



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

Two new vertebrate localities from the Early Pleistocene of Mygdonia Basin (Macedonia, Greece): Preliminary results



Deux nouvelles localités de vertébrés du Pléistocène inférieur du bassin de Mygdonia (Macédoine, Grèce): résultats préliminaires

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ARTICLE INFO

Article history:

Received 23 February 2015

Accepted after revision 18 May 2015

Available online 10 July 2015

Handled by Lars van den Hoek Ostende

Keywords:

Villafranchian

Tsiotra Vryssi

Platanochori-1

Fauna

Mammals

Age

ABSTRACT

Two new vertebrate fossiliferous localities from the Pleistocene of the Mygdonia Basin (Macedonia, Greece), Tsiotra Vryssi (TSR) and Platanochori-1 (PLN), are presented in this article. TSR belongs to the Gerakarou Formation and its preliminary faunal list includes the corvid *Corvus pliocaenus*, the hyaenid *Pachycrocuta brevirostris*, the canid *Canis etruscus*, the rhinoceros *Stephanorhinus* sp., two species of *Equus*, the bovid *Bison* sp., the cervid *Metacervoceros rhenanus* and the giraffid *Palaeotragus* sp. PLN belongs to the Platanochori Formation (overlying Gerakarou Formation) and its fauna includes the following taxa: *Stephanorhinus hundsheimensis*, *Equus apolloniensis*, *Bison* sp. and *Pontoceros ambiguus*. The preliminary comparison of these faunal assemblages with the already known localities from the Mygdonia Basin and the wider region, combined with the geological data, suggest a Late Villafranchian age for TSR, chronologically intermediate between the localities Gerakarou-1 and Apollonia-1, while the fauna from PLN is indicative of a Latest Villafranchian age, similar to that of Apollonia-1. These new localities will enhance our understanding of the crucial time period of the earliest dispersal of hominins into Europe.

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RÉSUMÉ

Deux nouveaux sites fossilifères de vertébrés du Pléistocène du bassin de Mygdonia (Macédoine, Grèce), Tsiotra Vryssi (TSR) et Platanochori-1 (PLN), sont présentés dans cet article. TSR appartient à la formation de Gerakarou et la liste faunique préliminaire comprend le corvidé *C. pliocaenus*, l'hyaenid *P. brevirostris*, le canidé *C. etruscus*, le rhinocéros *Stephanorhinus* sp., deux espèces d'*Equus*, le bovidé *Bison* sp., le cervidé *M. rhenanus* et la giraffidé

Mots clés :

Villafranchien

Tsiotra Vryssi

Platanochori-1

Faune

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Mammifères
Âge

Palaeotragus sp. PLN appartient à la formation Platanochori (recouvrant la formation Gerakarou), et sa faune comprend les taxons suivants: *S. hundsheimensis*, *E. apolloniensis*, *Bison* sp. et *P. ambiguus*. La comparaison préliminaire de ces assemblages faunistiques avec les localités déjà connues du bassin de Mygdonia et la région alentour, combinée avec les données géologiques, suggèrent un âge Villafranchien supérieur pour TSR, chronologiquement intermédiaire entre les localités Gerakarou-1 et Apollonia-1, tandis que la faune de PLN est indicative d'un âge Villafranchien terminal, similaire à celui d'Apollonia-1. Ces nouvelles localités permettront d'améliorer notre compréhension de la période cruciale qui vit la première dispersion des hominidés en Europe.

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1. Introduction

The Pleistocene fossiliferous localities of the Mygdonia Basin (Macedonia, Greece) are known since the end of the 1970s. During the last decades, numerous field-work campaigns, carried out by the Laboratory of Geology and Palaeontology of the Aristotle University of Thessaloniki (LGPUT), led to the discovery of several sites and to the excavation and study of a great number of fossils (Koufos, 2001; Koufos et al., 1995), enriching significantly the Pleistocene fossil record of Greece and rendering the Mygdonia Basin as one of the European reference regions for the study and comparison of Pleistocene mammals. Recently, a team of researchers from the Aristotle University of Thessaloniki and the Eberhard Karls University of Tübingen (Germany) started systematic field surveys in the Mygdonia Basin, under the framework of the PaGE project – “Paleoanthropology at the Gates of Europe: human evolution in the southern Balkans” (Harvati and Tourloukis, 2013). PaGE aims to explore potentially informative areas in Greece in order to identify sites with palaeolithic/palaeoanthropological interest and shed light on crucial palaeoanthropological questions, including the earliest human dispersals into Europe. Although Greece lies directly on the most likely hominin dispersal route from Africa to Europe, the Greek palaeoanthropological record is relatively sparse, and little evidence exists of human presence prior to the Late Pleistocene (see Galanidou et al., 2013; Harvati et al., 2009; Panagopoulou et al., 2015). Because of its geographic location in northern Greece and of its well-documented Pleistocene fossiliferous sediments, the Mygdonia Basin represents an important target for systematic investigations (Tourloukis and Karkanis, 2012).

