



# The Wolf From Dmanisi and Augmented Reality: Review, Implications, and Opportunities

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In the complex scenario of Plio–Pleistocene mammalian faunal turnovers, recent research on canids has revealed an increasingly higher number of species than previously thought. In this framework, Georgia had a key role in the biogeographic dispersion of fauna from/to Asia, Africa, and Europe. Historically attributed to *Canis etruscus*, the rich *Canis* material recovered from Dmanisi possesses certain peculiar cranial and dentognathic features, which cannot be regarded only as intraspecific variability. We revealed closer similarities between the Dmanisi wolf and the younger European *Canis mosbachensis*, rather than with other Early Pleistocene canids as *C. etruscus* and *Canis arnensis*. The discovery of a *Canis borjgali* sp. nov. in Dmanisi, with characteristics close to those of *C. mosbachensis*, changes radically the idea of *Canis lupus* evolution as it is conveyed today, invalidating the paradigm *C. etruscus*–*C. mosbachensis*–*C. lupus* lineage. Furthermore, the geographic position of Dmanisi in the Caucasian area offers interesting insights regarding the Asian canids and their dispersion into Europe and Africa, an aspect still poorly investigated. The exquisite state of preservation of the fossil from Dmanisi combined with novel 3D visualization and a digital imaging technique gives us the opportunity to increase the outreach of the research thanks to user-friendly and free tools. Here, for the first time, we employed augmented reality on a few specimens of *C. borjgali* sp. nov. through a simple web app. The extraordinary chance offered by these technologies has yet to be implemented in scientific research and dissemination, particularly in paleontology.

**Keywords:** Canidae, Carnivora, Georgia, augmented reality, early Pleistocene, morphology

## INTRODUCTION

In the last decades, genetic and paleontological studies have revealed an intricate evolutionary history of the genus *Canis* (Tedford et al., 2009; Koepfli et al., 2015; Viranta et al., 2017; Zrzavý et al., 2018). The genus *Canis* Linnaeus, 1758, since its early appearance in North American Late Miocene and its dispersal and radiation throughout Asia, is known to have reached the western part of Europe around 3 Ma (Lacombat et al., 2008), where the first species described is *Canis etruscus* Forsyth-Major, 1877 from several sites of Europe (Cherin et al., 2014). There

is wide consensus considering the modern wolf as the final stage of an evolutionary line starting with the Early Pleistocene *C. etruscus* through the Early–Middle Pleistocene *Canis mosbachensis* Soergel, 1925 (see inter alios Brugal and Boudadi-Maligne, 2011). Morphologically modern wolves appear in the early Middle Pleistocene of North America (Tedford et al., 2009) and in several mid Middle Pleistocene Asian and European localities (Bonifay, 1971). In the framework of the Early and Middle Pleistocene radiation of Eurasian mammals, the site of Dmanisi is celebrated for its outstanding record of early Homo Linnaeus, 1758 (Lordkipanidze et al., 2007, 2013; Krijgsman et al., 2019; Rightmire et al., 2019), for the state of preservations of the fossils (allowing molecular analyses on its fossils, Cappellini et al., 2019), and for the pivotal documentation of the biogeographic faunal dispersals between the three continents, Asia, Africa, and Europe. Indeed, the Georgian site offers a unique glimpse on the turnovers that took place around 1.8 Ma (during the late Villafranchian Land Mammal Age) (Ferring et al., 2011; Bartolini Lucenti et al., 2019; Krijgsman et al., 2019). Among the large number of mammalian taxa recovered, carnivores are abundant. At least 13 different species of the five most common families of carnivorans are represented. Of these, *Canis* (referred to *C. etruscus* by Vekua, 1995) is by far the most abundant taxon with eight almost complete crania and more than 270 cranial specimens. This rich and remarkably well-preserved sample allowed us to assess its variability, compared to that of other Early and Middle Pleistocene canids. We here suggest an early origin of modern wolves and related species, redescribing the *Canis* from Dmanisi as a new species.

## MATERIALS AND METHODS

### The Comparative Sample

The present study is based on the comparative morphological analysis of the medium-sized *Canis* from Dmanisi and other wolf-like canids (tribe Canini) of the Early–Middle Pleistocene from Europe. The described fossils are housed at the S. Janashia Museum of Georgia, Georgian National Museum (Tbilisi). As comparative fossil material, the late Villafranchian canids from Eurasia housed at AMNH, AUT, ICP, and IGF (see abbreviation below) were studied. This fossil comparative sample includes specimens of *Canis arnensis* Del Campana, 1913 and *C. etruscus* from the Italian sites of Olivola, Upper Valdarno Basin, Coste San Giacomo, and Pantalla (Cherin et al., 2014); *Canis apolloniensis* Koufos and Kostopoulos (1997) from Apollonia-I (Koufos, 2018); *Canis chihliensis* and *Canis palmidens* from Yushe Basin (Rook, 1993, 1994); remains of *C. mosbachensis* Soergel, 1925 from Cueva Victoria, Vallparadís (Bartolini Lucenti et al., 2017), Pirro Nord (Petrucci et al., 2013), 'Ubeidiya (Martínez-Navarro et al., 2009), Untermassfeld (Sotnikova, 2001), and Zhoukoudian (Jiangzuo et al., 2018). The relevant literature on the late Villafranchian canids was inspected (Del Campana, 1913; Crusafont Pairó, 1950; Thenius, 1954; Torre, 1967, 1974, 1979; Bonifay, 1971; Kurtén, 1974; Pons-Moyà and Moyà-Solà, 1978; Pons-Moyà, 1981; Koufos and Kostopoulos, 1997; Wang et al., 1999; Sotnikova, 2001; Garrido and Arribas, 2008; Lacombat et al., 2008; Tedford et al., 2009;

Petrucci et al., 2013; Cherin et al., 2014; Koufos, 2014, 2018; Bartolini Lucenti and Rook, 2016; Amri et al., 2017; Mecozzi et al., 2017; Jiangzuo et al., 2018). Extant specimens housed at the AMNH, MZUF, ICP, and MG-GNM (see abbreviation below) were also used for morphological and morphometrical comparisons. We examined specimens of *Canis aureus* Linnaeus, 1758, *Canis latrans* Say, 1823, *Canis lupaster* Hemprich and Ehrenberg, 1828–1834, *Canis lupus* Linnaeus, 1758, *Lupulella adusta* (Sundevall, 1847), *Lupulella mesomelas* (Schreber, 1775), and *Lycaon pictus* (Temminck, 1820).

The 3D surface scan of the fossil and extant specimens was obtained with the Artec Space Spider high-resolution 3D blue light technology scan at the Museum of Georgia and at the Paleo[Fab]Lab, Earth Science Department of the University of Florence. The 3D surface scans were subsequently elaborated in Artec Studio 12 Professional. The 3D visualization of the cranium D64 and upper and lower teeth comparison models in Augmented Reality was created following the protocols described by several authors (e.g., Etienne, 2017; Carpignoli, 2019) in Visual Studio Code ver. 1.41, using AR.js and A-Frame v. 0.9.2 (www.aframe.io).

### Morphometric and Statistical Analyses

Cranial and dental measurements were taken with a digital caliper to the nearest 0.1 mm following von den Driesch (1976) with minor modifications (see abbreviations below).

We performed a principal components analysis (PCA) on a dataset of selected  $\log_{10}$ -transformed cranial measurements, in order to establish the morphological similarities between various canid species, both extinct (*Canis* from Dmanisi, and *C. etruscus*) and extant (*C. aureus*, *C. lupus*, *C. lupaster*, *L. adusta*, *L. mesomelas*). We then used a permutational ANOVA on the most explicative principal components to test the statistical significance of the differences resulting from the analysis.

