The early hunting dog from Dmanisi with comments on the social behaviour in Canidae and hominins

Saverio Bartolini-Lucenti1,2, Joan Madurell-Malapeira3,4, Bienvenido Martínez-Navarro5,6,7, Paul Palmqvist8, David Lordkipanidze9,10 & Lorenzo Rook1

The renowned site of Dmanisi in Georgia, southern Caucasus (ca. 1.8 Ma) yielded the earliest direct evidence of hominin presence out of Africa. In this paper, we report on the first record of a large-sized canid from this site, namely dentognathic remains, referable to a young adult individual that displays hypercarnivorous features (e.g., the reduction of the m1 metaconid and entoconid) that allow us to include these specimens in the hypodigm of the late Early Pleistocene species *Canis* (*Xenocyon*) *lycaonoides*. Much fossil evidence suggests that this species was a cooperative pack-hunter that, unlike other large-sized canids, was capable of social care toward kin and non-kin members of its group. This rather derived hypercarnivorous canid, which has an East Asian origin, shows one of its earliest records at Dmanisi in the Caucasus, at the gates of Europe. Interestingly, its dispersal from Asia to Europe and Africa followed a parallel route to that of hominins, but in the opposite direction. Hominins and hunting dogs, both recorded in Dmanisi at the beginning of their dispersal across the Old World, are the only two Early Pleistocene mammal species with proved altruistic behaviour towards their group members, an issue discussed over more than one century in evolutionary biology.

Wild dogs are medium- to large-sized canids that possess several hypercarnivorous craniodental features and complex social and predatory behaviours (i.e., social hierarchic groups and pack-hunting of large vertebrate prey typically as large as or larger than themselves). Two extant species of wild dogs survive in the Old World, the Indian dhole, *Cuon alpinus* (Pallas, 1811), and the African hunting dog, *Lycaon pictus* (Temminck, 1820). Both are nowadays endangered or critically endangered according to the IUCN red list of threatened species1,2. The African hunting dog, known also as painted dog, and the dhole are among the top predators in their respective habitats3,4 thanks to the combination of several dental hypercarnivorous traits, skeletal adaptations to cursorial pack hunting and their highly developed social behaviour.

The evolution of these hypercarnivorous canids is still unknown and open to debate5,6. Furthermore, there is also a great deal of confusion in the taxonomy of the extinct large-sized and hypercarnivorous canids, which use to be referred to different systematic denominations (see Supplementary Information). Such names often hint implied or proposed affinities to extant taxa, yet seldomly based on phylogenetic analyses. Considering the results of molecular phylogenies7,8, from which it is evident that *Lycaon* and *Cuon* are sister taxa of the crown group of *Canis*, and that the large-sized members of the genus *Xenocyon* might be...
related to both Lycaon and Cuon, here we prefer to avoid names suggestive of a closer relationship to any of both genera, privileging the more parsimonious denomination Canis (Xenocyon) (for an in-depth discussion of the taxonomic issues, see the Supplementary Information).

The earliest record of a species of this group of hypercarnivorous canids corresponds to Canis (Xenocyon) cf. dubius (Teillhard de Chardin, 1940), which is represented by a single hemimandible from the Zanda Basin (3.81–3.42 Ma; Fig. 1). The species C. (Xenocyon) dubius is generally related to the lineage of Cuon10,6. A younger but more complete specimen from Fan Tsun (Taigu) was ascribed to Canis (Xenocyon) antoni (ca. 2.5 Ma)11. The latter canid is large-sized and displays evident dental features hinting to an incipient adaptation to a hypercarnivorous diet. Other records of large-sized canids with hypercarnivorous features are rather scanty across Eurasia and are of difficult attribution, considering the presence of hypercarnivorous Canis s.s. in Asia during the Early Pleistocene, e.g., Canis chihliensis Zdansky, 1924; Canis teilhardi Qiu et al., 2004; or Canis yuanmoensis You & Qi, 1973.

