SHORT COMMUNICATION

THE LATEST EUROPEAN PAINTED DOG

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The living African painted dog, *Lycaon pictus* (Temminck, 1820), is a successful predator, occupying a wide range of habitats, including short-grass plains, semidesert, bushy savannas, and upland forest. At present, this species is restricted to limited areas in sub-Saharan Africa and classified as endangered species by the International Union for Conservation of Nature (IUCN) (Githiru et al., 2007). The evolutionary origin of *Lycaon pictus* remains unresolved in spite of several morphologic and molecular studies (Van Valkenburgh and Koepfli, 1993; Tedford et al., 1995; Zrzavy and Rocanková, 2004; Lindblad-Toh et al., 2005). Phylogenetic relationships with the other wolf-like canids, especially the wolf and the dhole, remain unclear, but recent molecular studies only do not support a monophyletic group formed by these three species (Berdeleben et al., 2005).

Lycaon-like dogs are well recorded in the early Pleistocene of Europe, Asia, and Africa, being attributed to different taxa depending on the authors (Kretzoi, 1938; Torre, 1967; Sotnikova, 1989, 2001; Rook, 1994; Martínez-Navarro and Rook, 2003; Werdelin and Lewis, 2005; Moullé et al., 2006; Tedford et al., 2009; Hartstone-Rose et al., 2010; Petrucci et al., 2013). Unfortunately, the middle Pleistocene record of this lineage is very scarce throughout the Old World, with only one clear finding of a primitive large-sized mandible of *Lycaon pictus* at the site of Hayonim Cave (Israel), dated around 0.2 Ma (Stiner et al., 2001).

Martínez-Navarro and Rook (2003) first proposed a hypothesis for the origin of painted or wild dogs based on the gradual reduction of several dental cusps coupled with the predominance and increase of others, a tendency towards hypercarnivory, and the loss of the first metacarpal (an autapomorphic feature of the extant *Lycaon pictus*). According to them, all the *Lycaon*-like dogs of the early Pleistocene should be incorporated in the genus *Lycaon*, with three chronospecies: *Lycaon falconeri* (Forsyth Major, 1877), for the earliest early Pleistocene Eurasian forms; *Lycaon lycaonoides* (Kretzoi, 1938), for the forms of the second half of the early Pleistocene and the beginning of the middle Pleistocene of Eurasia and Africa; and *Lycaon pictus*, for the middle-late Pleistocene and extant African forms. However, other authors (Moullé et al., 2006; Tedford et al., 2009; Tong et al., 2012) have argued that most or all of these forms belong to the genus *Xenocyon*, which is sister to *Lycaon* and *Cuon*.

Here we describe new dentognathic material of a *Lycaon*-like dog from the latest early Pleistocene layer EVT7 of Vallparadís Estació (ca. 0.83 Ma, Vallès-Penedès Basin, Iberian Peninsula), and its implications for the origin and gradual evolution of the wild dogs.

Institutional Abbreviations—**EVT**, Estació de Vallparadís (Terrassa, Barcelona, Spain); **ICP**, Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain); **IGF**, Collections of the Department of Earth Sciences and Natural History Museum (Geology and Palaeontology section) of the Università degli Studi di Firenze (Florence, Italy); **RMCA**, Royal Museum for Central Africa (Tervuren, Belgium).

AGE AND GEOLOGIC SETTING

The Pleistocene Vallparadís composite section includes the paleontological sites of Cal Guardiola and Vallparadís Estació, which are situated in the Torrent de Vallparadís, within the town of Terrassa (Vallès-Penedès Basin; Madurell-Malapeira et al., 2010; Fig. 1A). Layer EVT7 of Vallparadís Estació corresponds to a 3-m-thick, mud-supported, greenish bed related to high-density flows divided into two major parts (Fig. 1C). The lower part has a thickness of 1 m, and is made up of medium to large pebbles that are mud-supported, probably as a result of debris-flow events. The upper part, with a thickness of 2 m, is composed of mud-supported and small-sized pebbles, and likely resulted from mud-flow events. On the basis of magnetostratigraphic and biostratigraphic correlations, this reverse-polarity layer corresponds to the post-Jaramillo interval of the Matuyama chron (ca. 0.99–0.78 Ma) (Madurell-Malapeira et al., 2010; Fig. 1B). Radiometric dating yielded an estimated age of 0.83 ± 0.07 Ma (Duval et al., 2011). Twenty-eight fossil mammal taxa were identified from layer EVT7, and show a predominance of typically Late Villafranchian species coupled with several new immigrants typically recorded from European Galerian associations (Madurell-Malapeira et al., 2010; Table 1).

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family CANIDAE Fisher von Waldheim, 1817
Genus *LYCAON* Brookes in Griffith, Smith, and Pidgeon, 1827
LYCAON LYCAONOIDES (Kretzoi, 1938)
(Figs. 2, 3, Table 2)

Referred Specimens—EVT22049, partial right hemimandible with p3, m1, and m2 (Fig. 2A–C); EVT23434, partial left hemimandibule with p2, p4, m1, and m2 (Fig. 2D–F). These specimens are housed in the ICP collections.