We compared the material of *Canis* from Dmanisi with that of other European Late Villafranchian species by means of boxplots, to inspect differences in values distribution, and statistical tests. At this purpose, selected cranial ratios were used to test for statistical difference between the sample of Dmanisi, the other fossil taxa, and the extant species of the genera *Canis* and *Lupulella*. We tested these ratios by means of permutational ANOVA computed in R statistical environment (ver. 3.6.). The difference between the samples in dental measures were tested using a permutational multivariate ANOVA (MANOVA), using the pairwise Adonis package (Martínez Arbizu, 2019) computed in R.

### Site and Institutional Abbreviations

AMNH, American Museum of Natural History, New York (United States); AUT, Earth Science Department of Aristotle University of Thessaloniki; D, Dmanisi site; ICP, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona (Cerdanyola del Vallès, Barcelona, Spain); IGF, Museum of Natural History, Geological and Paleontological section, the University of Florence (Italy); MG-GNM, S. Janashia Museum of Georgia, Georgian National Museum (Tbilisi, Georgia); MZUF, Museum of Natural History, “La Specola” Zoology section, University of Florence (Italy); 0X/D,

P, provisional catalog number of unregistered specimens from Dmanisi housed in MG-GNM.

## Anatomical Abbreviation

### Cranium

AB, height of the cranium without the sagittal crest (inion-basion); BL, basal length of the cranium; CBL, condylobasal length of the cranium; Ect, width across the zygomatic processes of the frontals; ECW, width of the muzzle at level of the upper canine; Eu, greatest neurocranium width; FL, facial length; GPW, greatest palatal width; GWOC, greatest width of occipital condyles; NcL, neurocranial length; PL, palatal length; POCW, smallest width of postorbital constriction; SCL, splanchnocranial

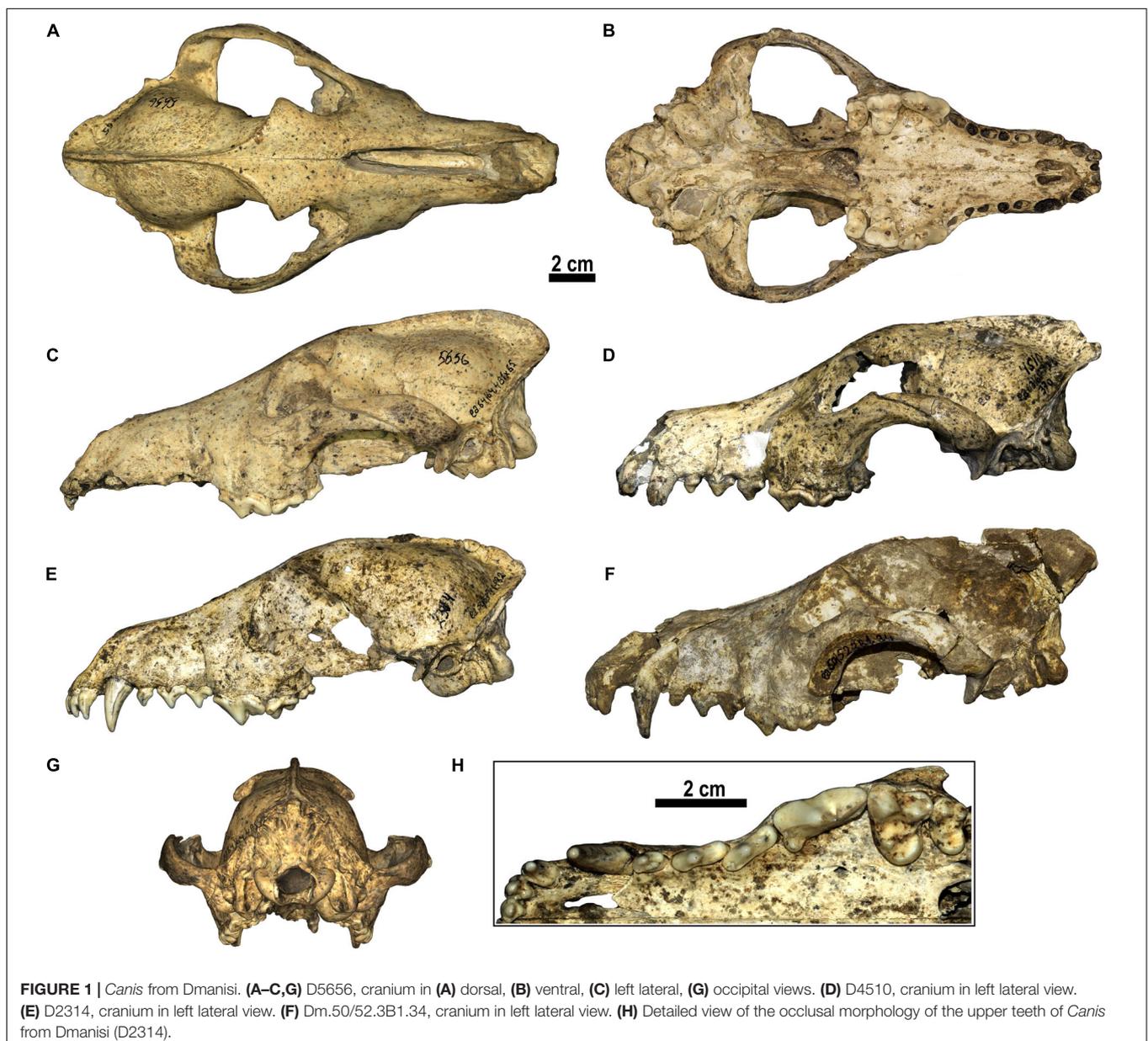
length; SH, skull height (with sagittal crest); TL, total length of the cranium (inion-prosthion); Zyg, zygomatic breadth.

### Dentition

L, mesiodistal length; LCR, upper cheek toothrow length (P1–M2); LMR, upper molar row length (M1–M2); LPR, upper premolar row length (P1–P4); tdm1, talonid of m1; trm1, trigonid of m1; W, buccolingual width.

### Mandible

HR, height of the mandible ramus; LLMR, length of the lower molar row (m1–m3); LLPR, length of the lower premolar row (p1–p4); Mm1B, mandibular corpus breadth below midpoint of m1; Mm1H, mandibular corpus height distal to m1 alveolus; Mp4H, mandibular corpus height distal to p4 alveolus; m1–m2



**FIGURE 1 |** *Canis* from Dmanisi. (A–C, G) D5656, cranium in (A) dorsal, (B) ventral, (C) left lateral, (G) occipital views. (D) D4510, cranium in left lateral view. (E) D2314, cranium in left lateral view. (F) Dm.50/52.3B1.34, cranium in left lateral view. (H) Detailed view of the occlusal morphology of the upper teeth of *Canis* from Dmanisi (D2314).

L, length of the first and second lower molars; p2–p4 L, length of premolar row between p2 and p4.

## SYSTEMATIC PALEONTOLOGY

Order Carnivora Bowdich, 1821

Family Canidae Fischer, 1817

Subfamily Caninae Fischer, 1817

Tribe Canini Fischer, 1817

Genus *Canis* Linnaeus, 1758

*Canis borjgali* sp. nov.

**Figures 1, 2, 3; Supplementary Tables S1, S2, S3, S4**

**Etymology.** From the Georgian “ბორჯღაღლი,” IPA: [bɔrdʒɔɖali], seven-rayed symbol of the sun and eternity typical of Georgia.