The two survey expeditions carried out in the Mygdonia Basin and in the surrounding smaller basins (Zagliveri, Doubia, Marathoussa) in 2013 and 2014 led to the discovery of two new fossiliferous localities: Tsiotra Vryssi (TSR) and Platanochori-1 (PLN) (Fig. 1). The aim of the present article is to provide preliminary results about the stratigraphy, fauna and age of these sites, based on the first collected material and its comparison with assemblages from the other known Pleistocene localities of the Mygdonia Basin and the wider region. The material is stored at the Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki.

Abbreviations: APD, antero-posterior diameter; di, deciduous incisor; dp/DP, lower/upper deciduous

premolar; DT, transverse diameter; H, height; L, length; m/M, lower/upper molar; W, width.

2. Geology, stratigraphy and localities

The Mygdonia Basin (basin of current lakes Koronia and Volvi) is located in central Macedonia (Greece), to the northeast of Thessaloniki, and represents an extensive and elongated east–west-trending tectonic depression, the formation of which started during the Early–Middle Miocene with the incipient development of the Pre-Mygdonia Basin (Fig. 1). During the Neogene–Early Pleistocene, the basin was filled with fluvial-fluvioterrestrial and lacustrine sediments, while at the beginning of the Middle Pleistocene a new tectonic event led to further subdivisions into smaller basins (basins of Mygdonia, Zagliveri, Doubia, Marathoussa), which were subsequently filled mostly by lacustrine sediments. The lakes Koronia in the west and Volvi in the east are the remnants of the initially single, large Mygdonia lake, which existed during the Pleistocene (Psilovikos, 1977). Geotectonically, the pre-Neogene basement in the central and eastern part of the basin consists of metamorphic rocks (schists, gneisses, amphibolites) belonging to the Serbomacedonian Massif, while in the western part it consists of slightly metamorphosed sediments (phyllites, limestones, sandstones) of the Circum-Rhodope Belt (Kockel et al., 1977). The Neogene and Quaternary deposits that filled up the basin overlie the basement unconformably. They are divided into two lithostratigraphic units: the Pre-Mygdonian Group and the Mygdonian Group. The Pre-Mygdonian Group, which includes the Neogene and Early Pleistocene deposits, is further subdivided into three successive formations (Koufos et al., 1995):

Chryssavgi Formation: This formation is the oldest of the basin and directly overlies the basement. It has a limited exposure in the northwestern part of the basin and consists mainly of alternating grey-white loose conglomerates and sands with silty-clayey lenses or lenticular intercalations (Figs. 1 and 2a). The thickness of the formation is 40–50 m. The fossiliferous locality Chryssavgi-1 (CHR) is situated in the upper part of this formation and provided mainly micro-mammalian fauna, but also some large mammals. The study of this material indicated a late Astaracian (Middle Miocene) age for the locality (Koliadimou and Koufos, 1998; Koufos and Kostopoulos, 2013).

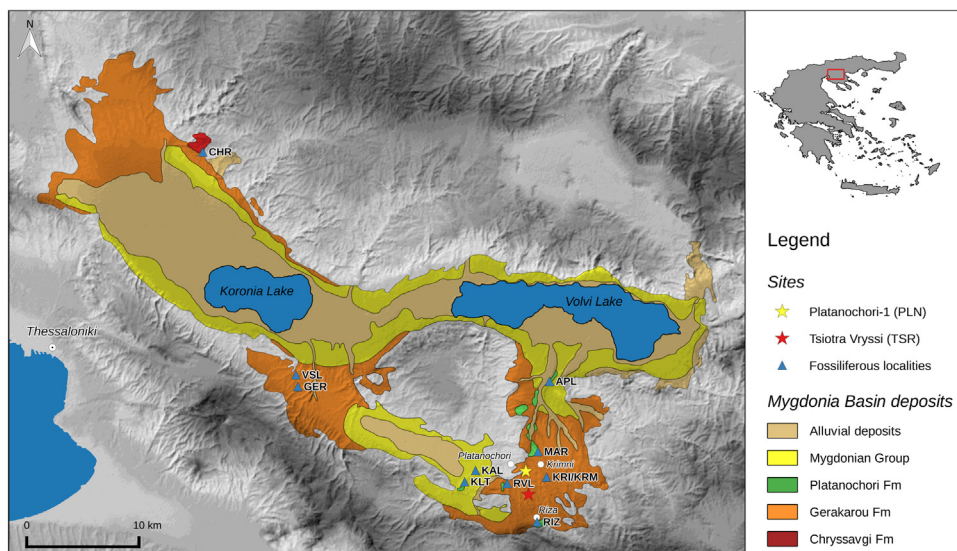


Fig. 1. (Color online.) Geological map of the Neogene and Quaternary lithostratigraphic units of the Mygdonia Basin.
Fig. 1. (Couleur en ligne.) Carte géologique des unités lithostratigraphiques du Néogène et du Quaternaire du bassin de Mygdonia.