Measurements—See Table 2.

Description—The two studied hemimandibles preserve most of the corpus, which is high and stoutly build. The masseteric fossa is deep, ending at the level of the m3 in lateral view. The premolars (p2, p3, and p4) display a high and asymmetric protoconid in lateral view, bearing individualized distal accessory cusps and strong distal cingulids (Fig. 2). The m1 (carnassial) displays a sharp and high trigonid, which bears a reduced and nonprotruding metaconid. The m1 talonid shows a large and sharp hypoconid and a very reduced, lingually situated entoconid (Fig. 2C, F). The m2 displays an oval occlusal outline, with two trigonid cusps
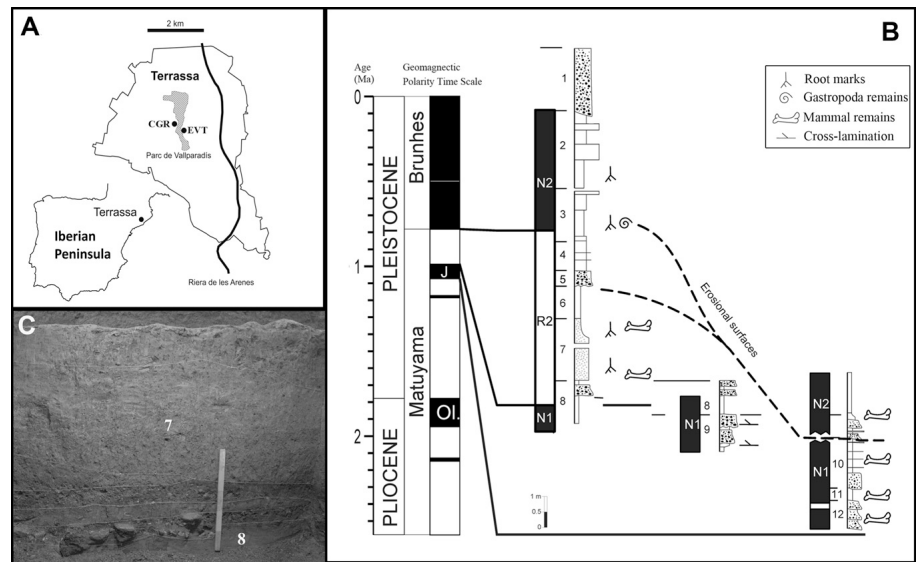
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FIGURE 1. **A**, location map of the two sites of the Torrent de Vallparadís section, Cal Guardiola and Vallparadís Estació, next to the city of Terrassa, and of the latter within the Iberian Peninsula; **B**, stratigraphic columns of the Vallparadís Estació local section, indicating the position of the fossiliferous layers and the magnetostratigraphic polarity; **C**, section along the thickness of layer EVT7.

(a large and sharp protoconid, and a reduced and lingually situated metaconid). The m2 talonid only shows a small and labially situated hypoconid (Fig. 2C, F).

DISCUSSION

Taxonomic Attribution

The studied material displays all the characters shown by other specimens of *Lycaon lycaonoides* from Eurasian localities, such as Pirro Nord (Italy, ca. 1.5 Ma; Rook, 1994; Petrucci et al., 2013), Venta Micena (Spain, ca. 1.5 Ma; Martínez-Navarro, 1991, Fig. 3C–E), Untermassfeld (Germany, ca. 1 Ma; Sotnikova, 2001), Vallonnet (France, ca. 1 Ma; Moullé et al., 2006), Lakhuti (Tajikistan, ca. 1 Ma; Sotnikova and Vislovokova, 1990), and Yunxian (China, ca. 1.2 Ma; Echassoux et al., 2008). These features (Martínez-Navarro and Rook, 2003; Fig. 3) include (1) reduced m1 talonid; (2) increased proportional size of the m1 hypoconid, which tends to be placed on the talonid central area; (3) proportionally reduced and lingually situated m1 entoconid; (4) m2 with protruding and sharp protoconid; and (5) reduced m2 metaconid.

Nevertheless, the specimens from Vallparadís Estació show several slight differences as compared with those from other lo-

TABLE 1. Mammal species recovered from layer EVT7 of Vallparadís Estació.