**Holotype.** D64, almost complete skull with I1–M2 and i1–m3.

**Hypodigm.** See **Supplementary Material**.

**Type Locality and Age:** Dmanisi, Georgia; ca 1.80 Ma.

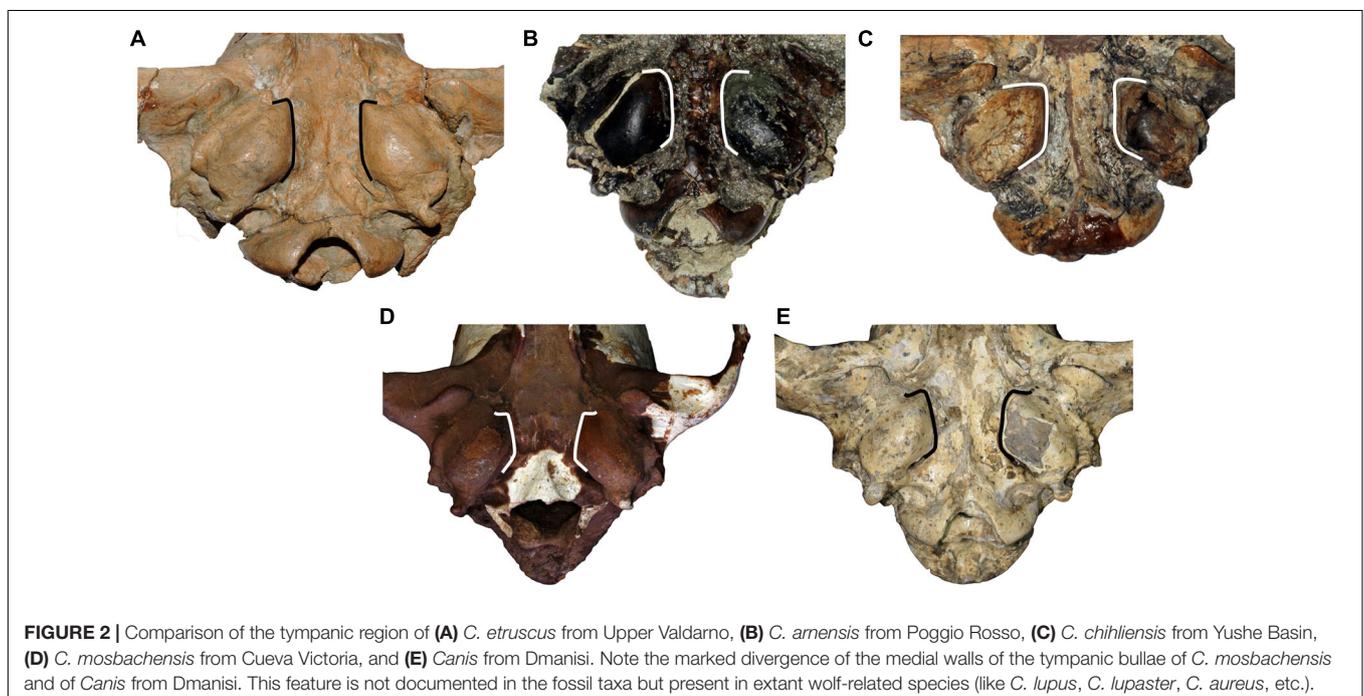
## Differential Diagnosis

A medium-sized canid, close or slightly smaller compared to *C. etruscus*, generally larger than other Villafranchian medium-sized canids. *Canis borjgali* differs from *C. arnensis* for the longer nasal bones, the well-developed frontal sinuses, the morphology of the upper molars, and the hypoconid on m1 larger than entoconid in the m1. It differs from *C. etruscus* for its overall cranial architecture, including the relatively higher cranium, the profile in lateral view, and shorter nasal bone and their morphology. It also differs in dental features, including the presence of accessory cusplids on the lingual margin of m1 talonid. It is distinguished from *C. arnensis* and *C. etruscus*

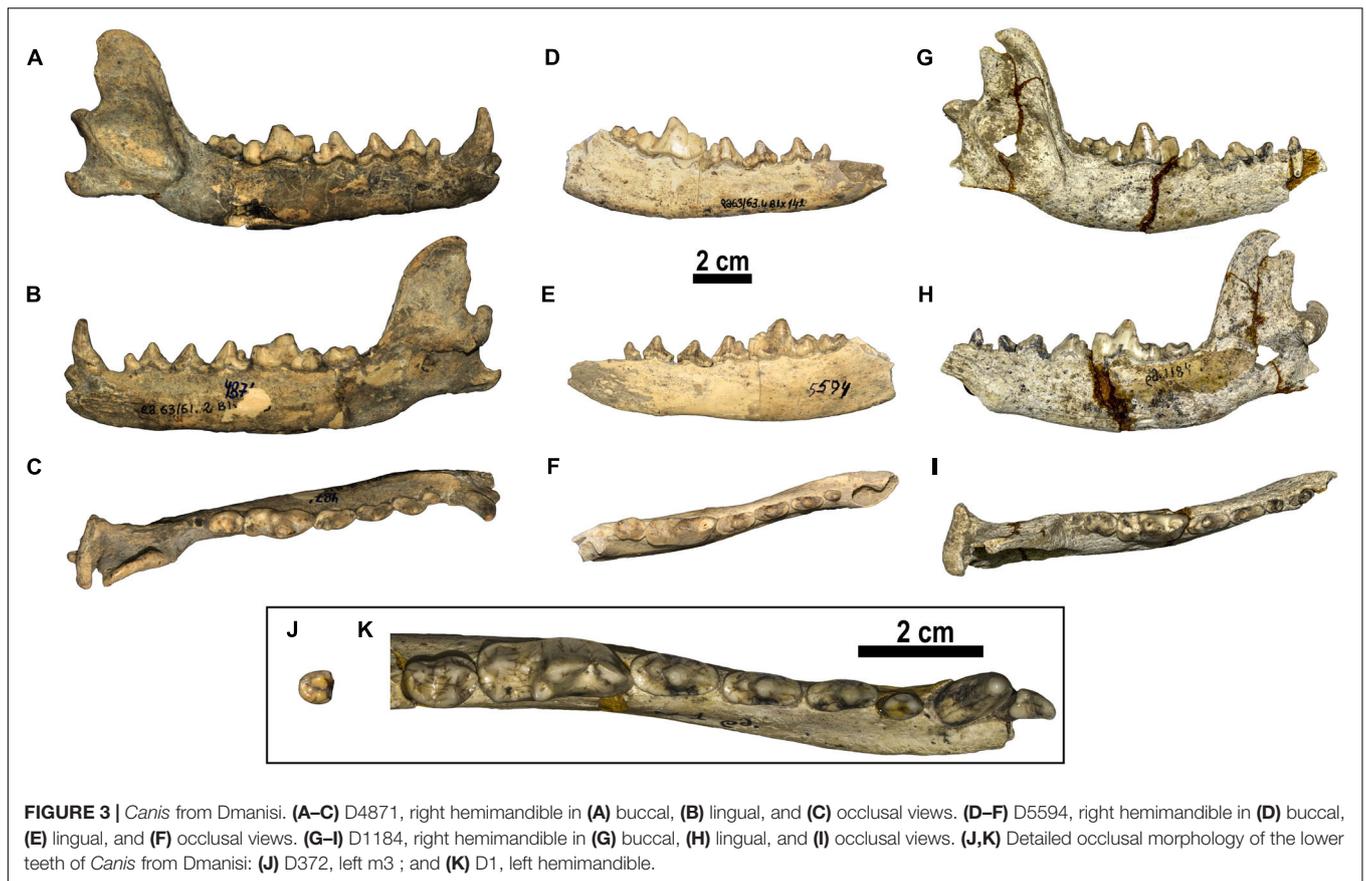
by the caudorostrally divergent medial walls of the tympanic bullae and few other dental features, including the deeper trigon basin compared to the talon basin on M1, the p3 that sets below the alveolar plane of p2 and p4. *C. borjgali* differs from *C. mosbachensis* for some less derived features, including the morphology of the second upper molar, the more arched lower toothrow, and larger metaconid on m1. *C. borjgali* possesses a marked apomorphy, i.e., the medial walls of tympanic bullae that diverge rostral direction.

