Original article

Canis accitanus nov. sp., a new small dog (Canidae, Carnivora, Mammalia) from the Fonelas P-1 Plio-Pleistocene site (Guadix basin, Granada, Spain)[☆]

Canis accitanus nov. sp., un nouveau petit canidé (Canidae, Carnivora, Mammalia) du gisement plio-pléistocène de Fonelas P-1 (bassin de Guadix, Grenade, Espagne)

Guiomar Garrido [*], Alfonso Arribas

Museo Geominero, Instituto Geológico y Minero de España, Ríos Rosas 23, 28003 Madrid, Spain

Abstract

This paper reports a new species of dog (*Canis accitanus* nov. sp.) from the Fonelas P-1 site (dated close to the Plio-Pleistocene boundary) in Granada, Spain. This new taxon shows cranial features more similar to coyote-like dogs (*C. lepophagus*, *C. priscolatrans*, *C. arnensis* or *C. latrans*) than to wolf-like dogs (*C. etruscus*, *C. mosbachensis* or *C. lupus*), such as a long and narrow muzzle, a little-developed sagittal crest and frontal bones raised only a little above the rostrum. However, it also shows a series of autapomorphic characteristics in its upper dentition, essentially in the first upper molar, which reflects a trophic adaptation towards a more abrasive diet than that eaten by other species of its genus. This new dog is the smallest representative of the genus *Canis* ever recorded for the European Pliocene or Pleistocene.
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Résumé

Ce travail décrit une nouvelle espèce de Canidé (*Canis accitanus* nov. sp.) du gisement de Fonelas P-1 (daté de la limite Plio-Pléistocène) à Grenade, Espagne. Ce nouveau taxon présente des traits crâniens plus proches de ceux des coyotes (*C. lepophagus*, *C. priscolatrans*, *C. arnensis* ou *C. latrans*) que de ceux des loups (*C. etruscus*, *C. mosbachensis* ou *C. lupus*), tel qu'un museau étroit et long, une crête sagittale peu développée et des os frontaux ne s'élevant que très légèrement au dessus du rostre. Cependant, il présente aussi un ensemble de caractéristiques autapomorphiques au niveau de la dentition supérieure, notamment la première molaire, qui présente une adaptation trophique à un régime plus abrasif que celui d'autres espèces de son genre. Ce nouveau canidé est le plus petit représentant du genre *Canis* jamais décrit dans le Pliocène ou le Pléistocène européens.
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1. Introduction

This paper reports a new species of dog (*Canis accitanus* nov. sp.) from the Fonelas P-1 site (dated close to the Plio-Pleistocene boundary) in Granada, Spain.

The fossil record of the genus *Canis* covers a period of some 4 million years from the Lower Pliocene to the present, during

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which time different species have belonged to palaeocommunities worldwide with the exceptions of Antarctica and, until recently, Australia. The taxonomy of the genus' fossil members is complex due to their anatomical homogeneity, the multitude of species described, and the wide geographical distributions of their different populations.

The modern day members of *Canis* are medium to large size Caninae with a lower dental formula of 3-1-4-3. Eight species are currently recognised (Nowak, 1999), including the three jackals:

C. mesomelas Schreber, 1775 (the black-backed jackal of Africa, which has been found at Pliocene sites; for a review see Garrido (2002));
C. adustus Sundevall, 1847 (the side-striped jackal, also of Africa and also reported for the Pliocene);
C. aureus Linnaeus, 1758 (the golden jackal, whose Asian populations met those of *C. mesomelas* and *C. adustus* in eastern Africa at some point during the last 500,000 years [Van Valkenburgh and Wayne, 1994]).

The Ethiopian species *C. simensis* Rüppell, 1840, sometimes known as the Simien jackal, Ethiopian wolf or Abyssinian wolf, and of which to date no fossils have been found, seems to be more closely related to the wolf and the coyote than the remaining African canids (Gotelli et al., 1994; Sillero-Zubiri and Gottelli, 1994). It probably represents a relic of an ancestral wolf population that dispersed over North Africa and Eurasia. Nonetheless, some authors remain of the opinion that it is related to the jackals (Rook and Azzaroli-Puccetti, 1996). *C. simensis* is found only in the mountains of Ethiopia, where it is threatened with extinction due to the risk of hybridisation with domestic dogs, among other dangers to its existence.

The wolf *C. lupus* Linnaeus, 1758, was found all over Eurasia during the Upper Pleistocene and continues to be present over much of Palaearctic Eurasia and certain areas of North Africa, North America and Mexico. The domestic dog, *C. familiaris* Linnaeus, 1758, appears to have arisen from *C. lupus* about 15,000 years ago. Most authors regard it as a subspecies of the wolf and give it the name *C. lupus familiaris* (Van Gelder, 1978). The coyote, *C. latrans* Say, 1823, appeared in North America during the Lower Pleistocene, although its fossils are not abundant until well into the Mid Pleistocene. It currently occupies large areas of the American continent from Alaska to Panama. Finally, the red wolf, *C. rufus* Audubon and Bachman, 1851, has long been considered a relic of the Plio-Pleistocene species *C. priscolatrans* Cope, 1899, which lived only in North America. However, according to recent genetic analyses, this taxon arose from hybridisation between wolves and coyotes at some point during the last 10,000 years (Reich et al., 1999). Currently, the red wolf occupies small territories in the south of the USA, and is threatened by extinction.

The great homogeneity of the morphological characteristics of the members of this genus renders distinction between certain fossil species difficult. Indeed, great historical disparities have existed in the classification of materials. The oldest representative of the genus *Canis* ''sensu stricto'' –

C. lepophagus Johnston, 1938 – was recorded in early Pliocene North American sites, and has been phylogenetically related to the modern day coyote *C. latrans* (Kurtén, 1974). It is difficult to identify the first Euroasiatic record of the genus *Canis*, since there are numerous doubtful citations from Miocene and Lower Pliocene sites, these have engendered very different opinions regarding the genus to which these materials really belong. The oldest reference corresponds to the species ''*Canis*'' *cipio* Crusafont, 1950, from the Turolian (end of the Miocene) of the Iberian Peninsula. This taxon appears to be related to ''*Canis*'' *michauxi* Martin, 1973, of the Perpignan Pliocene (Torre, 1979). Both forms show very primitive characteristics and are quite different from the genus *Eucyon* Tedford and Qiu, 1996. Therefore, until this taxonomic problem is solved, they remain included in *Canis* ''sensu lato'', although with some doubt. Morales (1981) identified *Canis* sp. at the Venta del Moro site, also from the end of the Miocene. However, these specimens were later determined to belong to *Eucyon monticinensis* (Rook, 1992). The species *E. davisi* (Merriam, 1911), *E. minor* (Teilhard de Chardin and Piveteau, 1930) and *E. odessanus* (Odinzow, 1967) were also originally classified as members of the genus *Canis*. Similar problems are seen with the African records. The oldest materials from the Pliocene and Plio-Pleistocene were originally classified as ''*Canis*'' *brevirostris* Barry, 1987, but are now included in *Eucyon* (Rook, 1993; Spassov and Rook, 2006). In the year 2000, Werdelin and Lewis described a canid species (*Canis* n. sp. A) from a Pliocene site at South Turkwel that represents the most ancient African testimony of this genus (Werdelin and Lewis, 2000, 2005).

With respect to the Asian continent, the oldest fossils assignable to the genus *Canis* come from deposits some 3.4 million years old in the Mazegu Formation of the Yushe Basin, China (Flynn et al., 1991). This form has anatomical characteristics similar to those of the Upper Villafranchian European species *C. etruscus* Forsyth-Major, 1877 (Tedford et al., 1991). Thus, although the genus *Canis* probably appeared during the Miocene, it is not until the Lower Pliocene that its presence can be confirmed in both the Old and New Worlds.