CARNIVORA	PRIMATES	PROBOSCIDEA
Pachycrocuta brevirostris	*Macaca sylvanus* cf. *florentina*	Elephantidae indet.
Meles meles atavus		
Ursus deningeri	PERISSODACTYLA	RODENTIA
Lycaon lycaonoides	*Equus altidens*	*Mimomys savini*
Canis mosbachensis	*Stephanorhinus hundsheimensis*	*Iberomys huescarensis*
Vulpes praeglacialis		*Stenocranius gregaloides*
Homotherium latidens	ARTIODACTYLA	*Apodemus* cf. *sylvaticus*
Panthera gombaszoegensis	*Hippopotamus antiquus*	*Eliomys quercinus*
Puma pardoides	*Sus* sp.	*Hystrix refossa*
Felidae indet. (large form)	*Dama vallonnentensis*	
Lynx sp.	*Megaloceros savini*	
	Bison sp.	
	Caprini indet.	

calities, namely: (1) more reduced m1 metaconid; (2) more protruding m1 hypoconid and highly reduced entoconid; and (3) more protruding m2 protoconid and highly reduced metaconid (Fig. 3H). When the hypothesis of Martínez-Navarro and Rook (2003), concerning the gradual evolution of European wild dogs, is taken into account, the above-mentioned slight differences displayed by the Vallparadís specimens agree with the chronology of the material (ca. 0.83 Ma), which is slightly younger than that of other European specimens of *Lycaon lycaonoides*. The studied specimens, in particular, display somewhat more derived dental features towards hypercarnivory as compared with similar-sized older remains of the same species. A mean body mass of 30 kg has been inferred for *L. lycaonoides* (Palmqvist et al., 2002).

Following the criteria of Martínez-Navarro and Rook (2003), we attribute the *Lycaon*-like dog material described in this paper to a derived form of the species *Lycaon lycaonoides* based on the above-described characters. In fact, the described material currently represents the latest record of this species, at least within a well-known geological and biochronological context (Madurell-Malapeira et al., 2010).

The Origin of the *Lycaon* Lineage

The geographic origin of the genus *Lycaon* is not clear; both Eurasia and Africa are possibilities (Martínez-Navarro and Rook, 2003; Hartstone-Rose et al., 2010; Tong et al., 2012). Shedding light in this issue, Hartstone-Rose et al. (2010) recently described the species *Lycaon sekowei*, on the basis of early Pleistocene specimens from South Africa and proposed that it was the ancestor of the painted dog lineage. According to them, the *Lycaon* lineage would have first developed a tendency towards hypercarnivory followed by subsequent adaptations to specialized cursorial locomotion, such as loss of the first digit on the manus. In fact, the recent discovery of first metacarpals of *Lycaon*-like dogs from the localities of Pirro Nord (Petrucci et al., 2013) and Yunxian (China; Echassoux et al., 2006), and the presence of this element in the partial skeleton of *L. sekowei* from Coopers Cave (Hartstone et al., 2010), suggests that *Lycaon* populations may have been polymorphic for this character for some period of time, further supporting the idea that adaptations for hypercarnivory preceded those for specialized cursoriality in this lineage.

On the other hand, both the fossil *Lycaon*-like dogs and their living counterparts display a high degree of intrapopulational
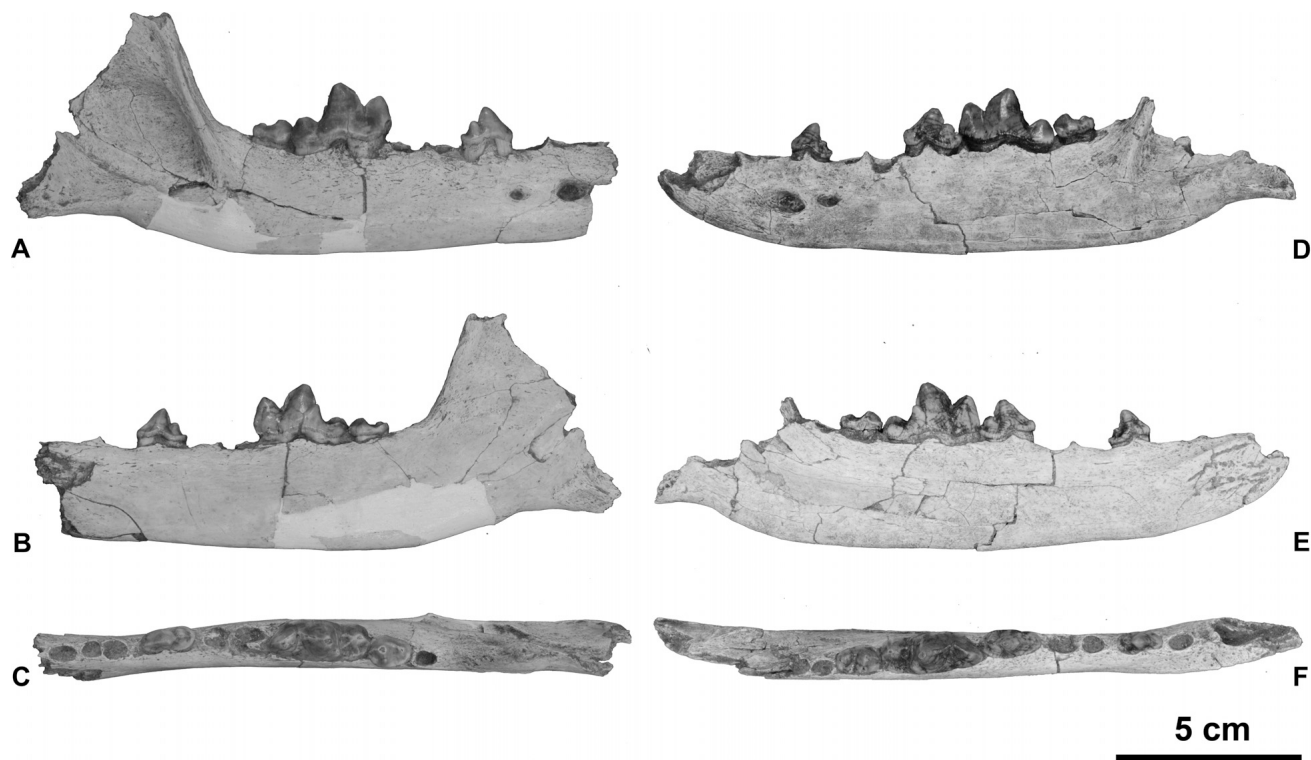
FIGURE 2.   Remains of *Lycaon lycaonoides* from layer EVT7. **A–C**, EVT22049, partial right hemimandible in **A**, buccal, **B**, lingual, and **C**, occlusal views. **D–F**, EVT23434, partial left hemimandible in **D**, buccal, **E**, lingual, and **F**, occlusal views.

