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Marie Meyer

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LES CARNIVORES DU PLIOCENE TERMINAL D'ARMENIE : ANATOMIE COMPAREE ET IDENTIFICATION

THESE D'EXERCICE

pour obtenir le titre de
DOCTEUR VETERINAIRE

DIPLOME D'ETAT

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devant l'Université Paul-Sabatier de Toulouse*

par

MEYER Marie, Albertine, Madeleine

Directeur de thèse : M. Giovanni MOGICATO

JURY

PRESIDENTE :
Mme Caroline LACROUX

Professeure à l'Ecole Nationale Vétérinaire de TOULOUSE

ASSESEURS :
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M. Benjamin CARTIAUX

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Abbreviations

- BL** basal length of the cranium (basion - prosthion)
- C/c** upper/lower canine
- c1 post - m3 L** length between the posterior border of the alveolus of the canine and the posterior border of the m3
- CBL** condylobasal length of the cranium (prosthion - occipital condyles)
- Ect** frontal breadth (ectorbitale - ectorbitale)
- Ent** least breadth between the orbits (entorbitale - entorbitale)
- Eu** greatest neurocranium breadth (euryon - euryon)
- FMB** greatest breadth of the foramen magnum
- FMH** height of the foramen magnum (basion - opisthion)
- GBPP** greatest breadth of the bases of the paraoccipital processes
- GDAB** greatest diameter of the auditory bulla
- GMB** greatest mastoid breadth (otion - otion)
- I/i** upper/lower incisor
- IGS** Institute of Geological Sciences of the National Academy of Sciences of Republic of Armenia
- L** antero-posterior length
- LBS** least breadth of skull (breadth at the postorbital constriction)
- LMR** length of the molar row (m1 - m3 or M1 - M2)
- NcL** neurocranium length (prosthion - frontal midpoint)
- M/m** upper/lower molar
- Mm1B** mandibular corpus breadth below m1
- Mm1H** mandibular corpus height behind m1
- Mp2-p3H** mandibular corpus height between p2 and p3
- MJSN** Jurassica Museum (former Musée Jurassien Sciences Naturelles)
- NHB** Naturhistorisches Museum Basel
- OTH** height of the occipital triangle (Akrikranion - Basion)
- P/p** upper/lower premolar
- p1 - p4 L** length of the premolar row starting from p1
- P1 - M2 L** length of cheektooth row starting from P1
- p1 - m3 L** length of cheektooth row starting from p1
- p2 - p4** length of the premolar row starting from p2
- p2 - m3 L** length of cheektooth row starting from p2
- SH** skull height (with sagittal crest)
- SL** snout length (oral border of orbits - prosthion)
- taL** length of m1 talonid
- taW** width of m1 talonid
- TL** total length of the cranium (akrokranium - prosthion)
- trL** length of m1 trigonid
- W** labio-lingual width.

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Résumé français

Jradzor est un site de fouilles archéologiques situé en Arménie, au pied de la province volcanique de Gegham, dont l'âge a été estimé à 4.3 – 3.03 millions d'années. Son exploration a débuté dans les années 2000, et une faune très riche y a été découverte - poissons, reptiles, mammifères -, ce qui revêt une importance capitale dans la compréhension des échanges ayant eu lieu en Caucase du Sud à cette période. En effet, à l'heure actuelle, et en raison des conditions climatiques de l'époque (région volcanique active), très peu de fossiles du Pliocène Terminal ont été découverts dans cette zone.

Si une partie des fossiles du site a déjà fait l'objet d'études et a pu être identifiée, ce n'est pas le cas des spécimens de carnivores, dont l'âge a été estimé à 3.3 +/- 0.3 millions d'années. Cette thèse est dédiée à leur description et à leur identification, à partir d'un travail bibliographique et d'ostéologie comparée. La terminologie dentaire, les spécimens étudiés ainsi que les méthodes de mesure utilisées sont décrits dans la partie **Material and methods**.

A l'issue de sept semaines de travail au sein du JURASSICA Museum de Porrentruy, 5 espèces ont pu être identifiées : 3 d'hyènes (*Chasmaporthetes lunensis*, Cf. *Pliocrocota perrieri* et *Miohyaenotherium* sp.) et 2 de canidés (*Nyctereutes tingi* et *Nyctereutes* cf. *vulpinus*). Une partie du matériel n'a pas pu être identifiée par manque de critères de diagnose.

Famille Hyaenidae – Gray, 1821

Genre *Chasmaporthetes* – Hay, 1921

***Chasmaporthetes lunensis* – Del Campana, 1914**

Description : Le matériel étudié comporte deux héli-mandibules appartenant au même individu. Les spécimens sont bien conservés ; il ne manque que les deux premières incisives droites et la première incisive gauche. Les incisives et les canines ont une racine unique. i2 et i3 sont asymétriques et comportent un grand cuspide principal et une cuspide postérieure. c1 présente des crêtes mésolinguales et postérieures. Les prémolaires et les molaires ont deux racines. Le protoconide des prémolaires est tranchant. En plus du protoconide, p2, p3 et p4 portent deux cuspides accessoires (un paraconide et un hypoconide), séparés du protoconide par une encoche. Sur p2, le paraconide est petit tandis que l'hypoconide est développé ; sur p3 le paraconide est légèrement plus petit, tandis que sur p4 les deux sont de taille

équivalente. En plus de ses 2 cuspides accessoires, p4 comporte un cingulum postérieur et un hypoconulide. Sur m1, le métaconide est vestigial, tandis que le paraconide et le protoconide sont bien développés. Le talonide est réduit : l'hypoconulide, bien développé, semble fusionné avec l'hypoconide et l'entoconide. Le talonide et le trigonide sont séparés par une entaille.

Discussion : d'après la taille de la mandibule, la formule dentaire et la forme des dents, ce spécimen appartient à la famille Hyaenidae (Thenius, 1989). A partir de différents critères d'identification, la mandibule de Jradzor a pu être distinguée des genres *Crocota* (Crégut-Bonnoure, 1996a) et *Pachycrocota* (Werdelin & Peigné, 2010) en se basant sur la taille du paraconide sur p2 et p3, du genre *Hyaena* d'après la morphologie de m1 (Crégut-Bonnoure, 1996a) et de p4 (Werdelin & Peigné, 2010), et de *Pliocrocota perrieri* d'après la morphologie des prémolaires (Vinuesa et al (2014) ; Werdelin & Solounias (1991)). En contrepartie, les critères d'identification du genre *Chasmaporthetes* tels que décrits par Kurtén & Werdelin (1988) permettent d'affirmer que la mandibule appartient à ce genre-là. Finalement, et d'après des critères morphologiques et morphométriques, les spécimens de Jradzor diffèrent de toutes les espèces de *Chasmaporthetes* du Pliocène Terminal exceptée une : *C. lunensis* (Werdelin & Solounias (1991), Kurtén & Werdelin (1988)).

Genre *Pliocrocota* – Kretzoi, 1938

Cf *Pliocrocota perrieri* – Croizet & Jobert, 1828

Description : Le matériel étudié comporte une m1 droite et une p4 droite biradiculées. Sur p4, on distingue un protoconide développé, un petit paraconide et un hypoconide bien développé. Les cuspides accessoires sont séparées du protoconide par une encoche. Sur sa face postérieure, p4 comporte un cingulum développé en partie linguale. Sur la carnassière inférieure, le paraconide et le protoconide sont de taille équivalente et bien développés, tandis que le métaconide est bien individualisé mais de petite taille. Sur sa face antérieure et en partie labiale se trouve un cingulum. Le talonide est réduit et comporte un hypoconide bien développé, tandis que l'hypoconulide et l'entoconide semblent fusionnés en une crête.

Discussion : d'après leur taille et leur forme, ces spécimens appartiennent à la famille Hyaenidae (Thenius, 1989). La taille du métaconide exclut le genre *Hyaena* (Crégut-Bonnoure, 1996a). Le genre *Chasmaporthetes* se distingue également des spécimens étudiés de par la présence du métaconide et la morphologie de p4 (Kurtén

& Werdelin, 1988). Le talonide bien développé sur m1 exclut également le genre *Crocota* (Werdelin & Lewis (2008), et *P. brevirostris* peut être écarté en raison de sa taille. Finalement et d'après des données morphologiques et morphométriques, ces dents appartiennent certainement à *P. perrieri* (Viret (1954), Kurtén & Poulianos (1981), Sotnikova (1989), Tseng et al. (2015), Tseng et al. (2016), Werdelin & Solounias (1991), Vinuesa et al. (2014)).

Genre *Miohyaenotherium* – Semenov, 1989

***Miohyaenotherium* sp. – Semenov, 1989**

Description : Le matériel étudié comporte une m1 droite dont les racines sont manquantes. Le protoconide et le paraconide sont développés et séparés par une large entaille. Un cingulum est présent sur la face antéro-labiale du paraconide. Le métaconide, bien que plus petit que les cuspidés labiales, est tranchant. Le talonide est réduit mais comporte un petit hypoconide, un hypoconulide et un entoconide (aussi haut que le métaconide), reliés en une crête. Le bassin du talonide est petit.

Discussion : La forme du talonide permet d'exclure la famille Canidae (Tedford et al. 1995). En revanche, cette carnassière ressemble au troisième éco morphotype de hyènes (Vinuesa, 2018) qui inclut les genres *Ictitherium*, *Thalassictis*, *Miohyaenotherium* et *Hyaenictitherium*. Toutefois, l'écomorphotype 5 (*Metahyaena confector*, *Palinhyaena reperta*, *Belbus beaumonti* et *Ikelohyaena abronia*) ne peut pas être exclu car il ne comporte pas de description de carnassière inférieure. Parmi les genres et espèces du Pliocène et Miocène eurasiatiques, *B. beaumonti* peut être écarté en raison de sa taille (Bonis et al, 2010) et de sa morphologie (Werdelin & Solounias (1991), Koufos (2011)). *P. reperta* présente également des caractéristiques très éloignées de la carnassière de Jradzor (Werdelin, 1988). En revanche, d'après ses dimensions, cette dent appartient à l'un des genres de la tribu Hyaenotheriini (sensu Semenov, 2008) - *Hyaenotherium*, *Hyaenictitherium* et *Miohyaenotherium* - ce qui permet d'exclure les genres *Ictitherium* et *Thalassictis*. Dans cette étude, les genres *Hyaenotherium* et *Hyaenictitherium* sont considérés synonymes en raison du peu d'arguments permettant de les distinguer (Zhang et al. (2002), Andersson & Werdelin (2005), Bonis (2004, 2005), Koufos (2011)). Semenov (1989) fournit des critères de diagnose des genres *Hyaenotherium/Hyaenictitherium* et *Miohyaenotherium*, entre autres basés sur la morphologie de m1, qui permettent d'exclure l'appartenance de la carnassière de Jradzor au premier genre. De plus, ses dimensions sont proches de

celles de *M. bessarabicum* (Semenov, 1989). Ainsi, d'après des données morphologiques et morphométrique, cette carnassière appartient très certainement au genre *Miohyaenotherium*. Toutefois, la seule espèce de ce genre connue à ce jour, *M. bessarabicum*, n'a été décrite que durant le Turolien (9.0 – 5.3 Ma) (Werdelin & Solounias, 1991). Il est donc probable qu'il s'agisse d'une espèce non documentée.

Famille Canidae – Fischer von Waldheim, 1817

Genre *Nyctereutes* – Temminck, 1838

***Nyctereutes tingi* – Depéret, 1890**

Description : Le matériel étudié comporte un crâne ainsi qu'une hémimandibule droite appartenant au même individu.

Mandibule et dentition inférieure : La mandibule est bien préservée mais il lui manque la branche ascendante, les deux premières prémolaires ainsi que m3. En vue latérale, elle est légèrement incurvée et sa partie postérieure est infléchie : cette flexion est appelée « lobe subangulaire » et il s'agit de l'insertion du muscle digastrique. Le premier foramen mentionner, en partie brisé, est situé sous p1 et le deuxième, bien préservé, sous la racine antérieure de p3. La fosse massétérique s'étend jusque derrière m2. La canine, plate en face linguale, porte une crête sur sa partie antérieure. Les prémolaires et molaires ont deux racines et un protoconide bien développé. Il n'y a pas de cuspide accessoire sur p3 et p4, mais p4 porte un hypoconide et un cingulum distal. Sur m1, le trigonide est bien développé : le paraconide est petit et court, le protoconide haut et rond, et le métaconide développé. Sur le talonide, l'hypoconide est large et relié par une crête à l'entoconide, légèrement moins saillant. Cette crête sépare le bassin du talonide en deux bassins. m2, subrectangulaire, porte un cingulum antéro-labial. Le protoconide et le métaconide sont larges, hauts, bien développés, et connectés en partie antérieure par une crête basse et arrondie. Sur le talonide, l'hypoconide – bien développé – et l'entoconide – difficilement individualisable – sont reliés par une crête.

Crâne et dentition supérieure : Le crâne est bien préservé et presque complet – il manque le processus frontal de l'os zygomatique, l'os temporal, une partie de l'os nasal, la bulle tympanique droite, le condyle occipital droit ainsi que les processus jugulaires. De plus, l'os ptérygoïde est en partie brisé. Le museau est fin, les processus post-orbitaires épais et bien développés. Les crêtes émanant du bord distal des processus post-orbitaires rejoignent la crête sagittale robuste au sommet du crâne. La

crête se joint à la crête supra-occipitale, bien développée. Enfin, la boîte crânienne est incurvée. La dentition supérieure est bien préservée ; il ne manque que les deux premières prémolaires. Les incisives et les canines n'ont qu'une seule racine. I1 et I2 comportent trois cuspides : une principale et deux accessoires. Si I1 présente un axe de symétrie, ce n'est pas le cas de I2 : la cuspide latérale est plus petite que les deux autres. I3 est également asymétrique : sa cuspide principale porte une petite cuspide accessoire en partie médiale. La canine, située en partie latérale de la mandibule, est petite, tranchante, légèrement courbée, et possède une crête sur sa face postérieure. P1 ne possède qu'une seule racine et possède une cuspide unique. P2 et P3 ont deux racines et une cuspide principale bien développée. Sur P3 se trouve un cingulum distal ressemblant à une cuspide. P4 comporte deux petites racines antérieures et une grande racine postérieure. Un petit cingulum lingual part de la bordure postérieure du métastyle et rejoint la base postérieure du protocone. Il y a également un petit cingulum lingual en partie postérieure de la dent. Le protocone est petit, et séparé du paracone – haut – par une dépression antéro-linguale. Le métastyle est petit et court. Les molaires sont quant à elles triangulaires et portent un cingulum en face antéro-linguale. Sur M1, ce dernier s'épaissit lingualement en hypocone. Le métacone est plus grand que le paracone, et le protocone presque aussi grand que l'hypocone. Le métaconule est bien développé. Sur M2, le paracone et le métacone sont petits comparés au protocone. Le métaconule n'est pas développé, tandis que le paraconule l'est.