Around 2.0–1.8 Ma, different forms appeared in several parts of the Old World. These forms showed distinctive dental features (i.e., broad and stoutly-built carnassials with enlarged buccal cusps), coupled with craniodental mandibles (robust mandibles and developed frontal sinuses). Their large size combined to these dental adaptations could have determined an advantage over the contemporaneous, medium-sized mesocarnivorous canids, as testified by the westward dispersion and radiation of Canis (Xenocyon) falconeri (Forsyth Major, 1877) in Western Europe and of Canis (Xenocyon) africanus (Pohle, 1928) from Olduvai Bed I (Tanzania) or Ain Hanec (Algeria) in Africa. A record of a primitive wild dog attributed to C. (Xenocyon) cf. falconeri was also reported from deposits of Tamagawa (near Tokyo)12, correlated to 2.1–1.6 Ma13. A close relationship between both taxa was suggested by13,14 who regarded them as the ancestor of modern L. pictus. However, such interpretation has not been shared by other researchers15. Recently, a new large-sized taxon was described as Lycaon sekeweri Hartstone-Rose et al., 2019, based on fragmented cranial material from Cooper’s Cave in South Africa (ca. 1.9 Ma) and an almost complete skeleton from Gladysvale (ca. 1.0 Ma)15. Some of the morphologies of the holotype from Cooper’s Cave (i.e., the high-crowned upper premolars, their mesial occlusal morphology, the lingual projection of P4 protocone, and the relative buccolingual length of the M1) cast doubts on its taxonomical attribution and its actual relation with Canis (Xenocyon)’s group. Moreover, the upper teeth resemble those of the Asian C. chihliensis, a large-sized canid possibly belonging to a hypercarnivorous lineage of Canis15.

During the late Early Pleistocene (i.e., Calabrian stage: 1.8–0.8 Ma), while other more primitive species remained in Africa [e.g., Canis (Xenocyon) atrox Broom in Broom & Schepers, 1946 from Kromdraai A; Fig. 1, although possibly synonym of C. (Xenocyon) africana11] a more derived form of Canis (Xenocyon) appeared and became widespread across the whole Old World (Fig. 1). Canis (Xenocyon) lycaonoides (Kretzoi, 1938) was a large-sized canid that resembled C. (Xenocyon) gr. falconeri but with more derived craniodental features (e.g., the P4 protocone tends to attach to the tooth; the M1 metaconule is crest-like; the M1 talon is reduced; the M1 hypoconid is enlarged and tends to be centred in the talonid, which functionally represents a lengthening of the trenched condition of the trigonid; the entoconid is reduced, being represented by a small crest-like cuspidul; and the m3 is single cusped). Its earliest record appears to be that of Venta Micena (Spain1, Fig. 1). In spite of its trenchant condition of the trigonid; the entoconid is reduced, being represented by a small crest-like cuspidul and the m3 is single cusped). Its earliest record appears to be that of Venta Micena (Spain1, Fig. 1). In spite of its uncertain chronology, this early occurrence suggests an eastern Asian origin for this hypercarnivorous species. Subsequently, during the late Early Pleistocene and the base of the Middle Pleistocene, from ca 1.6 to 0.7 Ma, C. (Xenocyon) lycaonoides became one of the most common and important members of the carnivoran palaeoguild of Eurasia (Fig. 1). Moreover, C. (Xenocyon) lycaonoides dispersed also in Africa, where it is documented in the northern and eastern part of the continent (e.g., Olduvai Bed II; Fig. 1). Considering the morphological and dental features, which confirm the original interpretation by Kretzoi17, Martinez-Navarro & Rook5 deemed C. (Xenocyon) lycaonoides as strictly related to extant L. pictus. Although some scholars do not favour this interpretation16,18, similar conclusions were shared by several other scholars10,19–21, who supported also a Eurasian origin for the living African hunting dog.

Among extant Carnivora, Lycaon pictus has one of the most complex, structured and unique social behaviours3,19. As one of the closest relatives to L. pictus, C. (Xenocyon) lycaonoides, the Eurasian hunting dog, might have had comparable complex sociality. Carbone and co-authors21 showed that the metabolic energy requirements for large-sized species (>21.5 kg) force them to predate on prey larger than themselves and thus, in hypercarnivorous Canidae, to hunt cooperatively. As such, this element allows us to figure the social behaviour of extinct hypercarnivorous canids, even with limited direct evidence. Nevertheless, apart from indirect and inferred evidence, direct proof of social behaviour in the Eurasian hunting dog have been reported24,25.

