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This is the author's manuscript

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/151531> since 2015-12-06T13:52:53Z

Published version:

DOI:10.1016/j.quascirev.2014.10.004

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UNIVERSITÀ DEGLI STUDI DI TORINO

This is an author version of the contribution published on:

Questa è la versione dell'autore dell'opera:

H.-A. Blain; J. Agusti; L. Rook; D. Lordkipanidze; M. Delfino, 2014.
Paleoclimatic and paleoenvironmental context of the Early Pleistocene hominins from Dmanisi
(Georgia, Lesser Caucasus) inferred from the herpetofaunal assemblage.

QUATERNARY SCIENCE REVIEWS, 105: 136-150

DOI: 10.1016/j.quascirev.2014.10.004

The definitive version is available at:

La versione definitiva è disponibile alla URL:

<http://www.sciencedirect.com/science/article/pii/S0277379114003916>

Paleoclimatic and paleoenvironmental context of the Early Pleistocene hominins from Dmanisi (Georgia, Lesser Caucasus) inferred from the herpetofaunal assemblage

Hugues-Alexandre Blain^{a,b}, Jordi Agustí^{a,b,c}, David Lordkipanidze^d, Lorenzo Rook^e, Massimo Delfino^{f,g,*}

^a IPHES, Institut Català de Paleoecologia Humana i Evolució Social, c/ Marcel·lí Domingo s/n (Edifici W3), Campus Sescelades, 43007 Tarragona, Spain

^b Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain

^c ICREA, Institut Català de Recerca i Estudi Avançat (ICREA), Barcelona, Spain

^d Georgian National Museum, 3, Rustaveli Avenue 0105 Tbilisi, Georgia

^e Dipartimento di Scienze della Terra, Università di Firenze, via G. La Pira 4, 50121 Firenze, Italy

^f Dipartimento di Scienze della Terra, Università di Torino, via Valperga Caluso 35, 10125 Torino, Italy

^g Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici Z (ICTA-ICP), Carrer de les Columnes s/n, Campus de la UAB s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain

*Corresponding author: E-mail address: massimo.delfino@unito.it

Dipartimento di Scienze della Terra

Università di Torino

via Valperga Caluso 35, 10125 Torino, Italy

phone: ++ 39 011 0915386

ABSTRACT

Dmanisi is currently the oldest Early Palaeolithic site discovered out of Africa. It has produced over 40 hominin remains, including a set of very informative skulls, in direct association with faunal remains and numerous lithic artifacts. Given the relevance of this locality, every effort is being made to reconstruct the landscapes where these hominins once lived. Amphibian and reptile remains from Dmanisi are here described for the first time and used as paleoclimatic and paleoenvironmental proxies. They comprise at least six taxa: a green toad (*Bufo* gr. *B. viridis*), the Greek tortoise (*Testudo graeca*), a green lizard (*Lacerta* gr. *L. viridis*), a four-lined snake (*Elaphe* gr. *E. quatuorlineata*), an indeterminate colubrid and a water snake (*Natrix* sp.). As these taxa are not extinct and their ecology can be directly studied, they can contribute to the reconstruction of the landscape and climate. The application of the Mutual Climatic Range method provides quantitative data indicating that during the hominin presence at Dmanisi climate was warm and dry, similar to the present-day Mediterranean climate. In comparison with today climate of Dmanisi, estimated mean annual temperature was 3.1°C higher, with a greater increase of temperature in summer (+7.1°C) than in winter (+4.7°C). The mean annual precipitation was slightly lower (-65 mm) than the current level, with precipitation higher than current one during winter (+104 mm) but strongly lower during the other seasons, suggesting a stronger contrast in the rainfall regime during the year. From a paleoenvironmental point of view, fossil amphibians and reptiles all suggest the predominance of arid environments, from steppe or semi-desert to open Mediterranean forest, with stony or rocky substrate and bushy areas. The presence of permanent aquatic environments is also documented. These results mainly agree with those for large mammals, small mammals and the archaeobotanical analysis that indicate an important water stress suggesting a period of increased aridity contemporaneous with human occupations of the site.

Keywords: Dmanisi; early *Homo*; Early Pleistocene; herpetofauna; paleoclimate; paleoenvironment

1. Introduction

Dmanisi (44° 21'E, 41° 19'N) is located at an elevation of 1015 m in the Masavera River valley (South East Georgia), in the Lesser Caucasus, 85 km southwest of Tbilisi (Fig. 1A). The archaeological site is situated on a promontory at the confluence of the Masavera and Pinezauri rivers, whose valleys were eroded into the local Cretaceous volcanoclastic and marine rocks, which form the hills surrounding the site. Early Pleistocene basaltic eruptions west of Dmanisi resulted in a flood of lavas down the Masavera Valley, which filled the valley, covered the lower part of the promontory, and spilled for a short distance up the Pinezauri Valley, creating a dam of that stream. The lavas cooled to form the Masavera Basalt, dated by $^{40}\text{Ar}/^{39}\text{Ar}$ to 1.85 ± 0.01 Ma (Maisuradze et al., 1989; Schmincke and van den Bogaard, 1995; Gabunia et al., 2000c); this basalt is conformably overlain by the hominin and artifact bearing Plio-Pleistocene volcanoclastic and colluvial deposits at the site.

The Dmanisi sequence is divided into two major stratigraphic units: A and B (Gabunia et al., 2000c; Fig. 1B). Stratum A is composed of different layers of ashfalls. The lowest layer (A1) consists of black sandy ashes. The upper A layers (A2-A4) are characterized by weak pedogenic features. Stratum B deposits include ashfalls, as well as a complex of deposits that filled pipes and gullies that had formed along collapsed pipes (Lordkipanidze et al., 2007). Rapid burial by low energy eolian and slope processes led to the superb stratification and preservation of bones in the pipe-gully facies of Stratum B1, which contain all of the hominin remains recovered thus far in the excavations in Blocks 1 and 2.

The geochronology of the Dmanisi deposits has been established by absolute dating, paleomagnetic analyses and biostratigraphic correlations. The Masavera Basalt and all of Stratum A deposits yield normal geomagnetic polarity, and are dated to 1.85-1.77 Ma, corresponding to the end of the Olduvai subchron. The 1.81 Ma $^{40}\text{Ar}/^{39}\text{Ar}$ age on Stratum A1a ashes (Lumley et al., 2002) is consistent with this dating interpretation. All of the Stratum B deposits at Dmanisi show reversed geomagnetic polarity, and

correspond to the Upper Matuyama Chron. The minor disconformity at the A-B contact, as well as microfaunal assemblages indicate that these deposits and the associated archaeological, hominin and megafaunal remains contained within these levels accumulated very quickly after the Olduvai-Matuyama reversal (Lordkipanidze et al., 2007). This interpretation is supported by the 1.76 Ma $^{40}\text{Ar}/^{39}\text{Ar}$ age on the Orozmani Basalt, which overlies the Dmanisi sediments at a locality west of the site (Gabunia et al., 2000c).

The archaeological deposits at Dmanisi have yielded large amounts of lithic and faunal remains associated with sediments from Stratum B. Their provenience suggests that they accumulated during the beginning of the Upper Matuyama Chron (Gabunia et al., 2000c, 2002; Rightmire et al., 2006; Lordkipanidze et al., 2007). Electron spin resonance (ESR) dating of dental remains confirms this geochronologic hypothesis in the Early Pleistocene (Garcia, 2004; Garcia et al., 2010). The first hominin specimen was discovered in 1991 and since then, over 40 hominin remains have been recovered, including teeth (Martínón-Torres et al., 2008), mandibles (Gabunia et al., 2000c, 2002), complete skulls (Rightmire et al., 2006; Lordkipanidze et al., 2013) and postcranial elements (Lordkipanidze et al., 2007). These hominin remains are in direct association with faunal remains (large and small vertebrates) and numerous lithic artifacts (Gabunia et al., 2000a,c, 2002; Lordkipanidze et al., 2007; Agustí and Lordkipanidze, 2011).

The presence of fossil herpetofaunal remains in the Early Pleistocene site of Dmanisi was first mentioned by A. Vekua (Chkhikvadze in Vekua, 1995) with a dentary of *Lacerta* sp. and a fragment of plastron of *Testudo* sp. (figured in Table 7, n°1 in Vekua, 1995), and probably pertaining to *Testudo graeca* (p. 78 in Vekua, 1995; Gabunia and Vekua, 1995; Gabunia et al., 1999). The following taxa were previously reported: *T. graeca*, *Lacerta* sp., *Eryx* sp., *Boiga* cf. *trigonata*, *Coluber najadum*, *Coluber robertmertensi* (now put in synonymy with *Hierophis viridiflavus*), *Elaphe* aff. *dione*, *Natrix* sp., *Pelias* sp. and *Daboia* cf. *raddei* (now *Montivipera raddei*) (Chkhikvadze and Kharabadze, 1995; Gabunia et al., 1998, 2000a,b). All these fossils (except the plastron of *T. graeca* figured in Vekua, 1995) were never described or figured, making it impossible to revise their taxonomic identifications. The fossils studied here come from the 1991

to 2009 excavations at Dmanisi. Part of these materials has been previously presented in an unpublished report (Delfino, 2003) and in the supplementary information of Lordkipanidze et al. (2007). The aim of the present publication is therefore to describe these fossil remains and, on the basis of the identified taxa, to infer new paleoclimatic and paleoenvironmental parameters for the period when the hominids were present in Dmanisi at ca. 1.8 Ma ago.

2. Material and methods

2.1. Systematic study

Amphibians and reptiles come from the level B1 of the two different sectors of Dmanisi excavations (Block 1 excavated from 1991 to 1999 and Block 2 from 2000 to 2009). Besides tortoise shells recovered directly from the excavation, the small-vertebrate fossil remains used for this study consist of disarticulated bone fragments collected by water-screening each year during the archaeological campaigns at Dmanisi. All the sediment was water-screened using superimposed 10,5 and 0.5 mm mesh screens and processed, sorted and classed in large categories directly in the site.

This assemblage includes a total of 118 elements, representing at least 6 taxa, including toads, tortoises, lacertids, and snakes (Table 1).