Discussion : d'après la formule dentaire et la forme du crâne, ces spécimens appartiennent à un Canidae (Pessutti et al., 2001). Parmi les genres ayant existé durant le Pliocène en Eurasie, les genres *Cuon* (Van Valkenburgh (1991), Ghezzo and Rook (2014) et *Eucyon* (Lucenti & Rook, 2020) peuvent être exclus. Tedford et al. ont publié en 1995 une matrice regroupant notamment les caractères morphologiques de *Nyctereutes*, *Canis* et *Vulpes*, les trois autres genres ayant vécu en Eurasie à cette époque. D'après cette matrice et d'autres publications, les genres *Canis* (Crégut-Bonnoure, 1996b) et *Vulpes* peuvent être écartés. De plus, la description faite par Ginsburg (1998) de *Nyctereutes* correspond parfaitement aux spécimens étudiés ; ainsi, en se basant sur des critères morphologiques, l'hémi-mandibule et le crâne appartiennent au genre *Nyctereutes*. Parmi les différentes espèces du genre, *N. procyonoides* peut être exclu de par sa taille. L'analyse de plusieurs critères morphologiques et morphométriques - développement du lobe subangulaire et rétrécissement du museau (Daguenet & Sen, 2019), caractéristiques de P4 (Lucenti (2017), Daguenet & Sen (2019), Depéret (1980), Tedford et al. (1991), Tedford et al.

(2009)) et des molaires supérieures (Daguenet & Sen, 2019) – permet d'exclure avec certitude les espèces *N. sinensis*, *N. vulpinus* et *N. megamastoides*. Toujours d'après la matrice de caractères établie par Daguenet & Sen (2019), il semblerait que la P4 du crâne arménien possède des caractéristiques de *N. tingi* et de *N. donnezani*. Toutefois, les caractéristiques morphologiques et morphométriques des molaires supérieures (Daguenet & Sen, 2019), et inférieures (Tedford et al. (1991), Daguenet & Sen (2019)) permettent d'affirmer que le crâne et la mandibule appartiennent à *N. tingi*.

Nyctereutes cf vulpinus

Description : Le matériel étudié comporte une P3 droite, une P4 droite et une M1 droite. Les prémolaires ont deux racines, mais l'antérieure n'est plus présente. La cuspide principale de P3 est tranchante et porte une cuspide accessoire postérieure ainsi qu'un cingulum postérieur. Le paracone de P4 est court et tranchant, et séparé du métastyle, long et tranchant, par une entaille. Le protocone est coupant mais petit, et situé sur la face antéro-linguale du paracone. La carnassière supérieure a trois racines et est de forme sub-triangulaire. Le paracone et le métacone sont de taille similaire. En face postéro-linguale, un cingulum s'épaissit en hypocone. Le métaconule est presque aussi développé que le protocone, tandis que le paracone est vestigial.

Discussion : étant donné le peu de matériel disponible, il est difficile d'identifier ces spécimens avec certitude, mais ils présentent de nombreuses similitudes avec *Nyctereutes vulpinus* de Saint-Vallier. Pour commencer, M1 présente les caractéristiques typiques du genre *Nyctereutes* (Viret (1954), Soria & Aguirre (1976), Ginsburg (1998), Werdelin & Peigné (2010)). La taille des spécimens diffère toutefois de celle de *N. procyonoides*. La morphologie de P4 quant à elle permet d'exclure *N. sinensis* (Lucenti, 2017) et *N. donnezani* (Depéret, 1890), et celle de M1 permet d'écarter *N. megamastoides* (Daguenet & Sen, 2019). Finalement et d'après les caractéristiques morphométriques et morphologiques décrites par Daguenet & Sen (2019), Lucenti (2017), et Argent (2004), le matériel découvert à Jradzor pourrait appartenir à *N. vulpinus*, bien qu'ils ne soient pas parfaitement identiques.

Canidae indet.

Description : Le matériel étudié comprend une i1 droite, une i2 droite, une P2 droite ou une p2 gauche, ainsi qu'une P2 gauche ou une p2 droite. Les incisives n'ont

qu'une seule racine. i2 est asymétrique : sa cuspide principale est bordée d'une cuspide latérale. Les prémolaires ont deux racines, leur cuspide principale est tranchante, et possède une cuspide tranchante.

Discussion : en raison du faible nombre de critères de diagnose basés sur les incisives et les prémolaires, il est impossible d'identifier ces spécimens. Ils pourraient appartenir au genre *Nyctereutes*, *Vulpes*, *Canis* ou *Eucyon*.

Considérations stratigraphiques, biogéographiques et écologiques : La faune du Pliocène terminal de Jradzor comprend 2 grandes hyènes, *Chasmaporthetes lunensis* et Cf *Pliocrocuta perrieri*, une petite hyène du genre *Miohyaenotherium*, 2 chiens viverrins *Nyctereutes tingi* et *Nyctereutes cf vulpinus*, et un Canidae indéterminé.

C. lunensis et *P. perrieri* étaient répandues en Eurasie durant le Pliocène terminal et sont toutes deux documentées dans des sites proches de Jradzor en Ukraine et en Turquie. Il est également courant de les trouver ensemble dans des localités du Villafranchien (Koufos, 1993). Ces dernières avaient des habitudes alimentaires différentes : si *C. lunensis* chassait pour se nourrir, (Kurtén & Werdelin (1988), Anton et al. (2006)), *P. perrieri* était un charognard. (Werdelin & Solounias (1996)). Toutefois et en raison des similarités en taille et des adaptations au charonnage présentes au sein des deux espèces, une compétition alimentaire ne peut être exclue (Anton et al., 2006).

Le genre *Miohyaenotherium* n'est quant à lui pas documenté après le Turolian (MN 11 – 12) en Ukraine, Moldavie et Georgie (Werdelin & Solounias, 1991). De taille relativement petite, il est peu probable que les espèces de ce genre se nourrissent des mêmes proies que les grandes hyènes, ce qui exclut une compétition alimentaire.

En ce qui concerne les deux canidés, *N. tingi* et *N. vulpinus* sont présents en Eurasie depuis le début du Pliocène, et sont aujourd'hui représentés par l'unique espèce *N. procyonoides* en Asie (Lucenti, 2018). Si *N. tingi* a été documenté dans plusieurs localités, l'espèce *N. vulpinus* a été créée spécialement pour les spécimens trouvés à Saint Vallier et n'a pas été découverte ailleurs ; il est donc étonnant de découvrir ces deux espèces à Jradzor. Une analyse des ratios molaires suggère que *N. tingi* et *N. cf vulpinus* avaient des régimes alimentaires relativement omnivores (Lucenti (2018), Asahara & Takai (2017)). La coexistence de deux espèces de *Nyctereutes* avec des habitudes alimentaires similaires à Jradzor est remarquable.

Introduction

Definitions

MN zones (Mammal Neogene zones): The MN zones are a system of biostratigraphic zones used to characterize periods of the **Neogene** (Pliocene and Miocene) (Figure 1). Each zone is associated with a particular fossil assemblage that is characteristic of that period; thus, each zone is defined through a well-known locality, that other sites can be correlated with. These zones enable geologists and paleontologists to correlate rock strata and date geological formations using fossils as temporal markers. There are seventeen consecutive zones: MN1 is the earliest zone, and MN18 is the most recent one (MN 7 and MN8 have been joined into MN 7/8).

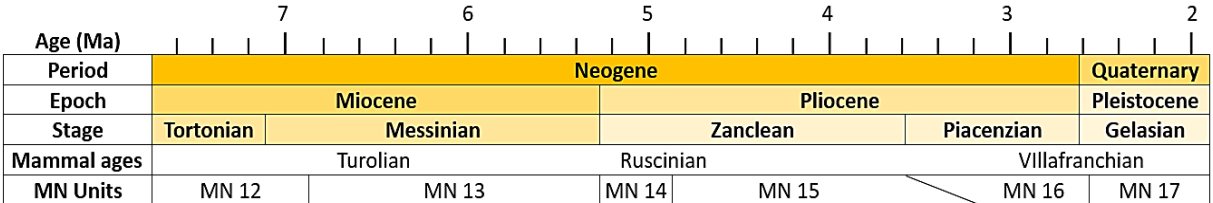


Figure 1 - Age limits of the MN-zones (Raffi et al. (2020))

Horizon: A horizon is a stratigraphic unit that represents a specific time period and is typically characterized by a distinct geological features and fossil assemblages.

Context

Remark: At this day, there is little data available in the literature concerning the Jradzor locality, that is studied in this thesis. The following introduction is based on an article published in 2023 that aims to study the paleoenvironmental evolution and biotic record of the locality (Lazarev et al. (2023)).

The contemporary Eurasian ecosystem has primarily been shaped by the faunal exchanges that took place during the Cenozoic era among Europe, Asia, Africa, and America. The South Caucasus, encompassing the present-day territories of Armenia, Georgia, Azerbaijan, and the easternmost part of Turkey, constitutes a mountainous region that acts as a biogeographic corridor connecting Asia, Europe, and Africa. According to the available studies, this corridor played a crucial role as a dispersal route for different vertebrate groups (including humans) during the late Cenozoic

(Paleogene – Neogene) period. But, while Late Miocene fossils records from this area have been discovered and studied, it is not the case for the Pliocene epoch (5.3 - 2.6 Ma). Indeed, during the late Pliocene, the region was a highly active volcanic region, and therefore, its geological records mainly consist of volcanic and volcanoclastic deposits. These deposits being formed by catastrophic and brutal events, they become quickly eroded and don't preserve vertebrate fossils very well. Therefore, the discovery of an excavation site containing fossils dating back to the late Pliocene in this region, such as the Jradzor locality, is a goldmine in the field of paleontology.

Jradzor is located at the foot of the Gegham volcanic province, in Armenia. (Figure 2). The excavation site is 57m thick and comprises 19 fossiliferous horizons with at least 48 identified vertebrate taxa. It is situated in an active diatomite mine, which was discovered in the 1960s and explored in the 2000s. Fish, reptiles and mammal fossils were discovered before (studies were published in 2008, 2013 and 2020), but its carnivora fauna has not yet been studied. Through a combination of $^{40}\text{Ar}/^{39}\text{Ar}$, magnetostratigraphic and biochronological dating methods, Lazarev et al. (2023) date the Jradzor locality between 4.3 - 3.03 Ma and/or as MN15 zone. When compared to other fossil collections in the area, Jradzor stands out by having the most diverse range of vertebrate species, including those from both aquatic and terrestrial environments; it plays a significant role in completing the MN15 mammalian zone in the South Caucasus biotic record.

The only horizon with large mammals' fauna is the JZ7 horizon (3.3 +/- 0.3 Ma) and it resides at the base of a lahar (a type of volcanic mudflow or debris flow, typically composed of water, volcanic ash, and debris, which can flow rapidly down the slopes of a volcano during or after an eruption).

This study is dedicated to the description and identification of the carnivore assemblage of the JZ7 horizon, that has never been studied before.



Figure 2 - Geographic position of the locality Jradzor (geosociety.org)

1. Material and methods

1.1. Referred specimens and comparative specimens

This study is based on anatomic and taxonomic analysis of the late Pliocene Carnivora from Jradzor, Armenia. The referred material, including 14 specimens, is stored in the collections of the IGS, Armenia. The actual and fossil specimens used for the comparative study are stored in the collections of the Jurassica Museum and the Naturhistorisches Museum of Basel, Switzerland (Table 1). The comparative morphological analysis – observation, measurement and comparison of anatomical characters – is completed with the relevant literature on Pliocene Carnivores. The pictures of the studied specimens were taken with a professional photographer, and then edited on photoshop.

Table 1 - Actual and fossil specimens used for the comparative analysis

Family		Species	Collection number			
			IGS	MJSN	NMB	
Hyaenidae	Referred material	<i>Chasmaporthetes lunensis</i>	JRD - 20/04 JRD - 20/05			
		<i>Cf Pliocrocuta perrieri</i>	JRD - 20/06			
		<i>Miohyaenotherium sp</i>	JRD - 19/04			
	Actuals	<i>Crocuta crocuta</i>		MJSN - OS 66	NMB - q156	
		<i>Hyaena hyaena</i>			NMB - 13939	
	Fossils	<i>Pachycrocuta brevirostris</i>			NMB - VA1940	
Canidae	Referred material	<i>Nyctereutes tingi</i>	JRD - 20/03 JRD - 19/03			
		<i>Cf Nyctereutes vulpinus</i>	JRD - 21/01			
		<i>Canidae indet</i>	JRD - 19/93 JRD - 20/24 JRD - 19/5 JRD - 19/94			
	Actuals	<i>Canis aureus</i>			NMB - C1568	
		<i>Canis lupus</i>		MJSN - OS 822	NMB - C2280	
		<i>Cuon alpinus</i>			NMB - 5432	
		<i>Nyctereutes procyonoides</i>			NMB - 8613	
		<i>Vulpes corsac</i>			NMB - C3901	
		<i>Vulpes lagopus</i>			NMB - C1934	
		<i>Vulpes vulpes</i>		MJSN - OS 876 MJSN - OS 887	NMB - C4100	
	Fossils	<i>Nyctereutes donnezani</i>			NMB - Rss45	
		<i>Nyctereutes megamastoides</i>			NMB - Se1779	
		<i>Nyctereutes vulpinus</i>			NMB - Se1779 NMB - StV764	
	Felidae	Actuals	<i>Lynx lynx</i>		MJSN - OS 10	
	Mustelidae	Actuals	<i>Martes foina</i>		MJSN - OS 875	
Procyonidae	Actuals	<i>Procyon lotor</i>		MJSN - OS 838		

1.2. Measurements and statistical analyses

This study follows the dental terminology of Tedford et al. 2009 for the P4 and for the molars (Figure 3) and Ginsburg (1999) for the other premolars (Figure 4). The dental measurement (Length x Width) is based on the Gingerich and Deutsch (1989) method, while the skull and mandible measurement follows Von Den Driesch (1976). Measurements were taken with an electronic digital caliper, and are given in the text and in the tables in millimeters to the nearest 0.1 mm.