Later, the Chinese Villafranchian record contains numerous discrepancies. The species *C. chihliensis* Zdanski, 1924, has been described in the villafranchian deposits of Nihowan, and although it has been proposed a synonym of *C. etruscus* (Torre, 1967), some authors believe it to be more closely related to the *C. (Xenocyon) falconeri* group (Rook, 1993). The subspecies *C. chihliensis palmidens* Teilhard and Piveteau, 1930, was also described from Nihowan, but was later identified as an Asiatic representative of the European species *C. arnensis* (Rook, 1993). Torre (1967), however, proposed it to be synonymous with *C. etruscus*.

The Republic of Tajikistan was thought to be home to a site that held evidence of the migration of the genus *Canis* from the American continent towards Europe and Africa some 2.5 million years ago. It is from here that the species *C. kuruksaensis* Sotnikova, 1989 was reported, although it was later definitively related to the genus *Eucyon* (Spassov and Rook, 2006). The canid from the Upper Villafranchian of

Siwaliks, *C. cautleyi* Bose, 1879, is a recent synonym of *C. etruscus* (Torre, 1967; Rook, 1993).

On the European continent, the Lower Pliocene species "*Canis*" *adoxus* Martin, 1973, shows the primitive anatomy and the smaller dimensions of the genus *Eucyon* (*E. adoxus* [Martin, 1973]; Rook, 1993).

The species *C. arnensis* Del Campana, 1913, has been reported from several European Lower Pleistocene sites, e.g., Tasso, Faella and Bucine in the Upper Valdarno region (Italy), Gerakarou (Greece) and Sainzelles (France), among others. Although the small *C. arnensis* was once related to the jackals (Torre, 1967, 1979; Kurtén, 1968), is considered in the present work as the ancestor of the Pleistocene wolf *C. mosbachensis* Soergel, 1925 (Soergel, 1928; Thenius, 1954; Kurtén and Poulianos, 1977; Beaumont, 1979, 1980), with a close relationship with the lineage of the coyote [as was proposed by Kurtén (1974)]. Kurtén and Anderson (1980) related the American species *C. lepophagus* with the European *C. arnensis*, arguing that they probably represented the extremes of a single population of coyotes of holarctic distribution that originated in North America. The species *C. senezensis* Martin, 1973, was reported from the French site of Senèze, thought to be some 2 million years old (Roger et al., 2000). The only elements recorded, however, were two hemimaxillary fragments that show no anatomical or metric differences to *C. arnensis,* it is therefore now considered a recent synonym (Garrido, 2002, 2006). When this is taken into account, *C. arnensis* appears not to belong only to the European ecosystems of the Tasso Faunal Unit, as traditionally proposed (Torre et al., 1992), but also to the Upper Pliocene.

In 1993, Rook identified a new taxon at Mediterranean sites dating from the end of the Villafranchian to the beginning of the Galerian (Venta Micena, Pirro Nord, Le Vallonet, Cueva Victoria, Huescar-1, Colle Curti, Cúllar de Baza-1, L'Escale, Petralona, and the Israeli site of Oubeidiyah). Given the provisional name of *Canis* aff. *arnensis* it was thought to be an advanced form of the last members of *C. arnensis*. Rook and Torre (1996) suggest, therefore, that in the Lower Pleistocene-Mid Pleistocene transition, Europe was home to two different lineages, that of *C. arnensis* (primitive form) plus *Canis* aff. *arnensis* (advanced form), which occupied Mediterranean areas, and that of *C. etruscus–C. mosbachensis*, which occupied the centre and north of Eurasia. In contrast, García and Arsuaga (1999) suggest *C.* aff. *arnensis* and *C. mosbachensis* to be synonyms, and therefore that only one species inhabited Europe from the beginning of the Pleistocene. This latter hypothesis may be more coherent with the values for the anatomical and metric variables analysed.

On the European continent, *C. etruscus* was well represented during the Upper Pliocene and Lower Pleistocene in Italy, its record is more sporadic in other countries. In 1971, Bonifay incorrectly identified this species (later classified as *C. mosbachensis*), among the materials of the L'Escale site in France, and concluded that *C. etruscus* persisted in Europe until the Mid Pleistocene. Some authors held to the opinion of Bonifay, citing the presence of *C. etruscus* in post-Villafranchian deposits (Morales and Soria, 1979; Pons-Moyà, 1987),

even giving it chronostratigraphic value by differentiating between two subspecies, the older *C. etruscus etruscus* and the more modern *C. etruscus mosbachensis* (Pons-Moyà, 1987; Agustí et al., 1987). In our opinion, records of *C. etruscus* younger than the Plio-Pleistocene transit are unlikely to exist: any individuals thus classified most probably belong to *C. mosbachensis*.

In 1997, Koufos and Kostopoulos reported a new canid from the Greek site of Apollonia-1, which dates from the end of the Villafranchian. This was intermediate in size between *C. etruscus* and *C. arnensis* and was given the name *C. apolloniensis*. It has also been reported from the Pirro Nord and Petralona sites. In agreement with García (2002), however, *C. apolloniensis* appears to have insufficient specific anatomical structures to justify its being recognised as a new species; rather, it may represent one of the first populations of *C. mosbachensis*.

The Pleistocene wolf *C. mosbachensis*, which has been recorded at numerous European Lower and Mid Pleistocene sites has for decades been considered the ancestor of the modern-day wolf (Thenius, 1954; Kurtén, 1968; Torre, 1974). It appears to be generally accepted that *C. etruscus* evolved into *C. mosbachensis*, before increasing in size and becoming *C. lupus* during the Mid Pleistocene (Torre, 1967, 1974, 1979; Kurtén, 1968; Martin, 1973; Sotnikova, 1989; Argant, 1991; Rook and Torre, 1996). Some authors consider *C. mosbachensis* to be a subspecies of the wolf, and give it the name *C. lupus mosbachensis* (Lumley et al., 1988). It is unlikely that *C. mosbachensis* and *C. etruscus* are directly related. Rather, *C. mosbachensis* probably descends from *C. arnensis*, as proposed by Soergel (1928).

Finally, in 2001, an almost complete skull of a small canid was discovered at the Fonelas P-1 site, which was provisionally designated as belonging to *Canis* sp. cf. *C. arnensis* (Arribas et al., 2001). A later review of the canids from this site revealed this skull to possess anatomical and metric differences to the Lower Pleistocene *C. arnensis*, showing it to belong to a new Iberian Plio-Pleistocene species of the genus *Canis* (Garrido, 2002, 2006; Garrido and Arribas, 2002).

2. The Fonelas P-1 site

The Fonelas P-1 site (Fig. 1), which was discovered in 2000 and has been investigated since 2001 under the auspices of the *Proyecto Fonelas* (Arribas et al., 2001), has become the reference site of the Iberian Peninsula for palaeontological research into the Plio-Pleistocene transition in a continental setting (http://www.igme.es/internet/museo/investigacion/paleontologia/fonelas/index.htm).