Taxonomic identifications were based on Sanchíz (1977), Bailon (1999) for anurans; Amiranashvili (2000) and Hervet (2000) for tortoises; Arnold (1973, 1989), Barbadillo and Sanz (1983), Barahona and Barbadillo (1997) and Arnold et al. (2007) for lizards; and Venczel and Sen (1994) and Szyndlar (1984, 1991a, 1991b) for snakes. Comparisons were drawn using the dry skeleton collections of Dipartimento di Scienze della Terra dell'Università di Torino (Massimo Delfino Herpetological Collection - MDHC), Museo Nacional de Ciencias Naturales (Madrid, Spain), Museum national d'Histoire naturelle de Paris (France), and Naturhistorisches Museums Wien (Austria).

Anatomical nomenclature follows Sanchíz (1998) for anurans, Zangerl (1969) for turtles, Rauscher (1992) for lizards, and Szyndlar (1984) for snakes.

2.2. Climatic and environmental reconstructions

Because amphibians and squamate reptiles are ectothermic vertebrates, the temperature and precipitation in their immediate environment mark their distribution. Numerous studies (e.g. Currie, 1991) evidence a strong relationship between amphibians and squamates and their environment. Like vegetation, their distribution and species richness on continental landmasses is more closely linked with climatic parameters such as the annual potential evapotranspiration, solar radiation and mean annual temperature than is the case with any other group of vertebrates. Moreover, with the exception of few taxa that are relicts of older groups now extinct (as the allocaudates that went globally extinct in the Early Pleistocene; Delfino and Sala, 2007), most of the species present in Pleistocene localities are still living (Rage and Roček, 2003; Rage, 2013; Roček, 2013), so uncertainty with respect to the paleoecological and/or paleoclimatic requirements of extinct taxa may be ruled out. All these characteristics make them sensitive, and therefore precise, indicators of past climatic conditions.

The Mutual Climatic Range (MCR) method was used to quantify paleotemperature and paleoprecipitation based on the presence of amphibian and reptile species (see Blain et al., 2009). We simply identified the geographic region (divided into 100 x 100 km squares in the Universal Transverse Mercator (UTM) coordinate system) where all the species represented as fossil in the locality currently live. Careful attention was paid so that real current distribution corresponds to potential ecological/climatic distribution, and was not strongly affected by other limiting or perturbing parameters, such as urbanization, landscape anthropization, predation, competition with other species, etc.

Analysis of the MCR was based on distribution atlases by Sindaco and Jeremčenko (2008), Sindaco et al. (2013), Gasc et al. (1997) and Kuzmin (1999). Climatic parameters (mean annual temperature [MAT] and mean annual precipitation [MAP]) were estimated for each 100 x 100 km UTM square, using the

corresponding climatic maps (Sensoy et al., 2008). Seasonal temperature and precipitation were estimated using 1961-1990 maps provided by Önal and Semazzi (2009). For comparison with current climatic data, we extrapolated the climatic values (1961-1990) from Dmanisi area (ENVSEC and Zoi Environment Network, 2011; Önal and Semazzi, 2009).

3. Systematic paleontology and paleobiogeographical implications of the Dmanisi herpetofauna

Amphibia Linnaeus, 1758

Anura Fischer von Waldheim, 1813

Bufo Gray, 1825

Bufo Garsault, 1764

Bufo viridis Laurenti, 1768

Bufo gr. *B. viridis*

(Fig. 2, A-H)

Material: ilium: 2 (DM-H-01,02); femur: 1 (DM-H-03); tibiofibula: 2 (DM-H-04,05).

Description: The best-preserved ilium (DM-H-01) is 19 mm long. The tip of the pars cylindriformis is broken off and the ventral edge of the pars descendens is partly eroded. The pars cylindriformis is roughly cylindrical because it does not show any dorsal laminar expansion. The tuber superior is relatively massive and, in lateral view, its edge is approximately rounded, without any protruding cusp, but weak grooves

define an anterior area that is slightly prominent in lateral direction. There is no supracetabular fossa (just a very shallow depression). Conversely, the preacetabular fossa is deep and well delimited. Below it, a small ridge delimits a second fossa pierced by a tiny circular foramen. The pars descendens is ventrally broad. As shown by the contact surface with the ischium, the body of the ilium is slightly thinned in correspondence of the pars descendens. A second ilium (DM-H-01-02) despite being not so well preserved shows a tuber superior that bears an evident anterior tubercle. A right femur (DM-H-03), 11 mm long, does not preserve the epiphyses but is relatively stout and fully hosts a high and undivided crista femoris. The two tibiofibulae (DM-H-04,05) share the presence of an evident ridge on the lateral margin of the tibia.

Identification: The material described above is morphologically congruent with the osteological characters of *Bufo viridis* (see Sanchíz, 1977; Bailon, 1999) a species that was recently split, on a genetic basis, into several species whose osteological differences are unknown, and whose generic identity is still debated (see Speybroeck et al., 2010, and literature therein). The material is therefore referred to this group of species that likely share the following characters: ilia characterized by the pars cylindriformis devoid of dorsal crest; presence of a well-developed preacetabular fossa and an evident tuber superior that usually expresses an anterior tubercle (as in DM-H-01-02); undivided and sharp crista femoris; lateral edge of the tibiofibulae with an evident ridge.

Present and past distribution: Green toads (*Bufo* gr. *B. viridis*) range in Central Europe, Central Asia, Arabia and the northernmost part of Africa. In Russia, the northern limit of its distribution area is comprised between the parallels 59°N and 55°N (Kuzmin, 1999; Stöck et al., 2006, 2008). *B. viridis* is reputed to be a typical steppe species not very sensitive to dryness, to warmth or to the cold. It was found up to an altitude of 4,500 metres. *B. viridis* has been mentioned in numerous localities of the former U.S.S.R. since the Late Pliocene (MN16) (Ratnikov, 2009), in the Pleistocene or Holocene of Devichi Skaly and in the Holocene of Talgar (Azerbaijan; in Sanchíz, 1998), in the Middle and Late Pleistocene of Azokh cave (Azykh in Sanchíz,

1998; Blain, in press), in the Pliocene of Çalta (Turkey; Rage and Sen, 1976), in the Middle Pleistocene of Emirkaya-2 (Turkey; Venczel and Sen, 1994) and in the Middle to Late Pleistocene of Karain E (Turkey; S. Bailon, pers. com.).

Anura indet.

(Fig. 2, I-K)

Material: pterygoid: 1 (DM-H-06); vertebra: 1 fragment (DM-H-07); humerus: 1 (DM-H-08); metapodial: 2 (DM-H-09,10); indeterminate elements: 3 (DM-H-11-13).

Description and identification: A few remains have been referred at order level because even if they show a morphology basically congruent with that of green toad they are devoid of diagnostic characters. Noteworthy is a fragment of the distal epiphysis of a left humerus that shows a deep and asymmetrically developed fossa cubitalis ventralis (Fig. 2K).

Reptilia Laurenti, 1768

Testudines Batsch, 1788

Testudinidae Batsch, 1788

Testudo graeca Linnaeus, 1758

(Fig. 2, L-T)

Material: 1 nearly complete shell associated to 3 cervical vertebrae and fragmentary pectoral and pelvic girdles (DM-H-14); neurals: 2 (DM-H-15-16); first costal: 1 (DM-H-17); peripheral: 1 (DM-H-18); hypoplastron: 1 (DM-H-19).

Description: A nearly complete shell, associated to 3 cervical vertebrae and fragmentary pectoral and pelvic girdles, is represented by several remains, 39 of which were not joined to the main portion of the reconstructed shell (DM-H-14) (Fig. 2, L to O). The shell is 230 mm long, 195 ± 5 mm (estimated) wide and 95 ± 10 mm (estimated) tall. The carapace preserves the following elements: nuchal bone; all the neurals except the IV; metaneurals I and II; pygal; all the right costals and the left costals from V to VIII; the right peripherals from III to XII and the left ones from IX to XII. All the plastral elements are preserved, but with the exception of the xiphiplastra, they are all incomplete (among others, the epiplastral pads are not preserved). The characters of the shell can be synthesized as follows: bony elements and sutures - neural formula: 4-8-4-8-4-8-4; trapezoidal costals with alternate shape; pleuro-marginal sulcus approximately coinciding with the costo-peripheral suture; pygal rather convex in lateral view; wide angle (about 70°) delimited by the ventral edge of the peripheral XI and the suture between this element and the pygal; absence of dorsal step ("d crochement" in Hervet, 2000) along this suture; presence of hinge between the hypoplastra and the xiphiplastra; horny elements and sulci - presence of cervical scute; vertebral scutes broader than the pleural scutes in dorsal view; the humero-pectoral sulcus intersects the entoplastron very close to its posterior edge; abdomino-femoral sulcus only partly preserved but moderately convex in the lateral sector and apparently close to the hypo-xiphiplastral hinge in the medial sector.

Morphologically congruent with this shell are some remains found in different layers. The two neurals (DM-H-15-16) are apparently contiguous and could represent the couple II-III or the couple IV-V. The anterior one, 24.0 mm long and 6.8 mm thick, is octagonal (but the right lateral edge is broken off), and its external surface does not host any sulcus. The posterior one, 19.0 mm long, 25.0 mm wide and 6.0 mm thick, is rectangular and hosts a transverse sulcus.

The first right costal (DM-H-17) is complete and approximately 57.5 mm broad and 31.7 mm long (the thickness at the periphery is of 6.5 mm). Both the surfaces are covered by a thin concretion that masks the fine morphology. However, on the external surface is visible at least the sulcus between the vertebral I and costal I (probably also the sulcus between vertebral I and II). A very fragmentary right hypoplastron (DM-H-19 - 25.2 mm long, 22.9 mm wide, and up to 11.0 mm thick) is represented by its postero-lateral area that hosts an evident abdomino-femoral sulcus placed very close to the hinge with the xiphiplastron.

Identification: According to the characters reported, among others, by Amiranashvili (2000) and Hervet (2000), the morphology of all the elements described above is congruent with that of *Testudo graeca* (here considered, in agreement with Fritz and Havaš, 2007, as including all the subspecies that have been recently elevated at species level). In particular, the alternation of rectangular and octogonal neurals, the alternation of trapezoid costals, the overlapping of the pleuro-marginal sulci with the costo-peripheral suture are typical of *Testudo*, whereas the broadness of the vertebral scutes, the absence of sagittal sulcus on the pygal, the width of the medial angle of the marginals XI and the presence of hinge between the hypoplastra and xiphiplastra clearly identify the species *T. graeca*. Noteworthy is that the presence of two metaneurals is a frequent character state in this species (Hervet, 2000) and that, considering that despite being fractured and incomplete, the shell is not significantly deformed, the ratio length / height of the shell approaches that of the living subspecies *T. graeca armeniaca* that is characterised by a length that surpasses the double of the height (Chkhikvadze and Bakradze, 1991).

