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(Canidae, Carnivora, Mammalia)
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ABSTRACT

The locality of Çalta has yielded one of the richest collection of fossil canids belonging to the raccoon dog genus *Nyctereutes* Temminck, 1838. This locality is situated in central Anatolia and its age is determined as early Pliocene, *c.* 4 Ma. Ginsburg (1998) studied these canid remains and identified them as *N. donnezani*, which was previously known from some early Pliocene localities in southern France and Spain. Some later studies questioned this attribution. The present study provides a new description of all available material, housed in collections in Paris, Lyon and Ankara, and a detailed comparison of the cranial and dental characters with other known species of *Nyctereutes*. This study is completed by a cladistic analysis of cranial and dental characters to document the phylogenetic relationships of the Çalta raccoon dog. This analysis was done on the locality-based data, using the main occurrences of each species. Both morphological and cladistic analyses favour attribution of the Çalta raccoon dog to *N. donnezani*, in agreement with Ginsburg (1998). In addition, this study reveals that possible sexual dimorphism in the size and proportions of some cranial elements, such as stronger sagittal and nuchal crests, a better defined temporal line, a thicker zygomatic process of the maxillary bone, a braincase that is elongated but less round and, in particular, stronger subangular lobe in male individuals.

KEY WORDS
Canidae,
Nyctereutes,
Pliocene,
Turkey,
phylogeny,
sexual dimorphism.

RÉSUMÉ
Relations phylogénétiques de Nyctereutes *Temminck, 1838 (Canidae, Carnivora, Mammalia) du Pliocène inférieur de Çalta, Turquie.*
La localité de Çalta a livré l'une des plus riches collections de canidés fossiles appartenant au genre *Nyctereutes* Temminck, 1838. Cette localité est située en Anatolie centrale et elle est datée du Pliocène inférieur, *c.* 4 Ma. Ginsburg (1998) a étudié les carnivores de Çalta et a identifié les fossiles de chien viverrin comme *N. donnezani,* une espèce précédemment connue dans quelques localités du Pliocène inférieur du sud de la France et de l'Espagne. Certaines études ultérieures ont remis en cause cette attribution. La présente étude fournit une nouvelle description de tout le matériel disponible, hébergé dans les collections de Paris, Lyon et Ankara, ainsi qu'une comparaison détaillée des caractères crâniens et dentaires avec d'autres espèces connues de *Nyctereutes.* Cette étude est complétée par une analyse cladistique de caractères crâniens et dentaires afin de documenter les relations phylogénétiques du chien viverrin de Çalta. Cette analyse a été réalisée par gisement plutôt que par espèce, en utilisant les principales occurrences de chaque espèce. Les analyses morphologiques et cladistiques sont toutes deux en faveur de l'attribution du chien viverrin de Çalta à *N. donnezani,* comme l'avait précédemment fait Ginsburg (1998). En outre, cette étude révèle qu'un dimorphisme sexuel se manifeste dans la taille et les proportions de certains éléments crâniens, tels que des crêtes sagittales et nuchales plus fortes, une ligne temporelle mieux définie, un processus zygomatique du maxillaire plus épais, une boite crânienne allongée mais moins ronde et en particulier un lobe sous-angulaire fort chez les individus mâles.

MOTS CLÉS
Canidae,
Nyctereutes,
Pliocène,
Turquie,
phylogénie,
dimorphisme sexuel.

INTRODUCTION

The Old World Canidae are immigrants from North America where the earliest fossil occurrences date back to the middle Eocene, whereas the oldest representatives of the family in Eurasia are from the late Miocene (McKenna & Bell 1997). Among the representatives of this large family, the genus *Nyctereutes* Temminck, 1838 occupies a particular position in having a wide distribution all over the three continents of the Old World. The only extant species of this genus, the raccoon dog *N. procyonoides* (Gray, 1834), is naturally restricted to East Asia, i.e., SE Russia, eastern China, Korea, Japan and north Vietnam (Ward & Wurster-Hill 1990). It was introduced in western Russia in 1920s for fur production, and individuals who escaped from production centres gradually populated eastern and central Europe. At present the raccoon dog is known as an invasive species in Europe from western Russia and the Caucasus to eastern France and northern Italy, and from Romania to Norway (Kauhala & Kowalczyk 2011).

Fossil species of *Nyctereutes* are known from Europe, Asia and Africa. The earliest fossil occurrence of this genus goes back to around 7 Ma in China (Tedford & Qiu 1991; Tedford *et al.* 2009). The canid remains from the latest Miocene locality Venta del Moro in Spain that Morales & Aguirre (1976) initially referred to as *N.* cf. *donnezani,* were later identified as a new species of *Eucyon* by Montoya *et al.* (2009). The main occurrences of *Nyctereutes* in the Old World are of Pliocene and early Pleistocene age. According to different authors, eight to ten fossil species are recognized, in addition to the extant species *N. procyonoides.*

The early Pliocene locality of Çalta in Turkey has yielded relatively abundant and well-preserved remains of *Nyctereutes.* Ginsburg (1998) described these fossils and attributed them to *N. donnezani* (Depéret, 1890), the type locality of which is Perpignan in southern France. To date, this is the unique occurrence of raccoon dog in Turkey. Ginsburg (1998) compared the Çalta fossils with *N. donnezani* and *N. megamastoides,* in addition to *Vulpes* and *Canis.* However, this identification was not sufficiently convincing since, as we will see below, some later studies have questioned the assignment of the Çalta raccoon dog to *N. donnezani.*

In the neighbouring countries of Turkey, raccoon dog fossils are recorded in Greece, Bulgaria and Romania. From Greece, Koufos (1997) referred a skull from Megalo Emvolon to *N. tingi,* while the remains of *N. megamastoides* are reported from several localities of late Pliocene and early Pleistocene age (Koufos 1993; Athanassiou 1996; De Vos *et al.* 2002). In Bulgaria, Spassov (1997, 2003) mentioned the presence of *N.* cf. *tingi* in the early Pleistocene locality of Varshets. In Romania, Simionescu (1930, 1932) described some cranial remains as *Vulpes donnezani* from the early Pliocene localities of Malusteni and Beresti that Radulescu *et al.* (2003) referred to *Eucyon odessanus.* These authors also mentioned the presence of *N. megamastoides* in two latest Pliocene localities in Romania, La Pietris and Valea Graunceanului, however without any description or illustration. It appears that raccoon dog fossils in south-eastern Europe are preferably referred to *N. tingi* and *N. megamastoides,* while the unique record in Turkey from Çalta was identified as *N. donnezani* by Ginsburg (1998).

Koufos (1997) and Tedford *et al.* (2009) noted that *N. donnezani* and *N. tingi* are similar in size and morphology, although they preferred to maintain both species based on some differences in the skull and tooth morphology and geographical distance between their type localities, Perpignan in France and Liujiagou in the Yushe Basin, China, respectively. More recently, Spassov (2003), Rook *et al.* (2017), Bartolini

TABLE 1. — List of the species referred to the genus *Nyctereutes* Temminck, 1838 from Asia, Europe and Africa, with indication of their type localities and ages.

Species authors, year	Type localities	Age
N. abdeslami Geraads, 1997	Ahl al Oughlam, Morocco	Latest Pliocene
N. barryi Werdelin & Dehghani, 2011	Upper Laetolil Beds, Tanzania	3.63-3.85 Ma
N. donnezani (Depéret, 1890)	Perpignan, France	Early Pliocene
N. lockwoodi Geraads, Alemseged, Bobe & Reed 2010	Dikika, Ethiopia	*c.* 3.35 Ma
N. megamastoides (Pomel, 1843)	Perrier-Les Etouaires, France	*c.* 2.78 Ma; MN16b
N. procyonoides (Temminck, 1833)	East Asia, introduced in Europe	Recent
N. sinensis (Schlosser, 1903)	Nihowan, China	Late Pliocene
"*N.*" *terblanchei* (Broom, 1948)	Kromdraai A, South Africa	Between 1.8-2.0 Ma
N. tingi Tedford & Qiu, 1991	Liujiagou, Yushe Basin, China	Early Pliocene
N. vinetorum (Bate, 1937)	Mount Carmel, Israel	?Late Pleistocene
N. vulpinus Soria & Aguirre, 1976	Saint-Vallier, France	Latest Pliocene

Lucenti (2018) and Bartolini Lucenti *et al.* (2018) questioned the systematic assignment of the Çalta material, and they suggested referring it to *Nyctereutes* sp.