The sedimentary environment and the genetic model of the site (*Sondeo B*) have been established (Viseras et al., 2006), and the biological processes associated with the genesis of its fossil association and the structure of the sedimentary matrix surrounding the fossils have been characterised. Its diverse association of large mammals (Arribas et al., 2004; Garrido, 2006) includes both native European species (*Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Eucladoceros* sp.,
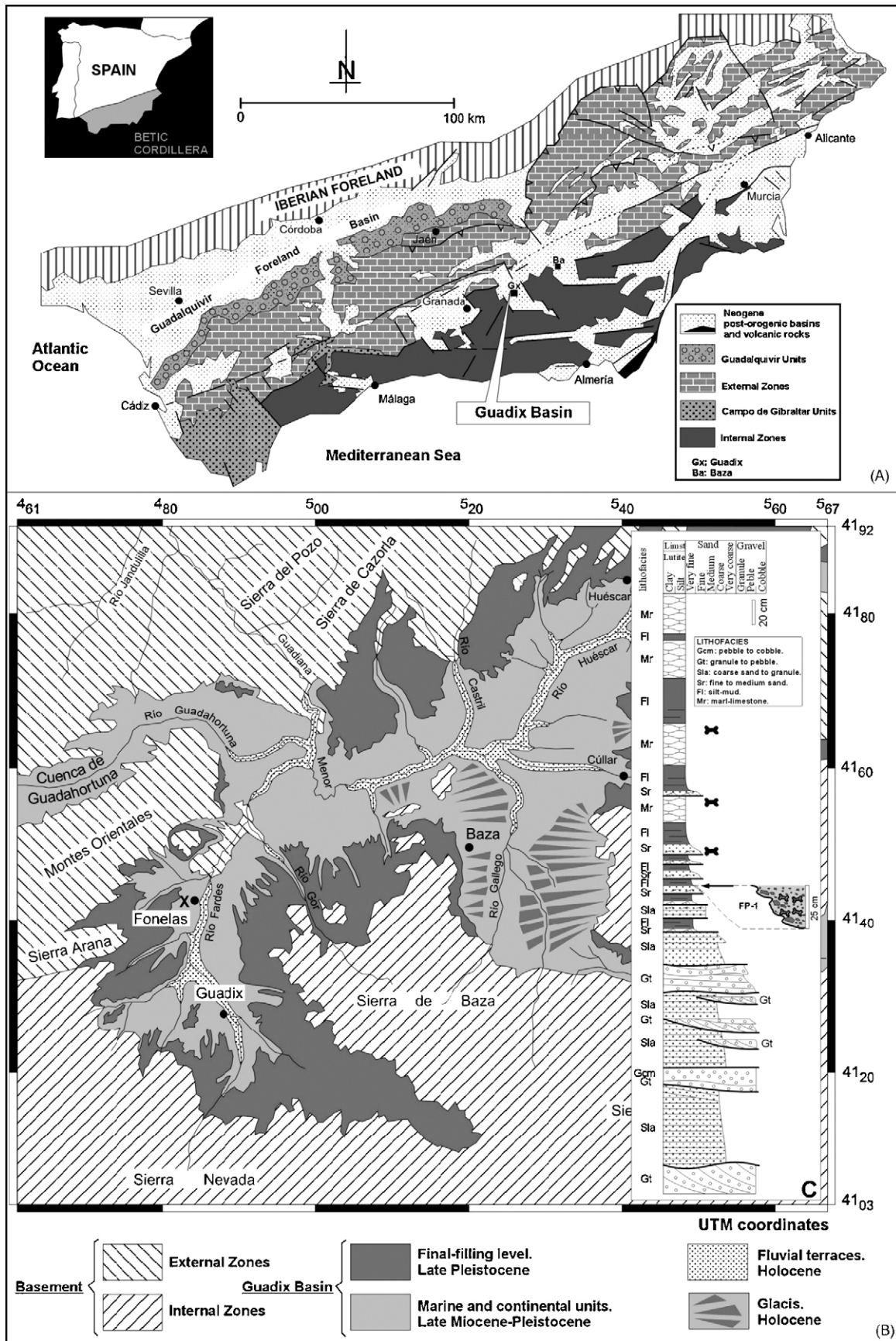
Fig. 1. Geographical and geological location of the Fonelas P-1 site. **A.** Geological map of the *Cordillera Bética* in southeastern Spain, showing the location of the Guadix Basin. **B.** Geological map of the Guadix Basin (the 'X' marks the location of the Fonelas P-1 site). **C.** Detailed stratigraphic log of the Fonelas P-1 site (*Sondeo B*, modified after Viseras et al. [2006]).
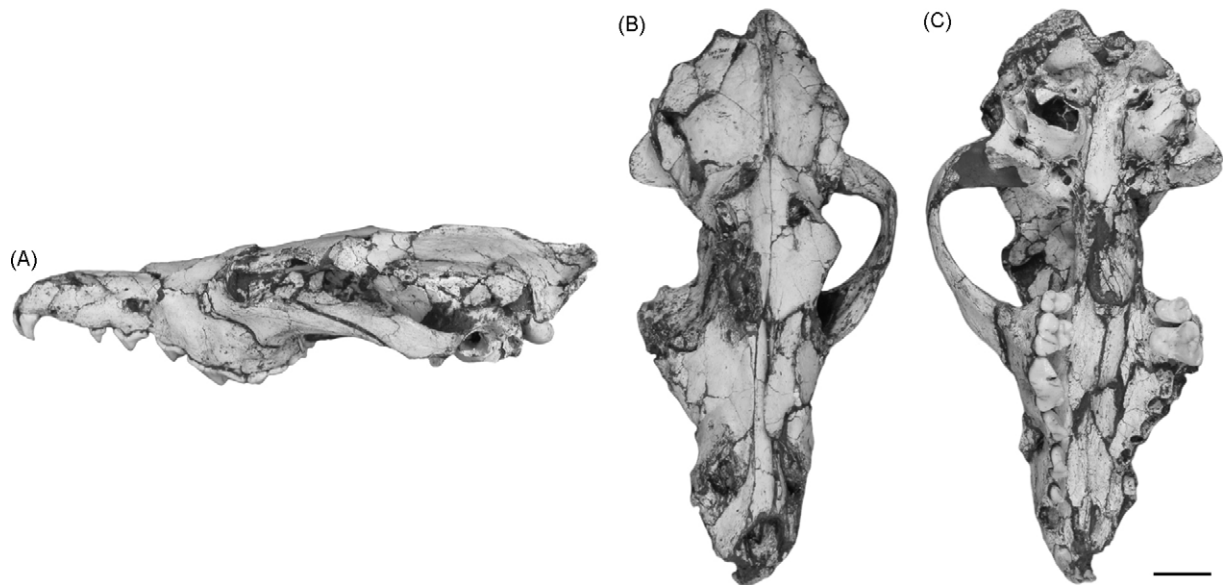
Fig. 2. Skull of *C. accitanus* nov. sp.; holotype FP1-2001-0434. **A.** Side view; **B.** Sagittal view; **C.** Ventral view. Scale bar = 2 cm.
Crâne de C. accitanus *nov. sp. ; holotype FP1-2001-0434. **A.** Profil ; **B.** Vue sagittale ; **C.** Vue ventrale. Échelle = 2 cm.*

Metacervoceros rhenanus cf. *phillisi, Croizetoceros ramosus* ssp., *Gazellospira torticornis* ssp., *Homotherium latidens, Megantereon cultridens* ssp., *Acinonyx pardinensis, Lynx pardinus spelaeus, Vulpes alopecoides, Meles iberica* and *C. accitanus* nov. sp.) and immigrants from Asia and Africa (*Equus* cf. *major, Potamochoerus* nov. sp., *Mitilanotherium* nov. sp., *Leptobos etruscus, Praeovibos* nov. sp., *Capra* nov. sp., *C. etruscus, C. falconeri, Hyaena brunnea* and *Pachycrocuta brevirostris*). Such a palaeobiological association is new for Eurasia.

Analysis of the Last and First Appearance Data (LADs and FADs) for the site's most important taxa assign the fossil association a position between the Olivola and Tasso Faunal Units (FU) (Raia et al., 2006), or, if the indications of other authors regarding French fossil associations (Palombo and Valli, 2003-2004) are taken into account, in zone MNQ-18. Carnivores are represented by eleven species, four of which are canids: *V. alopecoides, C. etruscus, C. falconeri,* and the new *Canis* member presented in this paper, *C. accitanus* nov. sp.

3. Systematic palaeontology

Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Family CANIDAE Fischer de Waldheim, 1817
Subfamily CANINAE Fischer de Waldheim, 1817
Tribe CANINI Fischer de Waldheim, 1817
Genus ***Canis*** Linnaeus, 1758
C. accitanus nov. sp.
Etymology: the species name is the Latin adjective describing the inhabitants of *Accitania* (Land of *Acci*), an Ibero-Roman term used for the Guadix region where the Fonelas site is found.

Holotype: FP1-2001-0434 (Fig. 2): a skull with the left dentition complete (except for the canine), and with the right P^1, M^1-M^2, held at the *Museo Geominero* (*Instituto Geológico y Minero de España, Ministerio de Educación y Ciencia*), Madrid, Spain.