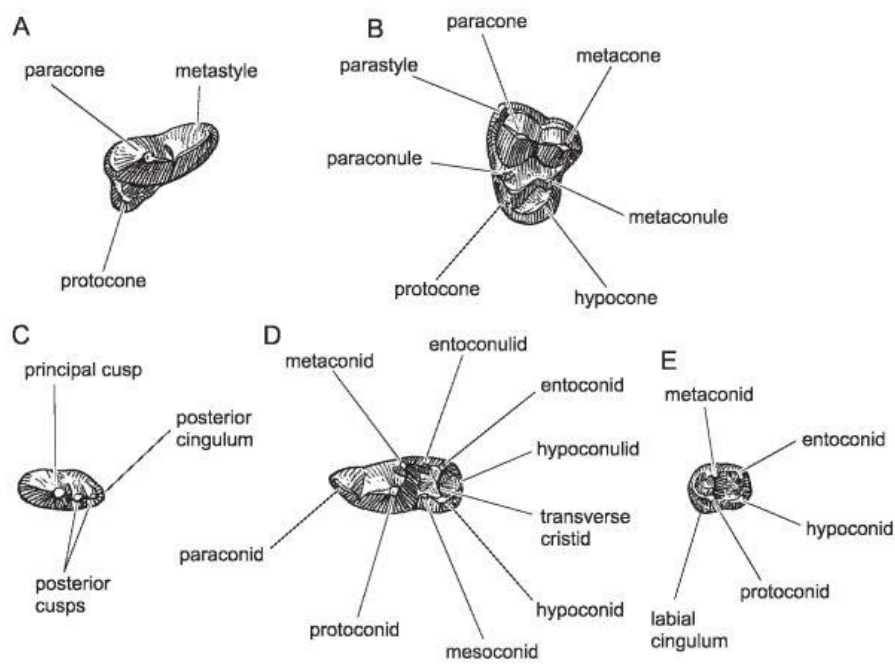


Figure 3 - Dental nomenclature (Tedford et al. (2009)). A : P4 ; B : Upper molars, C : Lower premolars, D : m1, E : m2.

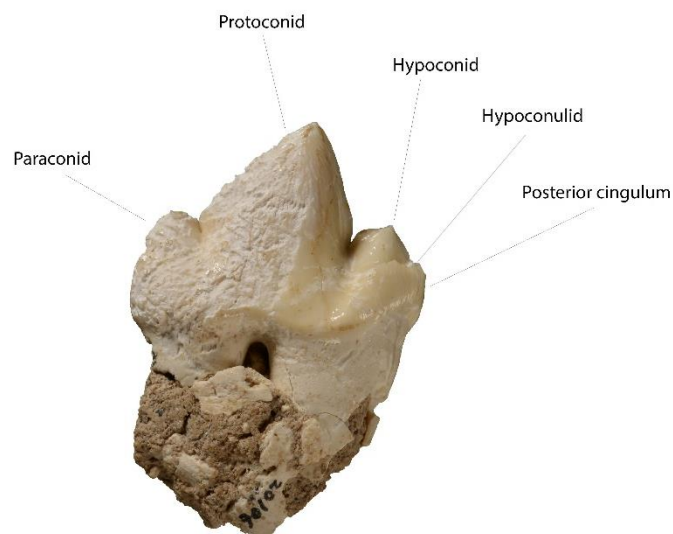


Figure 4 - Dental nomenclature (premolars other than P4)

2. Systematic paleontology

The families studied below belong to the order CARNIVORA – Bowdich, 1821.

2.1. Family Hyaenidae – Gray, 1821

Remarks: The Hyaenidae are a taxonomically diverse family of Neogene Carnivora, which's phylogeny has not always made consensus. For this study, we used the taxonomy described by Kurtén & Werdelin (1988), Werdelin & Solounias (1991), and Turner *et al.* (2008). Their work was used by Vinuesa (2018), who described the chronostratigraphic range (in Ma) and MN biozonation for all the known hyaenids species, as well as their geographical distribution by continents.

Following them, we consider the large-sized hunting hyaenas, previously referred to the genera *Chasmaporthetes*, *Euryboas*, *Lycaena* and *Ailuraena*, as belonging to the genus *Chasmaporthetes*. Moreover, we consider the characters distinguishing *C. kani* and *C. bielawskyi* from *C. lunensis*, as presented by Qiu (1987), invalid, and consider them synonymous. At last, following Werdelin & Solounias (1991), we consider *C. bonisi* to be synonymous with *Adcrocuta eximia*. To conclude, the following species are retained as valid : *C. borissiaki*, *C. exitelus*, *C. gangsriensis* Tseng et al. 2013, *C. lunensis* and *C. melei* in Eurasia, *C. australis* and *C. ossifragus* in Africa, and *C. ossifragus* in North America.

Moreover, we consider *Pliocrocuta perrieri* to be synonymous with *Pachycrocuta perrieri*, *Pliohyaena perrieri*, *Pliocrocuta pyrenaica*, *Plioheana pyrenaica* and *Pliocrocuta arambourgi* (Werdelin & Solounias, 1991).

2.1.1. Genus *Chasmaporthetes* – Hay, 1921

2.1.1.1. *Chasmaporthetes lunensis* – Del Campana, 1914

Referred material: mandible with a left lower jaw with i2 - m1 (JRD - 20/04) and a right lower jaw with i3 - m1 (JRD - 20/05) (Figure 5).

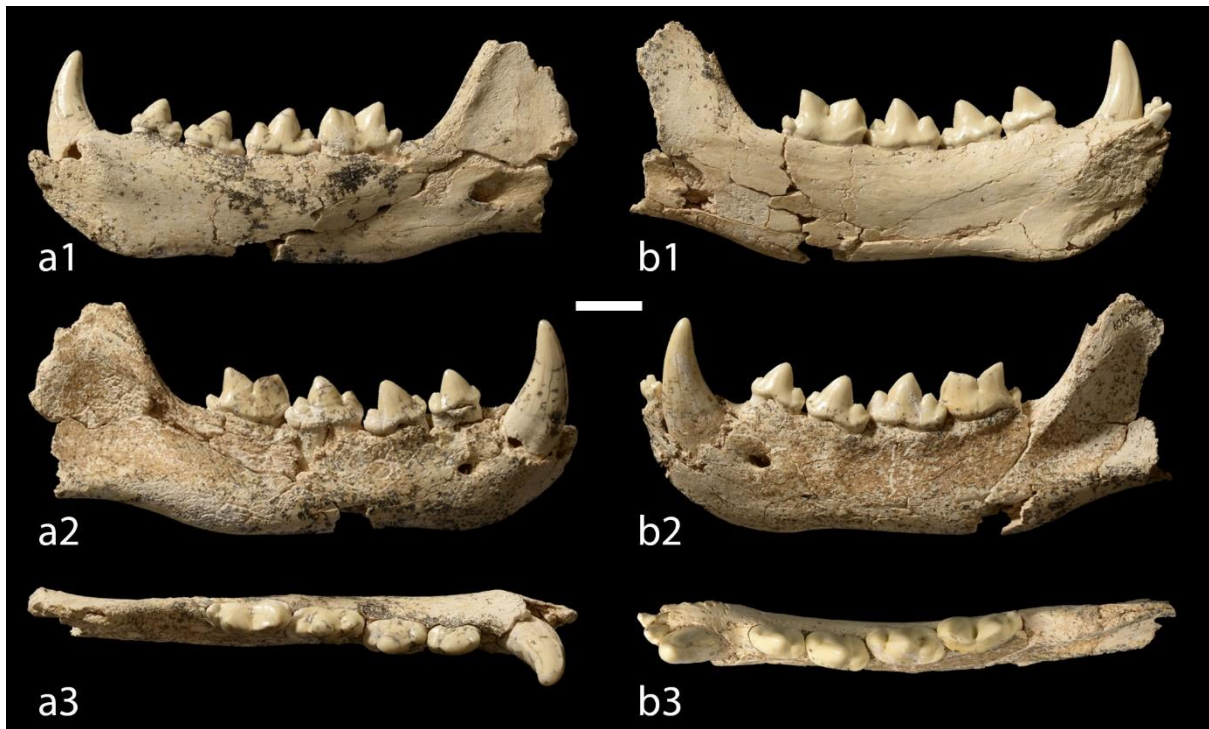


Figure 5 - *Chasmaporthetes lunensis* from Jradzor (a - b) : Right lower jaw (JRD - 20/05) in lingual view (a1), labial view (a2) and occlusal view (a3), Left lower jaw (JRD - 20/04) in lingual view (b1), labial view (b2) and occlusal view (b3). Scale bar equals 2 cm

Description: These two specimens belong to the same young adult individual: the occlusal outline of the teeth is sharp and the crown is quite unworn. The mandible is very well preserved, except for the ascending ramus, whose posterior part is missing. In lateral view, the ventral margin is linear. In occlusal view, the tooth row is slightly curved. The dentition is complete, except for the two first right incisors, and the left i1. The mental foramen is situated below the anterior root of p2. The masseteric fossa extends anteriorly to the level of the m1's talonid.

The incisors and the canines are single-rooted. The i2 and i3's crown is asymmetric as it bears a high main cusp and a distinct secondary posterior cusp. Their crown widens lingually. The i2 is tilted forward, and the i3, larger, is straight. The c1's lingual face is flat, while its labial face is rounded. It bears mesiolingual and posterior ridges.

The premolars and molars are double-rooted. The premolars are tilted backwards and their main cusp, the protoconid, is sharp and bears a ridge on its anterior and posterior side. The anterior cutting edge is longer than the posterior one. The p2 is separated from the canine by a 5.8 to 7.3 mm long diastema. p2 and p3's anterior cutting edge is slightly convex. The premolars bear 2 accessory cusps, separated from the main cusp by a notch. Their size increases from p2 to p4. The paraconid is small

on the p2, while the hypoconid is stronger. On the p3, they are almost of equal size, but the hypoconid remains slightly stronger. The p4's anterior and posterior accessory cuspid are equally developed, and free of the main cusp. It also bears a posterior cingulum and a second reduced accessory cusp (hypoconulid). The m1's metaconid is vestigial, while its paraconid and protoconid are developed. It bears an anterior cingulum. The talonid is reduced: the hypoconulid, well developed, seems merged with the hypoconid and entoconid, barely identifiable. The talonid basin is absent, a single linguo-labial notch separates the talonid from the trigonid.

Discussion: Based on the large size of the mandible, the dental formula (i1-3, c, p2-4, m1) and the shape of the tooth (tri-lobed premolars and molars in occlusal view), this specimen can be referred to the Hyaenidae family (Thenius, 1989). Among same age hyaenids genera, the Jradzor specimens can be distinguished from the genera *Crocota* (Crégut-Bonnoure, 1996a) and *Pachycrocota* (Werdelin & Peigné, 2010) in having a well-developed paraconid on the anterior side of the p2 and p3 protoconids. The lack of the metaconid on the trigonid of the m1 (Crégut-Bonnoure, 1996a) and the presence of a well-developed anterior accessory cusp on p4 (Werdelin & Peigné, 2010) also excludes the genus *Hyaena*. At last, the following characters of the premolars exclude *Pliocrocota perrieri*: the lack of the anterior accessory cuspid on the p3 and p2; the p4's anterior accessory cuspid, smaller than the distal cuspid, and situated on the lingual portion of the crown (Vinuesa et al, 2014). Moreover, according to Werdelin & Solounias (1991), the anterior accessory cusp of p4 in *P. perrieri* is appressed to the main cusp, which is not the case for the Jradzor specimens. Kurtén & Werdelin (1988) provided a revised diagnosis of the genus *Chasmaporthetes*: the p4 is elongated, with large accessory cusps; the m1 lacks a metaconid and the m1 talonid bears a single blade-like cusp, with a rounded lateral profile. *C. borissiaki* (Werdelin & Solounias, 1991) and *C. gangsriensis* (Tseng et al, 2013) exceptionally do possess two cusps on the talonid. Werdelin & Solounias (1991) described two other *Chasmaporthetes* features: a straight or slightly concave anterior face of the p3, and a the p4's anterior accessory cusp is free of the protoconid. The mandible found in Jradzor meets all those criteria. Based on morphological characteristics, these specimens belong without doubt to the genus *Chasmaporthetes*.

The specimens found in Jradzor differ from all of the Eurasian Late Pliocene fossils known so far, but one. Indeed, they differ from *C. melei* and *C. gangsriensis* by larger dimensions (Table 2), and from *C. gangsriensis* and *C. borissiaki* by the number

of cusps on the talonid. As described earlier, the mandible found in Jradzor only bears one developed cusp on its talonid, unlike *C. gangsriensis* and *C. borissiakii*. Moreover, *C. borissiakii*'s tooth row is straight (Werdelin & Solounias, 1991), while the mandible found in Jradzor has a slightly curved tooth row. Concerning *C. exitelus*, this species is only known from one specimen (Kurten & Werdelin, 1988), a palate, so it cannot be compared to the mandible found in Jradzor. At last, the specimens perfectly match *C. lunensis*' description: curved tooth row, talonid bearing one single cusp, large anterior accessory cusp on p4 (Werdelin & Solounias, 1991), and presence of anterior cusp on p2. Indeed, according to Kurten & Werdelin (1988), the p2 anterior cusp is normally very small or absent within the *Chasmaporthetes* genera, except for two species: the african specie *C. nitidula*, who's anterior cusp is well-developed, and *C. lunensis*, who's anterior cusp is smaller, but present. Based on morphological and morphometric criteria, these specimens undoubtedly belong to *Chasmaporthetes lunensis*.