Here we report the first occurrence of wild dogs from the Georgian site of Dmanisi (Fig. 1; 1.77–1.76 Ma26, see Supplementary Information). This locality preserves an outstanding fossil record, both in terms of abundance, completeness of skeletal remains and preservational status, as testified by the recently described molecular phylogeny based on a fossil rhino tooth27. In this paper, we describe the newly discovered remains, identifying them taxonomically and interpreting in the frame of Early Pleistocene diversity of Canis (Xenocyon). Moreover, the site of Dmanisi has yielded the earliest direct evidence of hominin presence out of Africa in their dispersal throughout Eurasia28,29 with also indication of complex sociality among individuals of this population30,31. The co-occurrence of two highly social species in the same locality around 1.8 Ma, a time of extreme diversification and expansion of the two clades from their centres of origin3,6, raises interest in the role played by social behaviour and by mutually-beneficial cooperation and reciprocity in the geographic expansion of these species. Questions to be explored in this paper.
Results

Implications for fossil hunting dogs diversity. The finding of a large-sized canid in the Georgian site of Dmanisi represents an important discovery, which adds valuable information to the current knowledge of canid radiation during the second half of the Early Pleistocene (early Calabrian). Despite the fragmented nature of...
the specimens, the set of features possessed by D6327 (Fig. 2a–f and Augmented Reality content) allow a confident attribution to *Canis* (*Xenocyon*) *lycaonoides* (see Supplementary Information), the plausible ancestor of the extant African hunting dog5,19. As such, this record is the oldest occurrence of Eurasian hunting dogs and precedes the burst of dispersal that the species experienced across the entire Old World during the Calabrian5,10,19.

**Dietary preferences of the Dmanisi hunting dog.** In order to test the dietary adaptations of the Dmanisi hunting dog and other Early Pleistocene forms, a linear discriminant analysis was performed over the extant canids (32 species, 247 specimens; craniodental measurements kindly provided by B. Van Valkenburgh), which were grouped in two feeding groups: (i) omnivores (i.e., meso- and hypocarnivores; 27 extant species, 210 specimens), in which vertebrate flesh represents less than 70% of their dietary requirements; and (ii) hypercarnivores (four extant species, 34 specimens), which diet consists almost entirely of vertebrate flesh and are pack-hunters of prey as large as or larger than themselves. Seven metric variables of this dataset for which the measurements were available in the Dmanisi specimens were used in the analysis: length and breadth of the third lower premolar (p3L and p3B, respectively), length and breadth of the trigonid basin of the lower carnassial (m1trigL and m1trigB, respectively), length and breadth of the talonid basin of the lower carnassial (m1talL and m1talB, respectively), and jaw depth measured at the limit between p3 and p4 (JDp4). The linear discriminant function was obtained with the direct method for inclusion of all variables. Reclassification of specimens to each dietary group were derived by cross validations using the leave one out method. After cross-validation, the discriminant function (Fig. 3) correctly allocated 98.8% of the specimens to their feeding group.

Indeed, all omnivores and all hypercarnivores, apart from the four specimens of the small-sized *S. venaticus*, were correctly classified in their feeding groups (Fig. 3). According to the loadings of the variables in the discriminant function, the hypercarnivores show third premolars that are relatively mesiodistally shorter and buccolingually narrower compared to those of omnivorous species, as well as a carnassial with an enlarged trigonid blade and a reduced talonid basin, and a deeper, more stoutly-built mandibular corpus, which is in agreement with previous analyses of adaptations in canids towards hypercarnivory33,34. This function reclassified...
Thecraniodental morphological features of the Eurasian hunting dog from Dmanisi (Fig. 2) were well suited for a diet consisting exclusively of vertebrate flesh. Moreover, they show that there was a gradual evolution of advanced adaptations towards hypercarnivory, like those of extant African hunting dogs. These results confirm that the craniodental morphological features of the Eurasian hunting dog from Dmanisi (Fig. 2) were well suited for a diet consisting exclusively of vertebrate flesh. Moreover, they show that there was a gradual evolution of these craniodental adaptations in C. (Xenocyon) lycaonoides from the oldest members analyzed of the lineage (Dmanisi) to the most derived ones (Untermassfeld), confirming the morphological evidence pointed out by other scholars.