Other materials: FP1-2001-0606: I^1 right, FP1-2001-0082: I^2 left, FP1-2001-0175: P^2 right, FP1-2001-0605: P^2 left, FP1-2001-0531: P^3 right, FP1-2002-1486: P^3 left, FP1-2001-0156: P^4 right, FP1-2001-0069: right radius.

MNI: 2 adults (P^2 and P^3 left).

Type locality: Fonelas P-1 (Fonelas, Guadix Basin, Granada, Spain) (Fig. 1). See Arribas et al. (2001) and Viseras et al. (2006) for details.

Stratigraphic level: facies association E (*Sondeo B*), Unit VI (*Sistema Axial*) of the Guadix Formation, in agreement with Viseras et al. (2006).

Geological age: Plio-Pleistocene boundary, *c.* 1.7-1.9 Ma, based on comparisons of the faunal association with older faunas from the Upper Pliocene of Saint-Vallier (MNQ-17) and Senèze (MNQ-18), contemporaneous faunas from the Plio-Pleistocene boundary (Olivola-Tasso Italian FUs), and younger faunas from the Lower Pleistocene (MNQ-19) (Arribas et al., 2001, 2004; Garrido, 2006).

Diagnosis: a small canid with a very long and narrow splanchnocranium showing two long and fine palatine fissures. The caudal margin of the nasal bones clearly lies beyond the caudal limit of the maxillary bones. The frontal bones of the neurocranium are only slightly prominent and have zygomatic apophyses that project strongly outward. The sagittal crest is

*Situations géologique et géographique du gisement de Fonelas P-1. **A.** Carte géologique du bassin de Guadix dans la cordillère Bétique au sud-est de l'Espagne. **B.** Carte géologique du bassin de Guadix (la croix indique le gisement de Fonelas P-1). **C.** Log stratigraphique du gisement de Fonelas P-1 (Sondage B, modifié d'après Viseras et al. [2006]).*

little developed. The upper premolars are separated by a diastema. P^1 has a conical crown and is very pointed, the basal cingulum is hardly visible and there is no distal platform. P^2 has a very tall protocone and no traces of a posterior accessory cuspid. P^3 shows a posterior accessory cuspid that is no more than a cusplet next to the distal margin of the protocone, giving the distal platform an inclined appearance. P^4 has a pointed, little-individualised protocone that projects mesially with respect to the mesial margin of the paracone, forming a continuum with lingual face of the tooth: the metacone is single lobed. M^1 shows pointed cusps and a protoconule close to the protocone; the tooth has a labiolingual ridge that joins the metacone with the entocone and a talon that projects weakly towards the caudal area of the skull. M^1 also has a bilobed hypocone divided by a labiolingual notch.

Description: the only skull recorded to date is practically complete (Fig. 2 and Table 1), although it shows strong dorsoventral fossil-diagenetic compression. This has caused the displacement of the left anterior region of the skull, which now lies over the right half. The zygomatic arch and most of the right dentition was probably lost prior to burial. The elements FP1-2001-0606 (I^1), FP1-2001-0175 (P^2), FP1-2001-0531 (P^3) and FP1-2001-0156 (P^4) may belong to the same individual as skull FP1-2001-0434 since these were found just a few centimetres below the latter. They may have become dislodged during putrefaction. The skull conserves its tympanic bullae, as well as the premaxillary, maxillary, nasal, frontal, parietal, occipital, sphenoid, pterigoid, vomer and palatine bones. The zygomatic arch of the right side has not been preserved, although the region posterior to it forms part of the squamous bone, where the condyles for the articulation of the jaw are situated.

The splanchnocranium is very long and narrow and shows a wide nasal orifice, with wedge shaped premaxillary bones; the caudal margin of this wedge ends at the level of the second premolar. The maxillary bones each contain a small, oval-shaped foramen above P^3. The caudal margin of the nasal bones lies well beyond the maxillofrontal suture. The neurocranium has frontal bones that show little prominence; a shallow longitudinal depression runs between them. Each frontal bone has a well developed zygomatic apophysis from which the frontal crests depart, and domed parietal bones (very deformed by compression) separated from one another by a mildly pronounced sagittal crest that reaches its maximum development in the caudal area where it meets a well developed occipital crest.

Ventrally, the palate is very long and narrow, but it dilates progressively after the distal margin of P^2 to reach its maximum width between the distal limit of the carnassial teeth. After this point, it becomes slightly narrower again. The palatine fissures are elliptical in shape and very elongated in the anterior-posterior direction. The palatine foramina open at the mean level of P^4. Secondary palatine foramina can also be seen. In the depression present in the palatine bone between P^4 and M^1 there is a deep hollow close to the lingual face of the metacone of P^4, into which a very sharp protoconid of M_1 enters when the mandible is completely closed. The alisphenoid bone has suffered great compression, its morphology cannot therefore be accurately described. The articulatory condyles, which have been preserved complete, are deep and show the typical elliptical shape of the family. The tympanic bullae also well preserved are oval: the dimensions of their main axes are 19.83 and 16.9 mm. Despite the compression it has suffered, an elliptical *foramen magnum* can be seen.

The left upper jaw conserves I^1-I^3, P^1-P^4 and M^1-M^2, the canine is missing (Fig. 2 and Table 2). In the right upper jaw, only P^1 (highly deformed by compression) and M^1-M^2 have been preserved. The implantation of P^1 and P^2 is practically parallel to the anterior-posterior axis of the cranium, however, it curves outwards at P^3 and P^4 and inwards at the molars. Diastemas are seen between I^3 and the alveolus of C, between the latter alveolus and P^1, between P^1 and P^2, P^2 and P^3, and P^3 and P^4, the size becoming slightly smaller from the first to the last.

The incisors become larger from I^1 to I^3. I^1 and I^2 show an external lateral denticle and a thick lingual cingulum. I^3 is caniniform: it has a mesiolingual and a distal ridge running its length, and a thick lingual cingulum. The first upper premolar is a simple tooth with a single root. It has a very pointed conical crown with two mesiolingual and distal ridges; the lingual cingulum is little developed, and there is no distal platform. The second upper premolar has a pointed protocone with mesiolingual and distal ridges: the linguodistal cingulum is little developed. The talon forms a small, flat surface along which runs a very sharp distal ridge. No true posterior accessory cuspid (pac) can be seen in P^2.

The third upper premolar has a mesiolingual and a distal ridge running the length of the talon. The platform formed by the talon is slightly larger than that of P^2. The cusplet of a pac can be seen next to the distal face of the protocone. A distal cingulum is also visible, which curves slightly to form another small denticle, the distal part of the tooth therefore has a clearly

Table 1

Measurements of the cranium FP1-2001-0434, following Driesch (1976) [() = estimate].

Mesures du crâne FP-2001-0434, d'après Driesch (1976) [() = estimation].

Anatomical features	Measurements (mm)
Total length	182
Condylobasal length	168
Basal length	160
Upper neurocranium length	80.14
Viscerocranium length	84.72
Facial length	102.47
Greatest length of the nasal bones	63.93
Snout length	76.26
Median palatal length	(90.02)
Palatal length	28.74
Greatest breadth of the occipital condyles	35.30
Greatest breadth of the *foramen magnum*	16.20
Height of the *foramen magnum*	12.95
Smallest breadth of skull (at the postorbital constriction)	31.20
Greatest palatal breadth	(47.11)
Smallest palatal breadth	27.61
Breadth at the canine alveoli	30.10

Table 2
Measurements (mm) of upper teeth. L = total length; w = maximum width.
Mesures (en mm) de la dentition supérieure. L = longueur totale; w = largeur maximale.