Modified from Koufos et al., 1995.

Gerakarou Formation: This formation is the most widely exposed across the Mygdonia Basin (Fig. 1) and its thickness is more than 100 m. It consists of red-brown sands, gravels, sandy-silts and clays, deposited in a fluvio-terrestrial environment. Five fossiliferous localities are situated in the upper part of the formation: Gerakarou-1 (GER), Vassiloudi (VSL), Krimni-1, 2 (KRI, KRM) and Kalamoto-2 (KLT) (Figs. 1 and 2). The study of the material indicated that, although the localities are not isochronous, all of them date to the late Villafranchian (Early Pleistocene) (Koufos et al., 1995; Tsoukala and Chatzopoulou, 2005).

Platanochori Fm: This formation has limited exposure in the south-eastern part of the basin and it mainly consists of sands, sandstones, conglomerates, silty sands, silts, clays, marls and marly limestones, indicating the local development of small lakes and swamps (Figs. 1 and 2), possibly correlated to the Pleistocene tectonic fraction of the initial basin. The formation is considered transitional from the fluvio-terrestrial depositional environment of the Gerakarou Fm to the merely lacustrine conditions characterizing the Mygdonian Group. Its thickness varies from 10–20 m. Five fossiliferous localities are situated in this formation: Ravin of Voulgarakis (RVL), Apollonia-1 (APL), Riza-1 (RIZ), Marathoussa (MAR) and Kalamoto-1 (KAL) (Figs. 1 and 2). The study of the material indicated that they are dated to the latest Villafranchian (Koufos et al., 1995; Tsoukala and Chatzopoulou, 2005).

The Mygdonian Group, dated from the Middle Pleistocene to the Holocene, overlies unconformably the Pre-Mygdonian Group, and consists mainly of lacustrine thin-bedded and fine sediments. In the upper part of the group, sandstones, gravels, sands and travertines are also present. Apart from some isolated fossils, no fossiliferous localities are known from this group thus far.

During the field survey conducted in 2013, a new fossiliferous locality, named Platanochori-1 (PLN), was

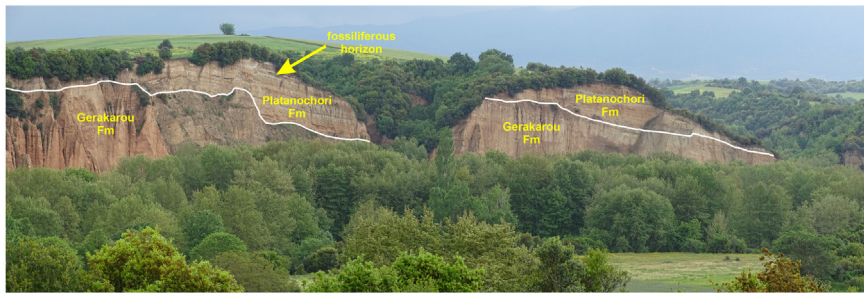
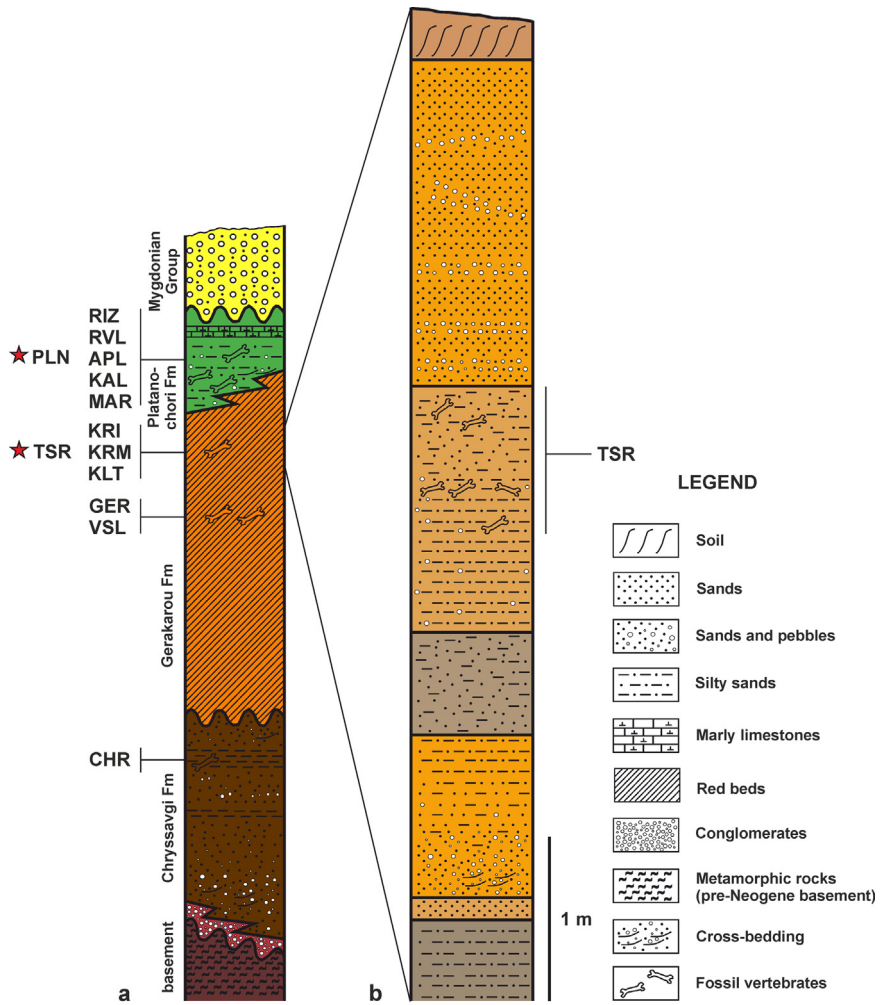
discovered in the Marathoussa Basin, about 60 km E–SE from Thessaloniki, near the villages of Platanochori and Krimni (northern Chalkidiki) (Fig. 1). Because it is situated in the uppermost part of a vertical cliff, systematic excavation is not possible. In the lower part of the section, the characteristic red sediments of the Gerakarou Fm are exposed, while green-white and green-grey sandstones, silty sands and silty clays, typical of the Platanochori Fm occur in the upper part (Fig. 2c, d). During the 2013 and 2014 field seasons, fossil mammals were collected from large intact blocks of sediment that collapsed from the cliff.