Discussion

Dmanisi, located in the Caucasus at the gates of Europe and near the crossway between Africa and Eurasia, is a key site to explain the dispersal of large mammal species, in a time of great faunal turnovers in the whole Old World. This Georgian site also records the earliest direct evidence of hominins presence out of Africa and their dispersal into Eurasia, at ca. 1.8 Ma. Here, we report the record of the Eurasian hunting dog, C. (Xenocyon) lycaonoides, which testifies to the beginning of the dispersal of this more derived, frankly hypercarnivorous canid from its eastern Asia region of origin, similarly to Canis borgi Bartolini-Lucenti et al., 2020 (the mesocarnivorous, wolf-like species also recorded in Dmanisi). During the Calabrian, C. (Xenocyon) lycaonoides became a common element of the entire Old-World faunas in the late Early-early Middle Pleistocene, when it even reached North America. In this dispersal, the Eurasian hunting dog followed at the same time the same dispersal pattern of hominins, just in the opposite direction. The co-occurrences of both species along their dispersal routes together with some other large-sized carnivore taxa, for instance the dirk-toothed cat of African origin Megantereon whitii (Broom, 1937), suggest that the ecological conditions favoured the dispersal of these species at that time. Large-sized carnivores like this felid has been recognized as important supplier of scavange resources for the hominins in direct competition with the large-sized scavenger Pachycrocuta brevirostris.

Social behaviour of Canis (Xenocyon) and Homo in the late Early Pleistocene. “There is, at the same time, as much, or perhaps even more, of mutual support, mutual aid, and mutual defense: Sociability is as much a law of nature as mutual struggle.” Probably, the most relevant common feature between the extinct hominins and the fossil hunting dogs is the fossil evidence on the mutually-beneficial cooperation, reciprocity and social behaviour of both species. This is well documented in Dmanisi by the finding at this site of an eden-hominins, just in the opposite direction. The co-occurrences of both species along their dispersal routes together with some other large-sized carnivore taxa, for instance the dirk-toothed cat of African origin Megantereon whitii (Broom, 1937), suggest that the ecological conditions favoured the dispersal of these species at that time. Large-sized carnivores like this felid has been recognized as important supplier of scavange resources for the hominins in direct competition with the large-sized scavenger Pachycrocuta brevirostris.

Canidae have some of the best-known examples of social organization of all mammals (e.g., the grey wolf, C. lupus). Probably less known, yet interesting is the case of the African hunting dogs. This hypercarnivore species display a more complex and peculiar set of behaviour, unique among Canidae, if not carnivores. This includes exclusive cooperative hunt, obligate cooperative breeding, prioritized access of the pups to the kills, widest variety of vocal repertoire in canidae and consensus decision making via “sneezing.” Many authors...
Figure 4. Two social species at Dmanisi. (a) altruistic behaviour of a group of Homo erectus sharing food with an individual who lived several years without teeth (as evidenced by edentulous skull D3444 and associated mandible D3900). This severe masticatory impairment would limit the diet of the individual to foodstuffs that did not require heavy chewing (e.g., soft plants, animal brain and marrow) or that were orally processed before by others. (b) a pack of hunting dogs chasing a prey (goat Hemitragus albus) by at Venta Micena, a site where a pathological skull (cranium and associated mandible VM-7000) of Canis (Xenocyon) lycanoides showing marked bilateral asymmetry and agenesis of several teeth was unearthed. The disabled dog, whose absence of an upper canine probably made it useless for hunting, is drawn running far behind the pack. Given that the individual managed to survive until a relatively advanced age, as indicated by tooth wearing, this suggests that the other members of its family group would have allowed it to feed on the prey captured by the hunting pack. Remains of this hypercarnivorous canid species are also preserved in the assemblage of large mammals from Dmanisi, as shown in this paper. Artwork made by Mauricio Antón with the scientific supervision by the authors of the manuscript.
noted a reduced degree of aggressivity between pack members in comparison to other social Canidae (C. lupus and C. alpinus40), even during the consumption of the kill3.