## Description and Comparison

The cranium is moderately elongated (**Figure 1**). Nasals are long, although not as long as in *C. etruscus* from Olivola and Pantalla. In lateral view, the profile of the cranium of *Canis* from Dmanisi is moderately arched, contrasting condition compared to the straight profile of *C. etruscus* from Olivola and Pantalla, but still less arched than in *C. mosbachensis* and *C. lupus*. The postorbital constriction is not marked for the considerable development of the frontal sinuses, which extend caudally toward the frontoparietal suture like in *C. chihliensis* from Yushe Basin, *C. etruscus* from Italy, *C. mosbachensis* from Eurasia, and *C. lupus*, although reduced compared to the latter (**Table 1**). The postorbital region is shorter compared to the elongated one of *C. lupus*, resembling other fossil species (e.g., *C. mosbachensis* from Cueva Victoria, Untermassfeld, and Zhoukoudian). The supraoccipital shield has the typical *Canis* triangular shape, although less sharp compared to that of *C. mosbachensis* from Eurasia (e.g., Cueva Victoria, Untermassfeld, and Zhoukoudian loc. 13) and extant *C. lupus* (**Table 1**). In ventral view, the tympanic bullae are oval shaped and moderately inflated. Their medial walls are not parallel, but tend to diverge in caudorostral direction, unlike *C. arnensis*, *C. etruscus*, and *C. chihliensis* from



**FIGURE 2 |** Comparison of the tympanic region of (A) *C. etruscus* from Upper Valdarno, (B) *C. arnensis* from Poggio Rosso, (C) *C. chihliensis* from Yushe Basin, (D) *C. mosbachensis* from Cueva Victoria, and (E) *Canis* from Dmanisi. Note the marked divergence of the medial walls of the tympanic bullae of *C. mosbachensis* and of *Canis* from Dmanisi. This feature is not documented in the fossil taxa but present in extant wolf-related species (like *C. lupus*, *C. lupaster*, *C. aureus*, etc.).



**FIGURE 3** | *Canis* from Dmanisi. (A–C) D4871, right hemimandible in (A) buccal, (B) lingual, and (C) occlusal views. (D–F) D5594, right hemimandible in (D) buccal, (E) lingual, and (F) occlusal views. (G–I) D1184, right hemimandible in (G) buccal, (H) lingual, and (I) occlusal views. (J,K) Detailed occlusal morphology of the lower teeth of *Canis* from Dmanisi: (J) D372, left m3; and (K) D1, left hemimandible.

Yushe Basin (Figure 2). There are no diastemata between the upper teeth. The protocone of the upper carnassial is poorly individualized and relatively reduced, condition similar to that found in *C. lupus*, whereas in *C. etruscus* from Italy, the protocone is well separated from the rest of the tooth. The P4 also possesses a high and stout paracone, a sharp metastyle, and a strong mesiolingual cingulum. On the M1, the paracone is larger and higher than the metacone as in *C. apolloniensis*, *C. etruscus*, *C. mosbachensis*, and *C. lupus* (Table 1). As in these species, there is a well-developed metaconule, a high protocone, and a rather individualized protoconule. The protocone basin is deeper and larger than the hypocone basin, like in *C. apolloniensis*, *C. mosbachensis*, and *C. lupus*. The M1 shows a strong and well-developed buccal cingulum, expanded on both the mesial and distal sides, unlike *C. lupus* in which the cingulum is present but subdued. The morphology of the M2, in occlusal view, tends to be similar to that of *C. etruscus*, with a large buccal side. Some specimens share this more buccolingually elongated shape resembling the morphology of *C. apolloniensis* from Apollonia-1, *C. lupus*, and *C. mosbachensis* from Eurasia (Table 1).

The mandible of *Canis* from Dmanisi generally has a moderately deep horizontal ramus (Figure 3), similar in dorsoventral height and morphology to that of *C. etruscus* from Italy, unlike *C. arnensis* from Upper Valdarno, in which it is more slender. The postcanine tooththrow is slightly arched (buccally convex at the p4–m1 commissure) as generally in

*C. apolloniensis*, *C. etruscus*, *C. mosbachensis*, and *C. lupus*, whereas it is moderately arched in *C. arnensis* from Upper Valdarno (Table 1). Diastemata are absent between the lower premolars. In *Canis* from Dmanisi, the p3 generally sets in the mandible below the alveolar level of the p2 and p4, as in *C. mosbachensis* and *C. lupus* (Figure 3 and Table 1). The p3 possesses a distal accessory cuspid, generally absent in *C. apolloniensis* and *C. mosbachensis*. The p4 occlusal shape is wide and oval similar to *C. mosbachensis* from Eurasia compared the more slender shape of *C. apolloniensis* from Apollonia-1, *C. arnensis* from Upper Valdarno. The m1 paraconid is higher than the p4 protoconid, like in *C. apolloniensis* from Apollonia-1, *C. mosbachensis* from Eurasia, and *C. lupus*, in contrast to *C. arnensis* and *C. etruscus*. In the lower carnassial, the metaconid is large and individualized from the protoconid. It is larger compared to *C. apolloniensis* from Apollonia-1, *C. mosbachensis* from Eurasia, and *C. lupus*, which possess a reduced metaconid, closely attached to the large protoconid. Nevertheless, the lower carnassial is less developed compared to *C. arnensis* and *C. etruscus*. On the talonid, the hypoconid is larger than the entoconid, although the difference between them is reduced compared to that visible in *C. lupus* and *C. etruscus* (Figure 3 and Table 1). The transverse cristid between the m1 hypoconid and entoconid is evident and generally sinuous, as in *C. mosbachensis* and *C. lupus*, unlike *C. arnensis* or *C. etruscus* from Italy. The m1 entoconid is more developed compared to

**TABLE 1** | Summarizing table of the main craniodental features of *C. etruscus*, *C. arnensis*, *C. mosbachensis*, and *C. apolloniensis* compared to those of the *Canis* sp. from Dmanisi.

Character	<i>C. etruscus</i>	<i>C. arnensis</i>	<i>C. apolloniensis</i>	<i>C. mosbachensis</i>	<i>Canis</i> sp. from Dmanisi	References
Nasal bones, in dorsal view	very long, end well beyond maxillo-frontal suture	short, end slightly before the level of maxillo-frontal suture	–	long, end beyond maxillo-frontal suture	Long, end beyond maxillo-frontal suture	Sotnikova, 2001; Bartolini Lucenti et al., 2017
Nasal bones, in lateral view	straight profile in lateral view	gently dorsoventrally curved	–	dorsoventrally curved	slightly dorsoventrally curved	Bartolini Lucenti et al., 2017
Distal elongation of the postorbital constriction	modest	reduced	–	generally marked	modest	
Outline of nuchal crest	blunt dorsal outline	rounded outline	–	triangular, sharp-pointed	blunt dorsal outline	
Medial walls of the tympanic bullae	straight, parallel one another	straight, parallel one another	–	markedly rostrocaudally divergent	markedly rostrocaudally divergent	Bartolini Lucenti et al., 2017, here
GWOC/AB	>0.9	<0.9	–	<0.9	<0.9	Cherin et al., 2014
Axis of P3	inline with that of P4	inline with that of P4	generally deviates laterally from that of P4	generally deviates laterally from that of P4	may deviates laterally from that of P4	Koufos, 2018
M1 paracone	larger than the metacone	slightly larger than the metacone	larger than the metacone	larger than the metacone	larger than the metacone	Sotnikova, 2001; Tedford et al., 2009
Trigon-talon basins on M1	same depth	same depth	trigon basin deeper	trigon basin deeper	trigon basin deeper	Sotnikova, 2001; Bartolini Lucenti et al., 2017
Occlusal shape of the M2	squared	short bean-like shape	generally buccolingually elongated bean-shaped	buccolingually elongated bean-shaped	generally triangular	Sotnikova, 2001
M2 metacone	smaller than the paracone	equal-sized with paracone	similar to the paracone	smaller than paracone	smaller than paracone	
Contact between M1-M2	reduced	broad	reduced	reduced	reduced	Cherin et al., 2014
Toothrow curvature	strong	slight	tend to be strong	tend to be strong	strong	Del Campana, 1913
Lower premolars protoconids	high	high	short	short	short	Bartolini Lucenti et al., 2017
p3 alveolus	at same level of p2-p4 alveoli	at same level of p2-p4 alveoli	at same level of p2-p4 alveoli	lower in the mandible, especially distally	lower in the mandible, especially distally	Sotnikova, 2001
p3 distal accessory cuspid	developed	developed	generally reduced	generally reduced	present	
p4 secondary distal cuspid and distal cingulid	separated	separated	fused	fused	fused	
Mesial margin of paraconid of m1	vertical and straight	vertical and straight	inclined distally and straight/slightly curved	inclined distally and straight/slightly curved	inclined distally and straight	Bartolini Lucenti et al., 2017
Hypoconid of m1	very large	similar size with entoconid	considerably larger than entoconid	larger than entoconid	larger than entoconid	Torre, 1967; Sotnikova, 2001
Transverse cristid	straight (rarely sinuous)	straight	straight (rarely sinuous)	generally sinuous	generally sinuous	Sotnikova, 2001; Bartolini Lucenti et al., 2017
m1 accessory cuspids	absent	can be present	generally present	generally present	can be present	Martinez-Navarro et al., 2009; Bartolini Lucenti et al., 2017
m2 protoconid	larger than the metaconid	equal-sized with metaconid	larger than the metaconid	larger than the metaconid	larger than the metaconid	Tedford et al., 2009
m2 distolingual cuspids	absent	entoconid evident	generally absent	generally absent	absent	Martinez-Navarro et al., 2009; Tedford et al., 2009

