NYCTEREUTES TEMMINCK, 1838 (MAMMALIA, CANIDAE): A REVISION OF THE GENUS ACROSS THE OLD WORLD DURING PLIO-PLEISTOCENE TIMES

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BULLET-POINTS ABSTRACT

- Although *Nyctereutes* is nowadays monospecific, the fossil record suggests a larger diversity and wider distribution.
- The study of large sample from numerous sites of the Old World allowed a critical revision at an intercontinental scale.
- Some specimens of Layna and the sample from Çalta reveal peculiar morphologies, contrasting with the attribution to *N. donnezani*.
- The peculiarities of two samples testify to the urge for new research on fossil *Nyctereutes*.

INTRODUCTION

Nyctereutes Temminck, 1838 is nowadays represented by the single species *Nyctereutes procyonoides* (Gray, 1834). This taxon inhabits two separated areas of Eurasia (Ward & Wurster-Hill, 1990): a natural one (spanning from the Eastern part of Russia, China, Korean peninsula and Japan) and an artificial one resulted from the accidental or intentional introduction during the 1920s and 1930s across Eastern and Central Europe (from Finland to Hungary and from France to the Caucasus). On the contrary, the fossil record reveals a much greater diversity as up to 10 species have been described in literature (Bates, 1937; Rook et al., 2017). Furthermore, the fossil distribution range was not limited to Eurasia since *Nyctereutes* spp. were recovered also from several regions of Africa (see among others Werdelin & Dehghani, 2011).

The dentognathic features possessed by *N. procyonoides* are diagnostic for the genus and, at least part of them, were acquired by the extant raccoon-dogs' ancestors as the result of progressive adaptations towards a hypocarnivorous diet. Among these characteristics, there are the reduction of slicing portions of the carnassials and enlargement of the crushing surface of the molars, the developed subangular lobe, the expansion of the angular process, and the development of the insertion areas of the muscle pterigoideus medialis, on the medial side of the mandible.

Thanks to a considerably large sample from more than twenty-five sites across the Old World, this study combines the summary of the state of art of the past research on the genus *Nyctereutes* together with the most recent findings in the Old World.

MATERIALS AND METHODS

The fossil sample studied for this research comes from numerous Eurasian and African localities, housed in several institutions (See Table 1). The considered species are *Nyctereutes abdeslami* Geraads, 1997, *Nyctereutes barryi* Werdelin & Dehghani, 2011, *Nyctereutes donnezani* (Depéret, 1890), *Nyctereutes megamastoides* (Pomel, 1842), *Nyctereutes sinensis* (Schlosser, 1903), *Nyctereutes tingi* Tedford & Qiu, 1991, *Nyctereutes terblanchei* Ficcarelli et al., 1984, *Nyctereutes vulpinus* Soria and Aguirre, 1976. The extant comparative sample includes specimens of *N. procyonoides*, *Vulpes vulpes* (Linnaeus, 1758), *Vulpes lagopus* (Linnaeus, 1758) and *Cerdocyon thous* Smith, 1839 housed in the MZUF and AMNH (See abbreviation below).

Institutional abbreviations

AMNH, American Museum of Natural History, New York (U. S. A.); AUT, Aristotle University Thessaloniki (Greece); GNM, Georgian National Museum, Tbilisi (Georgia); IGF, Geological and Paleontological Section of the Natural History Museum of the University of Florence; MdC, Musée des Confluences, Lyon (France); MNCN, Museo Nacional de Ciencias Naturales, Madrid (Spain); MNHN, Musée National d'Histoire Naturelle, Paris (France); MZUF, La Specola, Zoological section of the Natural History Museum of the University of Florence; UCBL-1, Université Claude-Bernard Lyon-1, Lyon (France).

DISCUSSIONS

The Old world record of *Nyctereutes*: an update

The earliest occurrences of the genus is in the Yushe

Species	Locality	Repository
<i>N. tingi</i>	Yushe Basin (Liujiagou, Nanzhuanggou) (China); Megalo Emvolon (Greece)	AMNH
<i>N. sinensis</i>	Yushe Basin (Beihai, Liujiagou, Xiachuang, Zhangwagou, Zhaozhuan), Nihewan Basin (China)	AMNH, MNHN
<i>N. donnezani</i>	Perpignan-Roussillon (France); Layna, La Gloria 4* (Spain)	AMNH, MdC, MNCN, UCBL-1
<i>N. vulpinus</i>	St. Vallier (France)	MdC, UCBL-1
<i>N. megamastoides</i>	Senéze, Perrier-L'Etouaires (France); Kvabebi (Georgia); Dafnero (Greece); Csarnota, Beremend (Hungary); Montopoli, S. Giusto (Italy); El Rincon, Villarroya (Spain)	AUT, GNM, HMNH, IGF, MNCN, MNHN, UCBL-1
<i>N. abdeslami</i>	Ahl al Oughlam (Morocco)	MNHN
<i>N. terblanchei</i>	Kroomdrai A* (South Africa)	IGF
? <i>N. barryi</i>	Upper Laetoli Bed* (Tanzania)	MNHN
<i>Nyctereutes</i> sp.	Çalta (Turkey)	MNHN

Tab. 1. List of the considered sample for this study: the species of *Nyctereutes*, the localities where they come from and the institutions in which they are housed in.