Sociality in fossorial canids had been investigated by numerous authors31 and Carbone and coauthors23 proved the necessity for large canids, weighing more than 21.5 kg, to hunt cooperatively to kill prey larger than themselves. The Eurasian hunting dog C. (Xenocyon) lycaonoides was indeed a large-sized hypercarnivorous species. Body-size estimates suggest that this canid was similar to L. pictus (whose average weight is 20–25 kg43 if not larger (estimated weight of C. (Xenocyon) lycaonoides = 28 kg44)). The individual from Dmanisi, despite being a young adult, would have been rather robust (around 30 kg, applying the regression equation for body mass on lower carnassial length53). Such a body mass, coupled with its marked hypercarnivorous features, support the idea that C. (Xenocyon) lycaonoides adopted cooperative hunting strategies, similar to the extant canids C. lupus, C. alpinus and L. pictus. Further support of a highly social group organization is provided by fossil pathological specimens. Recently, Tong et al.25 described injuries in the sample of Shanshenmiaozui, Nihewan Basin, dated to 1.2 Ma. One of the specimen records a dental infection likely inflicted by processing hard food, such as bone; the other suffered a displaced fracture of its tibia and, despite such a severe injury (which would represent a death sentence for a solitary predator) it managed to survive the trauma to heal. The long period that was presumably required for healing the compound fracture, as well as the incapacitating nature of this trauma for a cursorial predator during the rest of its life (as the healed tibia was considerably shortened), suggests social hunting strategies and provision by other members of the family/pack (primarily food-sharing). Similar pathologies have been also detected in the Late Pleistocene population of Canis dirus Leidy, 1858 (recently reassigned to Xenocyon dirus23) from La Brea tar pits in southern California55. This is not surprising considering that packs of extant canids temporarily support wounded or sick members of their group, as reported by many authors in both extant C. lupus and L. pictus45, despite the cost in terms of efficiency of the group46. Nevertheless, in the case of African hunting dogs, several studies describe the asymmetry as a result of increasing levels of population homozygosity61. This suggests that the malformations of the C. (Xenocyon) lycaonoides from Venta Micena were probably due to developmental instabilities resulting from a high level of genetic homozygosity in the relatively small population of wild dogs that inhabited the Baza Basin during late Early Pleistocene times55; anodontia (tooth losses) and cranial bilateral asymmetry have been both documented in extant populations of C. lupus of small size subject to severe bottlenecks and inbreeding, for example the wolf population of the Białowieża Primeval Forest in Poland86. In the case of modern L. pictus, a study of museum skulls that span a period of a hundred years, which records the dramatic decline in the populations of the species in sub-Saharan Africa during the last century, has shown a marked increase in fluctuating asymmetry as a result of increasing levels of population homozygosity61. This suggests that the malformations of the C. (Xenocyon) lycaonoides skull from Venta Micena would reflect developmental instabilities resulting from a high level of genetic homozygosity in the relatively small population of hunting dogs of the Baza Basin, which was geographically (and genetically) isolated from other populations. Moreover, the effective population size of modern painted dogs is typically reduced to 20–35% of the censused population size by reproductive suppression of subordinates and uneven sex ratios82. In the case of Venta Micena, this would have also promoted further inbreeding and homozygosity. However, despite the numerous congenital disabilities, the individual VM-7000 was able to reach adulthood, which probably affected or even precluded its ability in the pack-hunting activities (Fig. 4b). This suggests that cooperative behaviour and food provisioning from other members of the family group were the only way for this individual to survive until this age44. Similarly to the old human from Dmanisi, who managed to reach such an old age thanks to the altruistic help and care of other family members (Fig. 4a), this hunting dog reached adulthood. This truly altruistic behaviour probably applies also to the hunting dog population of Dmanisi, although the scarce record of this species in the site precludes a direct inference.