“–” represents missing information in the literature or on the specimens.

*C. apolloniensis* and *C. mosbachensis*, similarly to *C. etruscus*. Accessory cusplids may be present on the lingual side of the talonid, like in *C. apolloniensis* and *C. mosbachensis* from Eurasia. The m2 protoconid is larger compared to the metacone, unlike *C. arnensis* (Table 1). Distally on the m2, there is a hypoconid and a lingual cristid, generally with no accessory cusplids, as in *C. apolloniensis* and *C. mosbachensis* (although in the latter, the m2 occlusal shape is generally more rectangular). The m3 has two cusplids, with the buccal larger than the lingual one as in *C. etruscus* from Italy and *C. mosbachensis* from Europe, as opposed to *C. arnensis* (which has two equal-sized cusplids) and *C. lupus* (with a single and large cuspid).

## RESULTS

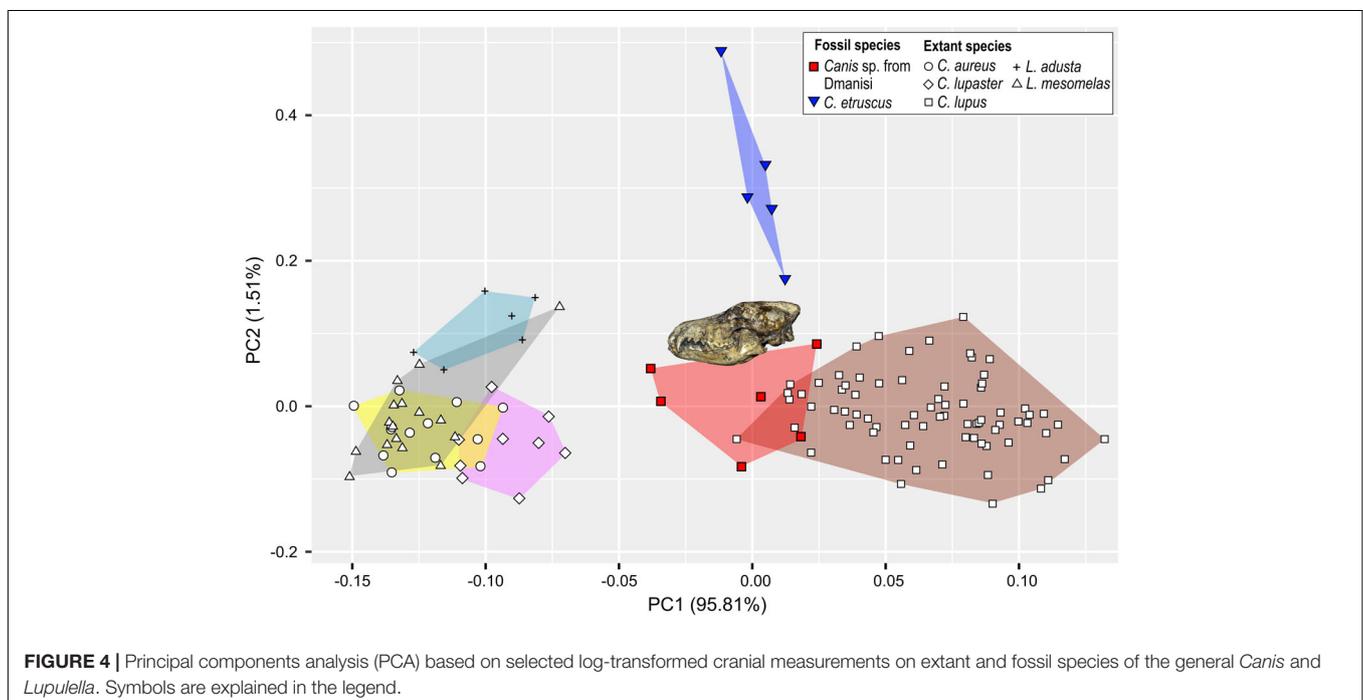
### Principal Component Analysis

The results of the PCA on cranial variables are reported in Figure 4. The PC1, which accounts for most of the variance (95.8%), has positive and similar loading for all the analyzed original variables (Supplementary Table S5), thus being positively influenced by cranial shape. Along the PC1, the modern wolves separate from other extant canids (jackals and golden wolves), the former on the positive end whereas the latter on the negative end. Extinct species (*Canis* from Dmanisi and *C. etruscus*) occupy an intermediate position, slightly overlapping with the modern wolf variation. *C. etruscus* variability on this axis is relatively limited, and its variance is included in that of *Canis* from Dmanisi. The PC2 only accounts for 1.5% of total variance, being dominated positively by greatest nasal length, splanchnocranial length, and facial length, whereas negatively by the skull height with the sagittal crest,

the neurocranial length, and the width of the muzzle across the upper canines. On this axis, *C. etruscus* is considerably separated from the range of the other canids; therefore, it is visibly distinguished from *Canis* from Dmanisi. The results of the ANOVA on the PC1 is reported in Supplementary Table S6. The analysis confirms the significant difference between *C. lupus* and the other extant canids visible in Figure 4. Both *C. etruscus* and *Canis* from Dmanisi are different from the extant canids, yet there is no statistical difference between them on the PC1 ( $F = 0.2576$ ,  $p = 0.99923$ ), as visible from Figure 4.