The second fossiliferous locality, discovered in 2014, was named Tsiotra Vryssi (TSR) after a local toponym. The site is also located in the Marathoussa Basin, to the southwest of Krimni and to the north of Riza (northern Chalkidiki), and belongs to the Gerakarou Fm (Fig. 1). The sediments consist of alternating beds of unconsolidated gravels, coarse sands and reddish-brown silts and clays (Fig. 2b). After collecting the surface remains and the exposed specimens from the section, we proceeded to conduct a test excavation. The fossil vertebrates appear in the middle – upper part of the section and occur as small pockets of concentrations along it. Most of the remains are of single isolated specimens, but also several anatomically connected bones were found. The preliminary faunal lists for TSR and PLN are given in Table 1.

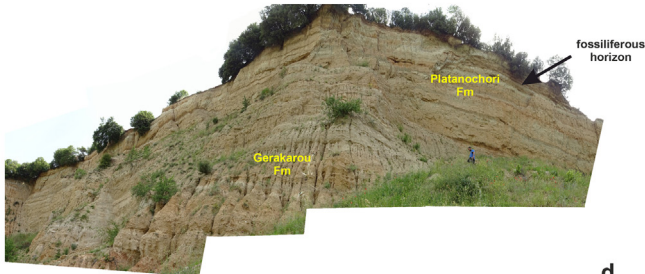
3. Palaeontology

3.1. Tsiotra Vryssi

Birds are represented in the TSR fauna by a few postcranial elements, which belong to a single taxon of a large-sized passeriform (Fig. 3a, b). They preserve morphological characters that are typical of corvids, such as



c



d

Table 1

Preliminary faunal lists of the localities Tsiotra Vryssi (TSR) and Platanochori-1 (PLN).

Tableau 1

Listes fauniques préliminaires des localités Tsiotra Vryssi (TSR) et Platanochori-1 (PLN).