Upper teeth	P1		P2		P3		P4		M1		M2		Series P^1-M^2	Premolar series	Molar series
	L	w	L	w	L	w	L	w	L	w	L	w	L	L	L
FP1-2001-0434	5.41	3.75	10.91	4.20	11.64	4.46	18.48	8.63	12.49	14.41	7.20	9.54	66.98	51.32	19.89
FP1-2001-0175	–	–	9.87	4.21	–	–	–	–	–	–	–	–	–	–	–
FP1-2001-0605	–	–	10.15	4.07	–	–	–	–	–	–	–	–	–	–	–
FP1-2001-0531	–	–	–	–	11.56	4.56	–	–	–	–	–	–	–	–	–
FP1-2002-1486	–	–	–	–	11.72	4.40	–	–	–	–	–	–	–	–	–
FP1-2001-0156	–	–	–	–	–	–	18.91	8.58	–	–	–	–	–	–	–

inclined platform. The upper carnassial tooth has a pointed paracone with a mesiolingual ridge that joins at its base with a mesial cingulum. At the base of the paracone, there is a second crest a few millimetres in height arising from the protocone. The protocone is very pointed: it is little individualised and projects slightly towards the mesial region with respect to the mesial margin of the paracone, forming a continuum with the lingual face of the latter. The distal region of the paracone has a very sharp crest that ends in an open V-shaped depression which, on the labial face, gives rise to a small hollow in the area of contact with the metacone. The metacone has a sharp, single lobed occlusal ridge whose posterior margin enters into contact with the distal cingulum. This cingulum continues along the lingual face of the metacone and the distal part of the paracone.

M^1 has a tall, pointed paracone (Fig. 3). It is subtriangular in cross-section, and has a very notable mesiolabial ridge running its length. It also has prominent lingual ridge more prominent at the tooth base, and a distal ridge that ends in the depression between the paracone and metacone. In the mesiolabial region of the paracone, there is an increase in the size of the labial cingulum to form a parastyle. The metacone is also very well developed although it is not as tall as the paracone. This cusp has a sharp ridge in the mesial position that reaches the depression that connects it with the paracone. It also has a distal ridge that joins with the basal cingulum to form a miniscule metastyle cusplet. The protocone is subtriangular in cross-section: it is a very prominent and very pointed cusp with a mesiolabial ridge that continues along the mesial face of the tooth until reaching the metastyle. A distal ridge connects the protocone with the entocone, leaving a slight U-shaped depression between them. Close to the mesial face of the protocone, and arising from the mesiolabial ridge, there is a small supernumerary cusp (protoconule). The entocone is well developed although it is smaller than the protocone. As well as the ridge that joins it to the protocone, two further ridges arise from the entocone: one in a labiodistal position that ends by joining up with the basal cingulum at the level of the metacone, and another, labiolingual in orientation, that joins the cusp to the base of the metacone at its mid point. Between the four cusps described (paracone, metacone, protocone and entocone) there is a large, subcircular depression. The talon of M^1 appears slightly curved towards the distal region, though this curvature is not very pronounced compared to that seen in other members of this genus. The hypocone is prominent and shows a very particular characteristic: it is bilobate due to the presence of a central notch. This notch divides two cusps, the larger in a linguodistal position (the hypocone) and the smaller in a lingual position. A very marked cingulum can also be seen on the labial and mesial faces of the base of the tooth.
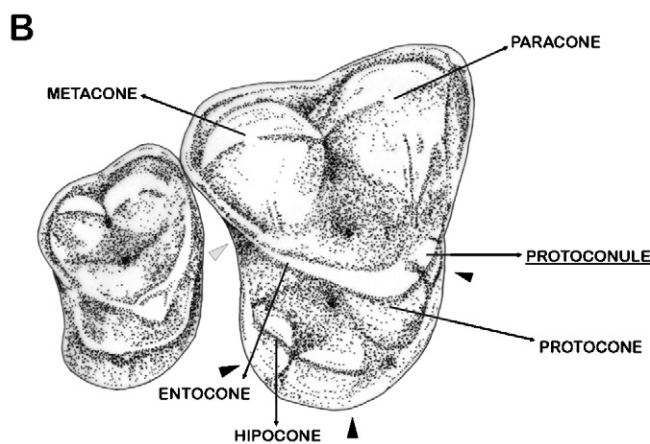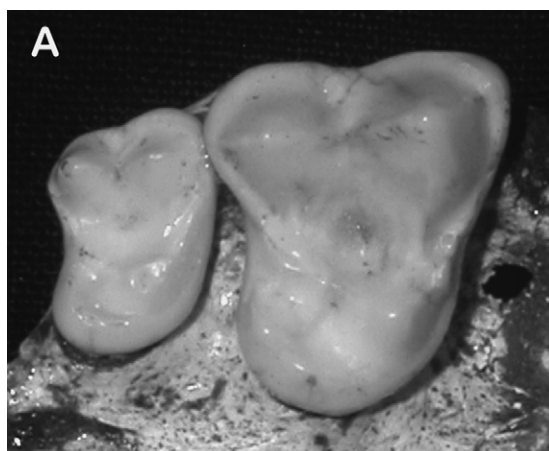

Fig. 3. Upper right jugal dentition (M^1-M^2) of *Canis accitanus* nov. sp. **A.** Detail of the upper molars. **B.** Distribution and nomenclature for the M^1 cuspids. The arrows show the position of the diagnostic features of *Canis accitanus* nov. sp. relating to this tooth.
Dentition jugale supérieure droite (M^1-M^2) de C. accitanus *nov. sp.* **A.** *Détail des molaires supérieures.* **B.** *Distribution et nomenclature des cuspides dans la M^1. Les flèches indiquent la localisation sur cette dent des traits diagnostiques de* C. accitanus *nov. sp.*

M^2 is a small, well developed tooth, the talon of which is slightly curved towards the posterior region of the skull. Its paracone is slightly larger than the metacone, although both cusps reach approximately the same height. The protocone, which is pointed and well developed, is joined to the basal cingulum by two well developed crests, one situated in a mesiolabial position, the other running towards the distal margin passing over a barely visible entocone. The hypocone appears as a thick lingual crest: no evidence of a cusp is visible.

The postcranial skeleton includes a complete radius; this has been slightly compressed and fractured but it conserves its original dimensions (*total length*: 144.96 mm; *DTprox*: 15.29 mm; *DAPprox*: 11.02 mm; *DTdistal*: 20.26 mm and *DAPdistal*: 10.60 mm) and the epiphyses are complete. The diaphysis is practically straight, ovoid in cross-section and very graceful in its constitution. The dorsal face of the diaphysis is convex while the plantar face is flatter. A long longitudinal crest runs along the latter face where the ligament joining the radius and ulna inserts. The joint surface of the proximal epiphysis has a kidney-like shape, is concave, and has a little developed oblique crest. The diaphysis becomes wider at its extreme distal end, giving rise to a transversally enlarged distal epiphysis with a very well-developed styloid apophysis.

4. Comparison and discussion

The general architecture of this small canid skull from Fonelas P-1, and the association of anatomical characteristics it presents – especially the presence of smooth (rather than rough) parietal bones plus the disproportion between the buccolingual (DBL) and mesiodistal diameters (DMD) of M^1 – exclude its owner from the genus *Nyctereutes*. In addition, the absence of the typical vulpine depression of the zygomatic process of the frontal bones, and the presence of an M^1 with a paracone larger than the metacone plus a little developed labial cingulum, rule out this animal as a member of the genera *Eucyon* or *Vulpes*; the members of these genera have substantially smaller dimensions than those of this new canid (Fig. 4). Nonetheless, the mesial projection of the protocone of P^4 with respect to the mesial margin of the paracone does approximate it anatomically to *Vulpes* (vulpines show a strong mesial projection of the protocone on this tooth). In essence, however, the animal's cranial and dental anatomical characteristics are similar to those shown by members of the genus *Canis*.