### Statistical Analyses

In both cranial and dental measures, *Canis* from Dmanisi is close to *C. etruscus* and other Early Pleistocene canids of Eurasia like *C. mosbachensis* and *C. apolloniensis*, and comparable to smaller subspecies of *C. lupus* (e.g., *Canis lupus arabs* or *Canis lupus pallipes*; Supplementary Material, Supplementary Tables S1–S4). Nevertheless, the cranial ratios (SCL/TL, GNL/TL, GWOC/AB, SH/TL) show significant difference between *C. etruscus* and *Canis* from Dmanisi (Figure 5). *C. etruscus* is considerably different in cranial proportions as opposed to the others species, fossil, and extant ones. The ratios of *Canis* from Dmanisi are more similar to *C. mosbachensis* and *C. lupus*. *C. arnensis* differs significantly from *C. etruscus* in three ratios (SCL/TL, GNL/TL, GWOC/AB) and cannot be distinguished from *Canis* from Dmanisi in these ratios. Nevertheless, the relative height of the skull is significantly different between *C. arnensis* and *Canis* from Dmanisi. The analysis of variance on the relative length of the nasals (Supplementary Table S7), the most numerous of the considered ratios, revealed to be statistically significant

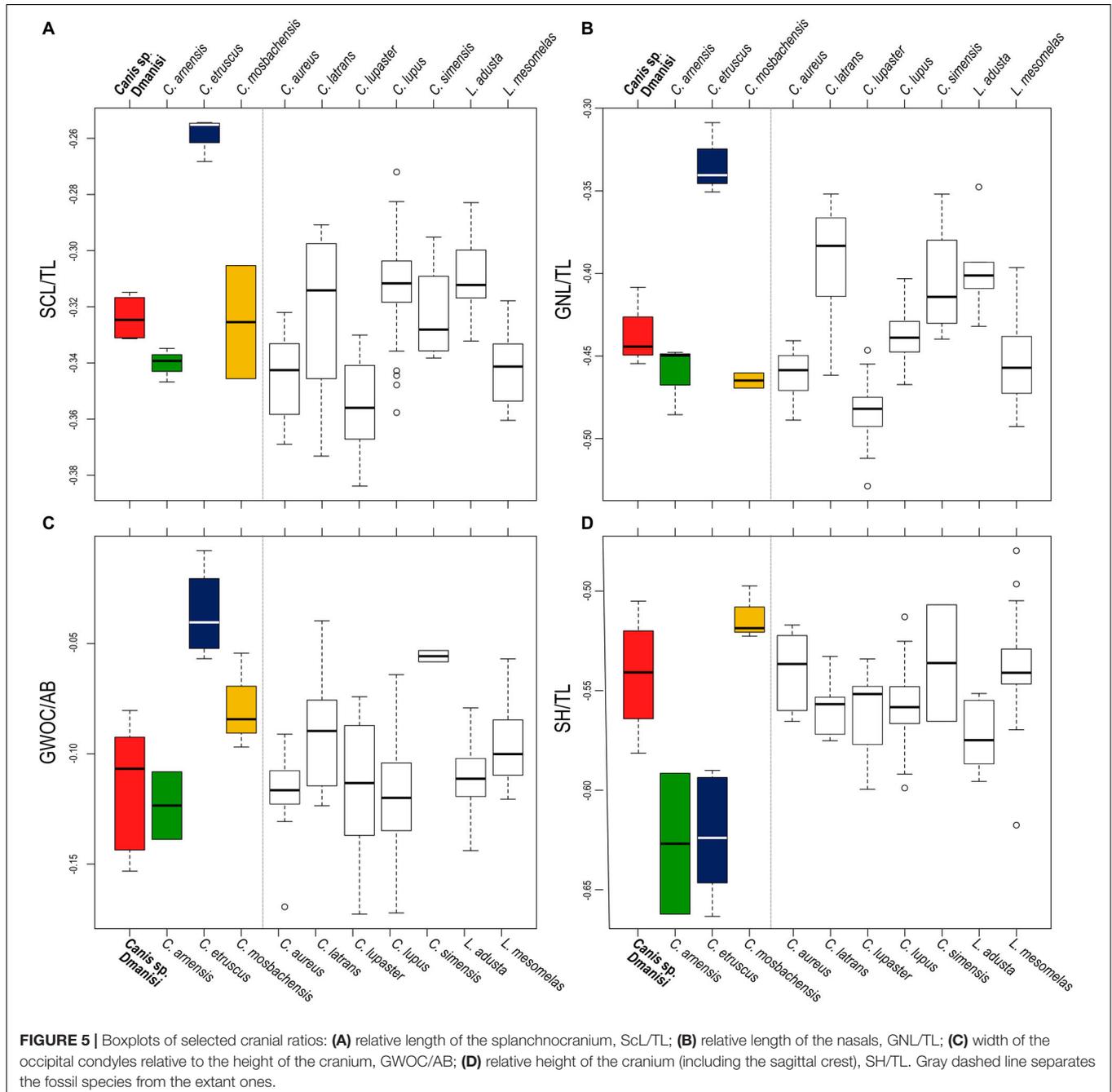


between *Canis* from Dmanisi and *C. etruscus* ( $F = -0.102498$ ;  $p << 0.01$ ; **Supplementary Table S7**). The MANOVA on dental measures (**Supplementary Tables S8, S9**) confirms the statistical difference between *Canis* from Dmanisi and *C. etruscus* (upper teeth:  $F = 33.403$ ;  $p = 0.04496$ ; lower teeth:  $F = 19.4091$ ,  $p = 0.04496$ ), on one side, and no difference between the former and *C. mosbachensis*, on the other. As for cranial ratios, the dental measures of *C. arnensis* are partially similar to *Canis* from Dmanisi, as the lower teeth values of the two species are significantly different ( $F = 33.403$ ;  $p = 0.04496$ ; **Supplementary Table S9**).

## DISCUSSION

### Taxonomic Attribution of *Canis* From Dmanisi and Implications for the Evolution of Canini

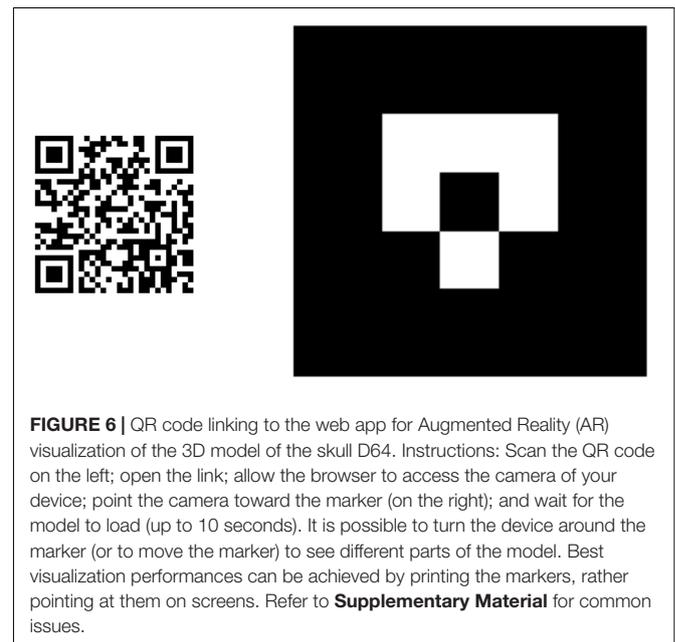
The results of the ANOVA on the PC1, the axis explaining the majority of the variability of the PCA (**Figure 4**), show no statistical distinction between *C. etruscus* and *Canis* sp. from Dmanisi (**Supplementary Table S6**). Nevertheless, the separation between these species in the plot of the principal component