Class	Order	Family	Genus	Species
<i>Tsiotra Vryssi (TSR)</i>				
Reptilia	Chelonii	indet.		
Aves	Passeriformes	Corvidae	<i>Corvus</i>	<i>pliocaenus</i>
Mammalia	Carnivora	Canidae	<i>Canis</i>	<i>etruscus</i>
		Hyaenidae	<i>Pachycrocuta</i>	<i>brevirostris</i>
	Perissodactyla	Equidae	<i>Equus</i>	sp. (medium-sized)
			<i>Equus</i>	sp. (large-sized)
		Rhinocerotidae	<i>Stephanorhinus</i>	sp.
	Artiodactyla	Giraffidae	<i>Palaeotragus</i>	sp.
		Cervidae	<i>Metacervocerus</i>	<i>rhenanus</i>
			indet. (large-sized)	
		Bovidae	<i>Bison</i>	sp.
<i>Platanochori-1 (PLN)</i>				
Mammalia	Proboscidea	indet.		
	Perissodactyla	Equidae	<i>Equus</i>	<i>apolloniensis</i>
		Rhinocerotidae	<i>Stephanorhinus</i>	<i>hundsheimensis</i>
	Artiodactyla	Cervidae	indet. (large-sized)	
		Bovidae	<i>Pontoceros</i>	<i>ambiguous</i>
			<i>Bison</i>	sp.

the presence of a single fossa pneumotricipitalis in the humerus, the large processus intermetacarpalis fusing with the os metacarpale minus in the carpometacarpus and the trochleae metatarsi II–IV, which are placed at almost the same plane in the tarsometatarsus. Compared to various extant European genera they are most similar morphologically and metrically to *Corvus*. The TSR specimens are closest in size to *C. cornix*. However, they are considerably more robust in general dimensions. Several fossil corvids have been described from the Plio-Pleistocene of Europe (Mlíkovský, 2002), but there is some ambiguity concerning the validity for some of them, while possible synonymies further complicate the taxonomy. The preliminary study of the TSR findings indicates that they show closer affinities with *C. pliocaenus*, the validity of which was recently suggested based on material from Pirro Nord (Italy) (Bedetti and Pavia, 2013), and therefore we tentatively attribute the TSR bird to this species.

The carnivores in the TSR fauna are represented by a canid and a hyaenid. The TSR canid is so far known by one isolated M1 (Fig. 3c). Its dimensions (L × W: 16.3 × 19.1 mm) are larger than *Lycaon* sp. from APL (15.7–15.8 × 17.6–17.8 mm), *Canis arnensis* from GER (13.2 × 17.5 mm), RVL (13.0 × 18.0 mm) and APL (13.8 × 19.1 mm), and *C. apolloniensis* from APL (13.0–14.3 × 16.4–16.9 mm), and are close to *C. etruscus* from APL (15.2–15.7 × 19.3–19.4 mm) and to some specimens from Upper Valdarno (Italy), including the lectotype of the species (Koufos, 1987, 1992a; Koufos and Kostopoulos, 1997; Rook, 1993). Additionally, the TSR M1 presents a more elevated paracone than metacone, which is a diagnostic feature of *C. etruscus* (Cherin et al., 2014). The