variability in dental characters, especially with regard to lower premolar morphology. For example, the presence or absence of mesial accessory cusps in the p3 and p4 is highly variable in the extant *L. pictus* (Fig. 3I, J; Table 3). This variability is also documented in the fossil record; for example, a hemimandible (VM-2255) from Venta Micena displays a p4 mesial accessory cusp, whereas no other known specimen of *L. lycaonoides* from the same locality does so (Fig. 3D). Hartstone-Rose et al. (2010) proposed *L. sekowei* as the ancestor of the wild-dog lineage on the basis of dental characters as compared with *L. pictus* and the European *Lycaon*-like dogs, largely based on the morphology of the premolar accessory cusps. However, given the substantial variability of such characters and the relatively scarce African record of *Lycaon*-like dogs, a Eurasian origin for the painted dogs with later dispersal into Africa by the Middle-Late Villafranchian transition at ca. 2.0–1.9 Ma seems more parsimonious (Martínez-Navarro and Rook, 2003; Rook and Martínez-Navarro, 2010).

Alternatively, it has been suggested that early Pleistocene hypercarnivorous dogs from Eurasia might represent the common ancestor of both extant painted dogs and dholes, thus including these forms in the genus *Xenocyon* Kretzoi, 1938 (Moullé, et al., 2006; Tedford et al., 2009). This hypothesis is mainly based on the hypercarnivorous adaptations of both extant forms, coupled with the moderate hypercarnivorous adaptations of large canids from the early Pleistocene of Eurasia. However, similarities between painted dogs and dholes can be alternatively explained by convergent evolution, because the origin of the Asian dhole currently remains unclear. Most fossil remains from the early Pleistocene of Asia are attributed to either *Canis*, *Xenocyon*, or *Lycaon*, depending on the particular criteria of the various authors (see discussion in Tong et al., 2012), and the genus *Cuon* Hodgson, 1838, is not unambiguously recorded until the early-middle Pleistocene in Europe (Tedford et al., 2009; Petrucci et al., 2012). It is therefore unclear which species of *Xenocyon* might have given rise to *Cuon* and *Lycaon*. Given the lack of a clear-cut link between either extant or fossil dholes and its purported ancestor *Xenocyon*, we favor the scenario proposed by Martínez-Navarro and Rook (2003) for the origin of the genus *Lycaon*.

TABLE 2.   Measurements in mm of the hemimandibles of *Lycaon lycaonoides* from Vallparadís Estació.

Specimen	p2		p3		p4		m1				m2		Hp2	Hp4
	L	W	L	W	L	W	L	Lt	Lw	W	L	W		
EVT22049			13.6	6.0			25.5	7.5	9.3	10.9	10.9	8.2	24.8	28.4
EVT23434	11.3	5.5			16.0	7.0	25.6	7.4	9.2	10.6	10.8	8.1	24.1	29.9

