with the lingual cuspid, entoconid and metaconid weaker than in *Sivanasua*. *Izmirictis* differs from *Lophocyon paraskevaidisi* by the elongated P3 and P4 with the cutting cuspid aligned antero-posteriorly, while the differences in the lower dentition are even more pronounced than with *Euboictis* and *Sivanasua*, particularly in the p4 which in *Lophocyon* species are clearly hypsodonts, with the lingual cuspid better developed than *Izmirictis*.

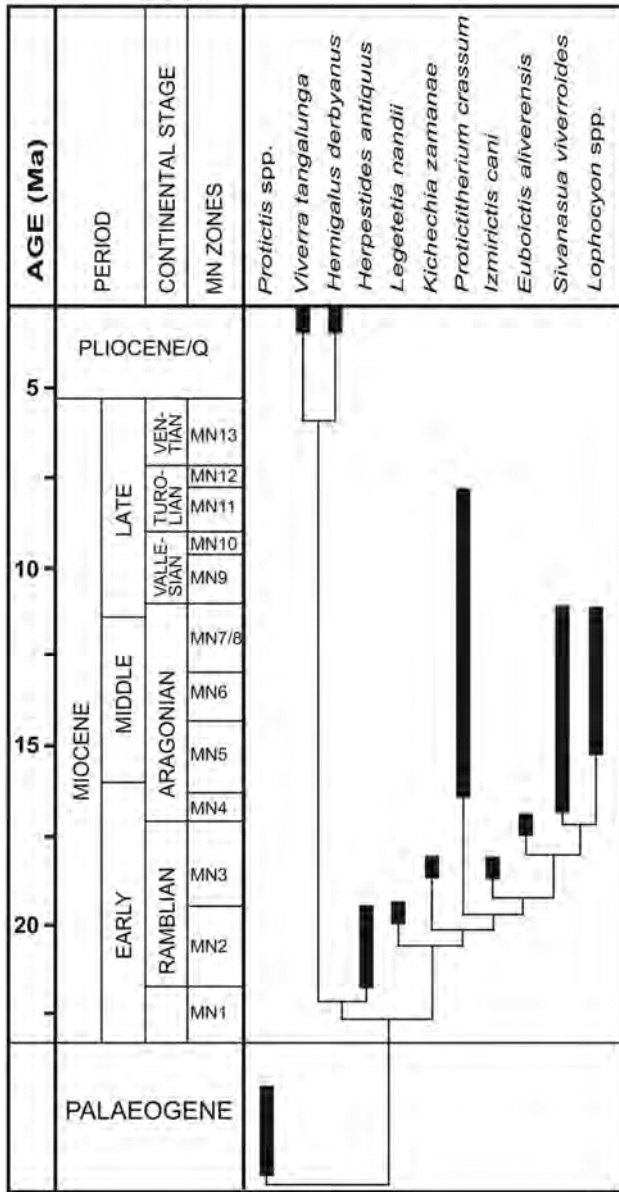


Figure 5. Biochronology and hypothesis of phylogenetic relationships of the species of Lophocyoniidae based on the obtained tree (Fig. 4). Chronological data after Hilgen *et al.* (2012). Temporal ranges of species based on Schmidt-Kittler (1983, 1987); Fejfar & Schmidt-Kittler (1984, 1997); Koufos *et al.* (1995); Hoek Ostende *et al.* (2015); Morales *et al.* (2015).

The differences between *Izmirictis* and the aforementioned genera justify the creation of a new genus and species for the Sabuncubeli fossils, *Izmirictis cani* gen. et sp. nov. The species can be included together with the Lophocyoniinae in a monophyletic group, for which, following Schmidt-Kittler (1999), we propose the elevation of Lophocyoniinae to family rank,

a category already employed by Morlo *et al.* (2010, table 10.1).