Another question is the sexual dimorphism that the species of *Nyctereutes* may display. In previous studies, we did not find any observations dealing with size and morphological differences between male and female individuals in fossil species of *Nyctereutes,* but some differences are known in the extant species (see below). The material from Çalta provides reliable morphological characters to address this issue.

Taking into consideration these remarks, we undertook a new study of the raccoon dog fossils from Çalta, and analysed its cranial and dental characters to build a matrix in order to investigate its relationships with species referred to the genus *Nyctereutes* using cladistic methods.

The locality of Çalta is situated about 50 km NW of Ankara in central Anatolia, Turkey. Its geographic coordinates are 40°14'21.8"N and 32°32'39.0"E. The geology of the Çalta region and its faunal content are studied in detail in a volume edited by Sen (1998). The fossiliferous horizon is situated in the upper part of the Sinap Formation in the Kazan Basin (see also Bernor & Sen 2017; Sen *et al.* 2017; Sen & Saraç 2018). The sediments of this formation consist of fluviatile and ephemeral lake deposits, which are particularly rich in vertebrate fossils (over one hundred localities) ranging in age from latest middle Miocene up to early Pliocene (Fortelius *et al.* 2003). The fossiliferous horizon at Çalta is a floodplain deposit in which bones are accumulated in a large pocket without apparent orientation. The Çalta locality yielded a rich and diverse vertebrate assemblage that consists of amphibians, reptiles, birds, and small and large mammals, in total 45 species including six carnivores (Ginsburg 1998; Sen 1998; Sen & Saraç 2018). This fauna indicates an early Pliocene age, correlated to Neogene mammalian zone MN 15.

MATERIAL AND METHODS

The material was collected in 1972 by a French-Turkish team and in 1977 by a team of the General Directorate of Mineral Research and Exploration (MTA, Ankara). The main part of the specimens is housed at the Natural History Museum of Paris (MNHN), except for a fragment of mandible that is in the collections of the University Claude Bernard in Lyon, and a palate with P4-M2 of both sides, an isolated M1 and two fragments of mandible with m1-m2 that are stored at the Natural History Museum of Ankara. The Paris material consists of two almost complete skulls, several lower jaw fragments and isolated upper and lower teeth. The specimens in the Paris collections are prefixed ACA (Ankara-Çalta), the lower jaw fragment preserved at the University Claude Bernard is numbered FSL 212 806, and the specimens at the Ankara Natural History Museum are either unnumbered or labelled AKÇ.

The nomenclature for description of cranial features follows Barone (1999) and for teeth Tedford *et al.* (2009). To compare the material of Çalta with other species, but also for the analysis of the morphological characters, we studied specimens belonging to several species of the genera *Nyctereutes*, *Vulpes* and *Canis* in the collections of the MNHN in Paris, and we also used all the literature allowing us to supplement these observations with specimens preserved in other institutions, in particular those studied by Depéret (1890), Boule (1889), Broom (1948), Viret (1954), Kurtén (1965), Martin (1971), Soria & Aguirre (1976), Kurtén & Crusafont Pairó (1977), Xue (1981), Tedford & Qiu (1991), Koufos (1993, 1997), Geraads (1997), Ginsburg (1998), Hidaka *et al.* (1998), Monguillon *et al.* (2004), Argant (2004), Geraads *et al.* (2010), Rook *et al.* (2017), Bartolini Lucenti (2017) and Bartolini Lucenti *et al.* (2018). Table 1 summarizes our current knowledge on the species referred to the genus *Nyctereutes*.

STATE OF PRESERVATION OF THE MATERIAL

It is important to consider the preservation state of fossils in descriptions of cranial and dental characters and to take this into account in the interpretations. The two skulls of *Nyctereutes* from Çalta show some deformation due to conditions during burial. The skull MNHN.F.ACA292 is slightly deformed and displays some anteroposterior distortion, as expressed in particular by the absence of symmetry in dorsal and ventral views (Fig. 1). The second skull, ACA291, has a much higher degree of deformation since it displays dorsal-ventral compaction, unequally distributed along the skull, and lateral deformation especially by the partial flattening of the left side, as seen in the parietal bone (Fig. 2). The zygomatic arches are incomplete, and the incisors, some canines, premolars and molars are lost.

ABBREVIATIONS

Institutions and collections

AKÇ   Ankara-Çalta, for specimens housed at the Natural History Museum of the General Directorate of Mineral Research and Exploration (MTA) in Ankara;

FSL   Faculté des Sciences de Lyon, now University of Claude Bernard, UFR Sciences de la Terre, where a fragment of mandible from Çalta is preserved.

MNHN   Muséum national d'Histoire naturelle, Paris, collection of Palaeontology;

MNHN.F.ACA   Ankara-Çalta, for specimens housed at the Muséum national d'Histoire naturelle, Paris, collection of Palaeontology.

Other abbreviations

L   length;
W   width.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family CANIDAE Fischer von Waldheim, 1817
Subfamily CANINAE Fischer von Waldheim, 1817

Genus *Nyctereutes* Temminck, 1838

TYPE SPECIES. — *Nyctereutes procyonoides* (Gray, 1834). Extant species, East Asia.

Nyctereutes donnezani (Depéret, 1890)

CRANIAL AND DENTAL REMAINS FROM ÇALTA

Two rather complete skulls (MNHN.F.ACA291, ACA292) belonging to fully adult individuals; damaged right upper canine (ACA300); right P4 on a piece of bone (ACA298); two isolated M1 (ACA296, ACA297); a palate (unnumbered) at the Natural History Museum of Ankara bearing right and left P4-M2 series; a left isolated M1 (AKÇ-136) at the same museum; right mandible with the alveolus of p1 and p2-m3 (ACA549); fragment of right mandible with p4-m2 (ACA294); fragment of right mandible with c-p3 (ACA295); fragment of left mandible with m1-m2 and alveolus of m3 (ACA387); fragment of left mandible with p4 and alveoli of p1-p3 (FSL-212806); right m1 on a piece of bone (ACA548); left lower canine (ACA299); fragment of left mandible with m1-m2 (AKÇ-134) and another fragment of left mandible with m1-m2 (unnumbered) in the collections of the Natural History Museum of Ankara. In addition to the cranial remains, there are a few postcranial bones that Ginsburg (1998) described and measured. They are not used in the present study.

DESCRIPTION AND COMPARISON

Skull

The description of the cranial and dental remains is largely inspired by Ginsburg (1998) who provided a detailed comparative description of the Çalta fossils with *Vulpes vulpes* (Linnaeus, 1758) and some species of *Nyctereutes*, in particular *N. donnezani* and *N. megamastoides* (Pomel, 1843).

In dorsal view, the Çalta skulls are narrow, elongated, and the muzzle thins progressively forward like in *Vulpes vulpes* but unlike in the extant *Nyctereutes procyonoides* (Gray, 1834), *N. sinensis* from China and *N. megamastoides* from western Europe, which have a much more massive skull and short muzzle. In dorsal view, the narrowing of the muzzle is progressive on the Çalta skulls, while it is abrupt in *N. sinensis* and *N. megamastoides*. The nasal bones are thin and long like in all other species of *Nyctereutes,* and they reach the level of the orbital constriction, distal to the maxillary-frontal suture. The posterodorsal part of the maxillae is slightly inclined as in *N. sinensis* and more than in *V. vulpes*. The postorbital processes are thick and well developed. They present a dorsal depression as in *V. vulpes*, *N. sinensis* and *N. megamastoides*. The ridges issuing from the distal margin of the postorbital processes join the sagittal crest behind the postorbital constriction, similar to *N. tingi* Tedford & Qiu, 1991. In *N. megamastoides*, *N. sinensis* and *N. procyonoides*, the fusion of the postorbital ridges with the sagittal crest takes place in the middle of the braincase, i.e. much more caudally than in *N. tingi* and in the skulls of Çalta. The sagittal crest is stronger than in *V. vulpes* and *N. megamastoides*. The braincase is curved as in the other species of *Nyctereutes* and *Vulpes.*

In lateral view, the jugal bone is larger in the specimens from Çalta than in *N. sinensis* and *V. vulpes*. The tympanic bullae are more rounded than in *V. vulpes* and *Canis lupus* (Linnaeus, 1758). The paroccipital process (or jugular process) is appressed to the tympanic bullae and descends ventrally the level or even below the level of the bullae. This process is much higher in *V. vulpes*, *N. tingi*, *N. sinensis* and *N. megamastoides*. The nuchal crest fully dominates the occipital surface. It is stronger than in *V. vulpes* and *C. lupus*, but is similar in thickness to that of *N. megamastoides*.