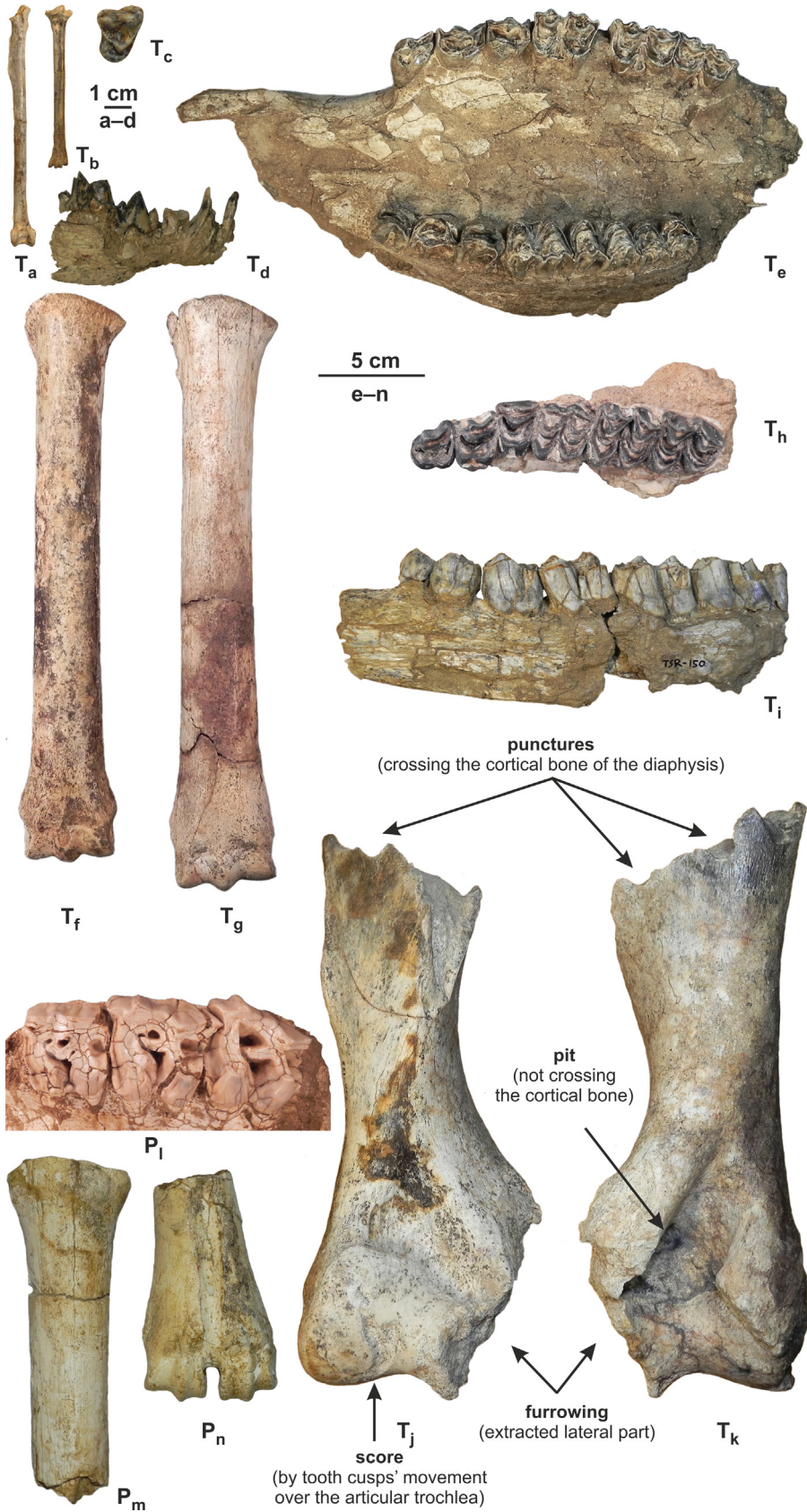
TSR hyaenid is represented by a mandibular fragment with deciduous dentition (Fig. 3d). Surpassing in size the teeth of *Pliohyaena perrieri*, the TSR dp3 (19.9 × 9.1 mm) and dp4 (21.3 × 8.8 mm) fit well morphometrically with those of *Pachycrocuta brevirostris* from GER (dp3: 19.1 × 8.4 mm; dp4: 20.2–21.8 × 8.0–8.7 mm), Fonelas P-1 (Spain), Untermassfeld (Germany), Ceysseguet and Vallonnet (France) (Arribas and Garrido, 2008; Koufos, 1992a; Moullé and Tréguier, 2006; Tsoukala and Bonifay, 2004; Turner, 2001).

The rhinocerotids of the TSR fauna are represented by few postcranial elements and some very fragmented dental ones. Noteworthy is a distal part of a humerus that was gnawed by a large carnivore as indicated by the presence of toothmarks (Fig. 3j, k). The lateral part is extracted but the remaining articular trochlea is not as oblique as in *Stephanorhinus etruscus*; rather, it is closer to *S. hundsheimensis*. The TSR humerus is smaller (H × W medial trochlea: 70.0 × 43.3 mm) than a humerus of *Stephanorhinus* from APL (pers. observ.). The proximal part of a third metacarpal is morphometrically closer to *S. hundsheimensis* (DT × APD proximal: 59.8 × 51.8 mm) from Untermassfeld, whereas a distal part of a tibia is closer to *S. etruscus* (DT × APD distal: 89.0 × 67.4 mm) from Senèze (France) and Upper Valdarno (Fortelius et al., 1993; Kahlke, 2001). Because the specimens exhibit morphological features and dimensions of both *S. etruscus* and *S. hundsheimensis*, and the transition/replacement between these species is not yet clear, we prefer to attribute the TSR specimens to *Stephanorhinus* sp. until further material is discovered.

The equids are relatively abundant in the TSR collection, represented mainly by postcranial elements, but also

Fig. 2. (Color online.) **a:** Simplified composite stratigraphic column of the Mygdonia Basin indicating the position of the old and new fossiliferous localities, data from Koufos et al., 1995; **b:** stratigraphic column of the Tsiotra Vryssi (TSR) locality; **c, d:** panoramic view of the Platanochori-1 (PLN) locality in distant (c) and close (d) view.

Fig. 2. (Couleur en ligne.) **a:** Colonne stratigraphique composite simplifiée du bassin de Mygdonia, indiquant la position des anciennes et nouvelles localités fossilifères; **b:** colonne stratigraphique de la localité Tsiotra Vryssi (TSR); **c, d:** vue panoramique de la localité de Platanochori-1 (PLN) en vue lointaine (c) et en vue proche (d).