Abbrevations: **L**, length; **W**, width; **Lt**, talonid length; **Lw**, talonid width; **Hp2**, height of the mandibular corpus behind p2; **Hp4**, height of the mandibular corpus behind p4.
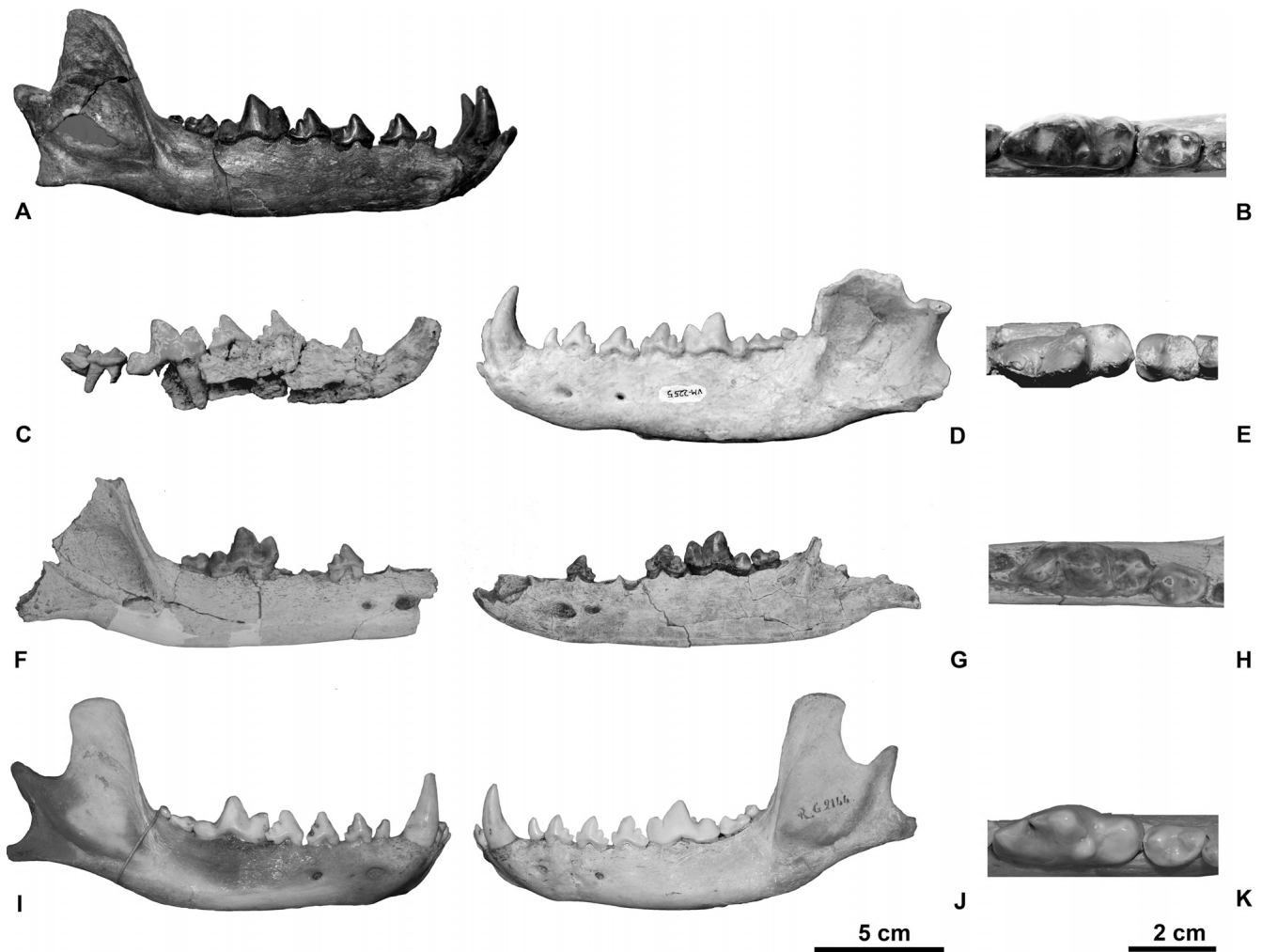
FIGURE 3. Different species of the genus *Lycaon* from the European Pleistocene compared with the extant wild dog. **A**, **B**, hemimandible of *Lycaon falconery* from Tasso (Upper Valdarno, Italy) IGF 865 in **A**, buccal view and **B**, detail of m1 and m2 in occlusal view. **C–E**, hemimandibles of *Lycaon lycaonoides* from Venta Micena (Iberian Peninsula): **C**, partial right hemimandible VM-2257 in buccal view; **D**, **E**, partial left hemimandible VM-2255 in **D**, buccal view and **E**, detail of the m1 and m2 in occlusal view. **F–H**, hemimandibles of *Lycaon lycaonoides* from Vallparadís Estació (Iberian Peninsula): **F**, partial right hemimandible EVT22049 in buccal view; **G**, **H**, partial left hemimandible EVT22434 in **G**, buccal view and **H**, detail of the m1 and m2 in occlusal view. **I–K**, hemimandibles of *Lycaon pictus* from Congo: **I**, right hemimandible RMCA 46B in buccal view; **J**, left hemimandible RMCA 2144 in buccal view; **K**, detail of m1 and m2 of hemimandible RMCA 11815.

Evolutionary Implications

According to Martínez-Navarro and Rook (2003), the genus *Lycaon* experienced a gradual evolutionary trend towards hypercarnivory, from the more ancestral *L. falconeri* towards the extant *L. pictus*. Such a trend can be discerned in the dental morphology of the fossil species *L. falconeri* and *L. lycaonoides*, with

TABLE 3. Variability in the development of the mesial accessory cusps of the lower premolars of *Lycaon pictus* on the basis of 29 individuals (21 from Congo, 3 from Burundi, 2 from Kenya and 3 of unknown origin) housed at the Royal Museum from Central Africa (Tervuren, Belgium).