Present and past distribution: The Greek tortoise (*Testudo graeca*) is one of the five species of western Palaearctic tortoises (Sindaco and Jeremčenko, 2008). It inhabits North Africa, southern Europe and southwest Asia. In the former Soviet Union, it is prevalent in the Black Sea coast of the Caucasus (from Russia Anapa to Abkhazia Sukhumi to the south) as well as in Georgia, Armenia, Azerbaijan and Dagestan. Its natural habitat includes semi-arid scrub and Mediterranean forest to the verges of semi-desert. Such

habitat is subject to marked seasonal fluctuations in vegetation - with peak availability of edible plants in winter and early spring. The earliest fossil record of *T. graeca* dates back to the Late Pliocene of North Africa (de Lapparent de Broin, 2000). *Testudo* sp. has been mentioned in the Pliocene of Çalta (Turkey; Rage and Sen, 1976) and *T. graeca* in the Middle and Late Pleistocene of Karain E (Turkey; Bailon, pers. com.) and in the Late Pleistocene of Wezmeh Cave (Iran; Mashkour et al., 2009).

Lepidosauria Haeckel, 1866

Squamata Opperl, 1811

Lacertidae Bonaparte, 1831

Lacerta Linnaeus, 1758

Lacerta viridis (Laurenti, 1768)

Lacerta gr. *L. viridis*

(Fig. 3, A-S)

Material: premaxilla: 1 (DM-H-20); maxilla: 1 (DM-H-21); jugal: 2 (DM-H-22,23); quadrate: 3 (DM-H-24-26); dentary: 2 (DM-H-27,28); presacral vertebra: 5 (DM-H-29-33); scapulocoracoid: 1 (DM-H-34); humeral fragment: 1 (DM-H-35); femur: 1 (DM-H-36); femoral fragments: 3 (DM-H-37-39); tibia 1 (DM-H-40).

Description: The only available premaxilla (DM-H-20) is relatively large in size being 4.4 mm tall (Fig. 3A). It preserves only the left half approximately and therefore shows only 5 tooth positions, 4 of which host pleurodont teeth which are long, cylindrical and unicuspid. It is possible to assume that originally there were 9 tooth positions. The premaxillary process is long, narrow and uniformly rectangular.

DM-H-21 is a right maxilla, 9.7 mm long, preserved in the area from the anterior tip of the external premaxillary process (the internal is broken off) to the level of the 16 tooth (Fig. 3B-C). All the tooth positions except two still bear pleurodont teeth, which are cylindrical and, if not worn, have a very small anterior cusp followed by a much larger cusp. The external surface is covered by an irregular ornamentation that does not allow us to clearly perceive the boundaries between the scales. Between the ornate area and the crista dentalis the external surface of the maxilla shows a marked concavity and below it is aligned a series of six foramina.

A fragmentary jugal (DM-H-22) is 6.2 mm long; for preservational reasons it is not possible to evaluate the presence/absence of the step along the suture with the maxilla (see Arnold et al., 2007). The three quadrates are variably complete: the two left elements (DM-H-24,25) are rather complete and measure 5.1 and 5.0 mm (from the condyle to the dorsal tip) (Fig. 3F-H); the right quadrate (DM-H-26) is more fragmentary and slightly smaller (4.6 mm).

DM-H-27 is a 9.2 mm long, nearly complete right dentary (only the posteroventral edge of the Meckelian canal is damaged) (Fig. 3I). This element shows 20 tooth positions, 19 of which preserve teeth. These are pleurodont, nearly cylindrical, with a mono- or bicuspid apex. The anterior teeth are monocuspid (or with a nearly invisible second cusp) and anterodorsally oriented, whereas the other teeth are bicuspid (the anterior cusp is the smallest) and dorsally oriented (i.e. approximately vertical). The relatively wide Meckelian canal is entirely open in medial direction. The external surface of the dentary hosts 5 nearly aligned foramina. A second dentary (DM-H-27) is slightly larger than the first but less complete (Fig. 3J). It is represented by the section corresponding to the first 17 or 18 positions, 9 of which preserve teeth morphologically congruent with those described above, but slightly larger. This specimen is 10.2 mm long.

The five presacral vertebrae (DM-H-29-33) are characterized by being relatively large: the centrum length varies from 2.5 to 3.2 mm (Fig. 3K-M). DM-H-29 is a mid trunk, nearly complete presacral vertebra that well represents all the others. The centrum is procoelous and has an evident ventral keel. Condyle and cotyle are slightly dorsoventrally flattened. The neural canal is broad and rounded, but flattened along the

centrum. The anterior edge of the neural arch does not show any zygosphenes. The neural spine is tall and overhangs the posterior edge of the postzygapophyses. The synapophyses are evident and laterally protruding in ventral view.

The preserved elements of the girdles and the limb bones have a size that matches that of the elements described above: the incomplete right scapulocoracoid (DM-H-34) has a length of 5.5 mm; the left humeral fragment (DM-H-35), despite not being complete (both the epiphyses are damaged), is 12 mm long; a proximal femoral fragment (DM-H-35) is 7.5 mm long; a left tibia (DM-H-40) is perfectly preserved and has a length of 9.9 mm.

Identification: The material here described can be confidently referred to a lacertid lizard on the basis of the characters discussed, among others, by Arnold (1973, 1989), Barbadillo and Sanz (1983), Barahona and Barbadillo (1997), and Arnold et al. (2007). Relevant characters present on the material from Dmanisi are: the pleurodont, bicuspid dentition; the broad Meckelian canal of the dentary; the procoelous vertebrae provided with a ventral keel. Conversely the specific identification is not straightforward and has to be limited to the referral of the material to the group of the green lizards (subgenus *Lacerta*) which is, at least in part, dimensionally congruent. The comparative osteology of most of the members of the group of the green lizards, collectively represented by the most widespread species, *Lacerta viridis* (Laurenti, 1768) is poorly known. Barahona and Barbadillo (1997) partly described the osteology of *Lacerta schreiberi* Bedriaga, 1878 and *L. viridis* (that includes here *Lacerta bilineata* Daudin, 1802 because the taxonomic status of the latter is not clear, see Sindaco and Jeremčenko, 2008), but the osteology of *Lacerta agilis* Linnaeus, 1758, *Lacerta media* Lantz and Cyrén, 1920, *Lacerta pamphylica* Schmidtler, 1975, *Lacerta strigata* Eichwald, 1831 and *Lacerta trilineata* Bedriaga, 1886 is nearly unknown. However, the size of all the elements listed in this section matches that of at least some of the green lizards: the quadrates are longer than 4 mm in *Lacerta viridis* and *L. schreiberi* (Barahona and Barbadillo, 1997) but also in *L. trilineata* (personal observations); the horizontal lamina of the maxillae of these species is longer than 7 mm and that

of the dentaries longer than 8.4 mm; the centrum length of the vertebrae of *L. viridis* does not exceed 4,38 mm (Barbadillo and Sanz, 1983). In conclusion, the size itself of the remains allows to exclude their referral to *L. agilis* but all the other species cannot be excluded on a morphological basis, and the material is therefore referred simply at group level as *Lacerta* gr. *L. viridis*.

Present and past distribution: Green lizards (i.e. *Lacerta bilineata* + *Lacerta viridis*) correspond to large lizards distributed across European mid-latitudes from North Spain and Western France to the Black Sea coasts of Ukraine and Turkey. They are often seen basking on rocks or lawns, or sheltering amongst bushes. In the fossil record, attributions have been made at family level (Lacertidae indet.) in the Late Pliocene of Çalta, Turkey (Rage and Sen, 1976), in the Middle to Late Pleistocene of Karain E, Turkey (S. Bailon, pers. com.) or genus level (*Lacerta* sp.) in the Middle Pleistocene of Emirkaya-2, Turkey (Venczel and Sen, 1994). *L. viridis* is known since the Pliocene (MN16) in the Russian Platform, (Ratnikov, 2009) and, in Europe, since the Late Pliocene from Italy, Hungary, Poland, Croatia and Serbia (Holman, 1998; Delfino, 2002).

Serpentes Linnaeus 1758

Colubridae Opperl, 1811

Elaphe Fitzinger, 1833

Elaphe quatuorlineata (Bonaterre, 1790)

Elaphe gr. *E. quatuorlineata*

(Fig. 3, T-X)

Material: cervical vertebra: 1 (DM-H-41).

Description: DM-H-41 is an incomplete cervical vertebra with a centrum length estimated to have originally reached 5 mm. Even if the prezygapophyses, the paradiapophyses, most of the neural spine, and the condyle are broken off or eroded, this vertebra can be referred to the cervical region because of the comparatively large (taller than broad) and vaulted neural canal. The nearly complete hypapophysis is robust and ventrally projecting, but its posterior edge is clearly anteroventrally directed when seen in lateral view.

Identification: A massive, anteroventrally directed hypapophysis is a character typical of the species *E. quatuorlineata* and *Elaphe sauromates* (Pallas, 1814) (Venczel and Sen 1994; Szyndlar 1984, 1991a) two species so closely related that the latter was considered for a long time a subspecies of the former. It is therefore possible to refer DM-H-41 to *Elaphe* gr. *E. quatuorlineata*, a group that comprises both these species. All the other characters of the vertebra (the dorsoventrally elongate shape of the vertebra; the large neural canal, taller than wide; zygosphene convex when seen in anterior view, and slightly concave in dorsal view; posterior edge of neural arch tall and moderately convex in posterior view) match well with the cervical vertebrae of the extant comparative material of *E. quatuorlineata* at our disposal (Fig. 3Y). More precisely, the morphology of the hypapophysis matches with that of the vertebrae from 15 to 35, and with those from 25 to 35 in particular. It seems that also *Elaphe schrenckii* (Strauch, 1873), an eastern Palearctic species, has a similar morphology (Venczel and Sen 1994; Szyndlar 1984, 1991a), but its possible presence at Dmanisi was tentatively excluded on biogeographical basis.