Phylogenetic relationships

Izmirictis cani represents an important link in the history of the Lophocyoniidae. Its membership in this family is clear, in spite of the primitive traits that it retains in its dentition compared with forms such as *Euboictis* or *Sivanasua*, and that differ even further from the highly derived *Lophocyon*. In the phylogenetic analysis (Fig. 4), the genera included in the Lophocyoniidae show a close relationship and allow us to include *Izmirictis* within a monophyletic group characterized by the molarization of the anterior premolars (P3 and p4), the lophodont adaptation of the molar dentition and the complex morphology of the incisors. Compared to other lophocyoniids these adaptations are present in *Izmirictis* in nascent form, maintaining a morphological pattern of more generalist carnivores. It is precisely these primitive traits that yield clues about the phylogeny of Lophocyoniidae, which was hitherto poorly constrained. The presence of abundant autapomorphies in the family, many of them unique at the ordinal level, drastically distances Lophocyoniidae from potential relatives in the suborder Feliformia, as was recognized by Fejfar *et al.* (1997, p. 107) when they pointed out that “Up to now, these genera are too peculiar in their features to be integrated within a cladogram together with other feliform carnivores”. Much of the discussion presented by these and other authors (Schmidt-Kittler 1983; Fejfar & Schmidt-Kittler 1984; Fejfar *et al.* 1987, 1997) was focused on the presence of an elongated m2 talonid, which was considered to be a synapomorphic character. This type of m2 can be observed in different clades among extant representatives of Feliformia, such as *Eupleres* (Eupleridae), *Liberictis* (Herpestidae) and *Hemigalus* (Viverridae), but none of these species reaches the degree of development and complexity observed in Lophocyoniidae. This statement serves for fossil forms also considered to be potential ancestors of Lophocyoniidae, in particular *Legetetia* Schmidt-Kittler, 1987, from the lower Miocene of Africa. In all of these cases we can reasonably assume that the presence of an elongated m2 is related to an increase in the molar grinding surface, so that the M1 and M2 are not reduced, as occurs in some viverrids, herpestids and euplerids. The increase in size in the m2 of these feliformes should definitely be considered a convergence reflecting the adaptation of slightly more hypercarnivorous dentitions. This is why it is difficult to find

phylogenetic support for a relationship between Lophocyoniidae and the rest of Feliformia, since among the numerous dental adaptations of the latter there are none that are similar or analogous to those of Lophocyoniidae. However, these adaptations have already occurred in some Caniformia, such the living red panda *Ailurus fulgens*. Of the taxa considered in our analysis only *Protictitherium* Kretzoi, 1938, a genus that is usually considered to be a primitive hyaenid (Werdelin & Solounias 1991), does not support the previous arguments. In fact, a relationship of this genus with Lophocyoniidae is reasonably supported in our analysis (Fig. 4). Derived characters shared between *Izmirictis* and *Protictitherium* occur in the morphology of the anterior premolars (P3 and p4) and in both carnassials, with the m1 of *Izmirictis* closely resembling that of *Protictitherium crassum*. In contrast, the upper molars and m2 of *Protictitherium* are reduced; in fact, a more advanced reduction would characterize most of the more modern hyaenids. Only the genera *Ictitherium* Wagner, 1848 and *Plioviverrops* Kretzoi, 1938 retained a moderately hypocarnivorous dentition similar to that of *Protictitherium*. Some even more recent species such as *Plioviverrops faventinus* Torre, 1988 from the lower Pliocene of the Mediterranean region have given rise to morphologies with strong development of the m2, and molarization of the premolars, but never reaching the degree of specialization seen in Lophocyoniidae. In addition, all of these forms are considerably younger than the cladogenesis of the group, which occurred during the lower–middle Miocene (Fig. 5). Thus, in the present state of our knowledge, a sister group relation between Lophocyoniidae and Hyaenidae could be proposed, at least as a working hypothesis. *Protictitherium* appears in Western Europe at the end of the lower Miocene (MN4) and its range extends to the upper Miocene (MN13) (Fig. 5). It is, therefore, somewhat younger than *Izmirictis*, and contemporaneous with other lophocyoniids, the temporal range of which extends to the end of the middle Miocene (MN7/8) (Schmidt-Kittler 1983; Fejfar & Schmidt-Kittler 1984; Fejfar *et al.* 1987, 1997; Koufos *et al.* 1995; Morales *et al.* 2015). The relationships of the Lophocyoniidae and *Protictitherium* to other hypocarnivorous Feliformia are less well supported. *Kichechia zamanae* Savage, 1965, is close to the advanced Lophocyoniidae in the morphology of the P4. It is characterized by a short metastyle and paracone that are well separated from the protocone. The m1 shows a low protoconid and a talonid/trigonid of the same size, which is relatively similar to Lophocyoniidae. However, although the premolars are robust, morphologically they are simple without signs of molarization. *Kichechia zamanae* has been related to the bunodont

viverrids, such as Paradoxurinae (Morales & Pickford 2011), which in a certain way show an opposite trend to Lophocyoniidae. *Legetetia nandii* Schmidt-Kittler, 1987 shares with Lophocyoniinae a great development of m2 and M2 and, as with *Kichechia*, it shares some similarities in the morphology of the P4 and m1. Nevertheless, the premolars are gracile and sectorial, which is far removed from the complexity present in the Lophocyoniidae.