Ginsburg (1998) did not note that the two skulls from Çalta are different in size, MNHN.F.ACA291 being clearly larger than ACA292. In particular, the former is more robust and has stronger sagittal and nuchal crests, better defined temporal line and occiput structures, thicker zygomatic process of the maxillary bone, elongated but less rounded braincase, and thicker postarticular process.

An anecdote deserves to be mentioned here. When the second author (S. Sen) was cleaning and preparing the fossils from Çalta in 1974, Björn Kurtén (1924-1988), the famous Finnish vertebrate paleontologist, visited the Institute of Paleontology of the Museum in Paris. He came to see the Çalta fossils under preparation, and asked for carnivores. He took the two *Nyctereutes* skulls of Çalta in his hands, observed them for a while, and said only "Monsieur et Madame", and he left. We agree with B. Kurtén in considering the differences noted here above as due to sexual dimorphism. We will see that such differences also exist on the mandibles.

Mandible

The ascending ramus is broken in all of the seven fragments of mandible from Çalta, which all represent parts of the corpus and bear various numbers of teeth. The corpus is quite long

Fig. 1. — *Nyctereutes donnezani* from Çalta, central Turkey, early Pliocene. Skull MNHN.F.ACA292, probably belonging to a female individual, in dorsal (**A**), occipital (**B**), ventral (**C**) and right lateral (**D**) views. Scale bar: 50 mm.

TABLE 2. — Measurements (in mm) of upper and lower teeth of *Nyctereutes donnezani* from Çalta.

Tooth	Length		N	Width	
	Range	Mean		Range	Mean
C	–	7.1	1	–	4.7
P4	15.0-15.3	15.2	6/5	7.2-7.8	7.3
M1	10.8-12.2	11.6	8	11.9-14.5	13.4
M2	7.3-9.7	8.5	5	10.9-11.5	11.2
c	–	8.0	1	–	5.1
p1	–	4.3	1	–	2.5
p2	8.2-8.5	8.3	3	3.3-3.4	3.3
p3	8.4-9.0	8.8	3	3.4-3.6	3.5
p4	9.8-10.2	10.0	3	4.2-4.7	4.4
m1	15.4-17.6	16.3	4	6.5-8.0	7.2
m2	9.1-10.5	9.8	4	6.2-7.8	7.0
m3	–	5.3	1	–	4.6

and moderately thick, and its depth increases progressively backward, more so on specimen MNHN.F.ACA549 than on ACA294 and FSL-212806. The ventral margin is slightly convex, mainly below the p4 and the molars. The symphyseal process is well defined under the p2, interrupting the ventral profile of the body (Fig. 3). This process is apparently absent in the extant species, but variably present in fossil species of *Nyctereutes*.

One of the diagnostic features of *Nyctereutes* is the presence of the subangular lobe, which is the insertion ridge of the digastric muscle. This muscle links the corpus of the mandible to the paroccipital process. The digastric muscle is involved in all complex jaw action, mainly by pulling the lower jaw backward and pivoting it at the jaw joint to open the mouth. The subangular lobe is strong on the specimen MNHN.F.ACA549, similar in importance to that of *N. donnezani* from Perpignan and *N. tingi* from the Yushe Basin (Depéret 1890; Tedford & Qiu 1991), but weak on specimen ACA294 (Fig. 3). The lobe is stronger and placed distally in *N. megamastoides*, *N. sinensis* and *N. abdeslami* (Boule 1889; Depéret 1890; Teilhard de Chardin & Piveteau 1930; Viret 1954; Martin 1971; Tedford & Qiu 1991; Koufos 1993; Geraads 1997; De Vos *et al.* 2002; Rook *et al.* 2017), as well as in the extant species *N. procyonoides* (Hidaka *et al.* 1998). The degree of development of this lobe, which is weak in the species from late the Miocene/early Pliocene (*N. donnezani* and *N. tingi*), but strong in the younger species (*N. megamastoides*, *N. sinensis, N. abdeslami* and *N. procyonoides*), is used to distinguish species. However, as shown by the specimens from Çalta, the robustness of this lobe may also be due to sexual dimorphism. To quantify the importance of the subangular lobe, we calculated the index (depth of the body behind m2/ depth of the body in front of p4) × 100. This index is 148 on the mandible with a strong subangular lobe (ACA549), and 130 on the mandible with a weak subangular lobe ACA294. We hypothesize that this difference in the development of the subangular lobe is due to sexual dimorphism, a strong subangular lobe being characteristic of male individuals. This value is 147 for the type mandible of *N. donnezani* from Perpignan, 133 for the mandible of Layna, Spain, 123 for the type mandible of *N. tingi*, but 142 for the other mandible

referred to this species from the Upper Gaozhuang Formation (Tedford & Qiu 1991: fig. 1G). In other words, all these specimens are similar in the robustness of the subangular lobe if we consider that the large values indicate male individuals and the small values female individuals. This index cannot be applied to *N. megamastoides*, *N. sinensis*, *N. abdeslami* and *N. procyonoides* because in these species the subangular lobe is situated in a different position, as we will see below.

Another character of the subangular lobe is its position and shape. On specimen MNHN.F.ACA549 it extends from beneath the distal half of m1 to behind m3, and its distal margin is curved. The mandibles of *N. donnezani* from Perpignan and *N. tingi* from the Yushe Basin have a similar shape and position of the subangular lobe (Depéret 1890; Tedford & Qiu 1991). On the fragment of mandible from Layna (Soria & Aguirre 1976: pl. 2, fig. 1; Bartolini Lucenti *et al.* 2018: fig. 4A-C), the subangular lobe is weaker and starts a little more distally than on the type mandible from Perpignan. We suggest that the Layna hemimandible may represent a female individual of *N. donnezani*. Koufos (1997) referred to *N. tingi* a well-preserved skull from Megalo Emvolon, Greece, but its mandible is unknown. In *N. megamastoides* from Perrier (France) and from many other localities in Europe, *N. vulpinus* from St Vallier, *N. abdeslami* from Morocco, as well as in the extant species *N. procyonoides*, the ventral margin of the body is almost flat and the subangular lobe is situated more posteriorly, its maximum development being under the coronoid process. In *N. sinensis* from China, the ventral margin of the mandible is irregularly curved, and the subangular lobe is situated a little more anteriorly than in *N. megamastoides* and *N. abdeslami.*

Distal to the subangular lobe, MNHN.F.ACA549 displays an open angle between the subangular lobe and the base of the ascending ramus; this part is not preserved on the other specimens of Çalta. In the mandibles of *N. donnezani* from Perpignan and Layna, this angle is also a rather open curve. In *N. megamastoides, N. abdeslami* and *N. sinensis* the distal margin of the subangular lobe is almost vertical, and the angle between this lobe and the angular process is sharp. For this character, *N. vulpinus* displays an intermediate position.

The labial face has two mental foramina, the larger one is under the p1 at the mid depth of the body, and the second smaller one is under p3 and situated in the upper part of the body. In *N. tingi,* the second foramen is placed under the anterior root of the p3. Although there are two mental foramina in all species, their position is somewhat variable between individuals.