Table 2 - Lower teeth measurements of JRD – 20/04, JRD – 20/05 and of different *Chasmaporthetes* species (length x width) in mm (*C. lunensis*, *C. borissiakii*, *C. melei* and *C. gangsriensis*: data taken from the literature: Qiu (1987)², Kurten & Werdelin (1991)¹ & ², Rook et al. (2004)³, Tseng et al. (2013)⁴)

		JRD – 20/04	JRD – 20/05	<i>C. lunensis</i> ¹		<i>C. borissiakii</i> ²		<i>C. melei</i> ³	<i>C. gangsriensis</i> ⁴	
				n		n		n = 1	n	
i2	L	5,4								
	W	4,4				1	4,7			
i3	L	6,4	6,3							
	W	6,1	6,2			1	5,8			
c1	L	16,5	17,1					14,99	1	16,2
	W	11	11,9					11,32	1	11,5
p2	L	17,3	16,5	15	16,42 [15,0 - 17,5]	2	15,6 [15,4 - 15,8]	13,04	2	17,35 [17,3 - 17,4]
	W	9,1	9,1	15	9,12 [8,1 - 10,2]	1	8,4	8,75	2	9,3 [9,2 - 9,4]
p3	L	20,5	20,5	12	19,47 [17,6 - 21,3]	2	19,15 [19 - 19,3]	17,15	1	20
	W	10,5	10,6	10	10,72 [9,9 - 11,8]	1	10,2	10	2	10,5 [10,3 - 10,7]
p4	L	24,5	24,3	19	23,35 [21,0 - 26,3]	2	22,05 [21,3 - 22,8]	20,05	2	22,15 [22,0 - 22,3]
	W	11,7	11,5	18	11,59 [10,3 - 13,2]	1	11,6	10,25	2	10,45 [10,3 - 10,6]
m1	L	25,6	26,1	15	25,05 [23,5 - 26,5]	2	24,4 [24 - 24,8]		2	23,3 [23,2 - 23,4]
	W	11	11,4	16	11,21 [9,3 - 12,7]	2	10,85 [9,8 - 11,9]		1	11,2

2.1.2. Genus *Pliocrocuta* – Kretzoi, 1938

2.1.2.1. *Cf Pliocrocuta perrieri* – Croizet & Jobert, 1828

Referred material: right m1, right p4 (JRD - 20/06) (Figure 6)

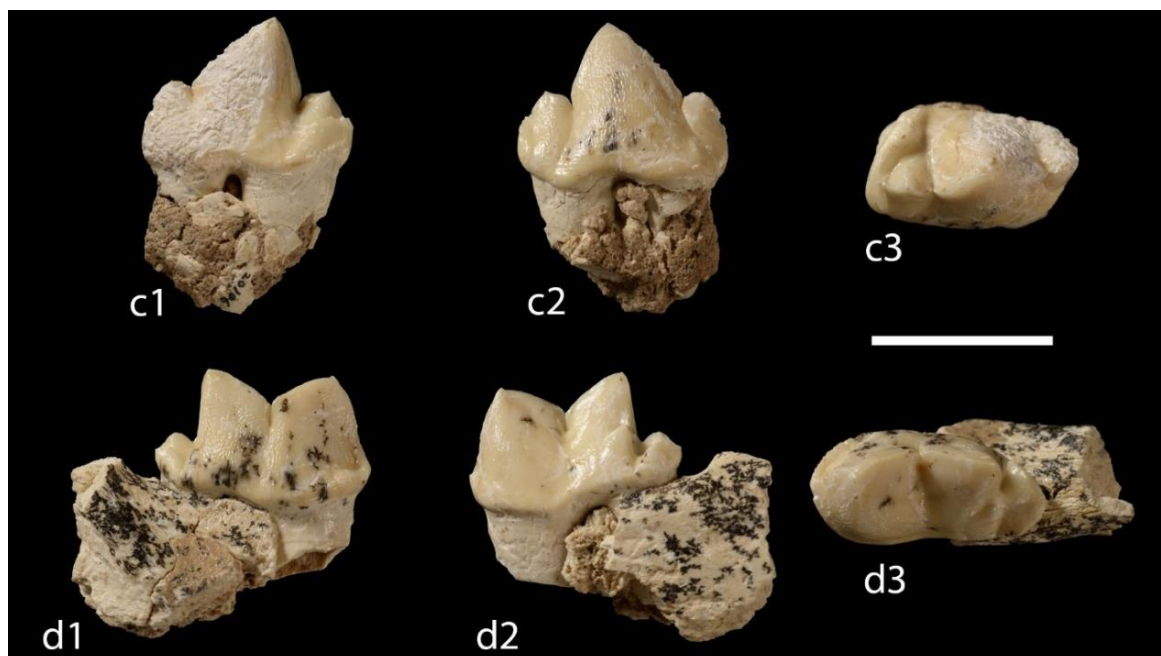


Figure 6 – *Cf Pliocrocuta perrieri* from Jradzor (c – d): c Right p4 (JRD - 20/06) in lingual view (c1), labial view (c2) and occlusal view (c3), d Right m1 (JRD - 20/06) in labial view (d1), lingual view (d2) and occlusal view (d3). Scale bar equals 2 cm

Description: The two specimens are double-rooted. Their occlusal outline is sharp, and the crown is unworn. The p4 bears a high protoconid and two accessory cusps: the paraconid is small but well-individualized and lingually deflected, while the hypoconid is developed. They are separated from the main cusp by a slight notch. On its posterior side, the p4's crown widens into a large cingulum, mainly lingually developed. The lower carnassial bears a large paraconid and large protoconid of equal height, and an individualized but small metaconid. On its anterior face, labially, the m1 bears a cingulum. The talonid, reduced, bears a well-developed hypoconid, while the hypoconulid and entoconid seem merged into a ridge.

Discussion: Based on the large size of the tooth and on their shape, these specimens belong to the Hyaenidae family (Thenius, 1989). Among same age hyaenids genera, the Jradzor specimens can be distinguished from the genus *Hyaena* by the small size of the metaconid (Crégut-Bonnoure, 1996a). The presence of the

metaconid, combined with p4's anterior accessory cusp, appressed to the protoconid, excludes the genus *Chasmaporthetes* (Kurtén & Werdelin, 1988). The genus *Crocuta* can also be excluded due to the well-developed talonid present on the right m1 from Jradzor: indeed, according to Werdelin & Lewis (2008), the talonid is greatly reduced within the *Crocuta* genus. Concerning *Pachycrocuta brevirostris*, it sets itself apart from the JRD - 20/06 specimen with its huge size (Table 3a and 3b). The *Pliocrocuta perrieri* fossil records shows some variability concerning the lower carnassial: a small metaconid can be present on the talonid of the m1, but some specimens don't have any (Viret, 1954). Moreover, the talonid can bear 2 cusps, the hypoconid being taller and longer than the entoconid (Viret, 1954), or one single cusp (Kurtén & Poulianos, 1981). Sotnikova (1989) illustrated these variations, describing 5 types of m1 who succeed each other in *P. pyrenaica*, *P. perrieri* and *P. brevirostris* that she considers chrono species. The first and most primitive type resembles the m1 found in Jradzor, and can only be found in *P. pyrenaica* individuals during the MN15. Tseng et al. (2016) add some other *P. perrieri* characteristics: the m1 paraconid is "swollen, longer than protoconid and is the same height as the protoconid". Werdelin & Solounias (1991), Vinuesa et al. (2014) and Tseng et al. (2015) gave some characteristic of p4 of *P. perrieri*: the anterior accessory cusp is large, but appressed to the main cusp, and situated on the lingual portion of the crown. Based on these elements and considering the morphometric data, these teeth certainly belong to *P. perrieri*. The morphometric data reported in Table 3a and 3b show an increase in the general size of the teeth within *P. perrieri*. By their dimensions, the teeth found in Jradzor resemble the *P. perrieri* individuals from the Zanda Basin (MN14) but also from the Odessa Catacombs, in Ukraine (MN15).

Table 3a - p4 and m1 measurements of JRD - 20/06 and different *P. perrieri* specimens (length x width) in mm (*P. perrieri*: data taken from the literature: Howell (1980)¹, Napoleone et al. (2003)⁴, Tseng et al. (2016)³)

		P. perrieri													
		JRD – 20/06	La Calera II (Spain) ¹	Wangjiagou (Yushe Basin) ³	Zanda Basin ³	Layna (Spain) ¹	Perpignan (France) ¹	Odessa Catacombs (Ukraine) ¹		Les etouaires (France) ¹		Val d'Arno (Italie) ¹		Villarroya (Spain) ¹	
			MN14 ³	MN14 ³	MN14 ³	MN15 ³	MN15 ³	n	MN15 ³	n	MN 16a ³	n	MN16a ⁴	n	MN 16a ³
p4	L	21,9	22,9	22,4	20,64	19,7	24,4	22	22,25 [20,5 - 24]	3	23,85 [22,5 - 25,2]	2	22,4 [21,5 - 23,3]	3	23,8 [23 - 24,4]
	W	12	12,4	13,3	12,06	9,3	13,3	21	12,75 [12,2 - 14,3]	2	15 [14,4 - 15,6]	2	13,7 [13,3 - 14,1]	3	14,3 [13,9 - 14,3]
m1	L	23,1	23	25,2	23,3	22,7	24,7	21	24,82 [23,1 - 28,7]	6	25,85 [24 - 26,8]	1	24,5	4	25,65 [25 - 26,5]
	W	11,3	10,9	12	11,2	10,8	12,6	21	11,42 [10,4 - 12,2]	4	12,95 [12,8 - 13,1]	1	12,5	3	14,3 [13,9 - 14,7]

Table 4b - p4 and m1 measurements of *P. brevirostris* and different *P. perrieri* specimens (length x width) in mm (*P. brevirostris* and *P. perrieri*: data taken from the literature: Howell (1980)¹, Qiu (1987)⁶, Sotnikova (1989)², Kostopoulos & Sen (1999)⁵, Tseng et al. (2016)³)

		<i>P. perrieri</i>										<i>P. brevirostris</i> ¹				
		Chang Wa Kou (Yushe Basin) ¹		St Vallier (France) ¹		Yassioren (Turquie) ¹	Kuruksai (Uzbekistan) ²		Xiachuang (Yushe) ¹		Malancun (Yushe) ³		Europe		Shansi (China)	
		n	MN16 ³	n	MN17 ³	MN17 ⁵	n	MN17 ³	n	MN 14 - 18 ³	n	Early Plio. ⁶	n		n	
p4	L	5	22,7 [21,4 - 24]	5	23,5 [21,7 - 25,5]	23,5	7	22,58 [20,4 - 23,9]	2	24,05 [23,3 - 24,8]	4	22,27 [21,8 - 22,8]	7	27,27 [25,5 - 28,1]	6	26,95 [25,7 - 28,5]
	W	5	13,26 [12,7 - 13,6]	4	14,67 [14,3 - 15,2]	14,8	4	14,27 [13,9 - 14,5]	2	15,40 [15,2 - 15,6]	4	13,92 [13,3 - 14,6]	6	16,77 [16,2 - 17,8]	6	17,31 [16,0 - 18,5]
m1	L	4	24,07 [23,2 - 24,9]	6	25,4 [23,9 - 26,9]	25	6	25,28 [23,7 - 26,3]	2	26,75 [26,2 - 27,3]	3	24,9 [24,3 - 25,9]	4	29,35 [27,5 - 31,2]	5	28,22 [26,7 - 30,6]
	W	3	12,37 [12 - 12,9]	5	12,74 [10,8 - 14,3]	12,6	4	13 [12,9 - 13,2]	2	14,30 [13,6 - 15]	3	12,63 [24,3 - 25,9]	4	14,42 [13,2 - 15]	4	14,9 [13,6 - 16,3]

2.1.3. Genus *Miohyaenotherium* – Semenov, 1989

2.1.3.1. *Miohyaenotherium* sp. - Semenov, 1989

Referred material: right m1 (JRD - 19/04) (Figure 7)



Figure 7 - *Miohyaenotherium* sp. : Right m1 (JRD - 19/04) in labial view (e1), lingual view (e2) and occlusal view (e3). Scale bar equals 2 cm

Description: The lower carnassial's roots are missing. The trigonid's 2 labial cusps (the protoconid, high, and the paraconid, quite long) are well developed, and separated by a large notch. Their occlusal outline seems worn out as it is abraded labially. On the anterior-labial side of the paraconid, the enamel thickens into a cingulum. The metaconid, on the lingual side, is smaller than the labial cusps but still sharp. The reduced talonid bears a broad but low hypoconid, a hypoconulid, and a high entoconid, all connected into a crest. The entoconid is as high as the metaconid. The talonid basin is small.

Discussion: Considering the shape of the talonid, this tooth doesn't belong to the Canidae family. Indeed, Tedford et al. (1995) compared and illustrated the lower dentition of representative *Caninae*, and none of the m1 correspond to the lower carnassial found in Jradzor. On the other hand, this tooth resembles the m1 of the *Hyaenidae* family. Indeed, it shows similarities with the third ecomorphotype of hyaenids (Vinuesa, 2018): compared with the ecomorphotypes 1 and 2, the third bears 28

a longer paraconid, a higher protoconid and a reduced talonid and metaconid. This ecomorphotype includes the genera *Ictitherium*, *Thalassictis*, *Miohyaenotherium* and *Hyaenictitherium*. If we can easily exclude the ecomorphotypes 1, 2, 4 and 6 based on the characteristics of their lower carnassial, it is not the case for the fifth, in which the m1 is not described. This ecomorphotype is formed by *Metahyaena confector*, *Palinhyena reperta*, *Belbus beaumonti* and *Ikelohyaena abronia*. Among the Pliocene and late Miocene Eurasian genera and species of the ecomorphotypes 3 and 5, *Belbus beaumonti* can be excluded based on its size (Table 4) (Bonis et al, 2010) and on the photograph of its mandible (Werdelin & Solounias (1991), Koufos (2011)). Indeed, the talonid of the m1 doesn't resemble the one of JRD - 19/04. *Palinhyena reperta* (Werdelin, 1988) is also out of question considering that its metaconid is too developed and that its talonid doesn't resemble the one of the specimen from Jradzor, even though it has the same dimensions as JRD - 19/04. Based on morphometric data (Semenov 2008), this tooth actually belongs to one of the genera of the tribe Hyaenotheriini (sensu Semenov, 2008). Indeed, with a length of 4.56 mm and a width of 5.73 mm, the talonid represents respectively 23.3% and 29.2% of the crown length. These measurements exclude the genera of the second group described by Semenov (2008), that is to say *Ictitherium* and *Thalassictis*. Semenov (2008) describes three genera within this tribe: *Hyaenotherium*, *Hyaenictitherium* and *Miohyaenotherium*, whose sole species is *M. bessarabicum*. This species might be a synonym of *Hyaenictitherium parvum* and Werdelin & Solounias (1991) suggested further investigation for taxonomical clarification. We consider the genus *Hyaenotherium* a junior synonym of *Hyaenictitherium*, due to a lack of arguments supporting a distinction between the two forms (Zhang et al. (2002), Andersson and Werdelin (2005), Bonis (2004, 2005), Koufos (2011)). The validity of this tribe was discussed by Werdelin & Solounias (1991), but the morphometric data provided by Semenov (2008) concerning its genera remain valid.