The morphological similarity between *Protictitherium* and *Herpestides* is evident and has served to establish a possible origin of the Hyaenidae from this basal form (Beaumont 1967). Although other authors have suggested a relationship between *Herpestides* and Viverridae (Hunt 1991), in our cladogram it appears to be associated with the extant *Hemigalus derbyanus* and *Viverra tangalunga* in accordance with this idea, but the relationship is weakly supported. It is evident that the basal record of the non-feloid feliforms from the lower Miocene is still poorly understood and needs an in-depth review. Probably for a short period of time, there was a great expansion of these forms from Asia that colonized Europe and Africa independently (Fig. 5). Within this first radiation it is difficult to recognize the present-day families. The case of Lophocyoniidae is paradigmatic, but the same occurs with Percrocutidae Werdelin & Solounias, 1991 and Barbourfelidae Schultz, Schultz & Martin, 1970.

Insights into the diet of *Izmirictis*

From an evolutionary point of view, the tendency described in *Izmirictis cani* to develop new crests and acquire more pronounced lophodonty may be understood as an adaptation towards increased herbivory. Although some of the enamel surfaces of *Izmirictis cani* examined at high magnification through scanning electron microscopy present alteration (probably due to the effect of taphonomic processes as a result of sedimentary transport of the teeth), it is worth noting the existence of a pattern of tooth microwear which corresponds to a high frequency of small subcircular pits and long striations, with a preferred orientation of the latter, which is typical of plant-eating species and differs from that found in classical (obligate) carnivorous mammals (Van Valkenburgh *et al.* 1990). This pattern is somewhat comparable to that seen in *Sivanasua moravica* as described by Fejfar & Schmidt-Kittler (1984). Because dental microwear provides some of the best evidence of tooth use and diet in extinct species (DeMiguel *et al.* 2008), we can presume, therefore, that the pronounced lophodonty present in *Izmirictis cani* is connected to an

herbivorous feeding habit. This suggestion needs to be further tested, however, and investigated by studies relying primarily on dental microwear in order to offer more understanding and insight into such an outstanding dietary transformation.

Conclusions

New fossils from the early Miocene locality of Sabuncubeli (Turkey) are attributable to a new genus and species, *Izmirictis cani*, which is included in the Feliformia family Lophocyonidae (new rank). The systematic relationships of this group with respect to other Feliformia is obscure, but the new species shows a greater proximity to primitive members of Hyaenidae than to the extant Viverridae. *Izmirictis cani* is the oldest known species of Lophocyonidae and is the first record in Anatolia. Therefore, it can be considered a link between Lophocyonidae and the other Feliformia, in particular Hyaenidae. Dental microwear analysis indicates that the pronounced lophodonty present in *Izmirictis cani* could be connected to a herbivorous feeding habit.

Acknowledgements

We thank Hans de Bruijn (Utrecht University) and Oldrich Fejfar (Charles University in Prague) for providing casts of some lophocyonid specimens from the Aliveri and Rothenstein localities, respectively. Thanks to Susana Fraile (Museo Nacional de Ciencias Naturales, CSIC), Marta March (Institut Català de Paleontologia Miquel Crusafont), Pip Brewer (Natural History Museum, London) and Christine Argot (Muséum national d'Histoire naturelle) for access to comparative material in their care. The Spanish Research Project CGL2015-68333-P (MINECO/FEDER-UE) and the Research Groups CSIC 641538 and CAM-UCM 910607 funded this research. We also thank the AEI/FEDER EU (CGL2016-76431-P) for support. Serdar Mayda and Tanyu Kaya were funded by EGE University Research Grants 2004/BIL/020, 2005/TTM/001, 2016/TTM/001 and 2016/TTM/002, and 2015/Fen/17 and the TUBITAK Research Grant YDABAG 102Y045. The support of the DST-NFR Centre of Excellence in Palaeosciences (CoE-Pal) towards this research for Alberto Valenciano (COE2018-09POST) is hereby acknowledged. Opinions expressed and conclusions arrived at are those of the authors and are not necessarily to be attributed to the CoE. Special thanks to Martin Pickford for improving the

English. We are also indebted to the Editors-in-Chief P. Barret and P. D. Taylor and two anonymous reviewer for their useful comments and suggestions, which improved the original manuscript.