Therefore, these findings seem to suggest that increased cooperation and altruistic behaviour may have been important factors for the survival and dispersal of both humans and large social carnivorans in the open environments of Africa, Eurasia and North America. Interestingly, hunting dogs and hominins are up to now the only late Early Pleistocene hypercarnivorous species with proved altruistic behaviour towards other members of their group, including food sharing to group members. As noted before, such a behaviour is specially developed in the extant African hunting dog, where individuals with limitations resulting from genetic abnormalities, pathologies and/or advanced age are helped and sustained by the other members of the family group45,49,50 Canis (Xenocyon) lycaonoides showed a similar pattern of cooperative and altruistic behaviour towards pack-members24,25. The occurrence of the Eurasian hunting dog in Dmanisi marks one the first and better chronologically-constrained record of this large-sized, pack-hunting canid. The success of this wide-ranging dispersion across continents5,50, unprecedented and never reached by any other large-sized canids, might be correlated also to the advantages of the mutually-beneficial cooperation and altruistic nature of these extinct hunting dogs, as the result of an evolutionary trend leading to co-operation among members of a species: “the best pathway to advantage for individuals”83.
It would not be necessary, but we have here a new evidence of the importance of Dmanisi for that, paraphrasing Dawkins\textsuperscript{6}, \textit{Homo} and highly social Canidae both are descended from highly social ancestors and their ancestors lived in groups; this was not an option but an essential survival strategy and from this mutual aid arose.

Materials and methods

The present study is based on the comparative morphological analysis of the large-sized \textit{Canis} (\textit{Xenocyon}) from Dmanisi and other Plio-Pleistocene hypercarnivorous canids of the Old World. The described fossils are housed at the S. Janashia Museum of Georgia, Georgian National Museum (Tbilisi) (MG-GNM). As comparative fossil material, the Villafrancharian and Epivillafrancharian canids from the Old World and North America housed at the American Museum of Natural History, New York (United States), Earth Science Dept. of the Aristotle University of Thessaloniki (Thessaloniki, Greece), Institut Català de Paleontologia Miguel Crusafont, Universitat Autònoma de Barcelona (Barcelona, Spain), Museo di Geologia e Paleontologia, Università degli Studi di Firenze (Italy), and Musée National d’Histoire Naturelle (Paris, France) were studied. This fossil comparative sample includes specimens of \textit{Canis} (\textit{Xenocyon}) \textit{dubius} from Zhoukoudian Loc. 18\textsuperscript{65}, \textit{Canis} (\textit{Xenocyon}) \textit{falconeri} from Upper Valdarno Basin and Tamagawa\textsuperscript{19}, \textit{Canis} (\textit{Xenocyon}) \textit{lycaonoides} from Apollonia-1\textsuperscript{186}, Campbellbore\textsuperscript{11}, Chukochya\textsuperscript{86}, Zhangsino\textsuperscript{35}, Cripplecreek Sump\textsuperscript{18}, Cueva Victoria, Valleparadis Estació\textsuperscript{19}, Lakhuti-2\textsuperscript{11,25}, Ma Fang\textsuperscript{11}, Naliakh\textsuperscript{135}, Olduvai Bed II\textsuperscript{17}, Pirro Nord\textsuperscript{11,35}, Shanxianmiaozui\textsuperscript{11,25}, Tighennif\textsuperscript{84}, Trlica\textsuperscript{95}, Untermassfeld\textsuperscript{15}, Venta Micena\textsuperscript{74}, Westbury-sub-Mendip\textsuperscript{70}.

Extant specimens housed at the American Museum of Natural History (New York, United States), Museo di Zoologia “La Specola”, Università degli Studi di Firenze (Italy), Institut Català de Paleontologia Miguel Crusafont (Barcelona, Spain), Royal Museum for Central Africa (Tervuren, Belgium) and MG-GNM were also used for morphological and metrical comparisons. We examined specimens of \textit{Canis} (\textit{Xenocyon}) \textit{lupus Linnaeus}, 1758, and \textit{Lycaon pictus} (Temminck, 1820). Moreover, a wide data set of craniodental measurements taken in modern canids (247 specimens from 32 species) by Prof. Blaire Van Valkenburgh was used also in some statistical comparisons, in order to deliver palaeoecological inferences for the Dmanisi wild dogs and also for others from different (and younger) sites, like Venta Micena in Spain and Untermassfeld in Germany. Analyses and graphs on dental values present in the supplementary were made in R ver. 3.6.1. (https://cran.r-project.org/) using package ggplot2 ver. 3.2.1 (https://ggplot2.tidyverse.org\textsuperscript{73}).

Cranial and dental measurements were taken with a digital calliper to the nearest 0.1 mm following von den Driesch\textsuperscript{74} with minor modifications.