Semenov (1989) provided some interesting diagnose criteria based, among others, on the m1. According to him, the individuals of the genus *Hyaenotherium* and *Hyaenictitherium* bear a hypoconid that is higher or equal in height to the entoconid. On the other hand, within *Miohyaenotherium bessarabicum*, the hypoconid of the m1 is lower than the entoconid. Based on these observations, the tooth from Jradzor doesn't belong to the *Hyaenotherium/Hyaenictitherium* genus, but shows similarities with *Miohyaenotherium bessarabicum*. The morphometric data provided by Semenov (1989) show that the tooth from Jradzor is close in dimensions to *M. bessarabicum*,

even though the m1 of this species seems to be a little bit larger. According to these data, combined with the picture of a *M. bessarabicum* mandible (Semnov, 2008), JRD - 19/04 very likely belongs to the genus *Miohyaenotherium*. Considering that *M. bessarabicum* was last recorded during the Turolian (Werdelin & Solounias, 1991), it is unlikely that this tooth belongs to this species. It probably is a new species of *Miohyaenotherium* that wasn't recorded yet.

Table 5 - m1 measurements of JRD - 19/04, *B. beaumonti*, *P. reperta* and *M. bessarabicum* (length x width) in mm (*B. beaumonti*, *P. reperta*, *M. bessarabicum*: data taken from the literature: De beaumont (1968)¹, Werdelin (1988)², Semenov (1989)³, Bukhsianidze & Koiva (2018)⁴)

	JRD – 19/04	<i>B. beaumonti</i> ¹	<i>P. reperta</i> ²		<i>M. bessarabicum</i> ³		
		Samos	China		Belka (Ukraine) 7 - 6 Ma (MN12)	Udabno ⁴ (Géorgie) 9 - 7 Ma (MN(?10)11(?12))	Chimishlia (Moldavie) 7 - 6 Ma (MN12)
			n		n = 1	n = 2	n = 2
m1 L	19,62	24,9	7	20,86 [20,3 - 21,5]	20,9	21,8	21
m1 W	7,8	10,7	8	9,18 [8,3 - 9,7]	9,6	9,2	10
m1 trL	15,16 (77,3%)		9	16,5 [15,3 - 18,6]	16 (76,6%)		16,5 (78,6%)
m1 taL	4,46 (22,7%)				4,9 (23,4%)		4,5 (21,4%)
m1 taW	5,73 (29,2%)				7,8 (37,3%)		

2.2. Family Canidae – Fischer von Waldheim, 1817

2.2.1. Genus *Nyctereutes* – Temminck, 1838

Remark: The Saint-Vallier material was studied by Viret (1954), Martin (1971) and Argant (2004) who referred it to *N. megamastoides*. In 1976, Soria & Aguirre reviewed the material and distinguished *N. megamastoides* in two subspecies: *N. megamastoides vulpinus* for the material from Saint-Vallier and Puebla de Valverde, and *N. megamastoides megamastoides*. Tedford & Qiu (1991), Koufos & Kostopoulos (1997), Spassov (2000) and Argant (2004) later agreed with this distinction. Monguillon et al. (2004) elevated the Saint-Vallier and Puebla de Valverde material to the species level, and refer to it as *Nyctereutes vulpinus*. In this article, we follow Monguillon et al. (2004).

2.2.1.1. *Nyctereutes tingi* – Depéret, 1890

Remark: Using size, Spassov (2003), Rook et al. (2017), Bartolini Lucenti (2018) and Lucenti et al. (2018) questioned the systematic assignment of the Calta material, identified by Ginsburg (1998) as *N. donnezani*. Daguinet & Sen (2019), based on morphological and cladistic analysis, agreed with Ginsburg, and attributed the specimen to *N. donnezani*. We follow this last point of view. Moreover, Geraads et al (2010) questioned the assignment of the Megalo material, identified by Koufos (1997) as *N. tingi*, and suggested its attribution to *N. donnezani*. Still, due to a lack of arguments supporting this second opinion, we follow Koufos (1997).

Referred material: skull (JRD - 20/03), right lower jaw with c1, p3 - m2 (JRD - 19/03) (Figures 8 and 9)

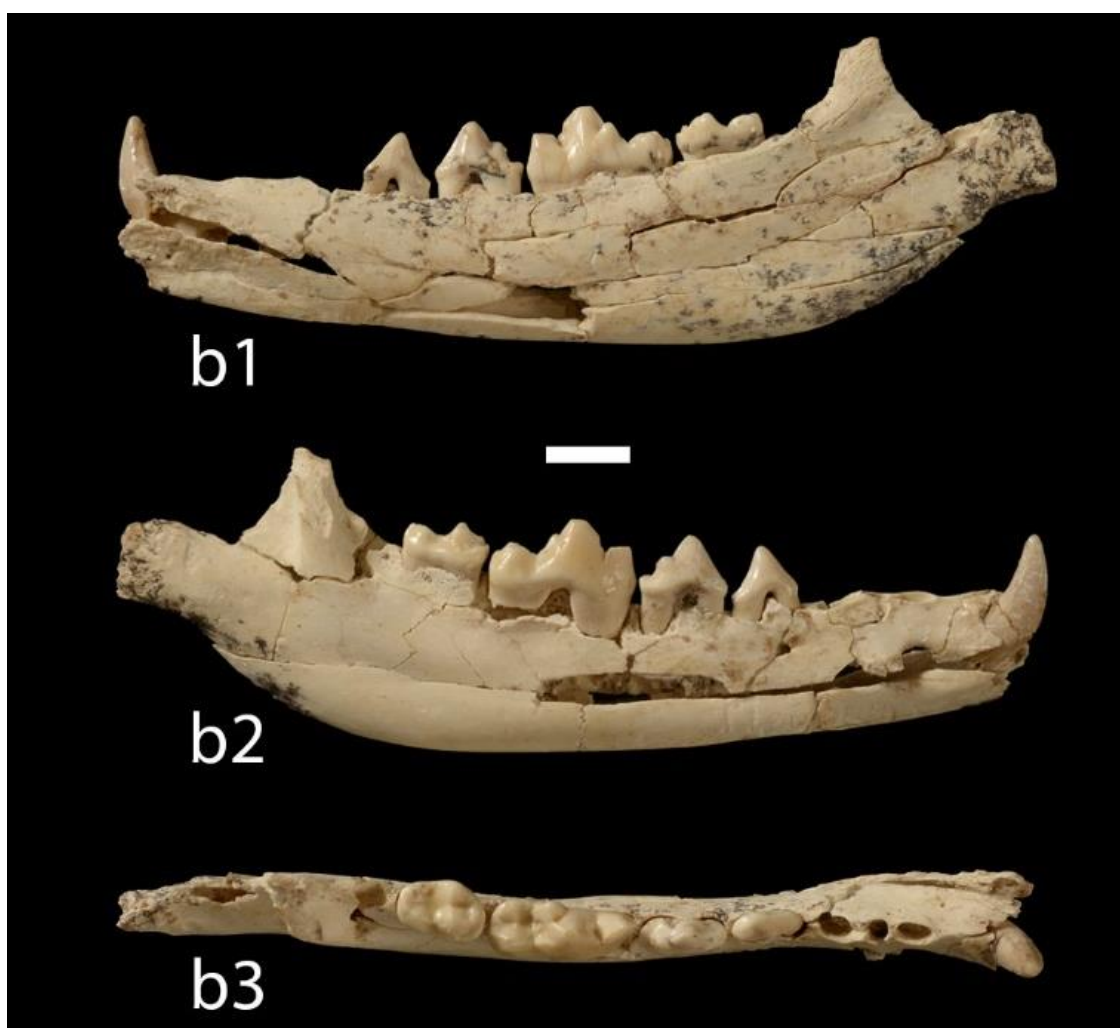


Figure 8 – *Nyctereutes tingi* from Jradzor: Right lower jaw (JRD - 19/03) in lingual view (b1), labial view (b2) and occlusal view (b3). Scale bar equals 1 cm



Figure 9 - *Nyctereutes tingi* from Jradzor: Cranium (JRD - 20/03) in lateral view (a1), dorsal view (a2) and ventral view (a3). Scale bar equals 1 cm

Description: The two specimens belong to the same relatively young individual: the crown is unworn, and the occlusal outline little worn.

Lower jaw: the mandible is well preserved and in fairly good state, but lacks the ascending ramus. The horizontal ramus is elongated and relatively low. In lateral view, it is slightly curved, and its posterior part is inflected - the curve is convex and then slightly concave. This flexion is called subangular lobe, and is the insertion ridge of the digastric muscle. In occlusal view, the lower dentition is well lined up, but partially complete: the incisors, the two first premolars and the m3 are missing. The first mental foramen is located at the mid depth of the body under the p1 alveolus and is partially broken, while the second foramen, under the anterior root of the p3 and in the upper part of the body, is well preserved. The masseteric fossa, quite deep, extends posteriorly to the m2.

Lower dentition: the canine bears a ridge on its anterior cutting edge. Its lingual face is relatively flat, while its labial face is more roundish. The premolars and molars are double-rooted, and bear a high protoconid. p3 and p4 lack an anterior accessory cusp. The p3's posterior cutting edge is longer than the anterior one. The p4 bears a hypoconid, strong and high on the protoconid, and a distal cingulum. The m1 bears a developed trigonid: the paraconid is low and short, the protoconid is high and roundish, and the metaconid is strong. Its talonid bears a large hypoconid and a slightly weaker entoconid, connected by a transverse crest, that separates the talonid basin in two basins. The m2, of sub rectangular shape in occlusal view, bears an anterior-lingual cingulum. The protoconid and metaconid, slightly higher, are large, high, and well developed. These cusps are connected anteriorly by a low and roundish crest. On the talonid, the hypoconid and entoconid are connected by a crest. The hypoconid is well-developed, while the entoconid is harder to distinguish from the crest.

Skull: The skull is well preserved, and almost complete: in dorsal view, the frontal process of the zygomatic bone, the temporal bone and a large part of the nasals are missing. In ventral view, the right tympanic bullae and the right occipital condyle are missing. Moreover, the pterygoid bones, normally located on both lateral sides of the sphenoid, are partially broken. On the posterior side of the skull, the jugular processes are also missing. In dorsal view, the skull is narrow and elongated. The muzzle is thin, and progressively widens backwards. It is hard to establish the nasal bones' length as they are broken, and therefore to determine if they exceed the fronto-maxillar suture. The postorbital processes are thick and well developed, and bear a slight dorsal depression. The ridges issuing from the distal margin of the postorbital processes join the strong sagittal crest on top of the skull. The crest joins the supraoccipital crest, well developed. At last, the braincase is curved.

Upper dentition: the upper dentition is well preserved, except for the two first premolars that are missing. The incisors and the canine are single rooted. The incisors, of same height, are slightly rounded on their labial face. The I1 and I2 bear 3 cusps: the main cusp is surrounded by two small accessory cusps, separated from the central cusp by a small slit. The I1's occlusal outline is linear, and the tooth is symmetrical. On the contrary, the I2 is asymmetrical, as the lateral accessory cusp is much shorter than the two other cusps. The I3 is also asymmetrical: its main cusp is peaked, and bears a very small accessory cusp on its medial side. A ridge separates its labial face from its lingual face, where it bears a small cingulum. The upper canine is separated from the incisors by a 4 to 6mm diastema, and located on the lateral side of the maxillary

bone. It is not very long, sharp, barely curved and bears a ridge on its posterior face. The P1 is separated from the canine by a 3 to 4 mm diastema. It is single rooted, and bears a single cusp, slightly rounded on its labial face. The P2 and P3 are double-rooted, and bear a strong main cusp whose posterior cutting edge bears a ridge. P3 bears a small distal cusp-like cingulum. The P4 has two small anterior roots, and one larger posterior root. A small lingual cingulum runs from the posterior edge of the metastyle to the posterior base of the protocone. It is thicker backwards. There is a small lingual cingulum on the posterior part of the tooth. The protocone is quite small, and diverts lingually compared with the lingual margin of the tooth. The paracone is high and anterior-posteriorly elongated and bears a sharp ridge on its anterior cutting edge. An anterior and rather lingual depression separates the paracone from the protocone. The metastyle is low and rather short compared to the paracone. The molars have a sub triangular outline and are slightly curved posteriorly. They both bear a cingulum on their antero-lingual side. On the M1, the cingulum thickens lingually into a large hypocone. The metacone is slightly higher than the paracone that is more roundish. The protocone is almost as high as the hypocone, and connected to a small paraconule. The metaconule is well developed. The M2's paracone and metacone are quite small compared with the protocone, more developed. The metaconule is underdeveloped, while the paraconule is quite large. The cranial and mandibular measurements of *N. tingi* are reported in the Tables 5 and 6.

Table 6 - Cranial measurements of JRD – 20/03 from Jradzor, in mm.