Supplementary material

Supplementary material for this article can be accessed at: <http://dx.doi.org/10.1080/14772019.2018.1529000>.

ORCID

Jorge Morales  <http://orcid.org/0000-0001-5170-5754>

Serdar Mayda  <http://orcid.org/0000-0001-5432-3559>

Alberto Valenciano  <http://orcid.org/0000-0003-1633-2248>

Daniel DeMiguel  <http://orcid.org/0000-0001-6138-7227>

References

- Beaumont, G. de.** 1967. Observations sur les Herpestinae (Viverridae, Carnivora) de l'Oligocène supérieur avec quelques remarques sur des Hyaenidae du Néogène. *Archives des Sciences, Genève*, **20**, 79–108.
- Blainville, H.** 1842. *Ostéographie ou description iconographique comparée du squelette et du système dentaire des cinq classes d'animaux vertèbres récents et fossils pour servir de base à la zoologie et à la géologie. Mammifères Carnassiers: Des Mustelas (G Mustela)*. J. B. Baillière, Paris, 100 pp.
- Bowdich, T. E.** 1821. *An analysis of the natural classifications of Mammalia, for the use of students and travellers*. J. Smith, Paris, 115 pp.
- Bruijn, H. de., Mayda, S., Hoek Ostende, L. W. van den., Kaya, T. & Saraç, G.** 2006. Small mammals from the Early Miocene of Sabuncubeli (Manisa, S. W. Anatolia, Turkey). *Beiträge zur Paläontologie*, **30**, 57–87.
- Crusafont-Pairó, M.** 1959. Trouvaille en Espagne du plus ancien Procyonidé d'Eurasie. *Annales de Paléontologie*, **45**, 127–140.
- DeMiguel, D., Fortelius, M., Azanza, B. & Morales, J.** 2008. Ancestral feeding state of ruminants reconsidered: earliest grazing adaptation claims a mixed condition for Cervidae. *BMC Evolutionary Biology*, **8**, 1–13.
- Depéret, C.** 1892. Les faunes de mammifères de la Grive Saint-Alban. *Archives du Muséum d'Histoire Naturelle de Lyon*, **5**, 32–96.
- Fejfar, O. & Schmidt-Kittler, N.** 1984. *Sivanasua* und *Euboictis* n. gen. – zwei pflanzenfressende Schleichkatzen vor laufer (Viverridae, Carnivora, Mammalia) im europäischen Untermiozan. *Mainzer Geowissenschaftliche Mitteilungen*, **13**, 49–72.
- Fejfar, O., Schmidt-Kittler, N. & Rummel, M.** 1997. *Sivanasua viverroides* (Schlosser, 1916) from the Lower Miocene fissure filling Rothenstein 1/13/. *Münchner*