Present and past distribution: The modern distribution range of the *Elaphe* gr. *E. quatuorlineata* (i.e. *E. quatuorlineata* + *E. sauromates*) covers from the Southern half of the Italian Peninsula to southern Russia and Ciscaucasia (eastwards to the Aral Sea), between the latitudes 49°N and 33°N. In Asia it is distributed in eastern Georgia, Armenia, Azerbaijan, the eastern part of Turkey, northwestern Iran, the extreme north-

west of Turkmenistan and western Kazakhstan (Sindaco et al., 2013). It is normally found in the arid landscapes, in steppes and semi-deserts, as well as in the forest-steppe zone (both on the plain and in the foothills), on the areas of stony and sandy semi-desert, on the slopes with bush vegetation and with rocky outcrops, on forest edges, in open steppe and tugai forests. In the Transcaucasia it goes up to 2500 m above sea level (Ananjeva et al., 2006). In the fossil record, *Elaphe* gr. *E. quatuorlineata* has been mentioned in the Middle Pleistocene of Emirkaya-2 (Turkey) (*E. cf. quatuorlineata*; Venczel and Sen, 1994) and from the Middle Pleistocene to the Holocene of Azokh Cave (Nagorno-Karabagh region) [cf. *Elaphe* sp. (probably *E. sauromates*); Blain, in press]. In Central and Eastern Europe, *E. quatuorlineata* is known since the Late Pliocene (Delfino, 2002; Venczel and Várdai, 2000; Szyndlar, 1991a).

Colubridae indet.

(Fig. 4, A-N)

Material: compound bone: 1 (DM-H-42); preloacal vertebra: 11 (DM-H-43-53).

Description: DM-H-42 is a relatively well preserved right compound bone: only the anterior extremity is partly eroded (Fig. 4A,B). The tip of the retroarticular process, despite being truncated, seems not to be broken. The total length is 13.0 mm. The medial flange is only moderately developed and slightly taller in the central portion. The supraangular foramen is relatively close to the mandibular fossa. The suprangular crest is represented by a faint ridge located at the base of the retroarticular process. Conversely, the medial surface of the medial flange bears an evident ridge.

The best-preserved vertebrae, showing the most characteristic morphologies, are briefly described below. DM-H-43-45 are three large-sized, well-preserved trunk vertebrae (centrum length is respectively: 7.2, 7.2, and 7.3 mm) found in association and morphologically so similar that they can be confidently referred to the same specimen. As shown by DM-H-45, the neural spine is long, moderately tall and probably

overhanging only posteriorly. The zygosphenes are relatively straight in dorsal view; the posterior edge is moderately depressed (not vaulted) and has nearly straight margins in posterior view. The prezygapophyseal processes can be variably developed but they are relatively massive, apically acute, and moderately long (the condition shown by the right process of DM-H-43 is related to its incompleteness; Fig. 4C-F). The exaggeratedly massive condition shown by DM-H-44, where only the left process is preserved, is here considered anomalous. In ventral view, the haemal keel is rounded anteriorly but flattens posteriorly, where it becomes slightly broader, with a moderately spatulated posterior end.

Slightly different is the partially preserved trunk vertebra DM-H-46 (Fig. 4G-J), which, even if congruent in terms of centrum length (estimated at about 7 mm) and other details, differs by the shape of the haemal keel. The latter is ventrally flattened and very thin in the anterior portion but becomes much wider posteriorly and ends with a truncated edge.

DM-H-47, having a centrum length of 3.1 mm, is a much smaller vertebra that is also morphologically different from the ones described above. In particular, the centrum is much broader than that of the previously described remains, the prezygapophyseal processes are short and pointed, and the haemal keel is uniformly very broad (Fig. 4K-N).

Identification: The development of the medial flange and the relative position of the supraangular foramen exclude the referral of the compound bone DM-H-42 to any natricine, elapid or viperid species, suggesting its referral to an undetermined colubrine. The moderate development of the medial flange excludes also the genus *Malpolon* Fitzinger, 1826. The marked ridge on the medial surface of the medial flange, not present in the compound bone of *E. quatuorlineata*, the only colubrine identified at Dmanisi, could suggest the presence of a member of the group *Coluber* s.l.

The trunk vertebrae DM-H-43-53, all devoid of hypapophysis and sharing a centrum length that exceeds the centrum width, clearly represent more than one taxon that is not possible to identify on the basis of the

available material. Therefore, they have been collectively referred to the working taxon Colubrines indet. (sensu Szyndlar, 1991a).

Natrix Laurenti, 1768

Natrix sp.

(Fig. 4, O-R)

Material: precloacal vertebra: 1 (DM-H-54).

Description: The precloacal vertebra DM-H-54 is nearly complete, but the neural spine, the right zygosphenial facet, the prezygapophyses, the right paradiapophyses, and the cotylar rim are broken off or eroded. The centrum length corresponds to about 3.6 mm (estimated because of the incompleteness of the cotylar rim). The zygosphene, now incomplete, was medially convex in dorsal view; the posterior edge is only moderately vaulted and with slightly convex edges in posterior view. The neural canal is slightly smaller than the cotyle but about as large as the condyle. The prezygapophyseal facets are approximately horizontal in anterior view. The dia- and parapophysis are clearly separated, and the parapophyseal process is anteriorly directed (also slightly ventrally) and vaguely pointed. The hypapophysis is very well developed and characterized by a sigmoid anterior edge and a relatively rounded tip.

Identification: According to Szyndlar (1984, 1991b), the morphological features described above unequivocally characterize the members of the genus *Natrix*, and they should discriminate among the three western Palearctic species of this genus, the shape of the tip of the parapophyseal processes and of the hypapophysis in particular. However, the direct comparison of DM-H-54 with extant comparative material

of *Natrix maura* (Linnaeus, 1758), *Natrix natrix* (Linnaeus, 1758), and *Natrix tessellata* (Laurenti, 1768) did not allow us to confidently identify it at species level.

Present and past distribution: Common Water Snakes (genus *Natrix*) have a large range in the Palearctic, from north-eastern Africa and Western Europe (southern Britain included) to western China and northern Mongolia and southwards to the Persian Gulf, Afghanistan, western Pakistan and north-western India (Ananjeva et al., 2006; Sindaco et al., 2013). In the fossil record, the genus is present since the Oligocene of France and Germany (MP 22; Rage, 1988, 2006, 2013; Szyndlar, 1994, 2012). In Asia, fossils of *Natrix natrix* and *Natrix tessellata* have been identified from the Late Pliocene of Southern Russia (MN16) onwards, and in the case of *N. tessellata*, some Early Pleistocene and Holocene records are from the Northernmost parts of its current distribution (Ratnikov, 2009). *Natrix* sp. has already been mentioned in the Early Pleistocene of Dmanisi (Gabunia et al., 2000a,b citing Chkhikvadze and Kharabadze, 1995). Natricine snakes have also been mentioned as fossil in Turkey: in the Middle Pleistocene of Emirkaya-2 (*N. cf. natrix*; Venczel and Sen, 1994) and in the Middle and Late Pleistocene of Karain E (*N. tessellata* and *N. cf. natrix*; Salvador Bailon, pers. com).

Serpentes indet.

(Fig. 4, S-U)

Material: compound bone: 1 (DM-H-55); cervical vertebra: 1 (DM-H-56); precloacal vertebra: 3 (DM-H-57-59); cloacal vertebra: 1 (DM-H-60); vertebral fragment: 5 (DM-H-61-65); rib: 4 (DM-H-66-69).

Description and identification: Several elements were identified at order level because they are undiagnostic even if well preserved (as the caudal vertebrae and the ribs) or too fragmentary to be identified (as the vertebral fragments and the fragmentary compound bone).

4. Paleoenvironmental and paleoclimatic implications

The Caucasus is a mountainous region located south of the East European plain, between the Black Sea in the west and the Caspian Sea in the east. Three entities can be recognized within the Caucasus: the Caucasus Foreland, the Greater Caucasus and Transcaucasia. South to the Rioni-Kura depression, stretching between the Black and the Caspian Seas, Transcaucasia, which is of interest here, includes the mountains of the Lesser Caucasus, the Armenian-Dzhavakhetian volcanic plateau extending beyond the borders of the former Soviet Union into Turkey and Iran. Each of the Caucasian provinces has a distinct character formed under the influence of the neighboring territories. The northern foothills of the Greater Caucasus have much in common with the steppes of the East European plain; environments of the Black Sea region are affected by the climate of the Mediterranean Sea; whereas in the eastern Caucasus and Transcaucasia the influence of Asia Minor climate is apparent (Volodicheva, 2002).

Almost every climatic zone is represented in the South Caucasus except for savannas and tropical forests (Volodicheva, 2002). To the North, the Great Caucasus range protects the region from the direct penetration of cold air. The circulation of these air masses has mainly determined the precipitation regime all over the region. Precipitation decreases from West to East and mountains generally receive higher amounts than low-lying areas. The absolute maximum MAP is 4,100 mm in southwest Georgia (Adjara), whilst MAP in southern Georgia, Armenia and western Azerbaijan varies between 300 and 800 mm per year. Temperature generally decreases as elevation rises. The highlands of the Lesser Caucasus Mountains in Armenia, Azerbaijan and Georgia are marked by sharp temperature contrasts between summer and winter months due to a more continental climate. The MAT at the Black Sea shore is 14-15°C, whereas in the plains of East Georgia MAT varies from 11 to 13°C (ENVSEC and Zoi Environment Network, 2011; Volodicheva, 2002).

Within this context, the Dmanisi region is located in the South Mountains of Georgia, which are part of Transcaucasia. Its territory is rising from east (820 m) to west (1900 m). Climate is mainly moderate-moist with cold winter (with 2 to 4 months with snow) and long warm summer. MAP are comprised between 650 and 1080 mm. Globally Dmanisi area receives today less precipitation than the Colchis region of western Georgia where the proximity of the Black Sea supports the present-day subtropical forests (Nakhutsrishvili, 1999; Denk et al., 2001; Volodicheva, 2002). The present vegetation cover around the site is composed of different formations depending on altitudinal gradients. On hilltops, forests of *Fagus orientalis* can sometime appear in humid conditions, but the prevailing ecosystems at the altitude of Dmanisi (1000 m a.s.l.) consist of oak (*Quercus iberica*) and oak-hornbeam (*Quercus iberica*, *Carpinus caucasica* and *Carpinus orientalis*) forests (Messenger et al., 2010a,b).