	TL	CBL	BL	NcL	FL	SL	P1 - M2 L	LMR	P1 - P4 L	GDAB
JRD - 20/03	181	171	162	78.6	102	76	59.5	18.8	40.7	25.4

	GMB	GBPP	FMB	FMH	Eu	LBS	Ect	Ent	SH	OTH
JRD - 20/03	53	54	15	12.8	53.6	34	48*	30*	46.1	36.6

Table 7 - Mandibular measurements of JRD – 20/03 from Jradzor, in mm.

	c1 post - m3 L	p1 - m3 L	p2 - m3 L	LMR	p1 - p4 L	p2 - p4 L	Mm1B	Mm1H	Mp2-p3H
JRD - 19/03	74.4	68.5	63	32.9	35.4	29.9	7.3	20.2	15.1

Discussion: Based on the dental formula (I3/3, C1/1, P4/4, M2/3) and the elongated skull, these specimens belong to a Canidae (Pessutti et al., 2001). Among the Eurasian Pliocene genera, the *Cuon* genus can be excluded. Indeed, this genus is characterized by the absence of the lower third molar, a reduced talonid on the m1, bearing one single blade-like cusp (Van Valkenburgh, 1991), and an upper first molar

bearing a single talon basin between the protocone, metacone and paracone (Ghezzi and Rook, 2014). The specimens found in Jradzor don't correspond to that description. Moreover, the presence of a transverse crest on the talonid of the m1 excludes the *Eucyon* genus (Lucenti & Rook, 2020). Tedford et al. (1995) build a Data Matrix of morphological characters that includes the genera *Nyctereutes*, *Canis* and *Vulpes*, the three other Eurasian Pliocene canids. Some of those characters can be used to determine which genus the skull and mandible belong to. Indeed, the lack of second accessory cusp on p4, the paracone not being enlarged relative to metacone and the I3's small size and weak cingulum don't match the *Canis* description. Crégut-Bonnoure (1996b) also pointed out the fact that in the *Canis* genus, the P2 and P3 bear a hypocone, which is not the case with the material from Armenia. Moreover, and still according to Tedford et al. (1995), the presence of a subangular lobe, and of short, slender, non-curved canines excludes the genera *Vulpes* (and *Canis*) and is characteristic of *Nyctereutes*. The well-developed sagittal crest, the transverse crest binding the hypoconid to the entoconid, and the high protoconid and metaconid on the m2 match the description made by Ginsburg (1998) of *Nyctereutes*. Based on morphological criteria, the specimens from Jradzor undoubtedly belong to the *Nyctereutes* genus.

Among the late Pliocene eurasian *Nyctereutes* species, *N. procyonoides* can be distinguished from the specimens found in Jradzor by its size (Tables 7 and 8). The other species can only be distinguished based on morphological criteria; the following paragraph is mainly based on Daguinet & Sen (2019). The first criteria that can distinguish the species is the degree of development of the subangular lobe. Indeed, it is weak in *N. donnezani* and *N. tingi* as in the specimen from Jradzor, but strong in *N. megamastoides*, *N. sinensis* and *N. procyonoides*. To quantify the importance of that lobe within *N. tingi* and *N. donnezani*, we can calculate the index (depth of the body behind m2/depth of the body in front of p4) x 100. This index is 148 and 130 on the mandibles of *N. donnezani* from Calta, 147 on the holotype from Perpignan and 133 on the mandible of Layna. Within the *N. tingi* species, it is 123 on the holotype and 142 on the specimen from the Upper Gaozhuang Formation. For the specimen from Jradzor, the index is 148. All these specimens are similar in the robustness of the subangular lobe, and sexual dimorphism could explain the larger or smaller values. The P4 also shows some interesting differences between the species, illustrated by Lucenti (2017): in *N. sinensis* from the Yushe basin, the protocone is located far anteriorly to the anterior margin of the paracone. On the other hand, the mesial margin

of *N. vulpinus* (from Nihowan, Yushe Basin and Saint Vallier) and *N. megamastoides* (from Montopoli, Dagnero, Sesklon, Kvabebi and Perrier) is straight (Daguenet & Sen, (2019), Lucenti (2017)). None of these descriptions fits the specimen from Jradzor. The upper carnassial of *N. donnezani* (specimen reported in Depéret 1980) “shows an embayment on the anterior margin of the tooth that separates the protocon from the rest of the paracon”. That embayment is also present on the specimen from Jradzor, and, based on the Fig. 2 provided by Tedford et al. (1991), on *N. tingi*. Still according to Lucenti (2017), the relative size of the paracone and metastyle of P4 also differs between species: the holotype of *N. megamastoides* has a rather “mesio-distally short paracone and elongated metastylar blade”, unlike *N. donnezani* from Perpignan and Layna, *N. tingi*, *N. vulpinus* from Saint-Vallier and the specimen from Jradzor. At last, a sharp ridge descends anteriorly from the tip of the paracone of the *N. donnezani* from Calta, and, based on the Fig. 2 provided by Tedford et al. (2009), of *N. tingi*. This ridge is also present on the P4 of the specimen from Jradzor. The upper molars have some interesting and different features within the different species (Daguenet & Sen, 2019). Indeed, the M1 of *N. donnezani*, *N. tingi* and *N. procyonoides* has a narrow lingual part that gives it a sub-triangular outline. Moreover, the occlusal outline of M1 and M2 of those species is curved backwards. On the other hand, the M1 of *N. megamastoides* and *N. sinensis* has a larger lingual part, so that the molar has a trapezoidal outline. Only the M2 is curved backwards within these two species. The M1 of the skull from Jradzor resembles the first group of species. The matrix of characters established by Daguenet & Sen (2019) highlights some other differences between the species : for example, in *N. donnezani* and *N. tingi*, the muzzle narrowing anterior to zygomatic process is not marked, while it is in *N. megamastoides*, *N. sinensis* and *N. vulpinus*. Moreover, *N. sinensis*, *N. vulpinus*, *N. procyonoides* and *N. tingi* of the Yushe Basin bear a posterior cusp on their P3, unlike *N. donnezani* from Perpignan and the *Nyctereutes* from Jradzor. Based on these elements, we can exclude with certainty *N. sinensis*, *N. vulpinus* and *N. megamastoides*. Concerning *N. donnezani* and *N. tingi*, Koufos (1997) and Tedfors et al. (2009) noted that these 2 species show many morphologic and morphometric similarities, but maintained both species based on some differences in the skull and tooth morphology. The matrix of characters provided by Daguenet & Sen (2019) highlights some of those differences. For a start, the P4 are not identical. The protocone of *N. donnezani* from Layna and Perpignan can either extend anterolingually beyond the anterior end of the paracone as it is the case in *N. tingi*, or more lingually and not beyond the anterior end of the paracone, as for *N.*

donnezani from Calta and the specimen from Jradzor. The P4 is broad, bears a strong anterior cingulum and its protocone is large in *N. donnezani* and *N. tingi* from Megalo. On the other hand, the upper carnassial is slender, its protocone is small, and the anterior cingulum is weak or absent on *N. tingi* holotype from the Yushe Basin. Based on this last criterion, the specimen from Jradzor resembles *N. tingi* from the Yushe Basin. At last, Daguinet & Sen (2019) compare the position of the anterior depression between the protocone and paracone. In *N. donnezani*, it is moderately deep, while in *N. tingi* it is more lingual. On the specimen from Jradzor, the anterior embayment is placed at the base of the ridge running the anterior face of the paracone, and slightly lingually deflected. Based on these descriptions, it seems like the P4 of the Armenian skull bears both *N. tingi* and *N. donnezani* features. When comparing the upper molars, other differences can be pointed out. Indeed, in *N. tingi* from the Yushe Basin, the paracone of the M1 is larger than the metacone, while in *N. donnezani* and *N. tingi* from Megalo, they are of equal size. On the M1 of JRD - 20/03, the metacone is smaller than the paracone, which resembles the first upper molar of *N. tingi* from the Yushe Basin. Moreover, the metaconule of the M1 from *N. donnezani* from Calta is well developed and slightly taller than the protocone, while the metaconule of the M1 of the skull from Jradzor is clearly smaller than the protocone. The hypocone of the first upper molar also show variability: it is small and barely differentiated from the lingual cingulum in *N. tingi* and *N. donnezani* from Calta, while it is enlarged and differentiated from the lingual cingulum in *N. donnezani* from Layna. Both states are found in *N. donnezani* from Perpignan. On the specimen from Jradzor, the hypocone is quite hard to distinguish from the cingulum, that is very well developed. At last, Daguinet & Sen (2019) use the metaconule of the M2 to compare both species: it is smaller than the protocone in both species, but underdeveloped in *N. tingi* from the Yushe Basin, as in JRD - 20/03. Finally, we can use the lower molars to distinguish *N. tingi* from *N. donnezani*. On the m1, the transverse cristid uniting the hypoconid to the entoconid is well-developed in *N. tingi* and the specimen from Jradzor (Tedford et al. 1991), which is not the case in *N. donnezani*. Still according to Daguinet & Sen (2019), the entoconid of the m1 is poorly differentiated as a low crest on the lingual border of the talonid in *N. tingi*, while it is a discrete conical or crest like cusp in *N. donnezani*. In the specimen from Jradzor, it could be described as “reduced relative to hypoconid, but retains cristid”. Based on these descriptions, the specimen from Jradzor resembles *N. donnezani* the most, since the entoconid is not “poorly differentiated”. Daguinet & Sen (2019) also compare the length ratio over the width of the m1: it is less than or equal

to 2.5 in *N. donnezani*, and greater than 2.5 in *N. tingi*. With a ratio of 2.6, JRD - 20/03 bears another *N. tingi* feature. Concerning the m2, the entoconid, metaconid and cingulum show differences between the two species. The entoconid is systematically not reduced in *N. donnezani*, while it can be both reduced or not in *N. tingi*. Since it is present on the mandible from Jradzor but not well individualized, it is closer to *N. tingi* than *N. donnezani*. The metaconid is then compared to the protoconid: it is almost as large as the protoconid in *N. donnezani*, and smaller or absent in *N. tingi*. But based on the Fig. 1 of Tedford et al. (1991), the metaconid of the *N. tingi* holotype seems as developed as the protoconid, so there could be some variability within the species. Since the metaconid and entoconid are both well developed in the mandible from Jradzor, it resembles both *N. donnezani* and *N. tingi*. At last, the anteriolingual cingulum is absent or weak in *N. tingi*, or present and well-marked in *N. donnezani*, as in JRD - 19/03. To conclude, the specimen from Jradzor bears *N. tingi* and *N. donnezani* features, but seems to be close to the *N. tingi* from the Yushe basin. Moreover, the morphometric data (Table 7 and 8) show that the size of the specimen from Jradzor doesn't correspond to *N. donnezani*: indeed, it is larger than the specimens documented at this day. Based on morphologic and morphometric data, the skull and mandible found in Jradzor undoubtedly belong to *N. tingi*.

Table 8a - Upper teeth (I1 – P1) measurements of JRD - 20/03, JRD - 21/01, *N. donnezani*, *N. vulpinus*, *N. tingi*, *N. procyonoides* and *N. megamastoides* (length x width) in mm (*N. donnezani*, *N. vulpinus*, *N. tingi*, *N. procyonoides* and *N. megamastoides* : data taken from the literature : : Sickenberg (1968)⁷, Tedford (1991)⁵, Ginsburg (1998)⁷, Monguillon (2004)^{1 & 4 & 6}, Rook (2017)⁷, Lucenti (2017)², Dagueneat & Sen (2019)³) *Data completed with measurements of specimens from the NMB collections

	JRD - 20/03		JRD - 21/01	<i>N. donnezani</i>					<i>N. vulpinus</i> ⁴		<i>N. tingi</i> ⁵		<i>N. procyonoides</i> ⁶		<i>N. megamastoides</i> ⁷		
	right	left		n	Perpignan ¹	n	Layna ²	n	Calta ³	n	St Vallier	n	China	n	Eurasia	n	Eurasia
I1	L	3,36	3,48											2	2,55 [2,5 - 2,6]		
	W	3	3,07											2	2,1 [2 - 2,2]		
I2	L	4	4,1											2	2,95 [2,9 - 3]		
	W	3,84	3,85											2	2,8 [2,8 - 2,8]		
I3	L	4,76	4,29											2	3,15 [2,8 - 3,4]		
	W	4,69	4,95											2	2,7 [2,6 - 2,8]		
C	L	7,73	7,96	4	6,5 [5,8 - 7,1]	2	6,8 [6,4 - 7,2]	1	7,1	6	6,1 [5,6 - 6,5]	2	7,55 [6,6 - 8,5]	2	5,4 [5,3 - 5,5]	3	5,73 [5,4 - 6,1]
	W	4,71	4,81	4	3,9 [3,7 - 4,3]	2	4,45 [4,3 - 4,6]	1	4,7	7	4,1 [3,8 - 4,4]	2	4,95 [4,3 - 5,6]	2	3,65 [3,5 - 3,8]	2	3,7 [3,7 - 3,7]
P1	L	\	4,73	2	4,5 [4,4 - 4,6]	1	3,8			8	4,1 [3,8 - 4,4]	2	4,7 [4,6 - 4,8]	78	3,5 [2,8 - 4,5]	6	4,27 [3,7 - 4,7]
	W	\	2,86	2	2,7 [2,6 - 2,8]	1	2,5			8	2,7 [2,6 - 3,2]	2	2,8 [2,6 - 3,0]	2	2,05 [2 - 2,1]	4	2,85 [2,5 - 3,2]

Table 9b - Upper teeth (P2 – M2) measurements of JRD - 20/03, JRD – 21/01, N. donnezani, N. vulpinus, N. tingi, N. procyonoides and N. megamastoides (length x width) in mm (N. donnezani, N. vulpinus, N. tingi, N. procyonoides and N. megamastoides : data taken from the literature : : Sickenberg (1968)⁷, Tedford (1991)⁵, Ginsburg (1998)⁷, Monguillon (2004)^{1 & 4 & 6}, Rook (2017)⁷, Lucenti (2017)², Daguinet & Sen (2019)³ *Data completed with measurements of specimens from the NMB collections