Judging by our reading of the literature, sexual dimorphism in fossil species of *Nyctereutes* is unknown. This may be partly explained by the limited number of specimens in most localities and their fragmentary nature, which is insufficient to demonstrate sexual dimorphism. However, some localities, such as Saint-Vallier (France, latest Pliocene) have yielded abundant remains of raccoon dog. The Saint-Vallier material has been studied by Viret (1954), Martin (1971) and Argant (2004) who referred it to *N. megamastoides*, by Soria & Aguirre (1976) who distinguished it as a new subspecies *N. megamastoides vulpinus,* and by Monguillon *et al.*

FIG. 2. — *Nyctereutes donnezani* from Çalta, central Turkey, early Pliocene. Skull MNHN.F.ACA291, probably belonging to a male individual, in dorsal (**A**), occipital (**B**), ventral (**C**) and right lateral (**D**) views. Scale bar: 50 mm.

(2004) who recognized a distinct species *N. vulpinus*. These authors did not mention any differences to be interpreted as sexual dimorphism in the Saint-Vallier assemblage.

On the other hand, Hidaka *et al.* (1998) and Kim *et al.* (2012) observed some features indicating sexual dimorphism in the extant species *N. procyonoides*, such as stronger canine width,
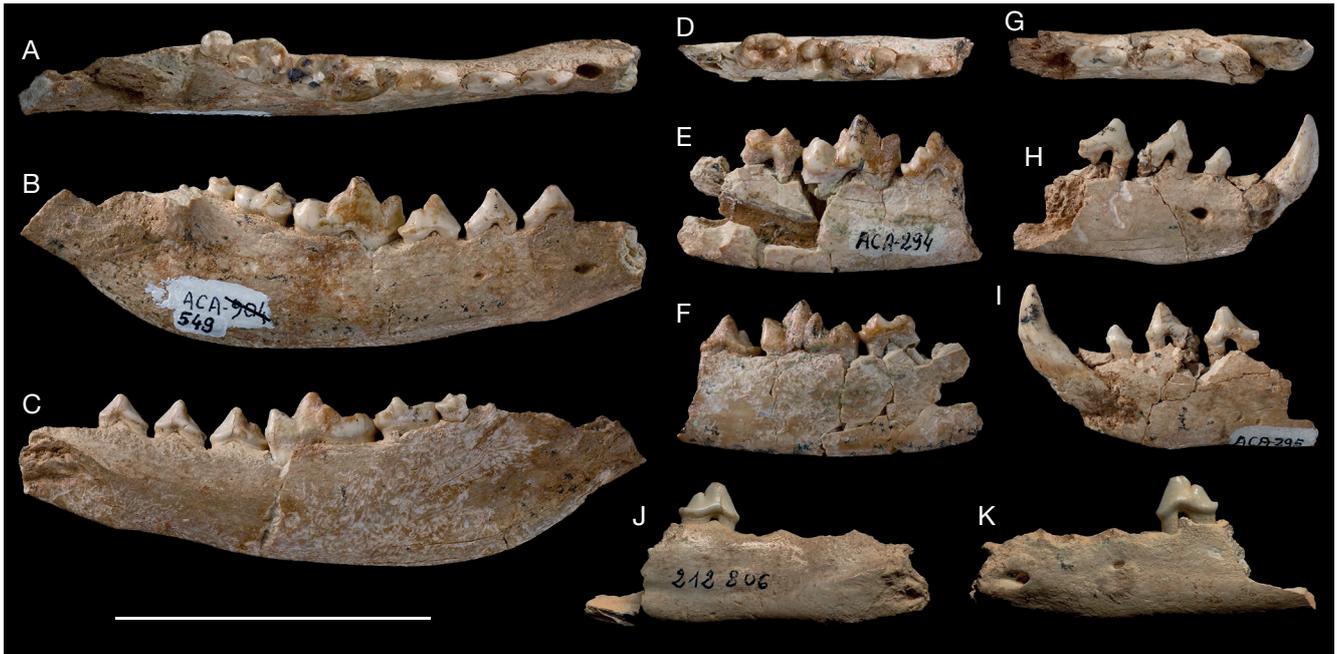
FIG. 3. — *Nyctereutes donnezani* from Çalta, central Turkey, early Pliocene: **A**-**C**, right mandible MNHN.F.ACA549 in occlusal (**A**), labial (**B**) and lingual (**C**), views; **D**-**F**, right mandible fragment MNHN.F.ACA294 in occlusal (**D**), labial (**E**) and lingual (**F**) views; **G**-**I**, right mandible fragment MNHN.F.ACA295 in occlusal (**G**), labial (**H**) and lingual (**I**) views; **J**, **K**, left mandible fragment FSL-212806 in lingual (**J**) and labial (**K**) views. Scale bar: 50 mm.

longer m3, thicker mandibular body and narrower postorbital constriction in male individuals, and a more globular braincase in female individuals. These observations partly overlap with the morphological differences that we noted as due to sexual dimorphism in the skulls and mandibles from Çalta.

Dentition

The only upper incisor preserved is an I3 of MNHN.F.ACA292, which has an asymmetric and rather sharp crown (Fig. 1). Its buccal face is slightly curved. The lingual face is curved mainly at the base of the crown. The morphology is quite similar to that of the I3 of *V. vulpes* and *N. procyonoides*.

The upper canine is long, sharp and barely curved. It is similar in size and thickness to that of *N. donnezani* of Perpignan (Fig. 2). In *N. megamastoides* from Dafnero in Greece and Kvabebi in Georgia (Vekua 1972; Koufos 1993; Rook *et al.* 2017), as well as in the extant *N. procyonoides*, the upper canine is rather gracile and curved distally, similar in that of *N. tingi* from China. The canines of *V. vulpes* are slightly more pointed than in the specimens of Çalta.

The P1, P2 and P3 are not preserved. There is a diastema of about 5 mm between the single alveolus of P1 and the anterior alveolus of the P2. The P4 is robust compared to that of *V. vulpes*, but similar to that of *N. donnezani* from Perpignan and Layna (Figs 1; 2). The anterior depression between the protocone and paracone is moderately deep, similar to *N. donnezani* (Perpignan and Layna). In *N. megamastoides* of Perrier this depression is more lingual, as it is in *N. tingi*, while in other specimens of *N. megamastoides* (Montopoli, Dafnero, Sesklon, Kvabebi) and *N. sinensis* (Nihowan and Yushe Basin), the anterior face of the P4 is almost straight. The latter two species differ in

having the protocone strongly projected antero-lingually like in *V. vulpes*, while on the Çalta specimens, it does not exceed the level of the anterior margin of the paracone or is barely anterior to it. In *N. tingi*, the protocone is small, protrudes anterior to the paracone and is situated near it, thus shaping slender the outline of P4. There is a sharp ridge descending from the tip of the paracone anteriorly. Bartolini Lucenti (2017) provided a detailed morphological analysis of P4 in different species of *Nyctereutes*. He noted that the metastylar blade is short in *N. donnezani* from Perpignan and Layna, and *N. vulpinus* from Saint-Vallier, France, while it is long in the type material of *N. megamastoides* from Perrier, indicating a more carnivorous diet. We tried to calculate the ratio of the metastylar blade to the total buccal length (paracone + metastylar blade) in all available records of *Nyctereutes* from Eurasia. Our results are not conclusive. The metastylar blade represents 37 to 46% of the total length, without, however, discriminating any species. For instance, on seven P4 from Çalta, this ratio varies between 38.8 and 43.1%. A continuous and thick lingual cingulum runs from the distal edge of the protocone to the distal base of the metacone. This cingulum is weak in *M. megamastoides* (Perrier, Montopoli, Dafnero, Sesklon, Kvabebi), *N. vulpinus* (St.-Vallier) and in the extant *N. procyonoides*, but similar in thickness to that of the Çalta specimens in *N. donnezani* (Perpignan, Layna) and *N. sinensis* (Nihowan). In summary, the P4 from Çalta is almost identical in proportions and morphology to that of *N. donnezani* from Perpignan and Layna (Fig. 4).