Data availability

All data generated or analyzed during the study are included in this published article, in its Supplementary Information Files and on the online repository Zenodo at the following link https://doi.org/10.5281/zenodo.4704327.
31. Lordkipanidze, D.
30. Lordkipanidze, D.
27. Cappellini, E.
26. Ferring, R.
25. Tong, H.
23. Carbone, C., Teacher, A. & Rowcliffe, J. M. The costs of carnivory. *Paleobiology* **34**(3), 340–362 (1998).
22. Chengetanai, S. The Latest European painted dog *Lycaon pictus*. *J. Vertebr. Paleontol.* **19**(2), 3245–3261 (2007).
21. Chavez, D. E. Human occupations at Dmanisi (Georgian Caucasus) dated to 1.85–1.78 Ma. *PNAS* **108**, 10432–10436 (2011).
20. Stiner, M. C. A fourth hominin skull from Dmanisi, Georgia. *Nature* **449**, 305–310 (2007).
19. Lordkipanidze, D. et al. The earliest toothless hominin skull. *Nature* **434**, 717–718 (2005).
18. Zrzavý, J. Six ecological factors that may limit African wild dogs. *Anim. Conserv.* **4**, 23–30 (1991).
17. Cappellini, E. et al. Early Pleistocene enamel proteome from Dmanisi resolves Stephanorhinus phylogeny. *Nature* **574**, 103–107 (2019).
16. Espigares, M. P. & Palmqvist, P. Presence of the African machairodont *Stephanorhinus* in the lower Pleistocene site of Venta Micena (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal events. *Quat. Int.* **37**, 77–100 (1998).
15. Palmqvist, B. & Martínez-Navarro, B. The earliest toothless hominin skull. *Anat. Rec.* **288**(3), 569–582 (2001).
14. Palmqvist, P. et al. A re-evaluation of the diversity of *Megantereon* (Mammalia, Carnivora, Machairodontinae) and the problem of species identification in extinct carnivores. *J. Vert. Paleontol.* **27**, 160–175 (2007).
13. Bergman, T. D. Canine behavior and the herbivorous prey: Sociomotor thresholds facilitated by sneezes in collective decisions. *Proc. R. Soc. B Biol. Sci.* **284**(1874), (2017).
12. Schaller, G. B. Human impacts on big carnivores: Implications for conservation. *J. Mammal.* **88**, 181–193 (2007).
11. Edwards, C. T. T., Rasmussen, G. S., Riordan, P., Courchamp, F. & Macdonald, D. W. Non-adaptive phenotypic evolution of the skull of the African painted dog. *J. Vert. Paleontol.* **31**(1), 52–70 (1967).
10. Walker, R. H., King, A. J., McNutt, J. W. & Jordan, N. R. Sneezing. *Anat. Rec.* **288**(3), 569–582 (2001).
9. Schaller, G. B. The Serengeti Lion: A Study of Predator–Prey Relations (University of Chicago Press, 1970).
8. Mehl, L. Canine dispersal. *Mamm. Species* **37**, 1–6 (1974).
7. Woodroffe, R., Lindsey, P. A., Romanič, S. S. & Ranah, S. M. O. A large carnivore in the world. *Quat. Int.* **295**, 113–125 (2013).
6. Lordkipanidze, D. At least two large carnivorans and great climatic shifts limiting factors for hominin dispersals? Evidence of an adaptation to the *Pachycrocuta brevirostris* during the Mid-Pleistocene Revolution in the Mapungubwe Section (Vallées-Penedes Basin, Iberian Peninsula). *Quat. Int.* **431**, 42–52 (2017).
5. Kropotkin, P. Mutual Aid: A Factor of Evolution 348 (Clague & Co. P., 1902).
4. Boucher, D. H. The Biology of Mutualism: Ecology and Evolution (Oxford University Press, 1985).
3. Mehl, L. Social living mitigates the costs of a chronic illness in a cooperative carnivore. *Ecol. Lett.* **18**, 660–667 (2015).
2. Courchamp, F. & Macdonald, D. W. Crucial importance of pack size in the African wild dog *Lycaon pictus*. *Anim. Conserv.* **4**, 169–174 (2001).
1. Woodroffe, R., Lindsey, P. A., Romanič, S. S. & Ranah, S. M. O. A large carnivore in the world. *J. Vert. Paleontol.* **27**, 160–175 (2007).
66. Koufos, G. New material and revision of the Carnivora, Mammalia from the Lower Pleistocene Locality Apollonia 1, Greece. *Quaternary* 1, 6 (2018).