Molar	Well-developed	Reduced	Absent
p2	2	12	14
p3	16	6	5
p4	12	10	7

the former representing the earliest stage characterized by the following features (Martínez-Navarro and Rook, 2003): (1) wider m1 talonid (Fig. 4); (2) m1 talonid with two independent cusps; (3) wider m2; and (4) m2 with two cusps in the trigonid (Fig. 3A, B). In turn, *L. lycaonoides* would represent a second stage, characterized by (1) reduced m1 talonid (Fig. 4); (2) increased size of the m1 hypoconid, which tends to be placed on the talonid central area; (3) reduced and lingually placed m1 entoconid; and (4) m2 with a protruding and sharp protoconid (Fig. 3C–E). The material studied here from Vallparadís Estació chronologically represents the latest phase of the second stage, just before the local extinction of *Lycaon* in Europe (Fig. 3F–H). In turn, from a morphologic viewpoint, these remains represent an additional small step in the gradual evolution of the wild-dog lineage, thus reinforcing the views of Martínez-Navarro and Rook (2003) that this lineage originated in Eurasia and initiated its gradual evolution towards hypercarnivory by the early Pleistocene.
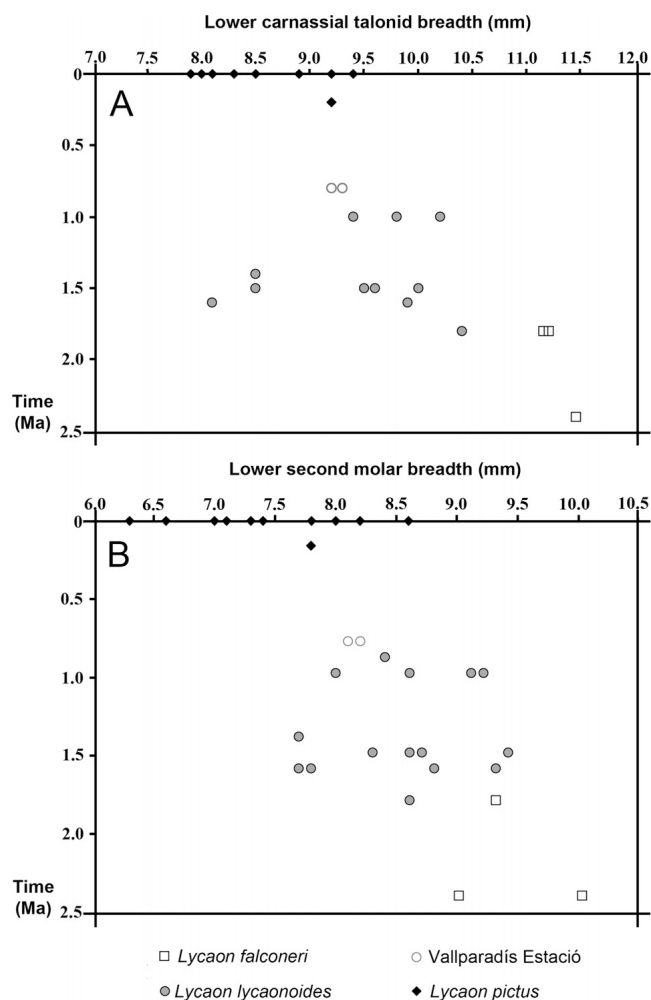
FIGURE 4.   Gradual reduction in breadth of the lower carnassial talonid (**A**) and in the breadth of lower second molar (**B**) in the species of the genus *Lycaon*. Data from Martínez-Navarro and Rook (2003) and J. M. M.'s unpublished data.

CONCLUSIONS

The *Lycaon*-like dog material from layer EVT7 of Vallparadís Estació described in this paper share several morphologic characters with *Lycaon lycaonoides*, including (1) reduced m1 talonid; (2) increased size of the m1 hypoconid, which tends to be placed on the talonid central area; (3) reduced and lingually placed m1 entoconid; (4) m2 with a protruding and sharp protoconid; and (5) reduced m2 metaconid. Nevertheless, the studied material shows some minor differences compared with other specimens of the same species, concerning the dimensions and sharpness of the main cusps of the m1 talonid and the m2 trigonid, as well as the reduction of the m1 and m2 entoconids. Such variation is interpreted here as a derived condition with respect to the 'typical' material of *Lycaon lycaonoides*, thus representing a small evolutionary step towards the hypercarnivory documented along this lineage (Martínez-Navarro and Rook, 2003), and further reinforcing the gradual nature of wild-dog evolution. Moreover, the reported material also represents the latest European record of the genus *Lycaon* at 0.83 Ma, just before the early-middle Pleistocene boundary, thus providing a more accurate date for the local extinction of this lineage in Europe and their concomitant geographical restriction to Africa and the Levant.