The M1 is almost as long as it is wide (Fig. 4). However, the typical feature of this molar is the narrowness of its lingual part, which gives it an almost triangular outline, a character shared with
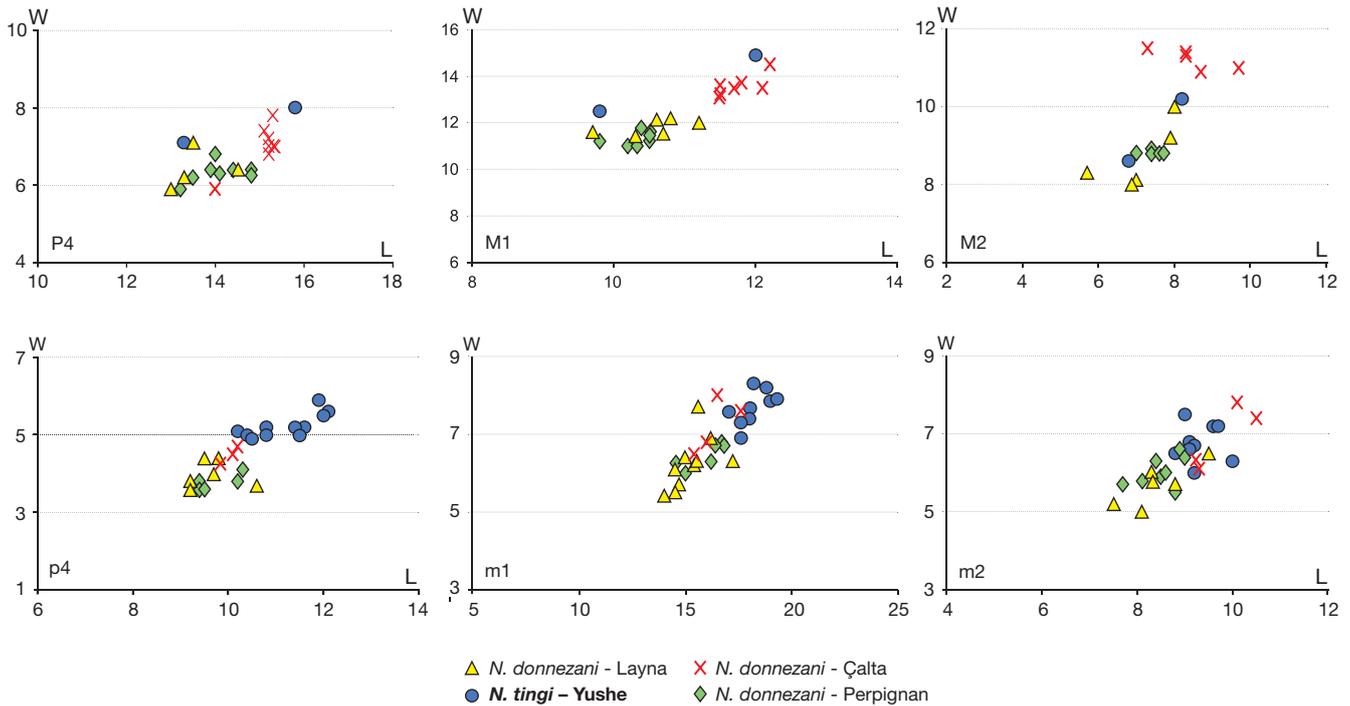
FIG. 4. — Length/Width dispersal diagrams of three upper (P4, M1 and M2) and three lower (p4, m1 and m2) cheek teeth for specimens from Perpignan, Layna and Çalta referred to *N. donnezani*, and *N. tingi* from Yushe Basin, China. Measurements for specimens from Çalta and Perpignan are our measurements; those for Layna are taken from Soria & Aguirre (1976) and for *N. tingi* from Tedford & Qiu (1991).

N. donnezani, *N tingi*, and *N. procyonoides*. In *N. megamastoides*, *N. abdeslami* and *N. sinensis*, the lingual part is larger, and the molar has a trapezoidal outline. In addition, the occlusal outline of M1 and M2 in the first group of species is curved distally in their lingual parts, as in *Vulpes* and *Canis*, while in the second group the M1 is not curved distally, but the M2 is. The paracone and metacone are equally large on the M1 of Çalta as in *N. donnezani* from Perpignan and Layna and *N. megamastoides* from Perrier, Dafnero, Sesklon and Kvabebi. In *N. tingi*, *N. sinensis* and *N. procyonoides,* the metacone is smaller than the paracone. The metaconule is well developed and slightly taller than the protocone. The M1 is surrounded by thick buccal and lingual cingula and thin mesial and distal cingula. The development of the cingula displays intra and interspecific variation and is rarely used for species distinction.

The M2 is wider than long. The paracone is a little stronger than the metacone, and the metaconule is weaker than the protocone. These features are also found in *N. donnezani*, *N. megamastoides*, *N. tingi* and *N. sinensis,* but the latter two species have a metaconule that is even smaller. The hypocone is well developed and strongly raised, as in *N. donnezani* of Layna and Perpignan. It is different from that of *N. sinensis*, which has a much more massive hypocone (Teilhard de Chardin & Piveteau 1930). The labial and lingual cingula are present, well developed and continuous. The lingual part is curved distally as in other species of *Nyctereutes*, but this curvature is a little stronger in *N. tingi*, *N. sinensis* and *N. procyonoides*.

The lower canine is sharp, a little shorter than in *N. sinensis*, *N. procyonoides* and *V. vulpes*, and in particular much less curved distally than in these species (Fig. 3). In these

characters, it recalls *N. donnezani* from Layna, and *N. tingi* from the Yushe Basin.

The p1 is small and single-rooted, and its crown is narrow, sharp and asymmetric, similar to that of *N. donnezani* and *N. procyonoides*. In *M. megamastoides*, *N. tingi* and *N. sinensis* this tooth is strongly asymmetric because of its tip is displaced mesially.

The other lower premolars are two-rooted, narrow, elongated and with a sharp tip (Fig. 3). Their length and width increase from p2 to p4. The mesial ridge is sharper than the distal one as in all other species of *Nyctereutes*. Only the p4 has a distinct distal accessory cuspid. *N. megamastoides* and *N. sinensis* frequently also have a distal accessory cuspid on the p3. The distal edge of the premolars is widened and only the p4 has a distal cingulum, similar to *N. donnezani* and *N. tingi*. In other species, the distal edge of the premolars is much wider, in particular in p4, and often surrounded by a cingulum.

The m1 is elongate and about twice as long as it is wide (Figs 3; 4). The anterior slope of the paraconid is almost vertical, while its posterior slope is inclined, similar like in *N. donnezani*. In other species, the distal slope of the paraconid is almost flat or slightly inclined near the protoconid. The protoconid is well developed, massive and greatly dominates the other cusps. The talonid is wide as, or even wider than the trigonid. This is also the case in other species of *Nyctereutes*, except in *N. sinensis* and *N. donnezani* from Perpignan, which have narrower talonids, while in the specimens of Layna, also referred to *N. donnezani*, the talonid is wider than the trigonid. The hypoconid is slightly more developed than the entoconid. In

TABLE 3. — List of phylogenetically informative characters of skull, mandible and dentition, and their character states used in the present cladistic analysis. Twelve characters, indicated in bold numbers, are defined in the present study. 21 other characters are inspired from Tedford *et al.* 1995, 2009 with some modification. Characters and character states used for cladistic analyses. The characters in bold numbers are those drawn from our own observations.