4.1. Local environment inferred from the fossil amphibians and reptiles

The paleoherpetofaunal assemblage from the Early Pleistocene of Dmanisi is relatively poor in terms of both taxa (6 taxa only) and individuals (some 11 individuals; Table 1) and does not permit a quantitative study for the reconstruction of the landscape. Nevertheless, the identified taxa may provide some paleoenvironmental indications. Most of the amphibians and reptiles recovered as fossil from Dmanisi suggest arid environments, from steppe or semi-desert to open Mediterranean forest (Kuzmin, 1999; Sindaco and Jeremčenko, 2008; Sindaco et al., 2013). Within the whole assemblage, only the water snake (genus *Natrix*) suggests the presence of permanent aquatic environments (rivers or lakes).

4.2. Climate inferred from the fossil amphibians and reptiles

Past climatic parameters were obtained by applying the MCR method (Blain et al., 2009) to the fossil herpetological assemblages (Table 2). The overlap of amphibians and reptiles represented as fossils in Dmanisi gives a total of 71 UTM squares occurring over Turkey, the Balkan Peninsula, Zagros mountains and the seashore of the Caspian Sea (Fig. 5A). In addition, two isolated squares occur: one on the northern shore of the Black Sea (Russia) and the other one centered over Israel. The estimated mean annual temperature MAT is $13.1 \pm 2.4^\circ\text{C}$, and the mean annual precipitation MAP is 635 ± 191 mm. The climate is of Mediterranean type, with a high atmospheric temperature range. The summer is hot and the winter is somewhat cold, with winter temperature of about 2.7°C . Rainfalls are scarce and their distribution is strongly irregular, with a particularly dry summer (Fig. 5B). In comparison with current climatic data (1961-1990 period) from the Dmanisi area, the MCR estimated MAT is 3.1°C higher, out of the range of the standard deviation, with a greater increase of temperature in summer ($+7.1^\circ\text{C}$) than in winter ($+4.7^\circ\text{C}$). The MAP is slightly lower (-65 mm) than the current level, with precipitations higher than current ones during winter (+104 mm) but strongly lower during the other seasons, suggesting a stronger contrast in the rainfall regime during the year (Fig. 5B).

5. Discussion and comparisons

5.1. Comparisons with other paleoclimatic and paleoenvironmental proxies from Dmanisi

At the beginning of the Early Pleistocene, Transcaucasia was a geographic outpost of Asia Minor. To the west and east it was flanked by the Black and Caspian Seas. The Caucasian range lay to the south where the waters of the Manich Strait washed the northern mountains. The Kura Strait, transformed by the Apsheron Basin at the beginning of the Pleistocene, occupied large parts of East Georgia and created a landscape of mountain masses dissected by deep valleys and ravines. Dmanisi at this time was situated about 60 km south-west of the Caspian Sea. Paleoenvironmental data indicate a semi-dry and warm

climate during this time, one similar to the present-day Mediterranean climate, with many rivers and lakes and rich animal and vegetable resources (Gabunia et al., 2000c; Agustí and Lordipaniidze, 2011; Messenger et al., 2010a,b). Because many sources of information are now available for the period of the hominin occupation at Dmanisi, it is possible to compare and discuss the results coming from the palaeoherpetofaunistic analysis with the other proxies like phytoliths, fruits and pollen, large and small mammals.

Archaeobotanical records (pollen, phytoliths and fossil fruits) indicate an environment in which grasses were well-represented, thus suggesting that the Dmanisi hominins occupied a relatively open environment of steppe forest, characterized by a temperate and dry climate (Messenger et al., 2011). Palynological analysis undertaken on the Dmanisi sediments (Kvavadze and Vekua, 1993; Messenger, 2006) indicates that the pollen spectra from stratum B sediments suggest the presence of a steppe-forest, dominated by grasses (Poaceae) with steppic elements. Palynological evidence for forested ecosystems show that these were present in the regional environment (Kvavadze and Vekua, 1993; Messenger, 2006), but the predominance of Poaceae indicates open, grassy environments. Phytoliths are very abundant in the overall stratigraphy of the Dmanisi deposits (Messenger et al., 2010a). Grasses (Poaceae) are the dominant taxon. Pooideae and Panicoideae appear to be the best represented subfamilies in the assemblages. Phytolith assemblages recovered in stratum B are evidence of the local herbaceous ecosystem. The climatically important water stress indices derived from the phytolith assemblages of Dmanisi suggest a period of increased aridity contemporaneous with human occupations of the site (Messenger et al., 2010a). Finally fossil fruit analyses at Dmanisi showed that almost all carpological remains recovered in the stratum B sediments belong to xerophilous taxa, which are adapted to open and dry environments (Messenger et al., 2008).

All paleobotanical results are consistent with the water stress index derived from the phytolith data (e.g. bulliform phytolith from Poaceae) that indicate the presence of rather dry conditions and local open vegetation (Messenger et al., 2010a,b). Most of the plants identified have a short biological cycle, annual or biannual, which confirms their pioneer behavior in sunny conditions. This kind of vegetation show clear

affinities with a pioneer and xeric meadow and is characteristic of ecological disturbance due to climatic and edaphic shifts (Messenger et al., 2010b).

In terms of small mammals, these are made up of 40% of gerbils (*Parameriones* aff. *obeidiensis*) and nearly 30% of migratory hamsters of the genus *Cricetulus*. These are typical rodents adapted to warm arid areas that populate today the desert areas from northern Africa to the Asian steppes. The other small-mammals are comprised of species of European affinity such as the water rats *Mimomys tornensis* and *Mimomys pliocaenicus* and the wild mouse *Apodemus atavus* (Muschelišvili, 1995; Gabunia et al., 2000a; Lordkipanidze et al., 2007; Agustí and Lordkipanidze, 2011) and the shrew *Beremendia fissidens* (Furió et al., 2010) suggesting aquatic environments and some riverine wooded areas.

On contrary, beside the presence of *Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Equus stenorhinus*, *Ursus etruscus*, *Megantereon cultridens*, *Pachycrocuta perrieri* and dry-adapted bovids such as diverse Antilopini, *Gallogoral sickenbergii*, *Soergelia* cf. *minor* and *Capra* sp., the Dmanisi large mammal assemblage is composed by more than 80% of deers (*Pseudodama* cf. *nestii*, *Cervus abesalomi*, *Eucladoceros* aff. *ctenoides*), pointing out large extension of forested areas (Gabunia et al., 2000a; Lordkipanidze et al., 2007). It is believed that the richness of the cervid fauna partially reflects the vertical zonation of the nearby forested mountainous areas. And consequently Dmanisi has been interpreted as located in a mixed mosaic environment of open landscapes, gallery forests along the river valleys and forested mountains (Gabunia et al., 2000a; Lordkipanidze et al., 2007).

These data agree with the results obtained from this new quantitative amphibian and reptile analysis (Table 3), which support a reconstruction of open, relatively dry environments and climate as dry and warm as those of Mediterranean type (i.e. with a period of aridity during summer months). And even if regional forest areas (suggested by the abundance of cervids in the Dmanisi assemblage) are not documented by any amphibian or reptile typical of dense forested areas, our interpretation does not exclude that forested areas may exist at a regional level (as indicated in a minor way by the presence of the four-lined snake, *Elaphe* gr. *E. quatuorlineata* currently living in open Mediterranean woodland environments). According to

all the climatic and ecological proxies (paleobotanical and paleozoological data), a reduction in precipitation took place in the Dmanisi area during the period of hominin occupation. MCR method applied to amphibians and reptiles shows that if effectively MAP was lower during the Early Pleistocene than today in the region of Dmanisi, the seasonal rainfall contrast was more pronounced with winter precipitation higher than today and summer precipitation strongly lower and cause of a period of aridity during summer months, as it occurs today in the Mediterranean climate.

5.2. Comparison with other terrestrial records at 1.8 Ma

Terrestrial paleoclimatic and paleoenvironmental records concerning the time range of Dmanisi (around 1.8 Ma) are not abundant in the literature. Most of such studies have been held in Africa (i.e. deMenocal, 1995, 2004) or in Spain in the Guadix-Baza Basin (Agusti et al., 2013). According to deMenocal (1995, 2004), marine sediment sequences demonstrate that subtropical African climate periodically oscillated between markedly wetter and drier conditions, paced by earth orbital variations, with evidence for step-like (-0.2 Ma) increases in African climate variability and aridity near 2.8 Ma, 1.7 Ma, and 1.0 Ma, coincident with the onset and intensification of high-latitude glacial cycles. The terrestrial dust records from the Arabian Sea (deMenocal, 1995, 2004), the eastern Mediterranean Sea (Larrasoña et al., 2003) and off subtropical West Africa (Tiedemann et al., 1994) suggest an increase in aridity and variability on the continent after ~1.9-1.5, which coincides with the development of a stronger Walker circulation (Trauth et al., 2009). At about the same time, there is also evidence for large deep, but fluctuating lakes occurring in East Africa (Trauth et al., 2005, 2007).

Within such high climate variability between dry and humid periods, direct comparison with other records may therefore be hampered by the lack of precise correlation between sites. In South-Eastern Spain, in the Guadix-Baza Basin, i.e. a very complete continental sequence ranging from Late Miocene to the Middle Pleistocene (Agustí, 1986; Hüsing et al., 2010), a paleontological site called Barranco de los Conejos has

recently been shown as being almost coeval with the Georgian site of Dmanisi (Agustí et al., 2013). The faunal record from Barranco de los Conejos includes a very diverse assemblage of small vertebrates (amphibians, squamates, insectivorans, rodents, lagomorphs) as well as one of the oldest evidence of the Ovibovini bovid *Praeovibos* in the Western Europe. The evidence from Barranco de los Conejos indicates that the lowermost levels in the upper Matuyama chron are characterized by a trend towards drier and, possibly, colder conditions than the preceding lower Matuyama levels. This is indicated by the evolution of the arvicolid local lineages towards developing ever-growing molars, but also from the evidence provided by the insectivorans (absence of Crocidurinae) and herpetofaunal assemblages (Agustí et al., 2009, 2010). MCR method applied to amphibians and reptiles from Barranco de los Conejos (Agustí et al., 2009) suggests mean annual temperature to be 1.3°C and mean annual precipitation 358 mm higher than present ones in southern Spain, so corresponding to a still globally warm and humid period.