The skull belongs to the smallest representative of *Canis* ever recorded at Fonelas P-1, and shows a series of anatomical characteristics similar to those seen in the lineage of the coyote (Kurtén, 1974; Sotnikova, 2001). Indeed, it would appear particularly similar to the Plio-Pleistocene species *C. arnensis*, with which it shares the features of a narrow muzzle, very mildly bowed frontal bones, and a little-developed sagittal crest. According to Koufos (1987) and Koufos and Kostopoulos (1997), the upper dentition of *C. arnensis* is characterised by a wide diastema between the upper premolars, a P^2 with no pac, a P^3 with a poorly developed pac, a P^4 with a small protocone, and tricuspid upper molars. These characteristics, however, are very general, and are seen in the majority of species belonging

to the genus *Canis*. Furthermore, the presence of a diastema between the premolars or the presence/absence of a pac in these elements are features that appear to be subject to a certain intraspecific variability. Therefore, the majority of determinations regarding *C. arnensis* are only based on metric data; the specific diagnosis of this taxon needs to be reundertaken, taking into account anatomical characteristics less common among the species of the genus *Canis*.

Bearing in mind the current diagnosis for *C. arnensis*, the presence of a very narrow maxillofacial region, the diastema between the upper premolars, the absence of a pac in P^2, and the presence of a small pac in P^3 in the new canid anatomically relate *C. accitanus* nov. sp. to *C. arnensis*.

The diagnosis of *C. apolloniensis* by Koufos and Kostopoulos (1997) is surprising in its brevity: "*small size; no diastema between the premolars; strong and well separated protocone; long M$_1$ with relatively short trigonid*". Certainly the majority of canid species diagnosed to date would fit perfectly with this diagnosis.

Once the ambiguity reigning within this group of small canids is accepted, it becomes clear that, despite the morphological homogeneity shown by these animals, skull FP1-2001-0434 shows a number of peculiar anatomical characteristics, e.g., the combination, on the first upper molar, of a well-developed protoconule plus a ridge between the entocone and metacone, along with the presence of a bilobate hypocone divided by a central notch.

A comparison of the skull of *C. accitanus* nov. sp. with those of modern-day *C. lupus*, *C. latrans*, *C. adustus*, *C. mesomelas* and *C. simensis* shows it to share features with some of these species. Indeed, a certain morphological affinity is seen with *C. simensis* in that both species share a very narrow maxillofacial region, narrow and very long palatine fissures, and an M^1 hypocone divided by a lingual notch. This last feature is also seen in some specimens of *C. lupus*, *C. adustus* and *C. latrans*. The presence of a ridge between the entocone and paracone has only been confirmed in *C. mesomelas*.

Apart from *C. accitanus* nov. sp., no protoconule was observed on M^1 in any canid studied, either fossil or modern. Similarly, the joint presence of a bilobate hypocone and a ridge between the entocone and metacone has never been described for any Eurasian taxon. Thus, no species of the genus *Canis* shows this association of characteristics.

Metrically, the new canid is clearly the smallest extinct member of the genus *Canis* that the European fossil record has ever provided (Fig. 4). It is even smaller than the smallest specimens of *C. arnensis*, including that examined by Martin (1973) and designated as *C. senezensis*. However, *C. accitanus* nov. sp. was substantially larger than extant jackals *C. mesomelas*, *C. adustus* or *C. aureus*.

To date, no lower dentition for *C. accitanus* nov. sp. has been found at Fonelas P-1, although given the presence of a deep hollow close to the metacone of P^4 and housed in the typical depression between P^4 and M^1, the presence of an M$_1$ with a long, pointed protoconid can be inferred.

With respect to the postcranial skeleton, the radius found at Fonelas P-1 shows the typical anatomical characteristics of the
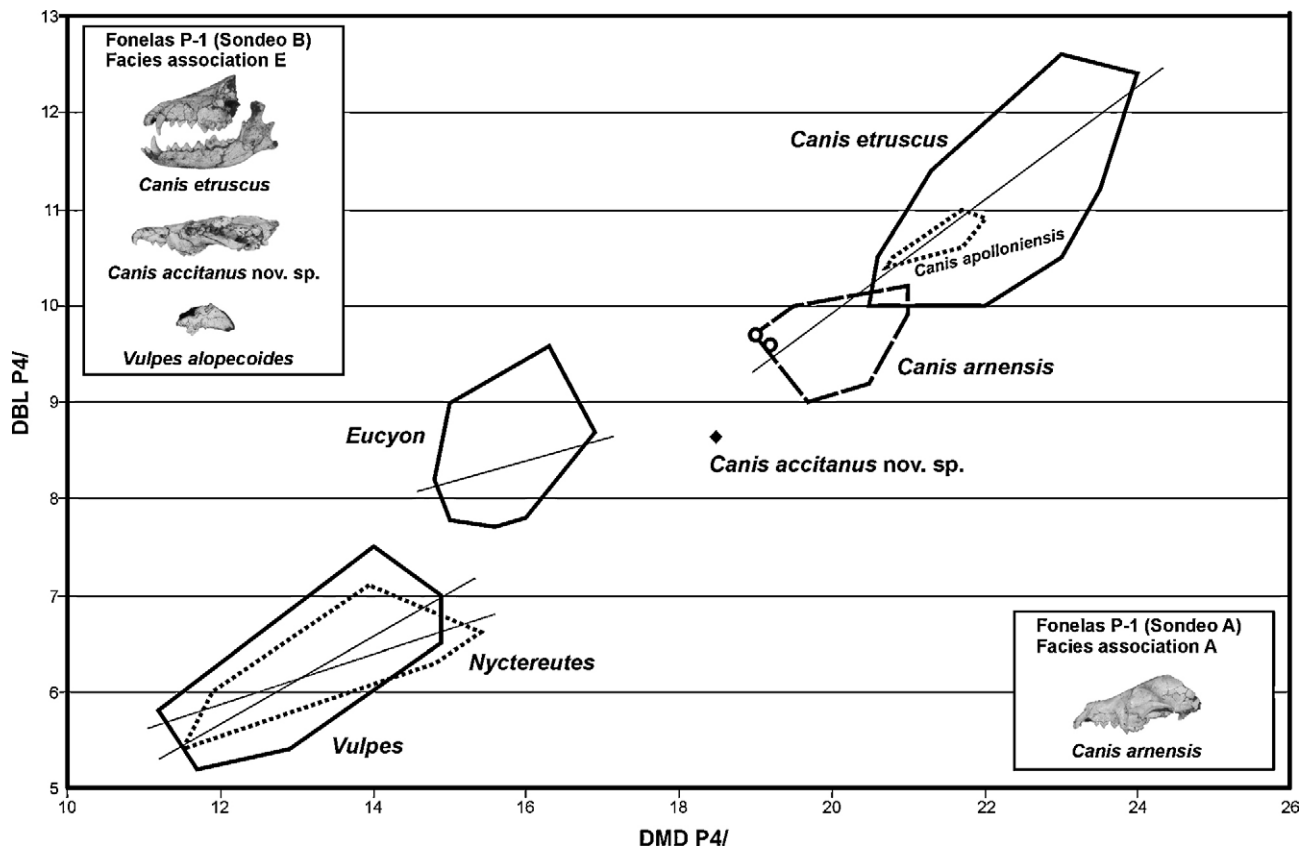
Fig. 4. Bivariate plot of the mesiodistal and buccolingual diameters of the upper carnassial teeth of a number of medium and large size fossil canids. Data for *C. etruscus* taken from Pons-Moyà and Moyà-Solà (1978), Rook (1993), Koufos (1992), Vekua (1996), and Koufos and Kostopoulos (1997), as well as from specimens from Fonelas P-1 (Garrido, 2006). Data for *C. apolloniensis* taken from Koufos and Kostopoulos (1997). Data for *C. arnensis* taken from Koufos (1987) and Rook (1993), including the two specimens known as "*C. senezensis*" (marked with white circles), a recent synonym of *C. arnensis*. For the genus *Eucyon*, data are taken from Tedford and Qiu (1996) for the species *E. davisi* and *E. zhoui*. The representation for *Nyctereutes* includes the species *N. donnezani* and *N. megamastoides* (Bonifay, 1971; Koufos, 1993). In *Vulpes*, the specimens classified as *V. alopecoides*, *V. praeglacialis* and *V. vulpes* (Villalta, 1952; Bonifay, 1971) have been included. *Diagramme bivarié des diamètres mesiodistal et buccolingual des dents carnassières supérieures de canidés fossiles de tailles moyenne à large. Les données concernant* C. etruscus *proviennent de Pons-Moyà et Moyà-Solà (1978),* Rook (1993), Koufos (1992), Vekua (1996), *et Koufos et Kostopoulos (1997), ainsi que de Fonelas P-1 (Garrido, 2006). Les données concernant* C. apolloniensis *ont été reprises de Koufos et Kostopoulos (1997). Les données de* C. arnensis *ont été relevées dans Koufos (1987) et Rook (1993), ainsi que celles des deux exemplaires connus comme « C. senezensis » (cercles blancs), un synonyme récent de* C. arnensis*. Pour le genre Eucyon, les données concernant* E. davisi *et* E. zhoui *ont été extraites de Tedford et Qiu (1996). La représentation de* Nyctereutes *inclut* N. donnezani *et* N. megamastoides *(Bonifay, 1971 ; Koufos, 1993). Pour* Vulpes*, ont été inclus les exemplaires classés comme* V. alopecoides, V. praeglacialis *et* V. vulpes *(Villalta, 1952 ; Bonifay, 1971).*