1	Nasal length: (0) long, usually extending posteriorly beyond the maxillary-frontal suture; (1) short, does not exceed the frontal-maxillary suture.
2	Muzzle narrowing anterior to zygomatic process of maxillary: (0) not marked; (1) marked.
3	Shape of palate: (0) V-shaped; (1) little narrowing at the level of P3s; (2) strong narrowing at the level of P3s.
4	Sagittal crest: (0) confined to parietal; (1) extends onto frontal.
5	Paroccipital process: (0) narrow mediolaterally; (1) broad mediolaterally.
6	Paroccipital process: (0) posteriorly directed; (1) ventrally directed; (2) anteriorly directed.
7	Paroccipital process: (0) free from bulla except at base; (1) fused with bulla through most of its length.
8	Paroccipital process: (0) ventrally does not exceed bulla; (1) ventrally it exceeds bulla.
9	Palate width at the level of P1: (0) narrow; (1) large.
10	I3: (0) only slightly larger than other incisors, posteromedial cingulum weak or absent; (1) markedly larger than I1–I2, posteromedial cingulum present and enlarged.
11	P3 posterior cusp: (0) present; (1) very weak or absent.
12	P4 shape: (0) broad, protocone large, anterior cingulum strong; (1) slender, protocone small, anterior cingulum weak or absent, particularly across paracone.
13	P4 protocone: (0) extends anterolingually beyond anterior end of paracone; (1) extends more lingually and not beyond anterior end of paracone.
14	P4 lingual cingulum: (0) absent or residual; (1) present.
15	M1 occlusal outline: (0) lingual part narrow; (1) lingual part wide.
16	M1 hypocone: (0) small, barely differentiated from lingual cingulum; (1) enlarged, differentiated from lingual cingulum.
17	M1 paracone: (0) not markedly enlarged relative to metacone; (1) paracone markedly enlarged.
18	M1 occlusal outline: (0) notably shorter than wide; (1) length and width almost similar.
19	M2 metaconule: (0) present; (1) very weak or absent.
20	Subangular lobe of mandible: (0) absent; (1) present, distally rounded; (2) present, distally angular.
21	Subangular lobe of mandible: (0) absent; (1) situated below molars; (2) situated behind molars.
22	The notch between subangular lobe and angular process: (0) wide; (1) narrow.
23	Angle between ventral margin of body and distal margin of subangular lobe: (0) more than 140°; (1) less than 140°.
24	p3, position of crown base vs that of p4: (0) approximately at the same level as p4 in lateral view; (1) crown base of p3 lies mostly below that of p4.
25	p3 posterior cusp: (0) present; (1) weak or absent.
26	m1 entoconid: (0) poorly differentiated as low crest on lingual border of talonid; (1) discrete conical or crestlike cusp; (2) conical cusp, enlarged, may be fused to the base of hypoconid to encounter talonid basin; (3) joined to hypoconid by cristids that form a transverse crest; (4) reduced relative to hypoconid, but retains cristid; (5) greatly reduced and lacks cristid.
27	m1, length ratio over the width: (0) less than or equal to 2.5; (1) greater than 2.5.
28	m2 talonid length: (0) talonid <90% trigonid length; (1) talonid >90% trigonid length.
29	m2 talonid : (0) as wide as trigonid ; (1) slightly narrowed ; (2) strongly narrowed.
30	m2 entoconid: (0) not reduced; (1) reduced or absent.
31	m2 metaconid: (0) approximately equal in size and height to protoconid; (1) reduced in size and height relative to protoconid or absent.
32	m2 anterolabial cingulum: (0) absent or weak; (1) present and well-marked.

N. megamastoides, they are almost equal in volume whereas the hypoconid is much more developed than the entoconid in *N. tingi* and *N. sinensis*. The presence of a weak hypoconulid can be noted like in *N. megamastoides* and *N. sinensis*.

The m2 is elongate, and its talonid is a little narrower than the trigonid (Fig. 3). In *N. megamastoides* the m2 is robust, almost rectangular in outline and more elongated. In *N. tingi*, *N. sinensis* and *N. procyonoides* the talonid of m2 is reduced. This is also the case with the specimens of *N. donnezani* from Perpignan and a right hemimandible from Layna (LC-3; Soria & Aguirre 1976: pl. 2, fig. 1), which have m2 with a narrow and reduced talonid, while on another right mandible from Layna (unnumbered; Soria & Aguirre 1976: pl. 2, fig. 2), the distal part of m2 is not reduced, and its shape is similar to that of the Çalta specimen. On the m2 of Çalta, the cusps are well developed, the metaconid is larger than the other cusps like in *N. sinensis* and *N. megamastoides*. There is a strong anterolabial cingulum as in *N. megamastoides* and *N. donnezani*. This cingulum is reduced or vestigial on the m2 of the Chinese species.

The m3 is small and ovoid in outline (Fig. 3). It has a well-developed protoconid and a weak metaconid. This tooth is different from m3 of *N. tingi* in having two cusps instead of one. In other species, the m3 has two or even three cusps of variable volume.

Regarding the size of teeth (Table 2; Fig. 4), the Çalta raccoon dog displays intermediate values between the larger *N. tingi* from the Yushe Basin in China and *N. donnezani* from Perpignan and Layna in western Europe. Using size criteria, Bartolini Lucenti (2018) suggested excluding the Çalta raccoon dog from *N. donnezani*, and referred it to *Nyctereutes* sp. In detailed comparison, the p4 and m1 of *N. tingi* are larger than all specimens referred to *N. donnezani*, including Çalta, while this is not obvious for the upper cheek teeth and the m3. The m3 of *N. tingi* is smaller than that of Çalta, Perpignan and Layna. The upper cheek teeth of *N. tingi* are poorly documented, with only two specimens for each, one small, similar in size to that of *N. donnezani*, while the other is larger than those of *N. donnezani* and Çalta. The dimensions of P4, M1, M2 and m2 from Çalta

TABLE 4. — The matrix of characters and character states of Table 3 used in the present cladistic analysis. It concerns 14 occurrences of nine species of *Nyctereutes* and two outgroup taxa *Vulpes* and *Canis*.

Characters/Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
N. procyonoides – Extant	0	1	0	0&1	0	0	1	0	1	1	1	0	0	1	0	0&1	0	1	1	2	2	1	1	1	1	1	0	0	1&2	0	0	0
N. abdeslami – Morocco	?	?	?	?	?	?	?	?	?	?	1	1	0	1	1	0	0	1	?	2	2	1	1	0	1	2	0	0	1	0	0	1
N. donnezani – Perpignan	?	0	1	0	0	0	1	1	0	1	0	0	0&1	1	0	0&1	0	0	0	1	1	0	0	?	1	1	0	0	2	0	0	1
N. donnezani – Layna	?	0	1	0	?	0	1	1	0	1	?	0	0&1	1	0	1	0	1	0	0&1	1	0	0	?	1	1	0	0	0&1	0	0	1
N. donnezani – Çalta	0	0	1	0	0	0	1	1	0	?	?	0	1	1	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0&1	0	0	1
N. lockwoodi – Ethiopia	1	1	2	0	0	0	1	0	0	0	0	1	0&1	1	0	0	0	1	0	1	2	0	0	?	?	?	?	?	?	?	?	?
N. megamastoides – Perrier	?	1	0	0	0	0	0	1	?	?	0	0	0&1	1	1	1	0	1	0	2	2	1	1	0	1	2	1	0	0	0	0	1
N. megamastoides – Dafnero	0&1	1	0	0	?	0&1	1	1	1	0	1	0	0	1	1	1	0	0&1	0	?	?	?	?	?	1	?	1	?	0	?	?	?
N. megamastoides – Kvabebi	0	1	1	0	?	0	?	0	0	0	0	0&1	1	1	1	0	1	1	?	1&2	?	1	1	1	2	0	1	0	0	0	0	1
N. m. vulpinus – St Vallier	0	1	2	0	?	1	1	0	0	0	1	0	0&1	1	0	0&1	0	0	1	2	2	0	1	0	1	2	1	1	1&2	1	0	0
N. sinensis – Nihowan	0	1	1&2	1	0	1	1	0	0&1	?	1	1	0	1	0&1	1	0	0	0	1	2	1	1	0	0	?	0	1	1&2	1	1	0
N. sinensis – Yushe	?	1	?	1	?	1	1	0	?	1	1	1	0	0	0&1	0	0	0	1	1	2	1	1	0	0	1	0	?	1&2	1	1	0
N. tingi – Megalo Emvolon	0	0	1	0	0	0	1	0	0	?	?	0	0	1	0	0	0&1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
N. tingi – Yushe	1	0	?	0	?	?	?	?	?	?	1	1	1	0	1	0	0	1	0	1	1	1	0	0	0	0&1	0	1	0	2	0&1	1
N. barryi – Tanzania	?	?	?	?	?	?	?	?	?	0	1	1	1	0&1	1	0	0	1	?	1	1	0	0	?	1	2	1	0	0	1	0	1
Vulpes vulpes – Extant	1	1	2	0	1	2	1	0	0	1	1	1	0	0	0	1	1	0	0&1	0	0	0	0	1	0	1	1	0	2	0	0	0&1
Canis lupus – Extant	1	0&1	0	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	2	0	0	2	1

are greater than those of *N. donnezani* from Perpignan and Layna, while the p4 and m1 are similar in size to the ones from these localities. In summary, the size of the cheek teeth from Çalta are intermediate between the smaller teeth from Perpignan and Layna (*N. donnezani*) and the larger teeth from the Yushe Basin (*N. tingi*). Regarding the lack of obvious size differences, one can wonder what is the effect of sexual dimorphism on the dentition of *Nyctereutes*. Kim *et al.* (2012: 1614) observed in *N. procyonoides* that "sexual difference is more apparent from data relating to the skull than that relating to the teeth". Taking into consideration these results, the size of the cheek teeth alone seems not useful for species differentiation given the lack of statistically significant samples for each species.