analysis is along the PC2 (as evident from **Figure 4**). The cranial ratios (SCL/TL, GNL/TL, GWOC/AB, and SH/TL) shown in **Figure 5** take into consideration those values that influence the dispersion of the specimens on this axis. A permutational ANOVA test on the GNL/TL, the most represented of the ratios and the most important parameter of PC2, clearly supports the distinction of *C. etruscus*. The result acknowledges the peculiarity of *C. etruscus* compared to other known fossil and extant species as noted by Cherin et al. (2014), including the sample from Dmanisi (**Supplementary Table S7**). The distinction between *Canis* sp. from Dmanisi and *C. etruscus* is confirmed also by the MANOVA on upper and lower teeth (**Supplementary Tables S8, S9**). Therefore, despite being considered as synonyms (Vekua, 1995), *C. etruscus* remarkably differs from the Georgian sample in both morphometrics and ratios measure (**Figure 5** and **Supplementary Tables S7–S9**). In this light, the material of *Canis* from Dmanisi cannot be ascribed to *C. etruscus*. Several of the morphometric and morphological results point out to a closer affinity of *Canis* from Dmanisi to the late Early Pleistocene *Canis* ex gr. *mosbachensis* (*C. mosbachensis*, e.g., from Untermassfeld, Sotnikova, 2001; Iberian Peninsula, Bartolini Lucenti et al., 2017; Pirro Nord, Petrucci et al., 2013; *C. mosbachensis variabilis* from Zhoukoudian localities, Jiangzuo et al., 2018; and *C. apolloniensis* from Apollonia-1, Koufos, 2018), rather than to *C. etruscus*. In addition to the affinity with these fossil taxa, *Canis* from Dmanisi shares also affinities with the group of wolf-related canids (see Lindblad-Toh et al., 2005), e.g., the caudorostrally divergent tympanic bullae; p3 alveolus at a lower level than p2–p4 (**Figures 1–3**). Indeed, the divergent walls of the bullae is shared by *C. lupus*, other wolf-related canids, and *C. mosbachensis* (see Bartolini Lucenti et al., 2017), as opposed to any other extinct species (**Figures 1–3**). Nevertheless, some other features of the sample from Dmanisi are more primitive, e.g., blunt or subrounded dorsal outline of the nuchal crest, reduced caudal elongation of the postorbital region; relatively developed crushing surface of the molars; and presence of an accessory cuspid on p3. This combined pattern of features (similar to both primitive- and derived-like canids), unlike any other early Early Pleistocene canids, supports the ascription of the sample to a new species, *C. borjgali* sp. nov.

The new identity of *Canis* from Dmanisi casts some doubts on the current interpretation of the origin of modern wolf. The wide consensus in scientific literature supports that *C. lupus* and its lineage originates during the Early Pleistocene with the primitive *C. etruscus* (Torre, 1967; Kurtén, 1968; Musil, 1972; Sotnikova, 2001; Sotnikova and Rook, 2010), from which derived *C. mosbachensis* in the second half of the Early Pleistocene to first half of the Middle Pleistocene. Despite the taxonomical debate (Mecozzi et al., 2017), *C. mosbachensis* is widely considered the ancestor of *C. lupus* (in addition to the former: Brugal and Boudadi-Maligne, 2011; Sardella et al., 2014). Sotnikova and Rook (2010) were the first to suggest a possible alternative classification for the *Canis* of Dmanisi and the plausible ancestry of *C. lupus*. Here, such an interpretation is supported, as *C. etruscus* appears more primitive than *C. borjgali* and should probably be regarded as one of the earliest taxa to disperse into Europe (around the end of the Pliocene–early Pleistocene).

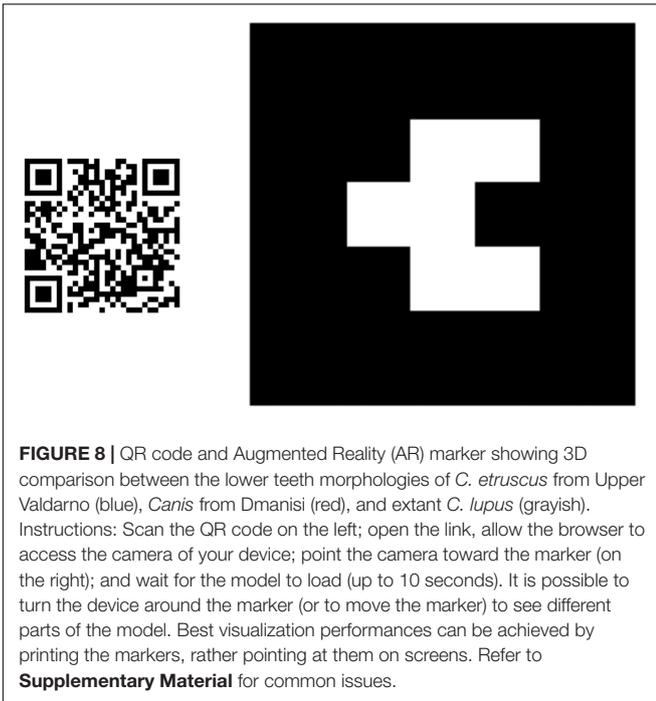
On the contrary, *C. borjgali* might represent the ancestor or, in any case, a close-allied taxon of the clade of more derived species of Eurasian Canini (e.g., *C. ex gr. mosbachensis*, *C. lupus*). The morphological and morphometrical similarity between the *C. borjgali* and *C. mosbachensis* supports the idea of close relationship between the two species. Some authors (Bartolini Lucenti et al., 2017; Jiangzuo et al., 2018) reinterpreted the idea of direct ancestry between *C. mosbachensis* and *C. lupus*, putting



**FIGURE 6** | QR code linking to the web app for Augmented Reality (AR) visualization of the 3D model of the skull D64. Instructions: Scan the QR code on the left; open the link; allow the browser to access the camera of your device; point the camera toward the marker (on the right); and wait for the model to load (up to 10 seconds). It is possible to turn the device around the marker (or to move the marker) to see different parts of the model. Best visualization performances can be achieved by printing the markers, rather pointing at them on screens. Refer to **Supplementary Material** for common issues.



**FIGURE 7** | QR code and Augmented Reality (AR) marker showing 3D comparison between the upper teeth morphologies of *C. etruscus* from Upper Valdarno (blue), *Canis* from Dmanisi (red), and extant *C. lupus* (grayish). Instructions: Scan the QR code on the left; open the link; allow the browser to access the camera of your device; point the camera toward the marker (on the right); and wait for the model to load (up to 10 seconds). It is possible to turn the device around the marker (or to move the marker) to see different parts of the model. Best visualization performances can be achieved by printing the markers, rather pointing at them on screens. Refer to **Supplementary Material** for common issues.