	JRD - 20/03		JRD - 21/01	N. donnezani						N. vulpinus ⁴		N. tingi ⁵		N. procyonoides ⁵		N. megamastoides ⁷		
	right	left		n	Perpignan ¹	n	Layna ²	n	Calta ³	n	St Vallier	n	China	n	Eurasia	n	Eurasia	
P2	L	\	8,38	1	6,8	2	7,15 [6,5 - 7,8]			13	7,3 [6,6 - 7,9]	2	7,9 [7,0 - 8,8]	87	5,5 [4,2 - 6,7]	8	6,74 [6 - 7,2]	
	W	\	3,16	2	2,8 [2,8 - 2,8]	2	2,85 [2,8 - 2,9]			12	2,9 [2,6 - 3,2]	2	3,45 [3,4 - 3,5]	2	2,4 [2,3 - 2,5]	6	2,88 [2,6 - 3,3]	
P3	L	9,89	9,95	8,8	2	8,3 [8,3 - 8,4]				9	8,5 [7,5 - 9,1]	2	9,3 [8,9 - 9,7]	99	6,5 [5,4 - 8]	7	7,93 [7 - 8,6]	
	W	3,47	3,6	3,8	2	3 [2,9 - 3,1]				9	3,2 [3 - 3,5]	2	3,95 [3,9 - 4]	2	3,05 [3 - 3,1]	5	3,26 [2,8 - 3,6]	
P4	L	15,26	15,23	13,7	5	13,9 [13 - 14,6]	4	13,83 [13,1 - 15,1]	6	15,2 [15 - 15,3]	20	14,8 [13,4 - 16,5]	2	14,5 [13,3 - 15,8]	123	10 [8,6 - 11,9]	9	13,21 [11,9 - 15,4]
	W	6,97	7,09	6,1	4	6,4 [6,2 - 6,9]	4	6,68 [6,1 - 7,4]	5	7,3 [7,2 - 7,8]	25	6,6 [5,8 - 7,6]	2	7,55 [7,1 - 8,0]	123	5,3 [4,2 - 6,6]	10	6,25 [5,6 - 7,2]
M1	L	12,63	12,5	11,2	5	10,4 [10,2 - 10,5]	5	10,13 [9,7 - 10,7]	8	11,6 [10,8 - 12,2]	25	10,6 [10,2 - 11,8]	2	10,9 [9,8 - 12]	125	8,4 [6,9 - 10,1]	13	10,96 [10 - 11,7]
	W	13,8	14,3	12,8	5	11,3 [11 - 11,6]	4	11,2 [10,5 - 11,9]	8	13,4 [11,9 - 14,5]	21	11,7 [11,1 - 13,2]	2	13,7 [12,5 - 14,9]	125	9,1 [7,8 - 10,2]	11	12,29 [10,4 - 13,7]
M2	L	8,39	8,6		5	7,5 [7,1 - 7,8]	3	6,77 [6,4 - 7,1]	5	8,5 [7,3 - 9,7]	17	6,6 [5,6 - 7,1]	2	7,5 [6,8 - 8,2]	125	5,3 [3,5 - 6,8]	12	7,24 [6,5 - 7,7]
	W	11,5	11,98		5	8,7 [8,5 - 8,8]	3	8,47 [8,1 - 9]	5	11,2 [10,9 - 11,5]	16	7,9 [7,3 - 8,9]	2	9,4 [8,6 - 10,2]	125	6,1 [3,6 - 7,5]	10	8,89 [7,1 - 10,1]

Table 10 - Lower teeth measurements of JRD - 19/03, N. donnezani, N. vulpinus, N. tingi, N. procyonoides, N. megamastoides and N. sinensis (length x width) in mm (N. donnezani, N. vulpinus, N. tingi, N. procyonoides*, N. megamastoides* and N. sinensis : data taken from the literature : Tedford⁵ (1991), Koufos⁷ (1993), Ginsburg⁷ (1998), Monguillon et al.^{1 & 4 & 6} (2004), Rook et al.⁷ (2017), Lucenti² (2018), Lucenti⁸ (2019), Daguinet & Sen (2019)³ *Data completed with measurements of specimens from the NMB collections

	JRD - 19/03		N. donnezani						N. vulpinus ⁴		N. tingi ⁵		N. procyonoides ⁶		N. megamastoides ⁷		N. sinensis ⁸	
	n	Perpignan ¹	n	Layna ²	n	Calta ³	n	St Vallier	n	China	n	Eurasia	n	Eurasia	n	China		
c	L	6,4	5	6,4 [5,3 - 6,8]	5	6,6 [6,1 - 6,8]	1	8	11	6,1 [5,2 - 6,8]	6	8,76 [8 - 9,6]	2	4,8 [4,8 - 4,8]	4	5,7 [4,5 - 7,1]		
	W	5,3	3	4,1 [3,6 - 4,5]	5	4,3 [4 - 4,5]	1	5,1	10	4,2 [3,4 - 4,8]	6	5,7 [5,3 - 6]	2	3,2 [2,9 - 3,5]	4	3,95 [3,6 - 4,4]		
p3	L	8,25	6	8,1 [7,7 - 8,6]	1	4,5	3	8,8 [8,4 - 9]	13	8,5 [7,5 - 9,2]	9	9,78 [3 - 10,6]	100	6 [4,9 - 7,3]	4	7,7 [7,4 - 8,1]		
	W	3,38	5	3 [2,8 - 3,1]	1	2,7	3	3,5 [3,4 - 3,6]	11	3,3 [3 - 3,6]	9	4,13 [3,8 - 4,5]	2	2,75 [2,6 - 2,9]	4	3 [2,8 - 3,2]		
p4	L	10,69	4	9,7 [8,6 - 10,7]	3	9,07 [9 - 9,1]	3	10 [9,8 - 10,2]	16	9,7 [9 - 10,3]	11	11,2 [10,2 - 12,1]	114	7 [5,7 - 9]	4	8,7 [8,3 - 9,1]		
	W	4,54	4	3,83 [3,6 - 4,1]	2	3,7 [3,5 - 3,9]	3	4,4 [4,2 - 4,7]	16	4,2 [3,7 - 4,7]	11	5,24 [4,9 - 5,9]	90	3,6 [3 - 4,5]	4	3,88 [3,6 - 4,2]		
m1	L	17,78	7	15,7 [14,6 - 17,3]	5	14,96 [13,6 - 15,7]	4	16,3 [15,4 - 17,6]	20	15,9 [14,7 - 16,8]	9	18,22 [17,5 - 19,3]	129	12,1 [10,1 - 13,8]	7	14,57 [13,5 - 15,9]	22	15,83
	W	6,82	7	6,3 [5,8 - 6,8]	4	5,93 [5,2 - 6,4]	4	7,2 [6,5 - 8]	20	6,4 [5,8 - 7,1]	9	7,19 [6,7 - 7,9]	129	5,1 [4,3 - 5,8]	7	6,21 [5,4 - 7,7]	22	6,47
m2	L	10,35	8	8,4 [7,9 - 9,1]	4	8,28 [7,8 - 8,9]	4	9,8 [9,1 - 10,5]	12	8,4 [7,7 - 9,1]	9	9,3 [8,8 - 10]	128	6,5 [5,2 - 8]	5	8,48 [7,9 - 8,9]	22	8,59
	W	7	8	5,7 [5,2 - 6,2]	3	6,13 [5,4 - 6,7]	4	7 [6,2 - 7,8]	12	5,9 [5,5 - 6,5]	9	6,76 [6 - 7,5]	127	4,3 [3 - 5,2]	5	6,08 [5 - 7,5]	22	6,29

2.2.1.2. *Nyctereutes cf vulpinus*

Referred material: right P3, right P4, right M1 (JRD - 21/01) (Figure 10)

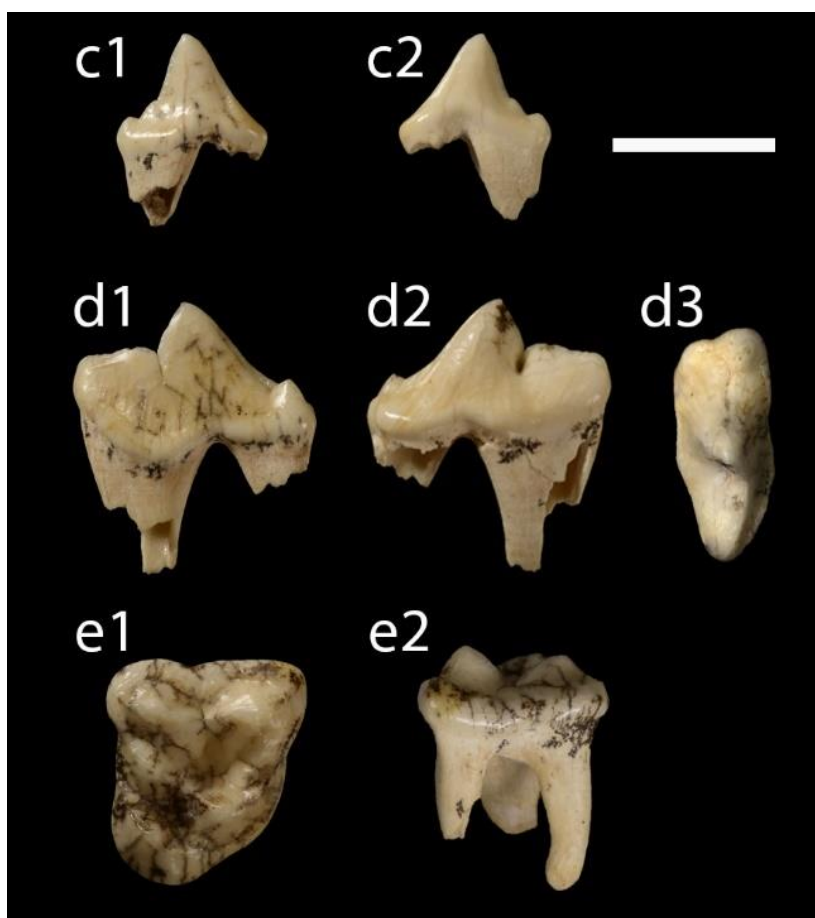


Figure 10 - *Nyctereutes cf vulpinus* from Jradzor (c - e): c Right P3 (JRD - 21/01) in lingual view (c1) and labial view (c2), d right P4 (JRD - 21/01) in lingual view (d1), labial view (d2) and occlusal view (d3), c right M1 (JRD - 21/01) in occlusal view (e1) and lingual view (e2). Scale bar equals 1 cm

Description: The premolars are double rooted. Their anterior root is missing, while the anterior part of the posterior root is broken. The P3's main cusp is sharp and bears a ridge on its posterior cutting edge, along with a small posterior accessory cusp and a posterior cingulum. The main cusp's anterior cutting edge is longer than the posterior one. The P4's paracone is short and sharp, and separated from the metastyle, long and cutting, by a notch. The protocone is sharp but small, and located on the paracone's anterior-lingual margin, so that the P4's anterior margin is almost linear. A lingual cingulum runs on the lingual side of the metastyle. The upper carnassial has 3 roots: a lingual, partially broken, and 2 labials. Its occlusal outline is sub-triangular. The paracone and the metacone are similar in size, sharp and quite

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small. Lingually, a posterior-lingual cingulum thickens into a well-developed hypocone. The metaconule is almost as developed as the protocone, while the paraconule is vestigial.

Discussion: Considering the few materials at our disposal, it is hard to identify those specimens for sure, but they show similarities with the *Nyctereutes vulpinus* from Saint-Vallier. The M1 from Jradzor is relatively large antero-posteriorly, massive, bears small labial cuspids of equal size and a relatively small basin, which is a typical *Nyctereutes* feature (Viret (1954), Soria & Aguirre (1976), Ginsburg (1998), Werdelin & Peigné (2010)). These specimens can be distinguished from *N. procyonoides* by their size (Table 7a and 7b). Lucenti (2017) compared the P4 morphology of some *Nyctereutes* species. JRD - 21/01 can be distinguished from *N. sinensis* from the Yushe basin by the position of the P4's protocone: indeed, it "lies far anterior of the anterior margin of the paracone" in *N. sinensis*, while it doesn't exceed by much the anterior margin of the P4 on the specimen from Jradzor. *N. donnezani* from Depéret (1890) shows a strong embayment on the anterior margin of the tooth, separating the protocone from the paracone. That embayment is absent on the P4 from Jradzor; on the contrary, the anterior margin of the P4 of JRD - 21/01 is straight like in *N. vulpinus* and *N. megamastoides*. The protocone of *N. megamastoides* and *N. donnezani* is deported lingually. It is not the case on the *N. vulpinus* from Saint Vallier, and that resembles the condition seen in the P4 from Jradzor. This affirmation is nuanced by Daguénet & Sen (2019), who describe two configurations in the *Nyctereutes* from Saint Vallier: the protocone on the P4 can either "extend anterolingually beyond anterior end of paracone", or "extend more lingually and not beyond anterior end of paracone". In their study, Daguénet & Sen (2019) provide a Matrix of characters based on 32 characters. According to this Matrix, the presence or absence of a posterior cusp on the P3 is variable. Still, this cusp is present on 2 of 3 of the studied *N. megamastoides*, and weak or absent on *N. vulpinus* and *N. sinensis*. This cusp is present on the posterior cutting edge of the P3 from Jradzor, but not free of the main cusp. The matrix also provides some interesting M1 characteristics: on *N. vulpinus* and *N. donnezani*, the lingual part of the tooth is narrow, while it is larger in *N. megamastoides*. Both situations can occur in *N. sinensis*. The hypocone shows some variability, even within a species: it can be either small and barely differentiated from the lingual cingulum, or enlarged and differentiated from the lingual cingulum. Both situations can occur in *N. donnezani*, *N. vulpinus* and *N. sinensis*, but *N. megamastoides* is characterized by the

second situation. The M1 found in Jradzor has a rather narrow lingual part, and a strong lingual cingulum barely differentiated from the hypocone, which excludes *N. megamastoïdes*.

Still, there are some differences between JRD - 21/01 and the material from Saint Vallier. According to Lucenti (2017), *N. vulpinus* and *N. donnezani* bear a short metastylar blade and a mesio-distally long paracone. But compared with the P4 of JRD - 20/03, the paracone of JRD - 21/01 is relatively short and its metastyle rather long. Moreover, according to Daguinet & Sen (2019), on the *Nyctereutes* from Saint Vallier the protocone is large, and the anterior cingulum strong, which is not the case on the P4 from Jradzor that bears a rather small protocone. Moreover, Argent (2004), while describing the *Nyctereutes* from Saint Vallier found by Faure and Guérin in 1993 - 1996, mentions an anterior-lingual ridge on the paracone of the P4, absent on the specimen from Jradzor. Based on morphometric and morphologic data, the tooth found in Jradzor could belong to *N. vulpinus*.