The skull, mandible and dentition of the Çalta raccoon dog have many morphological similarities with those of *N. donnezani* from its type locality Perpignan as well as from Layna. As noted above, they display several characters that are different from other species of the genus, in particular *N. tingi, N. sinensis, N. megamastoides* and *N. abdeslami*. In view of this, it is very likely that the specimens of Çalta belong to *N. donnezani*. This identification will be tested by the phylogenetic analysis of cranial and dental characters in various species of the genus *Nyctereutes*.

PHYLOGENETIC ANALYSIS

To date, there has been no phylogenetic study concerning the relationships between various species of *Nyctereutes*. In cladistic analyses based on morphology (Tedford *et al.* 1995, 2009), neuroanatomy (Lyras & Van den Geer 2003; Dermitzakis *et al.* 2004) or molecular biology (Wayne *et al.* 1997; Bardeleben *et al.* 2005), *Nyctereutes* has been included at the genus level, and the genera *Urocyon* or *Cerdocyon* appear as its sister groups.

For the present phylogenetic study, we identified 32 phylogenetically informative characters of skull, mandible and dentition. 21 characters are taken from Tedford *et al.* (2009), most of them with some modification, and 11 others are new and are indicated in Table 3 in bold numbers. Twenty-six characters are binary and six others are multi-state characters (Table 4). We preferred to carry out the cladistic analysis on locality-based data rather than species-based data. The main reason of our choice is that the species attribution of some records is disputed. For example, the material from Saint-Vallier (France) was referred to *N. megamastoides* by Viret (1954), Martin (1971) and Argant (2004), while Soria & Aguirre (1976) recognized a new subspecies that Monguillon *et al.* (2004) elevated to the species level, *N. vulpinus* Soria and Aguirre, 1976. Another example is the material of Megalo Emvolon in northern Greece. Koufos (1997) referred this to *N. tingi*, a species defined from China, while Geraads *et al.* (2010) suggested its attribution to *N. donnezani*. We also included in this analysis three species from the Pliocene of Africa, each known from a single locality. These species are *N. abdeslami* from Morocco, *N. lockwoodi* from Ethiopia and *N. barryi* from Tanzania. We coded the characters of these species after the descriptions by Geraads (1997), Geraads *et al.* (2010) and Werdelin & Dehghani (2011), respectively. Two species referred to *Nyctereutes* are excluded: *N. vinetorum* (Bate, 1937) from the Pleistocene of Palestine because of insufficient characters to be observed, and *N. terblanchei* (Broom, 1948) from the Plio-Pleistocene sites of South Africa. Ficcarelli *et al.* (1984) assigned the latter species to *Nyctereutes*, while Reynolds (2012) stated, after a careful study of the available material, that this species is better related to jackal or fox.

Taking into consideration these taxonomic problems, we analyzed as ingroup units the fossil record from fourteen localities, referred to eight species of *Nyctereutes*, in addition to the extant species *N. procyonoides*. The two outgroup taxa are *Canis lupus* and *Vulpes vulpes*, both extant canids. For *Nyctereutes donnezani*, we studied the type material from Perpignan in the Lyon and Paris collections, and we used the descriptions of Soria & Aguirre (1976) and Bartolini Lucenti *et al.* (2018) for the material of

Layna in Spain. *Nyctereutes donnezani* is also reported from at least three other localities in Spain (La Calera, La Gloria and La Gloria 4; Alcala *et al.* 1990) and one in southern France (Villeneuve de la Raho; Mein & Aymar 1984), but not described, and is not used for the present study.

Based on our observations and data from the literature, the data matrix of Table 4 was built under Mesquite 2.6a (Maddison & Maddison 2009) and the analysis was conducted using PAUP, version 4.0a164 (Swofford 1998). In the parsimony analysis, all the characters have the same weight, and are not ordered. A "branch & bound" search was performed, which resulted in 24 trees of 87 steps, from which a strict consensus tree was calculated. The values for the strict consensus tree are: consistency index 0.437 and retention index 0.570.

This study demonstrates, first of all, the monophyly of the genus *Nyctereutes,* as supported by several synapomorhies, in particular short nasal bones compared to *Canis* and *Vulpes* (1-0), presence of lingual cingulum on P4 (14-1), subangular lobe of mandible (20-1) and crown base of p3 below that of p4 (24-1), (Tables Table 3; 4). *Nyctereutes tingi* from China is basal in the tree and sister group to all the other species of *Nyctereutes*. Several other clades are clearly distinguished. All the European and African species, except *N. vulpinus* from France, are grouped at the Node 3, which also includes the extant species *N. procyonoides*. This node is supported by characters 18-1 (M1 with similar length and width) , 19-1 (metaconule weak or absent on M2), 29-0 (m2 with a wide talonid) and 32-1 (anterolabial cingulum well marked on m2). *Nyctereutes megamastoides* is grouped at the Node 5 with *N. abdeslami* from Morocco and *N. procyonoides*, without resolution to distinguish them based on any apomorphic feature. The raccoon dog of Çalta is grouped with that of Perpignan, the type locality of *N. donnezani*, and Layna (Node 7), which share several apomorphic characters: paroccipital process ventrally exceeds bulla (8-1), I3 markedly larger than I1 and I2 (10-1), subangular lobe of mandible situated below molars (21-1) and m1 entoconid conical, large, and even fused to the base of hypoconid to encounter talonid basin (26-2). *Nyctereutes "tingi"* from Megalo Emvolon appears as the closest sister taxon of the latter group (Node 6), in agreement with the suggestion of Geraads *et al.* (2010) for its attribution to *N. donnezani* rather than to *N. tingi*. The species *N. vulpinus* from Saint-Vallier is placed as the sister taxon of *N. sinensis* from two localities in China (Node 8) sharing three apomorphic characters: paroccipital process ventrally directed (6-1), on the mandible angle between ventral margin of the corpus and distal margin of the subangular lobe less than 140° (23-1), and m2 talonid length >90% trigonid length.

The interesting result of the present study is the grouping of the Çalta raccoon dog with *N. donnezani* from Perpignan and Layna. The other early Pliocene record from the eastern Mediterranean region, *N. "tingi"* as identified by Koufos (1997), appears closely related to the *N. donnezani* group, not to *N. tingi*.

Another result addresses to the supposed ancestral-descendant relationships between *N. donnezani* and *N. megamastoides* as suggested by Soria & Aguirre (1976), Argant (2004) and Monguillon *et al.* (2004). This relation is not supported by the present analysis since they appear in two different clades. Furthermore

in this tree, we can note that *N. lockwoodi* from Ethiopia appears as the closest sister species of *N. donnezani*, sharing apomorphies such as broad paroccipital process (5-1), protocone of P4 situated lingually and not protruding (13-1), strong lingual cingulum on P4 (14-1), short and wide M1 (15-1), and subangular lobe of mandible situated below molars (21-1). However, according to Geraads *et al.* (2010), *N. lockwoodi* is quite distant from *N. donnezani* and closer to the Asian species *N. tingi*, an opinion that is not supported by the present cladistic analysis.