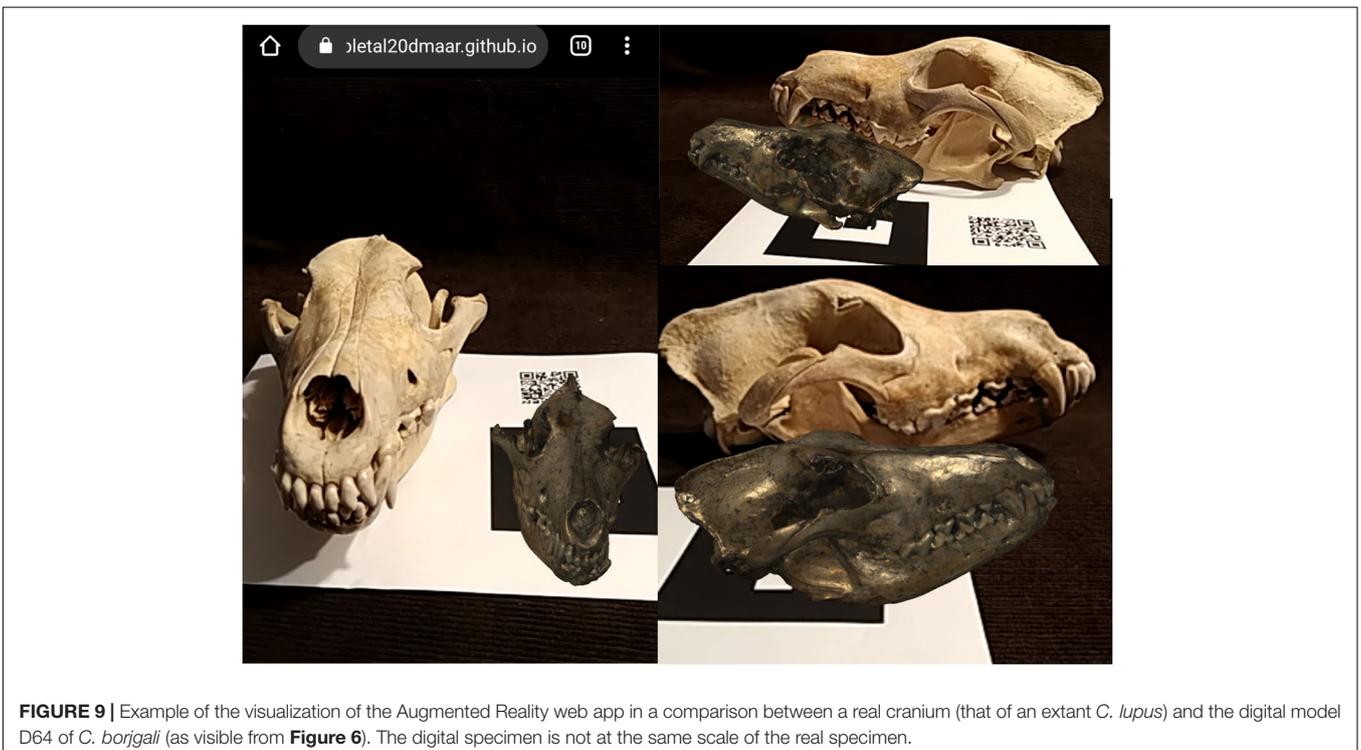


forward the idea that *C. mosbachensis*, as a large-ranged and time-spanned species, might actually be related to the crown species of the wolf clade (i.e., *C. latrans*, *C. lupaster*) rather than only to *C. lupus*. This might find support in recent molecular (e.g., Koepfli et al., 2015; Viranta et al., 2017) and paleontological

evidence (Tedford et al., 2009). Koepfli et al. (2015) estimated the time of divergence between the *C. lupaster* and the *C. latrans*–*C. lupus* clade around 1.3 Ma and between *C. latrans* and *C. lupus* around 1.1 Ma. This suggests that the Early Pleistocene was a time of high diversification in modern canids, as is also confirmed by fossil record. Tedford et al. (2009) reported the early presence of *C. lupus* in the early Middle Pleistocene deposits of Alaska. In the broader and more intricate framework of the evolutionary history of crown-Canini, the privileged geographical position of the Caucasian region reveals its importance in canids' evolutionary history, as noted by Sotnikova and Rook (2010). Indeed, the Caucasus sets as a crossroads between three continents, and its peculiar biotic evolution testifies to its role of key region in evolution of Old World faunas since Miocene times (Krijgsman et al., 2019). The discovery of a previously undescribed taxon in Dmanisi, with some modern features as opposed to *C. etruscus*, close but more primitive compared to *C. mosbachensis*, changes radically the idea of *C. lupus* evolution as it is conveyed today, invalidating the paradigm *C. etruscus*–*C. mosbachensis*–*C. lupus* lineage. As probable ancestor of *C. ex gr. mosbachensis*, *C. borjgali* sp. nov. might also represent one of the latest common ancestors of the crown clade of modern *Canis* species (*C. latrans*, *C. lupaster*, *C. lupus*).

## Augmented Reality: Opportunities and Perspectives

The exquisite conservation of the fossil specimens of *C. borjgali* offers the perfect subject for the application of 3D and digital imaging techniques, like Augmented Reality (AR), thanks to the use of Artec Space Spider. AR allows interacting with



computer-generated objects (*sensu lato*, from 2D pictures, videos to 3D objects) in the real world contexts in real time, allowing the users to perceive the real environment surrounding the digital rendering (Azuma, 1997; Zhou et al., 2008; Lee, 2012). Thus, differing from Virtual Reality (VR), in which users are immersed in a digital/computer-generated environment, AR can be considered a mixed-reality experience (Bower et al., 2014). It is not a brand-new technology, as its first applications date back to the 1990s. Currently, AR applications cover a diverse range of fields, from medicine to manufacturing, from aeronautics to entertainment and tourism (Bower et al., 2014). Particularly in educational sciences, AR has revealed its pedagogical potential, as much research documented (see Lee, 2012; Akçayır and Akçayır, 2017 and references therein). Nevertheless, no or little use has been made in scientific research, and its potentiality to paleontology and museology seems widely underestimated (at the very least, in Italian institutions). After the virtuous case of “Virtual Showcase” (Bimber et al., 2001, 2002), a multiuser AR display for museal exhibitions, no other use is reported in the literature. We propose here the first application of AR as support to paleontological research. Of the wide range of possible types of AR applications (see Bower et al., 2014’s review), a marker-based one was chosen (for further discussion see Kan et al., 2011) to allow remote and independent use by any interested user. The application of easy-to-use, open-source, and marker-based tools like AR.js and A-Frame allows to expand the accessibility to superb fossil specimens like D64 (Figure 6). A smartphone, a tablet, or any device with a camera and internet connection would suffice to grant access to the actual 3D morphology of the specimens and their tiniest features, such as dental cuspules/cuspidids. The same tool can be used to perform digital comparisons between different species or specimens, like in Figures 7, 8, where the upper and lower morphology of the teeth of *C. etruscus*, *C. borjgali*, and *C. lupus* can be compared as easily as would be with the three real specimens. Moreover, the use of a marker consent to even compare the 3D digital objects implemented in the app to real ones placed near the marker (for instance to a cranium of an extant canid, e.g., *C. lupus*, Figure 9), to directly see similarities and/or differences. In short, following the motto of the A-Frame team, “show, don’t tell.”

## CONCLUSION AND PERSPECTIVES

The extensive record of *Canis* from Dmanisi is outstanding both for its state of preservation and abundance. Several morphological and morphometric patterns challenge the previous attribution to *C. etruscus* and favor the ascription of the taxon to a new species, *C. borjgali* sp. nov. The record of Dmanisi has already changed our understanding of evolutionary history of different species, like in the case of the rhino “*Stephanorhinus*” (Cappellini et al., 2019) or of the genus *Homo* (Rightmire et al., 2019 and reference therein) as the first discovery of the earliest Out-of-Africa hominids. The description of *C. borjgali* sp. nov. offers a new picture of the evolutionary history of modern wolves and wolf-like canids. Instead of considering the rather

primitive species *C. etruscus* as the ancestor of *C. lupus*, the similarity between *C. borjgali* and *C. mosbachensis* suggests to acknowledge in the species from Dmanisi the ancestor of modern wolf-related canids. Furthermore, the present research reports the first application of Augmented Reality to a scientific paper in paleontology. Although especially used with pedagogical and educational purposes, scientific articles might benefit from the employment of AR contents thanks to its high interactivity and attractivity. Digital visualizations could be used to convey and communicate more easily the discoveries of a research, especially in life and physical sciences. In paleontology, the use of AR of digitalized fossil specimens in scientific articles might allow to increase the accessibility to superb fossils like D64 (Figure 6) without compromising the right and ownerships of institutions (museums or research ones) on these specimens. Undoubtedly, any 3D object, resulting from any different source (laser scan, CT scans, etc.), can be used. The implementation of web-based AR is valuable to other researchers, as it allows them to operate their observations of the 3D model better and more precisely than using 2D photos or even stereophotography. Relative height of cusps and cuspidids, development of the crests, and depth of depressions are all features that become directly observable and other workers might make their own opinion and verify the finding of the paper. Digital comparisons between different species (Figures 7, 8) and comparisons with real specimens placed near the marker (Figure 9). All of this can be achieved simply using a mobile device (smartphones, tablets, etc.). Digital technologies dealing with AR are constantly advancing while its potentials are already high; we just need to keep the pace.

## DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in the ZooBank (urn:lsid:zoobank.org:pub:93965532-1069-44E1-9430-DCC5706EA312).

## AUTHOR CONTRIBUTIONS

SB has studied the material together with the support of BM-N, MB, and DL. SB and MB digitalized the fossil specimens. SB designed the paper and wrote the manuscript with contributions from BM-N. DL and MB critically reviewed several parts and improved the first draft.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/feart.2020.00131/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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