- Geowissenschaftliche Abhandlungen Reihe A Geologie und Paläontologie*, **34**, 93–110.
- Fejfar O., Schmidt-Kittler N. & Zacharov, M.** 1987. *Lophocyon carpathicus* nov. gen. nov. sp. aus dem Jungtertiär der Ostslowakei und eine neue unterfamilie derschleikatzen (Viverridae). *Palaeontographica*, **199**, 1–22.
- Flynn, J. J. & Galiano, H.** 1982. Phylogeny of Early Tertiary Carnivora, with a description of a new species of *Protictis* from the Middle Eocene of northwestern Wyoming. *American Museum Novitates*, **2725**, 1–64.
- Fraile, S.** 2017. *Protictitherium crassum*, la pequeña hiena de 9 millones de años del Cerro de los Batallones. Pp. 216–232 in J. Morales (ed.) *La colina de los Tigres Dientes de sable. Los yacimientos miocenos del Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid)*. Museo Arqueológico Regional, Comunidad de Madrid, Spain.
- Geoffroy Saint-Hilaire, E. & Cuvier, F.** 1825. Panda. Pp. 1–3 in E. Geoffroy Saint-Hilaire & F. Cuvier (eds) *Histoire naturelle des Mammifères, avec des figures originales, coloriées, dessinées d'après des animaux vivans*, 3 (50). A. Belin, Paris.
- Gingerich, P. D. & Sahni, A.** 1984. Dentition of *Sivaladapis nagrii* (Adapidae) from the Late Miocene of India. *International Journal of Primatology*, **5**, 63–79.
- Gingerich, P. D. & Winkler, D. A.** 1985. Systematics of Paleocene Viverravidae (Mammalia, Carnivora) in the Bighorn Basin and Clark's Fork Basin, Wyoming. *Contributions from the Museum of Paleontology, The University of Michigan*, **27**, 87–128.
- Ginsburg, L. & Morales J.** 1999. Le genre *Sivanasua* (Lophocyoninae, Hyaenodontidae, Creodonta, Mammalia). *Estudios Geológicos*, **55**, 173–180.
- Gray, J. E.** 1832. On the family of Viverridae and its generic sub-divisions, with an enumeration of the species of several new ones. *Proceedings of the Committee of Science and Correspondence of the Zoological Society of London*, 63–68.
- Gray, J. E.** 1837. On a new species of paradoxure (*Paradoxurus derbianus*) with remarks on some Mammalia recently purchased by the British Museum, and characters of the new species. *Proceedings of the Zoological Society of London*, **5**, 67–68.
- Hilgen, F. J., Lourens, L. J. & Dam, J. A. van.** With contributions by **Beu, A. G., Boyes, A. F., Cooper, R. A., Krijgsman, W., Ogg, J. G., Piller, W. E. & Wilson, D. S.** 2012. The Neogene Period. Pp. 923–978. In Gradstein F.M., Ogg J. G., Schmitz M. D. & Ogg G. M. (eds) *The geologic time scale*. Elsevier, Amsterdam.
- Hoek Ostende, L. W. van den., Mayda, S., Oliver, A., Madern, A., Hernández-Ballarín, V & Peláez-Campomanes, P.** 2015. Aliveri revisited, a biogeographical appraisal of the early Miocene mammals from the eastern Mediterranean. *Palaeobiodiversity and Palaeoenvironments*, **95**, 271–284.
- Hunt, R. M.** 1991. Evolution of the Aeluroid Carnivora. Viverrid affinities of the Miocene carnivoran *Herpestides*. *American Museum Novitates*, **3023**, 1–34.
- Kaya, O., Ünay, E., Göktaş, F. & Saraç, G.** 2007. Early Miocene stratigraphy of central west Anatolia, Turkey: implications for the tectonic evolution of the Eastern Aegean area. *Geological Journal*, **42**, 85–109.
- Koufos, G. D.** 2011. The Miocene carnivore assemblage of Greece. *Estudios Geológicos*, **67**, 291–320.
- Koufos, G. D., Bonis, L.de & Sen, S.** 1995. *Lophocyon paraskevaidisi*, a new viverrid (Carnivora, Mammalia) from the Middle Miocene of Chios Island, Greece. *Geobios*, **28**, 511–523.
- Kretzoi, M.** 1938. Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfauna. *Annales Musei Nationalis Hungarici*, **3**, 88–157.
- Kretzoi, M.** 1945. Bemerkungen über das Raubtiersystem. *Annales Historico-Naturales Musei Nationalis Hungarici*, **38**, 59–83.
- Krijgsman, W., Duermeijer, C. E., Langereis, C. G., Bruijn, H. de., Saraç, G. & Andriessen, P. A. M.** 1996. Magnetic polarity stratigraphy of late Oligocene to middle Miocene mammal-bearing continental deposits in Central Anatolia (Turkey). *Newsletters on Stratigraphy*, **34**, 13–29.
- Mayda, S.** 2004. Early Miocene fauna from Western Anatolia (Sabuncubeli-Manisa). Pp. 330–332 in *5th International Symposium on Eastern Mediterranean Geology*. Volume 1. Thessaloniki, Greece.
- Mayda, S.** 2010. The Early Miocene Carnivores from Sabuncubeli, Turkey. *Geologica Balcanica*, **39**, 245–246.
- Meehan, T. J. & Wilson, R. W.** 2002. New viverravids from the Torrejonian (middle Paleocene) of Kutz Canyon, New Mexico and the oldest skull of the order Carnivora. *Journal of Paleontology*, **76**, 1091–1101.
- Morales, J. & Pickford, M.** 2011. A new paradoxurine carnivore from the Late Miocene Siwaliks of India and a review of the bunodont viverrids of Africa. *Geobios*, **44**, 271–277.
- Morales, J., Cantalapiedra, J. L., Valenciano, A., Hontecillas, D., Fraile, S., García-Yelo, B. A., Montoya, P. & Abella, J.** 2015. The fossil record of the Neogene carnivore mammals from Spain. *Palaeobiodiversity and Palaeoenvironments*, **95**, 373–386.
- Morlo, M., Gunnell, G. F. & Nagel, D.** 2010. Chapter 10. Ecomorphological analysis of carnivore guilds in the Eocene through Miocene of Laurasia. Pp. 269–310 in A. Goswami & A. Friscia (eds) *New contributions to the natural history of Carnivora*. Cambridge University Press, Cambridge, UK.
- Peppe, D. J., McNulty, K. P., Cote, S. M., Harcourt-Smith, W. E. H., Dunsworth, H. M. & Van Couvering J. A.** 2009. Stratigraphic interpretation of the Kulu Formation (early Miocene, Rusinga Island, Kenya) and its implication for primate evolution. *Journal of Human Evolution*, **56**, 447–461.
- Pilgrim, G. E.** 1932. The fossil Carnivora of India. *Memoirs of the Geological Survey of India. Palaeontologia Indica*, **18**, 1–232.
- Savage, R.** 1965. Fossil mammals of Africa: 19. The Miocene Carnivora of East Africa. *Bulletin of the British Museum (Natural History), Geology*, **10**, 241–316.
- Schlosser, M.** 1916. Neue Funde fossiler Säugetiere in der Eichstätter Gegend. *Abhandlungen der Mathematisch-physikalischen Classe der Königlich bayerischen Akademie der Wissenschaften*, **28**, 1–78.
- Schmidt-Kittler, N.** 1983. The Mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). III. On a new species of *Sivanasua* Pilgrim, 1931 (Feliformia, Carnivora) and the phylogenetic position of this genus. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, C*, **86**, 301–318.