Another very interesting record is the paleobotanical assemblage from Sisian (Armenia, Lesser Caucasus; Bruch and Gabrielyan, 2002). From Late Miocene onward, a trend towards cooler and drier conditions appears with increasing climatic instability in Armenia. Nevertheless, up to the Early Pleistocene, temperatures, especially winter temperatures, and precipitations were still far higher than today. In Sisian 1, located at 1400 m of altitude and with an age estimated at around 2 Ma, climatic parameters suggested that MAT were 4 to 6°C, mean temperature of the coldest month 6°C, mean temperature of warmest month 1°C and MAP 500 mm higher than current climatic data (Bruch and Gabrielyan, 2002). When compared with Dmanisi estimated parameters, MAT are consistent (+3.1°C in Dmanisi), but with a much greater increase of temperature in summer (+7.1°C) than in winter (+4.7°C), a pattern opposite to that observed in Sisian 1. Also if Sisian's MAT is strongly higher in comparison with present one, at Dmanisi MAP is slightly lower (-65 mm) than the current level, except during winter (+104 mm).

Finally, even if dealing with a more recent period, the analysis of vegetation dynamic by Joannin et al. (2010) of the late Early Pleistocene paleo-lake of Shamb in Armenia (Lesser Caucasus) is instructive. Although Caucasus vegetation was largely controlled by arid continental climate during the entire Pleistocene, in Shamb paleo-lake, the presence of *Liquidambar*, *Tsuga*, *Zelkova carpinifolia*, *Parrotia*

persica, *Pterocarya* and *Cedrus* taxa, suggests that moisture availability during the late Early Pleistocene was high enough for the development of warm and humid relict taxa, and low enough for the development of arid continental climate and mosaic-shaped vegetation pattern. Such data, according to Joannin et al. (2010), contradicts previous interpretation that Early Pleistocene temperatures and precipitations were far higher than today. However such environmental pattern can also be explained by a difference in the precipitation regime as evidenced at Dmanisi, with higher precipitations in winter and increasing aridity during summer. According to the same authors, forests developed during interglacials, and herbs during glacials, without significant mountainous forests during the interglacial to glacial transition. In such a flora dynamic, Dmanisi thus may be putted in relation with a fully interglacial period with high temperatures and well represented forest areas.

6. Conclusions

Although they are not as abundant and as diverse as in other Pleistocene localities, the fossil amphibians and reptiles from the Early Pleistocene site of Dmanisi (Georgia, Lesser Caucasus) help to understand the climatic and environmental background of the first registered hominin “out of Africa” at roughly 1.8 Ma. Fossil remains of amphibians and reptiles coming from the 1991 to 2009 excavations at Dmanisi and stored in the collections of the Georgian National Museum have been described and quantified for the first time in order to apply the Mutual Climatic Range Method and reconstruct the paleoenvironment. This has enabled us to produce a precise interpretation of the climatic and environmental conditions that were prevailing in the Early Pleistocene of Dmanisi at the time of the hominid occupation of the site. Our conclusions are as follows:

1. Fossil remains have documented the presence of a green toad (*Bufo* gr. *B. viridis*), the Greek tortoise (*Testudo graeca*), a green lizard (*Lacerta* gr. *L. viridis*), a four-lined snake (*Elaphe* gr. *E. quatuorlineata*), an indeterminate colubrid (Colubridae indet. probably *Coluber* s.l.) and a water snake (*Natrix* sp.).

2. All these taxa suggest the presence of arid environments, from steppe or semi-desert to open Mediterranean forest, with stony or rocky substrate and bushy areas and indicate a semi-dry and warm climate during the hominin occupation, similar to the present-day Mediterranean climate. Small, also temporary, water bodies could have been present.

3. The estimated mean annual temperature MAT was $13.1 \pm 2.4^{\circ}\text{C}$, and the mean annual precipitation MAP was 635 ± 191 mm. The climate was of Mediterranean type, with a high atmospheric temperature range. The summer was hot and the winter was somewhat cold, with winter temperature of about 2.7°C . Rainfalls were scarce and their distribution was strongly irregular, with a particularly dry summer. In comparison with today in the Dmanisi area, estimated MAT is 3.1°C higher, with a greater increase of temperature in summer ($+7.1^{\circ}\text{C}$) than in winter ($+4.7^{\circ}\text{C}$). The MAP is slightly lower (-65 mm) than the current level, with precipitations higher than current ones during winter ($+104$ mm) but strongly lower during the other seasons, suggesting a stronger contrast in the rainfall regime during the year.

4. These new estimated parameters are in accordance with the other climatic and ecological proxies (paleobotanical and paleontological data) that indicate an important water stress suggesting a period of increased aridity contemporaneous with human occupations of the site and support a reconstruction of open, relatively dry environments and climate as dry and warm as the Mediterranean type.

Acknowledgments

The Editor, J.S. Carrión, as well as J.-C. Rage and an anonymous reviewer improved the quality of the manuscript. The Dmanisi excavation team helped with the extraction, sieving and washing of sediments. M. Delfino was supported by a CNR-NATO Outreach Grant (221.34) and by a Synthesys Grant at Naturhistorisches Museums Wien (AT-TAF-1281). This paper is also an output of projects CGL2012-38358

and CGL2011-28681 (Spanish Ministry of Economy and Competitiveness), SGR2014-901 and SGR2014-416 GRC (Government of Catalonia), and DGSP-VI grants (Italian Ministry of Foreign Affairs - to LR).

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Figure legends

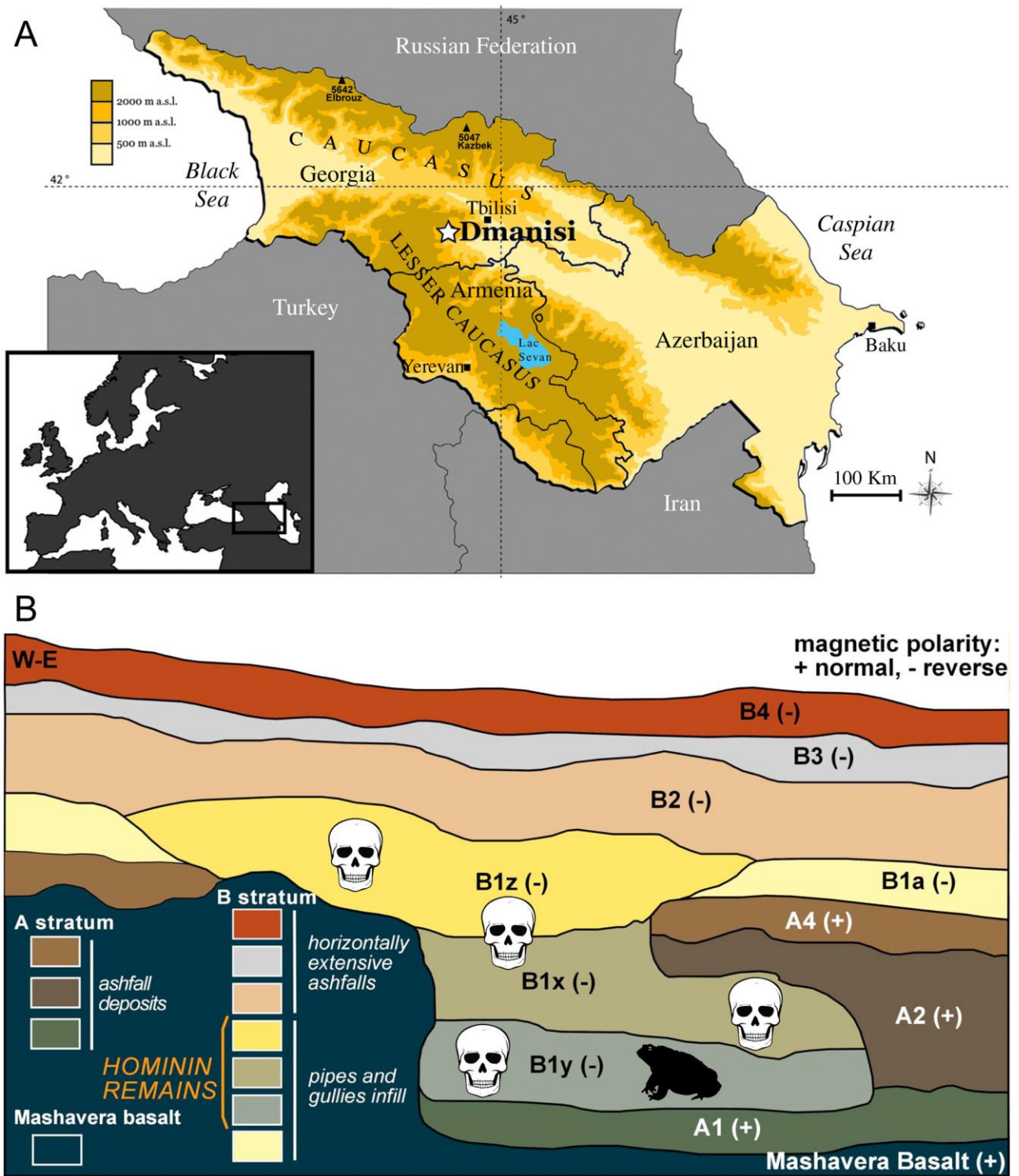


Fig. 1. A. Location of the Dmanisi site in Georgia. B. Schematic stratigraphic section of Block 2, with indication of the units where hominin remains and herpetofauna were found. Section is 10 m long, with ca. 1.8x vertical exaggeration (modified from Lordkipanidze et al., 2007).