genus, although it is substantially smaller than those of specimens of *C. mosbachensis* from L'Escale (Bonifay, 1971). In addition, the right radius FP1-2001-0069 is substantially larger than that of modern-day *V. vulpes*. Together, these data suggest this element belongs to the smallest member of the genus *Canis* ever discovered at Fonelas P-1.

5. Conclusions

Both the anatomical and metric characteristics of the studied material show it to belong to the smallest member of the genus *Canis* ever recorded at Fonelas P-1, a new fossil species: *C. accitanus* nov. sp.

The new species shares a series of basic morphological characteristics with *C. arnensis*. However, its upper dentition shows certain anatomical structures and associations of structures that have never been described before in this genus (e.g., those mentioned for P^4 and M^1), and it has a number of

features resembling those of *Vulpes* that are not seen in other members of *Canis* (*C. etruscus, C. arnensis, C. lupus* and *C. latrans*), e.g., the general form of P^1 and the mesial projection of the P^4 protocone. It also appears to share certain characteristics with *C. etruscus* and *C. lupus* (not present in *C. arnensis* and *C. latrans*) such as the reduced longitudinal development of the distal platform of P^3, a consequence of the presence of a posterior accessory cuspid at the distal margin of the protocone which forms an inclined rather than a level distal platform. The general structure of M^1 and the number and distribution of cusps on this tooth are homogeneous across *C. etruscus, C. arnensis, C. lupus* and *C. latrans*, but different in *Vulpes*, whose members show linguodistal development of the talon and a strong thickening of the labial cingulum. It should be noted that both patterns are different to that seen in *C. accitanus* nov. sp.

This new species of *Canis* shows a combination of autapomorphic and plesiomorphic features essentially in its jugal dentition. The autapomorphic features are interpreted to

be those resulting from adaptation to a more abrasive diet, this is inferred from the presence of elements showing anatomical affinities with the vulpines, and the existence of the combination of characteristics described above. Together, these indicate the development of an occlusal surface more efficient for grinding food (a convergent adaptation for feeding on carrion in a manner similar to jackals such as *C. mesomelas*). The plesiomorphic features are those also present in the lineage *C. arnensis–C. latrans*. Probably, the members of this new species derive from a local, ancestral population of *C. arnensis*, for which remarkable evidence exists in an older lithostratigraphic layer at the Fonelas P-1 site (Facies Association A in *Sondeo A* [Viseras et al., 2006]).

Finally, this new canid was substantially smaller than *C. arnensis*, and is the smallest European member of *Canis s.s.* recorded to date.

References

Agustí, J., Moyà-Solà, S., Martín-Suárez, E., Marín, M., 1987. Faunas de mamíferos en el Pleistoceno inferior de la región de Orce (Granada, España). Paleontología i Evolució, memoria especial 1, 73–86.

Argant, A., 1991. Carnivores quaternaires de Bourgogne. Documents des Laboratoires de Géologie de Lyon 115, 1–301.

Arribas, A., Baeza, E., Bermúdez, D., Blanco, S., Durán, J.J., Garrido, G., Gumiel, J.C., Hernández, R., Soria, J.M., Viseras, C., 2004. Nuevos registros paleontológicos de grandes mamíferos en la Cuenca de Guadix-Baza (Granada): aportaciones del Proyecto Fonelas al conocimiento sobre las faunas continentales del Plioceno-Pleistoceno europeo. Boletín Geológico y Minero 115, 567–581.

Arribas, A., Riquelme, J.A., Palmqvist, P., Garrido, G., Hernández, R., Laplana, C., Soria, J.M., Viseras, C., Durán, J.J., Gumiel, P., Robles, F., López-Martínez, J., Carrión, J., 2001. Un nuevo yacimiento de grandes mamíferos villafranquienses en la Cuenca de Guadix-Baza (Granada): Fonelas P-1, primer registro de una fauna próxima al límite Plioceno-Pleistoceno en la Península Ibérica. Boletín Geológico y Minero 112, 3–34.

Beaumont, G. de, 1979. Note sur quelques carnivores (Mammifères) du Quaternaire ancien de la province de Foggia (Italie). Bulletin de la Société Vaudoise des Sciences Naturelles 74, 217–226.

Beaumont de, G., 1980. Säugerfaunen von der Grenze Pliozän/Pleistozän aus Rheinessen 2. Les carnivores du Quaternaire ancien de Neuleiningen (Pfalz). Mainzer Geowissenschaften Mitteilungen 8, 7–16.

Bonifay, M.F., 1971. Carnivores quaternaires du Sud est de la France. Mémoires du Muséum National d'Histoire Naturelle Sér. C 21 (2), 1–377.

Driesch, A. von den, 1976. A guide to the measurement of animal bones from archaeological sites. Peabody Museum Bulletin 1, 1–137.

Flynn, J.J., Tedford, R.H., Qiu, Z., 1991. Enrichment and stability in the Pliocene mammal faunas of North China. Paleobiology 17, 246–265.

García, N., 2002. Los carnívoros de los yacimientos pleistocenos de la Sierra de Atapuerca. Ph. D. thesis, Universidad Complutense de Madrid (unpublished).

García, N., Arsuaga, J.L., 1999. Carnivores from the Early Pleistocene hominid-bearing Trinchera Dolina 6 (Sierra de Atapuerca, Spain). Journal of Human Evolution 37, 415–430.

Garrido, G., 2002. El registro del género *Canis* (Canidae, Carnívora, Mammalia) en el yacimiento villafranquiense de Fonelas P-1 (Cuenca de Guadix-Baza, Granada, España). Trabajo de Investigación del Doctorado Inter-universitario en Paleontología para la obtención del Diploma de Estudios Avanzados. Universidad Complutense de Madrid (unpublished).

Garrido, G., 2006. Paleontología sistemática de grandes mamíferos del yacimiento del Villafranquiense superior de Fonelas P-1 (Cuenca de Guadix, Granada). PhD thesis, Universidad Complutense de Madrid (unpublished).

Garrido, G., Arribas, A., 2002. Nuevos registros del género *Canis* en el Villafranquiense Ibérico: Fonelas P-1 (Cuenca de Guadix-Baza, Granada). Libro de Resúmenes de las XVIII Jornadas de la Sociedad Española de Paleontología. II Congreso Ibérico de Paleontología, Salamanca, pp. 50-51.

Gotelli, D., Sillero-Zubiri, C., Applebaum, G.D., Roy, M.S., Girman, D.J., García-Moreno, J., Ostraders, E.A., Wayne, R.K., 1994. Molecular genetics of the most endangered canid: the Ethiopian wolf, *Canis simensis*. Molecular Ecology 3, 301–312.

Koufos, G.D., 1987. *Canis arnensis* del Campana, 1913 from the Villafranchian (Villanyian) of Macedonia (Greece). Paleontologia i Evolució 21, 3–10.