67. Petrucci, M., Cipullo, A., Martinez-Navarro, B., Rook, L. & Sardella, R. The Late Villafranchian (Early Pleistocene) carnivores (Carnivora, Mammalia) from Pirro Nord (Italy). *Palaeontogr. Abteilung A Palaeozoologie - Stratigr.* 298, 113–145 (2013).

68. Geraads, D. A revision of the fossial Canidae (Mammalia) of north-western Africa. *Palaeontology* 54, 429–446 (2011).

69. Vidofova, I. A. & Agadjanian, A. K. New data on large mammals of the Pleistocene Trilica fauna, Montenegro, the Central Balkans. *Palaeontol. J.* 49, 651–667 (2015).

70. Bishop, M. J. The mammal fauna of the early Middle Pleistocene cavern infill site of Westbury-sub-Mendip, Somerset. *Spec. Pap. Palaeontol.* 28 (1982).

71. Del Campana, D. I cani pioveci di Toscana. *Palaeontogr. Ital.* XIX, 189–254 (1913).

72. Sher, A. V. Olyorian land mammal age of Northeastern Siberia. *Palaeontogr. Ital.* 74, 97–112 (1986).

73. Wickham, H. *ggplot2: Elegant Graphics for Data Analysis.* Use R. (Springer, 2009).

74. Von den Driesch, A. A guide to the measurement of animal bones from archaeological sites: as developed by the Institut für Paläoanatomie, Domestikationsforschung und Geschichte der Tiermedizin of the University of Munich (Peabody Museum Press, 1976).

**Acknowledgements**

The authors are indebted to the kindness and availability of the curators who granted access to the collections of their institutions and museums: M. Bukhsianidze of the MG-GNM; P. Agnelli of Museo di Zoologia “La Specola”, Università degli Studi di Firenze; E. Cioppi of Museo di Geologia e Paleontologia, Università degli Studi di Firenze; J. Galkin, and J. Meng of the American Museum of Natural History; G. Koufos of Aristotle University of Thessaloniki and E. Gilissen and W. Wendelen from Royal Museum for Central Africa. Dmanisi research is supported by Shota Rustaveli Georgian National Science Foundation, Laboratory equipment is provided by Alexander von Humboldt Foundation. This study is framed within a wider Georgian-Italian collaborative project (bilateral agreement between the University of Florence and the Tbilisi State University “I. Javakhishvili” / Georgia National Museum) supported by the Italian Embassy in Georgia. The latter is acknowledged for the continuous support to L.R. and S.B.L. while working in Tbilisi. The authors are indebted to M. Bukhsianidze for the fruitful discussion on a previous version of this manuscript that helped improve the text, and to L. Salimei for the rewarding conversations on mutually beneficial cooperation and reciprocity. The Italian Ministry for Foreign Affairs (DGPCC-V) is acknowledged for financially supporting Italian palaeontological research in Georgia. This study has been funded by the University of Florence (Fonti di Ateneo to L.R. and Fondi di Internazionalizzazione to L.R. and S.B.L.), the Spanish Agencia Estatal de Investigación (grants CGL2016-78577-P, CGL2016-80975-P, CGL2017-82654-P, AEI/FEDER-UE) and the Generalitat de Catalunya (CERCA Program GENCAT 2017SGR 859; SGR 416 GRC, AGAUR, Generalitat de Catalunya). Part of this research was also funded by the Synthesys project to J.M.-M. (BE-TAF-5471).

**Author contributions**

S.B.L., J.M.-M., B.M.N., P.P., L.R. and D.L. conceived and designed the experiments. S.B.L., J.M.-M., B.M.N., P.P. and L.R. wrote the paper and prepared figures and tables. All authors analyzed the data and reviewed drafts of the paper.

**Competing interests**

The authors declare no competing interests.

**Additional information**

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1038/s41598-021-92818-4.

**Correspondence** and requests for materials should be addressed to S.B.-L. or B.M.-N.

**Reprints and permissions information** is available at www.nature.com/reprints.

**Publisher’s note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2021