DISCUSSION AND CONCLUSION

After the above analysis, it appears that the size is not the most reliable criterion to distinguish species of *Nyctereutes*, except for *N. tingi* from China that is a little larger, and the extant *N. procyonoides* that is smaller than all other species. In other words, the dimensions of the skull, mandible and teeth from Çalta are close to those of *N. donnezani*, *N. megamastoides* and *N. sinensis*, although some differences may be observed in some measurements. However, the limited number of specimens and obvious sexual dimorphism in fossil and extant species of *Nyctereutes* do not allow for an evaluation of the size range of fossil species, and consequently some size differences noted in previous studies (Soria & Aguirre 1976; Koufos 1997; Rook *et al.* 2017; Bartolini Lucenti 2018; Bartolini Lucenti *et al.* 2018), as well as in the present work, cannot be used for clear species distinction. Morphology is instead more helpful than size for distinguishing species. The skulls from Çalta have an elongated face, and the anterior narrowing is progressive, similar to *N. donnezani* from Perpignan and Layna, and "*Nyctereutes tingi*" from Megalo Emvolon. In the skulls of *N. megamastoides* from Perrier (Boule 1889) and Dafnero (Koufos 1993), *N. vulpinus* from St Vallier (Viret 1954; Argant 2004, Monguillon *et al.* 2004), and *N. sinensis* from China (Teilhard de Chardin & Piveteau 1930; Xue 1981; Tedford & Qiu 1991) the face is shorter and the narrowing of the face is abrupt in front of the orbits.

On the specimens of Çalta, the dorsal profile of the skull is similar to that of "*N. tingi*" from Megalo Emvolon, but different from that of *N. megamastoides*, *N. tingi* and *N. sinensis*. In the skull of Çalta and Megalo Emvolon, the profile is almost flat at the level of the nasals anterior to the level above P4, then rises progressively up to the anterior part of the braincase, and drops distally until the occipital crest with a stronger curvature. The profile of the skull of *N. donnezani* from Perpignan, as illustrated by Kurtén & Crusafont Pairó (1977) and from Layna, as illustrated by Bartolini Lucenti *et al.* (2018), is identical to that of Çalta. On the skulls of *N. megamastoides*, *N. tingi*, *N. sinensis* and *N. procyonoides* the profile has a curvature that is almost continuous from the nasals up to the middle of the braincase, which gives the skull a rounded outline.

The mandible displays the most distinctive features in the position, shape and size of the subangular lobe. *Nyctereutes donnezani* and *N. tingi*, as well as the mandibles from Çalta, have subangular lobe that is rather weak, situated below the molars and its distal angle is wide, between 150 and 160°. In *N. megamastoides*, *N. vulpinus* and *N. abdeslami*, the subangular lobe
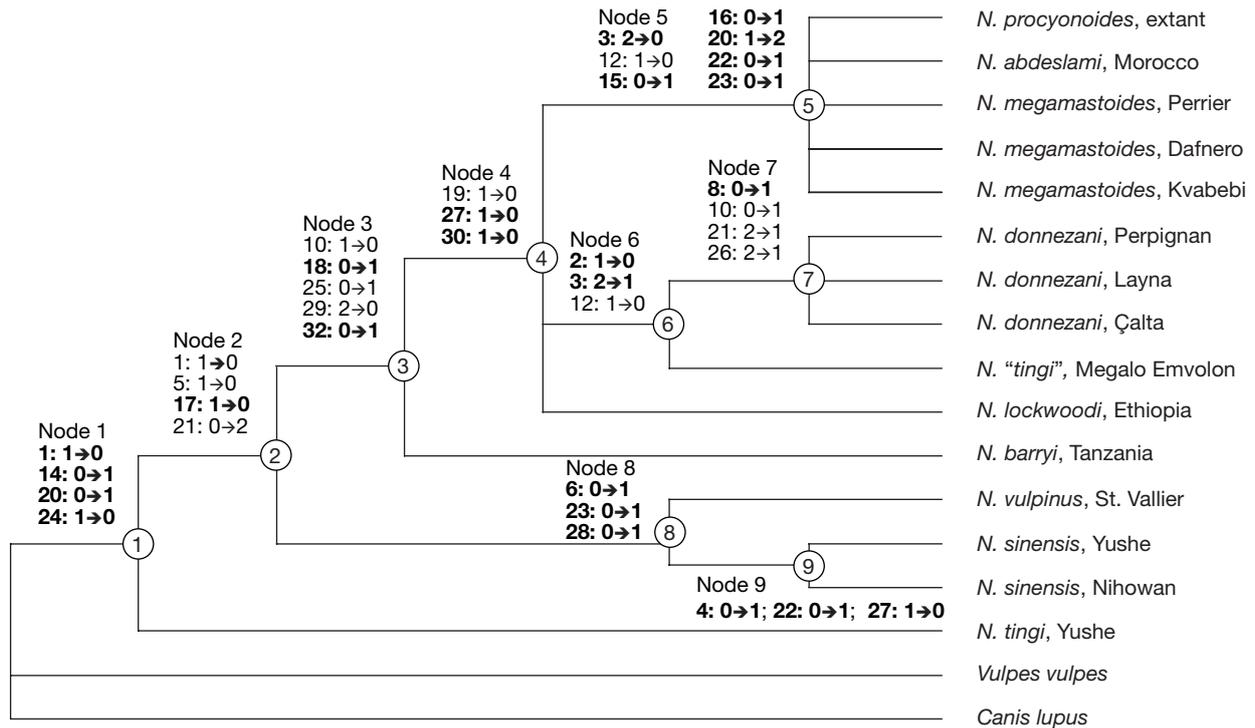
Fig. 5. — Cladogram showing the relationships among the species of *Nyctereutes*. The two outgroup taxa are the extant *Vulpes vulpes* and *Canis lupus*. For data matrix see Tables 3 and 4. Character state changes at nodes 1 to 9 are reconstructed using DELTRAN assumptions for ambiguous (**in normal digits**) and unambiguous (**in bold digits**) character transformations.

is strong, situated distally below the ascending ramus and its distal margin has a narrow angle of 110° in *N. megamastoides* (Perrier), between 120 and 125° in *N. vulpinus* (St. Vallier) and about 130° in *N. abdeslami* (Ahl al Oughlam). In *N. sinensis* and *N. procyonoides*, the subangular lobe is a little smaller than in *N. megamastoides*, situated similarly below the ascending ramus and the distal angle is about 120-130°.

Concerning the upper dentition, Rook *et al.* (2017) analysed dental features and demonstrated differences between the species of *Nyctereutes*. In *N. donnezani* and *N. tingi*, as well as the specimens from Çalta, the lingual part of M1 and M2 is narrow and curved backward. This is also the case in *N. procyonoides*. In *N. megamastoides* and *N. abdeslami* these molars have a wide lingual part and their outline is almost subquadrate. In *N. vulpinus* and *N. sinensis* the shape of M1 and M2 is intermediate between the two groups. The P4 from Çalta, as in *N. donnezani*, is robust and wide compared to that of other species, and its protocone does not protrude anteriorly as it does in other species. Bartolini Lucenti (2017) also noted that *N. donnezani* and *N. tingi* have a shorter metastylar blade compared to the other species. Although this character seems variable as discussed above, the P4s from Çalta have a rather short metastylar blade.

Regarding the characters of the lower dentition, the specimens from Çalta are similar to those of Perpignan and Layna in having a p3 without an accessory cuspid, a p4 with a relatively narrow talonid, and an m1 with talonid as wide as the trigonid.

Although the size of most cheek teeth from Çalta is apparently a little greater than in the type material of *N. donnezani*, morphological characters of the skull, mandible and dentition

do not show any clear difference to distinguish the Çalta raccoon dog from *N. donnezani*. This view is also supported by a cladistic analysis that we performed with a locality-based dataset. The phylogenetic tree distinguishes several well-resolved clades, including the one grouping the Çalta raccoon dog with *N. donnezani* from Perpignan and Layna.

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