2.3. Canidae indet.

Referred material: right i1 (JRD - 19/93), right i2 (JRD 20/24), right P2/left p2 (JRD - 19/94), left P2/right p2 (JRD - 19/5) (Figure 11).

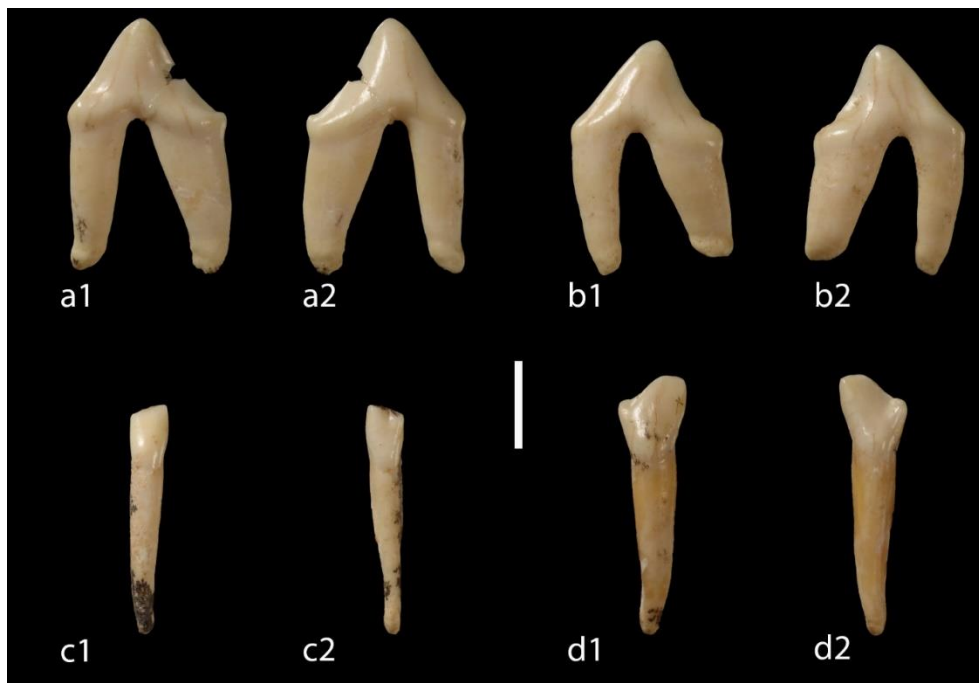


Figure 11 - Canidae indet. from Jradzor (a - c): a Left P2/right p2 (JRD - 19/5) in lingual view (a1) and labial view (a2), b Right P2/left p2 (JRD - 19/94) in labial view (b1) and lingual view (b2), c Right i1 (JRD - 19/93) in labial view (c1) and lingual view (c2), d Right i2 (JRD 20/24) in labial view (d1) and lingual view (d2). Scale bar equals 5 mm

Description: the incisors are single rooted. i1's occlusal outline is linear and culminates mesially. Its labial face is convex. i2's crown is asymmetrical: it bears a high main cusp and a small secondary lateral cusp. The premolars are double rooted. Their main cusp is sharp, and bears a ridge on its anterior and posterior cutting edge. The crown thickens slightly into a small bulge on the protoconid's posterior basis. The teeth measurements are reported in the Table 9.

Discussion: Due to a lack of diagnose criteria based on the incisors and the p2, and by lack of materials, we were unable to identify those specimens. We can not exclude the possibility of them belonging to one of the *Nyctereutes* species identified in Jradzor, but they could also belong to *Vulpes*, *Canis* or *Eucyon*.

Table 11 - Teeth measurements of Canidae indet.

	JRD - 19/93	JRD - 20/24	JRD - 19/94	JRD 19/5
L	2.8	3.6	8.4	9.1
W	2.2	4.0	3.1	3.6

3. Stratigraphic, biogeographical and ecological considerations

The Late Pliocene fauna of Jradzor includes two large hyenas, *Chasmaporthetes lunensis* and *Cf Pliocrocuta perrieri*, a small hyaena of the genus *Miohyaenotherium*, two raccoon dogs *Nyctereutes tingi* and *Nyctereutes cf vulpinus* and an undetermined *Canidae*.

The genus *Chasmaporthetes* is known in Eurasia from the Turolian to the Villafranchian (Kurtén & Werdelin, 1991). *C. lunensis* was first recorded at Olivola (MN 17) in Italy, and later on several occurrences from Spain, France, Germany, Italy, Greece, Ukraine, Turkey (Kurtén & Werdelin (1988), Turner et al. (2008)), China and Eastern Russia (Kurtén & Werdelin (1988), Werdelin & Solounias (1991), Sotnikova (1994)). This species is known from the latest Ruscinian to the late Villafranchian (Anton et al. (2006)), and some localities are close in age to the one of Jradzor : Calta in Turkey (Sen & Serac, 2017), Layna in Spain (Anton et al. 2006) and the Odessa Catacombs in Ukraine (Turner et al. 2008) are correlated to the MN 15 biozone, while the Spanish locality Villarroya, the French locality Etouaires, the Turkish locality Gülyazi (Anton et al. 2006) and the Greek locality Dafnero (Sen & Serac, 2017) are correlated to the MN 16 biozone. In Eurasia, the stratigraphic range of *Pliocrocuta perrieri* is quite wide; indeed, its earliest occurrence is Taoyang in China during the MN13 - 14 biozone, and it was last recorded during the MN18 biozone in Europe (Tseng et al. 2016). During the MN15 and MN16 biozones, it was recorded in Morocco (Ahl al oughlam), Tunisia (AinBrimba), Italy (Montopoli), Spain (Layna, Villarroya, El Rincon), France (Etouaires, Arde, Perpignan, Viallete), Turkey (Gulyazi), China (Niuwagou, Zhaozhuang, Zhangwagou, Xiachuang), Czech (Hajnacka) and Ukraine (Odessa Catacombs). Regarding the above-mentioned biostratigraphic information, these two species were common during the Late Pliocene of Eurasia, and are documented in localities relatively close to Jradzor such as Ukraine or Turkey. Moreover, according to Koufos (1993), it is very common to find *C. lunensis* and *P. perrieri* together in the Villafranchian localities. Indeed, these two large hyaenas are recorded in some identical localities, such as Perrier (Schaub, 1941), Saint Vallier (Viret, 1954), Sènèze (Schaub, 1943), Villarroya (Villalta, 1952), Layna (Crusafont & Aguirre, 1971), La Puebla de Valverde (Kurtén & Crusafont, 1977) and Upper Valdarno (Schaub, 1941). On the other hand, the genus *Miohyaenotherium* is not documented after the Turolian (MN 11-12), and is only known from the Ukraine (Belka), Moldavia

(Cimislia) and Georgia (Udabno) (Werdelin & Solounias, 1991). The presence of a representative of this genus in Armenia would make it its first occurrence during the Late Pliocene of Eurasia.

The two large hyaenas have different diet habits; indeed, even though they are both hypercarnivores, *Chasmaporthetes lunensis* is a hunting hyena (Kurtén & Werdelin (1988), Anton et al. (2006)), while *Pliocrocuta perrieri* is a bone-cracking species (Werdelin & Solounias, 1996). Anton et al. (2006) suggested that the small fossil record of *C. lunensis* could reflect its solitary lifestyle, while *P. perrieri*'s more furnished fossil record could reflect a group-denning scavenger. But, based on the shape of the muzzle and the elongated and gracile forelimbs, the authors suggest that *Chasmaporthetes* would “still require group action in order to kill medium and large prey”. Considering the similarities in their body size and the presence of adaptations for bone cracking in both species, Anton et al. (2006) point out the problem of the competition between the two species for the carcasses. While *P. perrieri*, due to its greater bone-cracking abilities, was well adapted to scavenging the carcasses of animals it had not hunted, *C. lunensis* would have used its crushing premolars on its own prey, and “not so much to consume scavenged carrion”. This could explain why, in sites where the presence of hyaenids is correlated to their capacity to scavenge carcasses of other animals, *P. perrieri* was more abundant. Moreover, regarding the relatively small size of the *Miohyaenotherium* genus, the individuals of this genus probably don't eat the same prey as the large hyaenids, so there is no competition on this aspect.

Concerning the two Canidae, the genus *Nyctereutes* is present in Eurasia since the Early Pliocene, and is nowadays represented by the single species *Nyctereutes procyonoides* in Asia (Lucenti, 2018). During the Pliocene, *N. tingi* was documented in the Zanda Basin and in Megalo, while the species *Nyctereutes vulpinus* was created for the specimens from Saint Vallier. Considering this data, it is surprising to find a *Nyctereutes cf vulpinus* and a *Nyctereutes tingi* in the same location, especially since *N. vulpinus* was never recorded elsewhere than in Saint Vallier. On the other hand, *N. vulpinus* co-existed with *C. lunensis* and *P. perrieri* in Saint Vallier while *N. tingi* is recorded in the Yushe Basin, where *C. lunensis* and *P. perrieri* are also documented.

To compare and estimate the dietary differences between extant species of the raccoon dogs, Lucenti (2018) and Asahara & Takai (2017) used the molar ratio method. Indeed, higher values of the molar ratio would imply a more omnivorous diet than lower ones. According to Lucenti (2018) and with a m2/m1 score of 0.48, *N. tingi*

would have had a relatively omnivorous diet but so would *N. vulpinus*, who's m2/m1 score is 0.49. If *Nyctereutes* species were already found in the same location (for example *N. tingi* and *N. sinensis* (relatively carnivorous) in the Yushe Basin (Lucenti et al. 2018)), it is quite surprising to find two species with the same dietary habits in the same locality.

Conclusion

This study was dedicated to the description and identification of the carnivores from Jradzor, an archeological excavation site from the Late Pliocene located at the foot of the Gegham volcanic province, in Armenia. It enabled us to highlight two large hyenas, *Chasmaporthetes lunensis* and *Cf Pliocrocuta perrieri*, a small hyaena of the genus *Miohyaenotherium*, two raccoon dogs *Nyctereutes tingi* and *Nyctereutes cf vulpinus*, and an undetermined *Canidae*.

The two large hyenas were common during the Late Pliocene of Eurasia, and were already found several times in the same localities. On the other hand, this would be the first occurrence of the genus *Miohyaenotherium* during the Late Pliocene of Eurasia. Even though the two large hyaenas had different diet habits – *C. lunensis* was a hunter while *P. perrieri* was a scavenger –, some authors point out the problem of the competition regarding the carcasses. Indeed, *C. lunensis* also bears some adaptations for bone-cracking. Still, *P. perrieri* was more adapted to scavenging carcasses, and this could explain why, in sites where the presence of hyaenids is correlated to their capacity to scavenge carcasses of other animals, *P. perrieri* was more abundant. Finally, concerning the *Miohyaenotherium* individual and regarding its relatively small size, it is very likely that it ate different preys, and thus was not in competition with the other species.

As for him, the genus *Nyctereutes* is present in Eurasia since the Early Pliocene, but the species *N. vulpinus* was created for the specimens from Saint Vallier and was never recorded elsewhere. Considering this data, it is unexpected to find this two *Nyctereutes* species in the same location. On the other hand, *N. vulpinus* co-existed with *C. lunensis* and *P. perrieri* in Saint Vallier while *N. tingi* is recorded in the Yushe Basin, where the two large hyaenas are also documented. Concerning their dietary habits, the two *Canidae* would both be omnivores, which makes it surprising to find them in the same locality.

The discovery and study of the Jradzor locality is a gold-mine in the field of the paleontology. Indeed, compared with other fossil collections in the area, Jradzor stands out by having the most diverse range of vertebrate species, including those from both aquatic and terrestrial environments. It plays a significant role in completing the MN15 mammalian zone in the South Caucasus biotic record, and represents an essential tie point for the Eurasian paleobiogeography.

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Titre : Les carnivores du Pliocène Terminal d'Arménie : Anatomie comparée et identification

Mots clés : Arménie, Pliocène Terminal, Identification, Carnivores, Ostéologie Comparée

Résumé : Jradzor est un site de fouilles archéologiques **arménien** où une faune intéressante a récemment été découverte. Parmi ses différents horizons, l'horizon JZ-7 (3.3 +/- 0.3 Ma) est caractérisé par son riche assemblage de mammifères du **Pliocène Terminal**. Durant 7 semaines, j'ai travaillé à l'**identification** des **Carnivores** de cet horizon au sein du JURASSICA Museum de Porrentruy. A partir d'une étude bibliographique et d'un travail d'**ostéologie comparée**, j'ai pu discerner 5 espèces de carnivores : 3 d'hyènes (*Chasmaporthetes lunensis*, Cf. *Pliocrocuta perrieri* et *Miohyaenotherium* sp.) et 2 de canidés (*Nyctereutes tingi* et *Nyctereutes* cf. *vulpinus*). Une partie du matériel n'a pas pu être identifiée par manque de critères de diagnose. L'identification de ces spécimens permettra de mieux comprendre l'histoire évolutive et la répartition stratigraphiques des espèces identifiées. Elle fournit également du matériel de comparaison intéressant pour les diagnoses futures.

Title : The carnivores of the Late Pliocene of Armenia: Comparative Anatomy and Identification

Key words: Armenia, Late Pliocene, Identification, Carnivores, Comparative Osteology

Abstract: Jradzor is a locality in **Armenia** where an interesting fauna was recently discovered. Among its different horizons, the horizon JZ-7 (3.3 +/- 0.3 Ma) is characterized by its large mammalian assemblage of the **Late Pliocene**. For 7 weeks, I worked on **identifying** the **carnivores** from this horizon at the JURASSICA Museum in Porrentruy. Based on a bibliographic study and on **comparative osteology**, I could identify 5 species: 3 species of hyenas (*Chasmaporthetes lunensis*, Cf. *Pliocrocuta perrieri* and *Miohyaenotherium* sp.) and 2 species of canids (*Nyctereutes tingi* and *Nyctereutes* cf. *vulpinus*). A part of the material was left unidentified due to a lack of diagnose criteria. Thanks to the identification of these specimens, we will have a better comprehension of the evolutive and stratigraphical history of the identified species. It also provides some interesting comparison material for the future identifications.