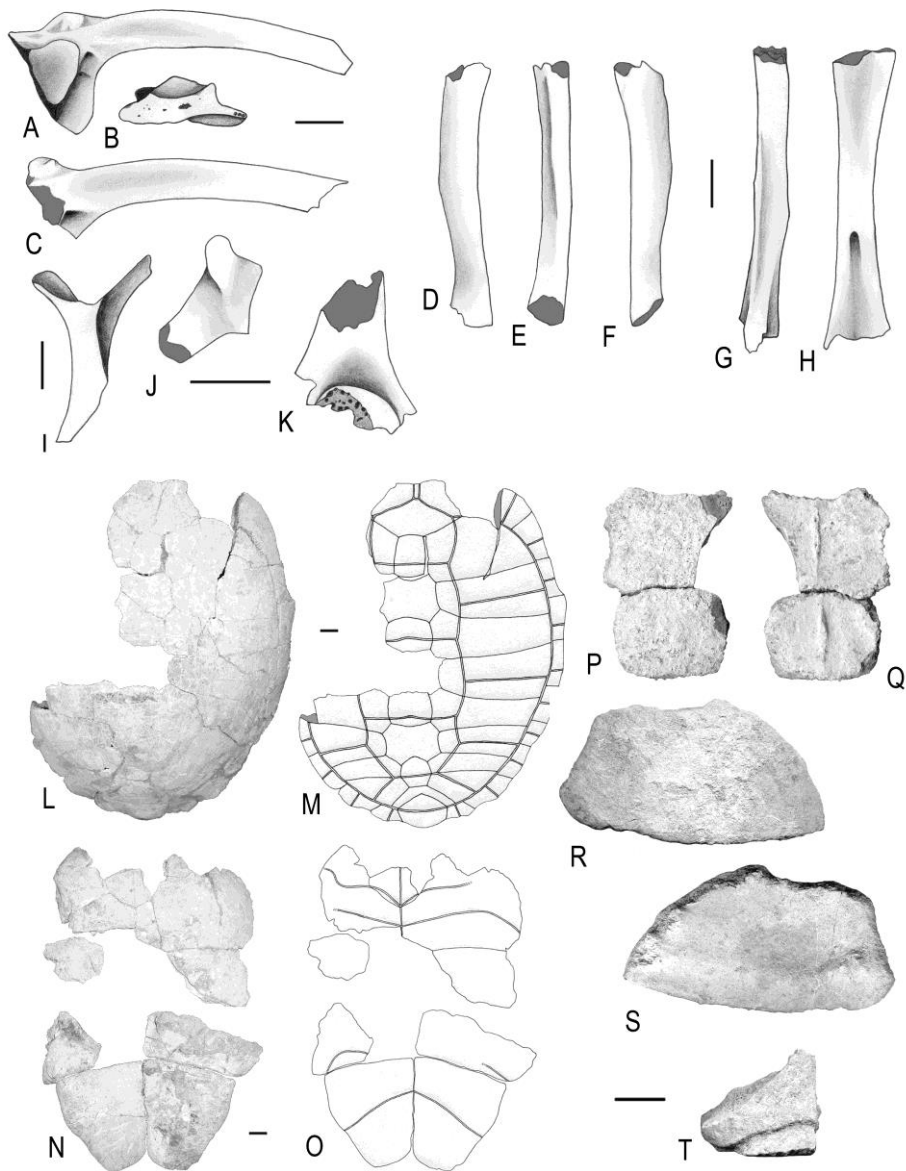


Fig. 2. Anurans and tortoises from the Early Pleistocene of Dmanisi, Georgia. *Bufo* gr. *B. viridis* - **A,B**: right ilium (DM-H-01) in lateral and posterior views; **C**: right ilium (DM-H-02) in lateral view; **D-F**: left femur (DM-H-03) in right lateral, internal and left lateral views. **G,H**: left tibiofibula (DM-H-04). Anura indet. - **I**: left pterygoid (DM-H-06); **J**: fragment of presacral vertebra (DM-H-07) in dorsal view; **K**: left humerus (DM-H-08) in ventral view. *Testudo graeca* - **L,M**: carapace (DM-H-14) in dorsal view. **N,O**: plastron (DM-H-14) in ventral view. **P,Q**: neural (DM-H-15) in dorsal and ventral views; **R,S**: first right costal (DM-H-17) in dorsal and ventral views; **T**: fragment of right hypoplastron (DM-H-19) in ventral view. Scales = 2 mm (A-K) and 10 mm (L-T).

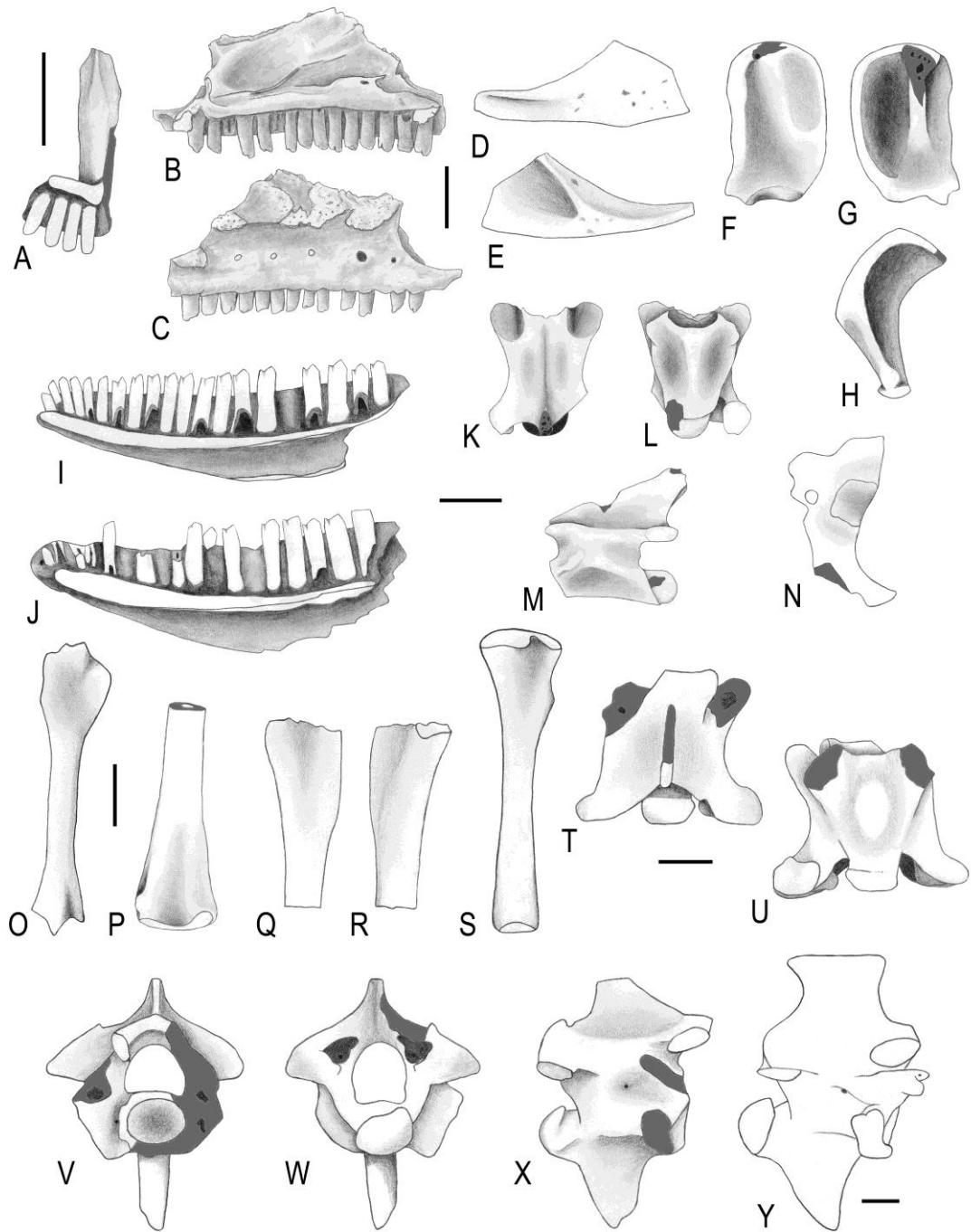


Fig. 3. Lizards and snakes from the Early Pleistocene of Dmanisi, Georgia. *Lacerta* gr. *L. viridis* - **A**: premaxilla (DM-H-20) in posteroventral view; **B,C**: maxilla (DM-H-21) in mesial and lingual views; **D,E**: left jugal (DM-H-22) in mesial and lingual views; **F,G**: left quadrate (DM-H-24) in anterior and posterior views; **H**: left quadrate (DM-H-25) in lateral view; **I,J**: right dentaries (DM-H-27 and DM-H-28) in lingual view; **K,L,M**: presacral vertebra (DM-H-29) in dorsal, ventral and left lateral views; **N**: right scapulocoracoid (DM-H-34); **O**: left humerus (DM-H-35); **P**: distal fragment of femur (DM-H-36); **Q,R**: proximal fragment of femur (DM-H-37); **S**: left tibia (DM-H-40). *Elaphe* gr. *E. quatuorlineata* - **T-X**: cervical vertebra (DM-H-41) in dorsal, ventral, anterior, posterior and right lateral views. *Elaphe quatuorlineata* (modern comparative specimen MDHC 169) - **Y**: cervical vertebra in right lateral view. Scales = 2 mm.