Koufos, G.D., 1992. The Pleistocene Carnivores of the Mygdonia basin (Macedonia, Greece). Annales de Paléontologie 78, 205–257.

Koufos, G.D., 1993. Late Pliocene carnivores from Western Macedonia (Greece). Paläontologische Zeitschrift 67, 357–376.

Koufos, G.D., Kostopoulos, D., 1997. New Carnivore material from the Plio-Pleistocene of Macedonia (Greece) with a description of a new canid. Münchner Geowissenschaften Abhandlungen 34, 33–63.

Kurtén, B., 1968. Pleistocene mammals of Europe. Weidenfeld and Nicholson, London.

Kurtén, B., 1974. A history of coyote-like dogs (Canidae, Mammalia). Acta Zoologica Fennica 140, 1–38.

Kurtén, B., Anderson, E., 1980. Pleistocene mammals of North America. Columbia University Press, New York.

Kurtén, B., Poulianos, A.N., 1977. New stratigraphic and faunal material from Petralona Cave, with special reference to the Carnivora. Anthropos 4, 47–130.

Lumley, H. de, Kahlke, H.D., Moigne, A.M., Moulle, P.E., 1988. Les faunes de grands mammifères de la grotte du Vallonet Roquebrune-Cap-Martin, Alpes-Maritimes. L'Anthropologie 92, 465–496.

Martin, R., 1973. Trois nouvelles espèces de Caninae (Canidae, Carnivora) des gisements Plio-Villafranchiens d'Europe. Documents des Laboratoires de Géologie de Lyon 57, 87–96.

Morales, J., 1981. Venta del Moro, su macrofauna de mamíferos, bioestratigrafía continental del Mioceno final mediterráneo. PhD thesis, Universidad Complutense de Madrid (unpublished).

Morales, J., Soria, D., 1979. Nuevos datos sobre los carnívoros del área de Teruel: Síntesis y bioestratigrafía. Estudios Geológicos 35, 497–540.

Nowak, R.M., 1999. Walker's Mammals of the World. Volumes I y II. Johns Hopkins University Press, Baltimore and London.

Palombo, M.R., Valli, A.M.F., 2003-2004. Remarks on the biochronology of mammalian faunal complexes from the Pliocene to the Middle Pleistocene in France. Geologica Romana 37, 145–163.

Pons-Moyà, J., 1987. Los carnívoros (Mammalia) de Venta Micena (Granada, España). Paleontología i Evolució, memoria especial 1, 109–128.

Pons-Moyà, J., Moyà-Solà, S., 1978. La fauna de Carnívoros del Pleistoceno medio (Mindel) de la cueva Victoria (Cartagena, España). Acta Geológica Hispánica 13, 54–58.

Raia, P., Piras, P., Kotsakis, T., 2006. Detection of Plio-Quaternary large mammal communities of Italy. An integration of fossil faunas biochronology and similarity. Quaternary Science Reviews 25, 846–854.

Reich, D.E., Wayne, R.K., Goldstein, D.B., 1999. Genetic evidence for a recent origin by hybridization of red wolves. Molecular Ecology 8, 139–145.

Roger, S., Coulon, C., Thouveny, N., Féraud, G., Van Velzen, A., Fauquette, S., Cochemé, J.J., Prévot, M., Verosub, K.L., 2000. ^{40}Ar/^{39}Ar dating of a tephra layer in the Pliocene Senèze maar lacustrine sequence (French Massif Central): constraint on the age of the Reunion-Matuyama transition and implications on paleoenvironmental archives. Earth and Planetary Science Letters 183, 431–440.

Rook, L., 1993. I cani dell'Eurasia dal Miocene superiore al Pleistocene medio. Ph.D. thesis. Universitá ''La Sapienza'', Florencia (unpublished).

Rook, L., Azzaroli-Puccetti, M.L., 1996. Remarks on the skull morphology of the endangered Ethiopian jackal, *Canis simensis* Rüppell, 1838. Atti della Academia Nazionale dei Lincei, Classe di Science Fisiche Matematiche e Naturali. Rendiconti Lincei Scienze Fisiche e Naturali 7 (9), 277–302.

Rook, L., Torre, D., 1996. The latest Villafranchian-early Galerian small dogs of the Mediterranean area. Acta Zoologica Cracoviensia 39, 427–434.

Sillero-Zubiri, C., Gottelli, D., 1994. *Canis simensis*. Mammalian Species 485, 1–6.

Soergel, W., 1928. Ein Kleiner Wolf aus dem Kiesen von Süssenborn. Zeitschrift der Deutschen Geologischen Gesellschaft 80, 227–255.

Sotnikova, M.V., 1989. Late Pliocene-Early Pleistocene Carnivora. Stratigraphic significance. Trudy Akademia Nauk 440, 1–123.

Sotnikova, M.V., 2001. Remains of Canidae from the Lower Pleistocene site of Untermassfeld. In: Kahlke, R.D. (Ed.), Das Pleistozän von Untermassfeld bei Meiningen (Thüringen), 2. Römisch-Germanisches Zentralmuseum, Mainz, pp. 607-632.

Spassov, N., Rook, L., 2006. *Eucyon marinae* sp. nov. (Mammalia, Carnivora), a new canid species from the Pliocene of Mongolia, with a review of forms referable to the genus. Rivista Italiana di Paleontologia e Stratigrafia 112, 123–133.

Tedford, R.H., Flynn, J.L., Qiu, Z., Opdyke, H., Doens, W.R., 1991. Yushe basin, China, Paleomagnetically calibrated mammalian biostratigraphic standard for the Late Neogene of eastern Asia. Journal of Vertebrate Paleontology 11, 519–526.

Tedford, R.H., Qiu, Z., 1996. A new canid genus from the Pliocene of Yushe, Shanxi Province. Vertebrata PalAsiatica 34, 27–40.

Thenius, E., 1954. Die Caniden (Mammalia) aus dem Altquartär von Hundsheim (Niederösterreich) nebst Bemerkungen zur Stammesgeschichte der Gattung *Cuon*. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 99, 230–286.

Torre, D., 1967. I cani villafranchiani della Toscana. Palaeontographia Italica 63, 113–138.

Torre, D., 1974. Affinità dentali del canide della grotta di L'Escale. Rivista Italiana di Paleontología e Stratigrafia 80, 147–156.

Torre, D., 1979. The Ruscinian and Villafranchian dogs of Europe. Bolletino della Società Paleontologica Italiana 18, 162–165.

Torre, D., Ficcarelli, G., Masini, F., Rook, L., Sala, B., 1992. Mammal dispersal events in the early Pleistocene of Western Europe. Courier Forschungsinstitut Senckenberg 153, 51–58.

Van Gelder, R.G., 1978. A review of canid classification. American Museum Novitates 2646, 1–10.

Van Valkenburgh, B., Wayne, R.K., 1994. Shape divergence associated with size convergence in sympatric East African jackals. Ecology 75, 1567–1581.

Vekua, A., 1996. Die Wirbeltierfauna des Villafranchium von Dmanisi und ihre biostratigraphische Bedeutung. Jahrbuch des Römisch-Germanischen Zentralmuseums Mainz 42, 77–180.

Villalta, J.F., 1952. Contribución al conocimiento de la fauna de mamíferos fósiles del Plioceno de Villarroya (Logroño). Boletín del Instituto Geológico y Minero de España 64, 3–204.

Viseras, C., Soria, J.M., Durán, J.J., Pla, S., Garrido, G., García-García, F., Arribas, A., 2006. A large mammals site in a meandering fluvial context (Fonelas P-1, Late Pliocene, Guadix Basin, Spain). Sedimentological keys for its palaeoenvironmental reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology 242, 139–168.

Werdelin, L., Lewis, M., 2000. Carnivora from the South Turkwel hominid site, Northern Kenya. Journal of Paleontology 74, 1173–1180.

Werdelin, L., Lewis, M., 2005. Plio-Pleistocene Carnivora of eastern Africa: species richness and turnover patterns. Zoological Journal of the Linnean Society 144, 121–144.