- Schmidt-Kittler, N.** 1987. The Carnivora (Fissipeda) from the lower Miocene of East Africa. *Palaeontographica A*, **197**, 85–126.
- Schmidt-Kittler, N.** 1999. Subfamily Lophocyoninae. Pp. 149–153 in G. Rössner & K. Heissig (eds) *The Miocene mammals of Europe*. Verlag Dr. Friedrich Pfeil, Munich, Germany.
- Schultz, C. B., Schultz, M. R. & Martin, L. D.** 1970. A new tribe of saber-toothed cats (Barbourofelini) from the Pliocene of North America. *Bulletin of the University of Nebraska State Museum*, **9**, 1–31.
- Swofford, D. L.** 2002. *PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4*. Sinauer Associates, Sunderland, MA.
- Torre, D.** 1988. *Plioviverrops faventinus* n. sp. a new carnivore of the late Messinian age. *Bolletino Della Societa Paleontologica Italiana*, **28**, 323–327.
- Van Valkenburgh, B., Teaford, M. F. & Walker, A.** 1990. Molar microwear and diet in large carnivores: inferences concerning diet in the sabretooth cat, *Smilodon fatalis*. *Journal of Zoology*, **222**, 319–340.
- Viret, J.** 1929. Les faunes de Mammifères de l'Oligocène supérieur de la Limagne bourbonnaise. *Annales de l'Université de Lyon, Nouvelle série 1*, **47**, 1–329.
- Wagner, A.** 1848. Urveltliche Säugethiere-Oberreste aus Griechenland. *Abhandlungen der Bayerischen Akademie der Wissenschaften*, **5**, 335–378.
- Werdelin, L.** 2010. Chronology of Neogene mammal localities. Pp. 27–43 in L. Werdelin & W. J. Sanders (eds) *Cenozoic mammals of Africa*. University of California Press, Berkeley.
- Werdelin, L. & Solounias, N.** 1991. The Hyaenidae: taxonomy, systematics and evolution. *Fossils and Strata*, **30**, 1–104.