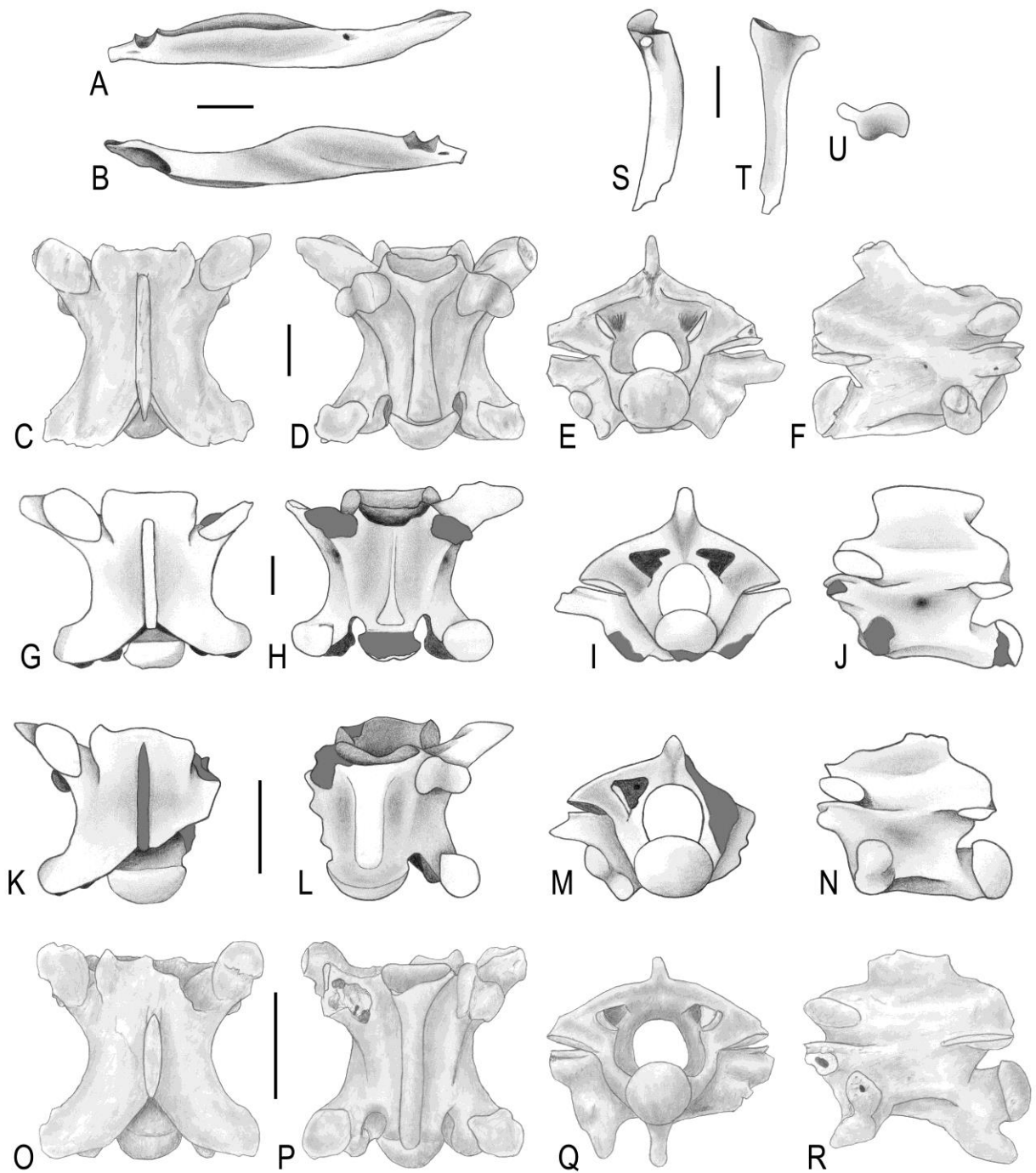


Fig. 4. Snakes from the Early Pleistocene of Dmanisi, Georgia. Colubrines indet. - **A,B:** compound bone (DM-H-42) in mesial and lingual views; **C-F:** preloacal vertebra (DM-H-43) in dorsal, ventral, posterior and left lateral views; **G-J:** preloacal vertebra (DM-H-46) in dorsal, ventral, posterior and right lateral views; **K-N:** preloacal vertebra (DM-H-47) in dorsal, ventral, posterior and left lateral views. *Natrix* sp. - **O-R:** preloacal vertebra (DM-H-47) in dorsal, ventral, posterior and left lateral views. Serpentes indet. - **S-U:** right rib (DM-H-66) in dorsal and posterior views and view of the surface of articulation. Scales = 2 mm.

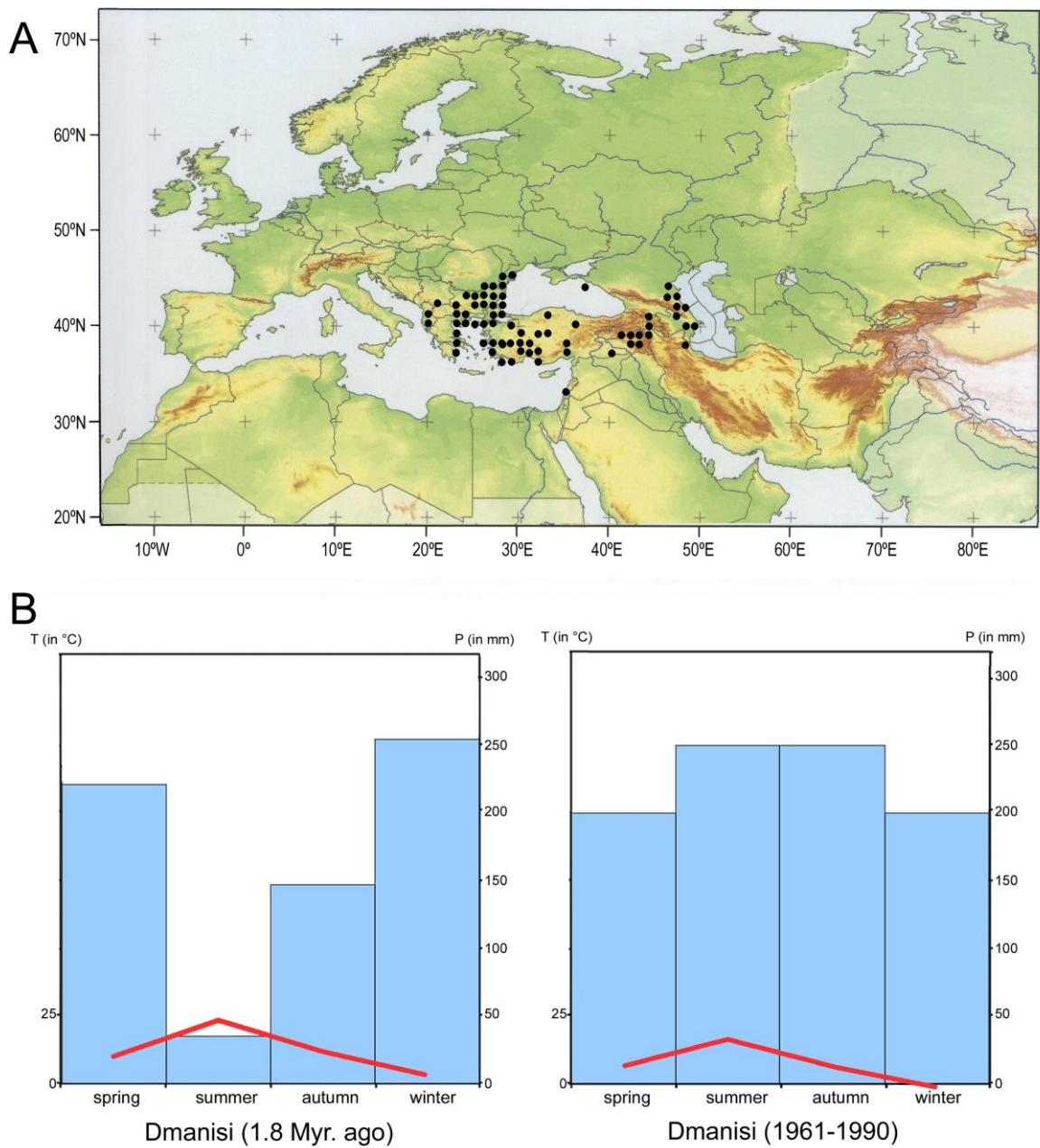


Fig. 5. A. Overlap of all the amphibian and reptile taxa represented as fossil in Dmanisi. Black points represent 100 x 100 km in an UTM grid. B. Climatograms showing on the left the reconstructed climate for Dmanisi archaeological site according to the MCR method and on the right the current climatic conditions in Dmanisi area (1961-1990, according to Önal and Semazzi, 2009). Scale as $T = 2 \times P$ permits to see directly dry periods.

	NR	MNI	%
<i>Bufo</i> gr. <i>B. viridis</i>	5	2	18.2%
Anura indet.	8		
<i>Testudo graeca</i>	55	4	36.4%
<i>Lacerta</i> gr. <i>L. viridis</i>	21	2	18.2%
<i>Elaphe</i> gr. <i>E. quatuorlineata</i>	1	1	9.1%
Colubrines indet.	12	1	9.1%
<i>Natrix</i> sp.	1	1	9.1%
Serpentes indet.	15		
TOTAL	118	11	100,0%

Table 1. Amphibians and squamates from Dmanisi in number of remains (NR) and minimum number of individuals (MNI).

	Temperature (in °C)					Precipitation (in mm)				
	MAT	winter	spring	summer	autumn	MAP	winter	spring	summer	autumn
N	71	71	71	71	71	71	71	71	71	71
MEAN	13.1	2.7	10.0	23.1	11.5	635	254	221	35	146
SD	2.4	3.8	2.8	2.7	3.0	191	119	65	53	86
MIN	8.0	-4.0	6.0	18.0	8.0	400	50	50	0	50
MAX	18.0	8.0	16.0	32.0	18.0	1200	750	350	200	350
Δ	+3.1	+4.7	+4.0	+7.1	+5.5	-65	104	-79	-215	-104
1961-1990	10.0	-2.0	6.0	16.0	6.0	700	150	300	250	250

Table 2. Climatic parameters calculated for Dmanisi by the mutual climatic range method and comparison with current (1961-1990) data (ENVSEC & Zoi Environment Network, 2011; ÖnoI and Semazzi, 2009). N = number of UTM squares, SD = standard deviation, Δ = difference between Dmanisi and current values, MAT = mean annual temperature, MAP = mean annual precipitation.

Proxy Climate Environment References

Pollen Temperate and dry Steppe forest Kvavadze and Vekua, 1993; Messenger, 2006

Phytoliths Arid Open Messenger et al., 2010a

Fossil fruits Dry Open and dry Messenger et al., 2008

Herpetofauna Warm and dry (but in winter) Open and dry, with some open woodlands and bushy areas

this work

Rodents Warm and arid Open and dry Muscheli svili, 1995; Gabunia et al., 2000a;

Lordkipanidze et al., 2007; Agustí and

Lordkipanidze, 2011

Insectivorans Aquatic environments and riverine woodland Furio et al., 2010

Large mammals Mediterranean warm and dry Mixed mosaic environment of open landscapes and large extension of forested areas

Gabunia et al., 2000a; Lordkipanidze et al., 2007

Table 3. Paleoclimatic and paleoenvironmental synthesis of the archaeological site of Dmanisi.