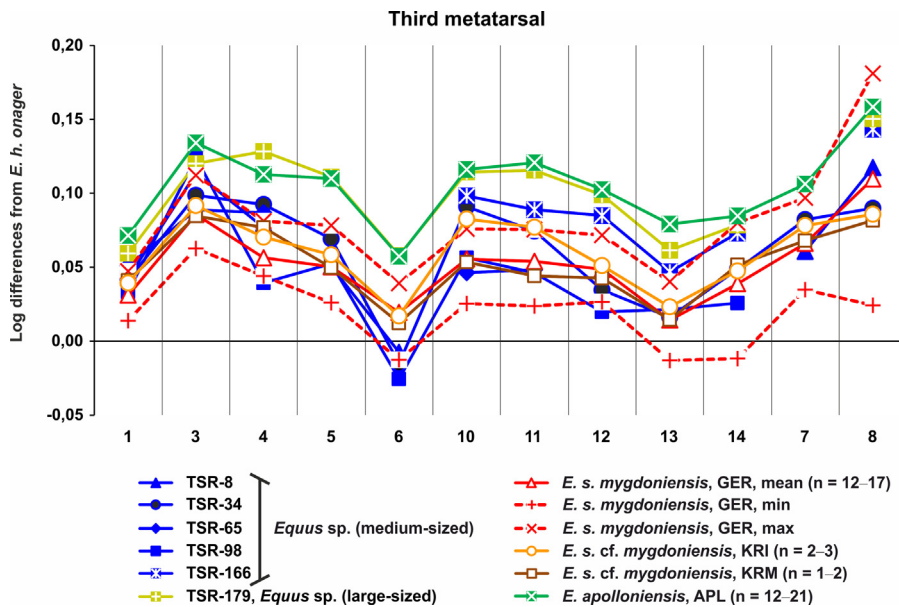


Fig. 4. (Color online.) Logarithmic ratio diagram comparing the third metatarsal measurements of *Equus* from Tsiotra Vryssi (TSR) to those of *E. stenon mygdoniensis* from Gerakarou-1 (GER), *E. s. cf. mygdoniensis* from Krimni-1, 2 (KRI, KRM) and *E. apolloniensis* from Apollonia-1 (APL). Standard of comparison: *E. hemionus onager* ($n = 14-16$).

Fig. 4. (Couleur en ligne.) Écart logarithmique comparant les mesures du troisième métatarsien d'*Equus* de Tsiotra Vryssi (TSR) à ceux de *E. stenon mygdoniensis* de Gerakarou-1 (GER), *E. s. cf. mygdoniensis* de Krimni-1, 2 (KRI, KRM) et *E. apolloniensis* de Apollonia-1 (APL). Standard de comparaison: *E. hemionus onager* ($n = 14-16$).

The measurements are taken from Eisenmann and Beckouche (1986), Koufos (1992b) and Koufos et al. (1997).

by some dental, and fragmentary cranial and mandibular remains (Fig. 3f, g). The metrical study of the metapodials revealed the presence of two distinct taxa: a medium-sized and a large-sized species. The medium-sized equid dominates in the fauna and it is similar in size to *Equus stenon mygdoniensis* from GER and *E. s. cf. mygdoniensis* from KRI and KRM (Fig. 4). At the moment, the limited number of finds and the absence of cranial remains do not allow for a more precise determination and we refer to this equid as *Equus* sp. (medium-sized). The other equid was recognized by a third metatarsal and some associated tarsals; the metatarsal is longer and more robust than the rest of the TSR specimens and fits well in size with *E. apolloniensis* from APL (Figs. 3f, g and 4). Due however to the limited material, we prefer to attribute this to *Equus* sp. (large-sized). The dental material, although scarce, also indicates

two forms that differ in size, supporting the presence of two equids in TSR.

Artiodactyles are represented in the TSR fauna by bovids, cervids and giraffids. A large-sized bovid is known by a cranium fragment (Fig. 3e) and some post-cranial remains. The combination of dental features, such as the abundant cement, the strong entostyle reaching the half of the crown and connected with the second lobe, the enamel islets on the M1, the strong and distolabially projected metastyle on the M3, the rectangular-shaped enamel around the central cavities, as well as the presence of well-pronounced tubercles in the distal end of the metacarpal, are distinct from *Leptobos* and *Bos*, and more closely resemble the primitive forms of *Bison*, known from Venta Micena (Spain), Pirro Nord and APL (De Giuli et al., 1987; Kostopoulos, 1997; Moyà-Solà, 1987; Sala, 1986).