LITERATURE CITED

Aymard, A. 1846. Communication sur le gisement de Sainzelles. Annales de la Société d'Agriculture, Sciences et Arts du Puy 12:153–155.

Bardeleben, C., R. L. Moore, and R. K. Wayne. 2005. A molecular phylogeny of the Canidae based on six nuclear loci. Molecular Phylogenetics and Evolution 37:815–831.

Bowdich, T. E. 1821. An Analysis of the Natural Classification of Mammalia, for Use of Students and Travelers. J. Smith, Paris, 115 pp.

Broom, R. 1937. On some new fossil mammals from limestone caves of the Transvaal. South African Journal of Science 33:750–769.

Duval, M., D. Moreno, Q. Shao, P. Voinchet, C. Falguères, J. J. Bahain, T. García, J. Garcia, and K. Martínez. 2011. Datación por ESR del yacimiento arqueológico del Pleistoceno inferior de Vallparadís (Terrassa, Cataluña, España). Trabajos de Prehistoria 68:7–24.

Echassoux, A., A. M. Moigne, P. E. Moullé, T. Y. Li, X. B. Feng, W. S. Li, and Z. Z. Wu. 2008. Les faunes de grands mammifères du site de l'Homme de Yunxian; pp. 253–364 in H. De Lumley and T. Y. Li (eds.), Le Site de l'Homme de Yunxian. CNRS Édition, Paris.

Fischer von Waldheim, G. 1817. Adversaria zoologica. Mémories de la Société Impériale des Naturalistes de l'Université Impériale de Moscou 5:368–428.

Forsyth Major, C. I. 1877. Considerazioni sulla fauna dei mammiferi pliocenici e post-pliocenici della Toscana. III. Cani fossili del Val d'Arno Superiore e della Valle d'Era. Memorie della Società Toscana di Scienze Natural 3:207–227.

The remains of *Lycaon* from Vallparadís Estació represent the latest record of this genus in Europe at 0.83 Ma. Wild dogs vanished from Europe at the same time as other carnivorous species, such as *Puma pardoides* (Owen, 1846), *Pachycrocuta brevirostris* (Aymard, 1846), and *Megantereon whitei* Broom, 1937, among others (Madurell-Malapeira et al., 2010). Somewhat surprisingly, these species survived one of the coldest glacial stages (MIS22, ca. 0.88 Ma), probably in Iberian and Italian refuges, but disappeared slightly later (in the MIS21, ca. 0.83 Ma), with their last record corresponding to layer EVT7 of the Vallparadís section (Madurell-Malapeira et al., 2010). The local extinction of the European wild dogs was probably related to the progressive cooling associated with the 'Mid-Pleistocene Revolution' (Torre et al., 2001; Madurell-Malapeira et al., 2010). After MIS21, wild dogs were apparently restricted exclusively to Africa and the Levant, but this cannot be more conclusively ascertained because *Lycaon*-like dogs are not recorded from Africa and/or Eurasia during the middle Pleistocene, with the exception of the remains from Hayonim Cave in Israel (Stiner et al., 2001).

Griffith, E., C. Smith, and E. Pidgeon. 1827. The Animal Kingdom Arranged in Conformity with Its Organization by the Baron Cuvier, with Additional Descriptions of all the Species Hitherto Named, and of Many Not Before Noticed. G. B. Whittaker, London, 392 pp.

Githiru, M., T. Njeri, F. K. Muthoni, R. Yego, M. Muchane, P. Njoroge, and A. Giani. 2007. African Wild Dogs (*Lycaon pictus*) from NE Kenya: Recent Records and Conservation Issues. Zoology Department Research Report No. 7. National Museum of Kenya, Nairobi, 8 pp.

Harstone-Rose, A., L. Werdelin, D. J. deRuiter, L. R. Berger, and S. E. Churchill. 2010. The Plio-Pleistocene ancestor of wild dogs, *Lycaon sekowei* n. sp. Journal of Paleontology 84:299–308.

Hodgson, B. H. 1838. Proceedings of learned societies. Annals of Natural History 1:1–152.

Kretzoi, M. 1938. Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfauna. Ein Beitrag zur Stratigraphie des Altquartaera. Annales Musei Nationalis Hungarici 31:88–157.

Lindblad-Toh, K., C. M. Wade, T. S. Mikkelsen, E. K. Karlsson, D. B. Jaffe, et al. 2005. Genome sequence, comparative analysis and haplotype structure of the domestic dog. Nature 438:803–819.

Madurell-Malapeira, J., R. Minwer-Barakat, D. M. Alba, M. Garcés, M. Gómez, J. Aurell-Garrido, S. Ros-Montoya, S. Moyà-Solà, and X. Berástegui. 2010. The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. Quaternary Science Reviews 29:3972–3982.