basin (China, ~MN14-15, [Tedford et al., 2013](#)) with the primitive species *N. tingi* (Fig. 1A). Its morphologies strongly differ from all the other *Nyctereutes* spp. for the modest or scarce development of mandibular and dental features (as pointed out by [Tedford & Qiu, 1991](#)). Around 4-3.5 Ma, there is a first burst in diversity (Fig. 1B): i) firstly, the African record starts at this time with the dubious and primitive ?*N. barryi* from the Upper Laetoli Bed (Tanzania); ii) secondly, the occurrence of *N. sinensis*, in the same Chinese basin of *N. tingi*, which marks the appearance of a taxon that resembles the extant *N. procyonoides* for the degree of development of its dentognathic features. Then in Western Europe, *N. donnezani* was described from French and Spanish sites. Some authors deem that this first European species corresponds to *N. tingi* (see [Tedford & Qiu, 1991](#)). In contrast to the Asian record (see [Tedford et al., 2013](#)), during the late Pliocene in Europe, primitive and derived forms of raccoon-dogs never co-existed: *N. donnezani* was replaced by *N. megamastoides*.

A second burst is dated between 3.5-2 Ma (Fig. 1C). *N. megamastoides* appears in Europe at this time ([Bartolini Lucenti, 2017](#)), and, partially due to its large range of distribution (from Spain to Georgia, [Rook et al., 2017](#)), it is one of the most renowned fossil species of this genus. The retention of strongly derived dental and cranio-mandibular features in *N. megamastoides*, led some scholars to suggest the idea that this taxon

and *N. sinensis* are closely related ([Soria & Aguirre, 1976](#)), although some morphological differences remain ([Rook et al., 2017](#)). The sample from St. Vallier (France), historically attributed to *N. megamastoides* ([Viret, 1954](#); [Martin, 1971](#)) should be classified as a separate taxon from *N. megamastoides* and in this respect, for the presence of some features resembling the genus *Vulpes*, ([Soria & Aguirre, 1976](#)) suggested for this remains the attribution to the species *N. vulpinus*. Apart from the controversial taxon ?*N. barryi*, the African record of *Nyctereutes* is relatively scanty but diverse. Younger although still early Pliocene in age, the primitive *Nyctereutes lockwoodi* [Geraads et al., 2010](#) from Dikika (Ethiopia) shows several peculiar morphologies, which justify the separation in a different species. Other findings in Africa are the Early Pleistocene *N. abdeslami* from Morocco, and the South African *N. terblanchei* (both derived species).

After 2 Ma, and during the last part of the Early Pleistocene, the findings of *Nyctereutes* across the whole Old World become more and more scarce and the diversity of the genus declined. The first record of the extant *N. procyonoides* appears in Middle Pleistocene deposits of China (Zhoukoudian 1 and 13, [Tedford & Qiu, 1991](#)) and remained the only species of the genus until today, with the exception of the Palestinian *Nyctereutes vinetorum* [Bates, 1937](#) (which may simply represent a larger form of the extant species).

The record of Layna and Çalta

The ongoing revision of the material from two important localities referred to MN15 (Layna, Spain; Çalta, Turkey) yielded some unexpected results. In literature, these samples are referred to *N. donnezani* ([Soria & Aguirre, 1976](#); [Ginsburg, 1998](#)). Nevertheless, at Layna few specimens show morphological similarities and morphometric proportions that cannot be explained as intraspecific variability, as they suggest affinity with derived forms. The *Nyctereutes* from Çalta possesses an undeniable primitive-like morphology of the mandible corpus with a reduced subangular lobe (as noted by [Ginsburg, 1998](#)) albeit its dental proportions or the shape of the molars (especially upper ones) does not fit with the attribution to *N. donnezani*. On the contrary, the dental characters showed by the Çalta *Nyctereutes* are close to those of forms like *N. sinensis*, *N. vulpinus* or, even more, *N. megamastoides*.

CONCLUSIONS

The fossil record of the genus *Nyctereutes*, spanning in whole Old World in the last 5 Ma, testifies to a great variety in morphologies and adaptations in diet. Many scholars have investigated the evolutionary history of this genus, yet many issues are still matters of debate and fertile grounds for research (e.g., the phylogenetic relationships between the species). This short overview of *Nyctereutes* spp. summarizes our current know-

Fig. 1. Geographic and temporal distribution of *Nyctereutes* spp. from the earliest Early Pliocene to present times across the Old World. **A**, earliest Early Pliocene, 5.3-4.5 Ma. **B**, Early-Late Pliocene, 4.5-3.5 Ma. **C**, Latest Pliocene-Early Pleistocene (*partim*), 3.5-1.5 Ma. **D**, Middle Pleistocene-Present times, 800-0 ka.

ledge of their diversity and evolutionary history, and points out peculiar two cases (i.e. those of Layna and Çalta), which certainly require deep studies in the future. Should the hypothesis of an early appearance of form with mixed pattern of morphologies in the MN15 be validated, it could reveal the presence in the Early Pliocene of an alternative lineage of raccoon-dogs, with serious implications on *Nyctereutes* dispersion and evolution across the Palearctic, the Afrotropical and the Indomalayan regions.

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