Martínez-Navarro, B. 1991. Revisión sistemática y estudio cuantitativo de la fauna de macromamiferos del yacimiento de Venta Micena (Orce, Granada). Ph.D. dissertation, Universitat Autònoma de Barcelona, Bellaterra, 334 pp.

Martínez-Navarro, B., and L. Rook. 2003. Gradual evolution in the African hunting dog lineage. Systematic implications. Comptes Rendus Palevol 2:695–702.

Moullé, P. E., F. Lacombat, and E. Echassoux. 2006. Apport des grands mammifères de la grotte du Vallonnet (Roquebrune-Cap-Martin, Alpes-Maritimes, France) à la connaissance du biochronologique de la seconde moité du Pléistocene inférieur d'Europe. L'Anthropologie 110:837–849.

Owen, R. 1846. A History of British Fossil Mammals and Birds. John Van Voorst, London, 560 pp.

Palmqvist, P., M. Mendoza, A. Arribas, and D. R. Gröcke. 2002. Estimating the body mass of Pleistocene canids: discussion of some methodological problems and a new 'taxon free' approach. Lethaia 35:358–360.

Petrucci, M. 2008. Analisi sistematica dei macromammiferi di Pirro Nord (Apricena, Foggia, Puglia). Ph.D. dissertation, University of Turin, Turin, 201 pp.

Petrucci, M., S. Romiti, and R. Sardella. 2012. The Middle-Late Pleistocene *Cuon* Hodgson, 1838 (Carnivora, Canidae) from Italy. Bollettino della Società Paleontologica Italiana 51:137–148.

Petrucci, M., A. Cipullo, B. Martínez-Navarro, L. Rook, and R. Sardella. 2013. The late Villafranchian (Early Pleistocene) carnivores (Carnivora, Mammalia) from Pirro Nord (Italy). Palaeontographica Abteilung A 298:113–145.

Rook, L. 1994. The Plio-Pleistocene Old World *Canis (Xenocyon)* ex gr. *falconeri*. Bollettino della Società Paleontologica Italiana 33:71–82.

Rook, L., and B. Martínez-Navarro. 2010. Villafranchian: the long story of a Plio-Pleistocene European large mammal biochronologic unit. Quaternary International 219:134–144.

Sotnikova, M. V. 1989. Carnivora of the Pliocene and Early Pleistocene. Trudy Geologicheskogo Instituta AN SSSR 440:1–125.

Sotnikova, M. V. 2001. The fossil Canidae from the Pleistocene deposits of Untermassfeld near Meiningen; pp. 607–632. in R. D. Kahlke (ed.), Das Pleistozän von Untermassfeld bei Meiningen (Thüringen). Römisch-Germaisches Zentralmuseum, Bonn.

Sotnikova, M., and I. A. Vislovokova. 1990. Pleistocene mammals from Lakhuti, Southern Tajikistan, USSR. Quatärpaläontologie 8:237–244.

Stiner, M. C., F. C. Howell, B. Martínez-Navarro, E. Tchernov, and O. Bar-Yosef. 2001. Outside Africa: Middle Pleistocene *Lycaon* from Hayonim Cave, Israel. Bollettino della Società Paleontologica Italiana 40:293–302.

Tedford, R. H., B. E. Taylor, and X. Wang. 1995. Phylogeny of the Caninae (Carnivora: Canidae): the living taxa. American Museum Novitates 3146:1–37.

Tedford, R. H., X. Wang, and B. E. Taylor. 2009. Phylogenetic systematics of the North American fossil Caninae (Carnivora: Canidae). Bulletin of the American Museum of Natural History 325:1–218.

Temminck, C. J. 1835–1841. Monographies de Mammalogie, ou Description de Quelques Genres de Mammifères, dont les Espèces ont été Observées dans les Différens Musées de l'Europe. C. C. van der Hoek, Leiden, 392 pp.

Tong, H. W., N. Hu, and X. Wang. 2012. New remains of *Canis chihliensis* (Mammalia, Carnivora) from Shanshenmiaozui, a lower Pleistocene site in Yangyuan, Hebei. Vertebrata PalAsiatica 50:335–360.

Torre, D. 1967. I cani Villafranchiani della Toscana. Palaeontographica Italica 64:113–138.

Torre, D., A. Abbazzi, A. Bertini, F. Fanfani, G. Ficcarelli, F. Masini, P. Mazza, and L. Rook. 2001. Structural changes in Italian Late Pliocene-Pleistocene large mammal assemblages. Bollettino della Società Paleontologica Italiana 40:303–306.

Van Valkenburgh, B., and K. P. Koepfli. 1993. Cranial and dental adaptations to predation; pp. 15–37. N. Dunstone, M. L Gorman (eds.), Mammals as Predators. Oxford University Press, Oxford, UK.

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

Zrzavy, J., and V. Ricánková. 2004. Phylogeny of recent Canidae (Mammalia, Carnivora): relative reliability and utility of morphological and molecular datasets. Zoologica Scripta 33:311–333.