Fig. 3. (Color online.) Fossil remains from Tsiotra Vryssi, TSR (T) and Platanochori-1, PLN (P), Mygdonia Basin, Macedonia, Greece. **a:** *Corvus plicicaenus*, right tibiotarsus, TSR-120, cranial view; **b:** *Corvus plicicaenus*, left tarsometatarsus, TSR-94, dorsal view; **c:** *Canis etruscus*, right M1, TSR-46, occlusal view; **d:** *Pachycrocuta brevirostris*, right mandibular fragment with di3-dp4, TSR-155, labial view; **e:** *Bison* sp., cranial fragment with right and left P2-M3, TSR-161, ventral view; **f:** *Equus* sp. (medium-sized), third metatarsal, TSR-34, anterior view; **g:** *Equus* sp. (large-sized), third metatarsal, TSR-179, anterior view; **h:** *Metacervoceros rhenanus*, left upper tooth-row with P2-M3, TSR-135, occlusal view; **i:** *Palaeotragus* sp., left mandibular fragment with p2-m3, TSR-150, lingual view; **j-k:** toothmarks produced by a large carnivore in the left humerus of *Stephanorhinus* sp., TSR-133, terminology after Sala et al., 2014; **j:** cranial view; **k:** caudal view; **l:** *Stephanorhinus hundsheimensis*, maxillary fragment with left DP2-DP4, PLN-1; occlusal view; **m:** *Equus apolloniensis*, proximal part of third metacarpal, PLN-2, anterior view; **n:** *Bison* sp., distal part of third and fourth metatarsal, PLN-13, anterior view.

Fig. 3. (Couleur en ligne.) Restes fossiles en provenance de Tsiotra Vryssi, TSR (T) et Platanochori-1, PLN (P), bassin de Mygdonia, Macédoine, Grèce. **a:** *C. plicicaenus*, tibiotarsien droit, TSR-120, vue crâniale; **b:** *C. plicicaenus*, tarsométatarsien gauche, TSR-94, vue dorsale; **c:** *C. etruscus*, M1 droite, TSR-46, vue occlusale; **d:** *P. brevirostris*, fragment de mandibule droite avec di3-dp4, TSR-155, vue labiale; **e:** *Bison* sp., fragment de crâne avec P2-M3, TSR-161, vue ventrale; **f:** *Equus* sp. (taille moyenne), troisième métatarsien, TSR-34, vue antérieure; **g:** *Equus* sp. (grande taille), troisième métatarsien, TSR-179, vue antérieure; **h:** *M. rhenanus*, rangée dentaire supérieure gauche avec P2-M3, TSR-135, vue occlusale; **i:** *Palaeotragus* sp., fragment de mandibule gauche avec p2-m3, TSR-150, vue linguale; **j-k:** marques de dents produites par un grand carnivore dans l'humérus gauche de *Stephanorhinus* sp., TSR-133; **j:** vue crâniale; **k:** vue caudale; **l:** *S. hundsheimensis*, fragment de maxillaire avec DP2-DP4 gauche, PLN-1; vue occlusale; **m:** *E. apolloniensis*, partie proximale du troisième métacarpien, PLN-2; vue antérieure; **n:** *Bison* sp., partie distale des troisième et quatrième métatarsiens, PLN-13, vue antérieure.

The presence of a medium-sized cervid in the TSR fauna is recognized by two upper tooth-rows bearing the P2–M3 (Fig. 3h). The dimensions of the teeth clearly separate the TSR cervid from the Villafranchian smaller *Croizetoceros*, and the much larger *Eucladoceros*, *Praemegaceros* and *Arvernoceros*. The TSR cervid is characterized by a large angle ($\sim 45^\circ$) between the labial and lingual slopes and a weak to moderate cingulum on the molars; in these traits it differs from the Villafranchian “*Cervus*” *nestii* and “*Dama*” *eurygonos* (Croitor, 2006). Additional features include the presence of protoconal folds and hypoconal spurs, and the prominent parastyles and mesostyles on the molars, while the premolars exhibit a hypoconal spur. The premolar/molar ratio of the tooth-rows is 73% and 76%, respectively. Although crania or antlers are so far absent from TSR, the morphology and dimensions of the teeth fit well with corresponding specimens of *Metacervoceros rhenanus* from Tegelen (Netherlands), Senèze, Ceysaguet, Vallonnet, Upper Valdarno, Fonelas P-1, Volakas and Dafnero (Greece) (Croitor, 2006; Garrido, 2008; Kostopoulos and Athanassiou, 2005; Spaan, 1992) and therefore an attribution to this species seems plausible. The presence of a large-sized cervid is also confirmed in the TSR fauna from a first phalanx.

Giraffids are known from a palaeotragine mandible fragment bearing the complete tooth-row and from a first phalanx (Fig. 3i). Only few giraffid lower teeth and phalanges are known so far from the Pleistocene, but the morphology of the TSR specimens matches those from Valea Grăunceanului (Romania), Liventsovka (Russia), Fonelas P-1 and Huélago (Spain); nevertheless, the TSR molars (m1: 31.2×20.7 ; m2: 38.0×21.0 ; m3: 46.1×19.8 ; all in mm) are longer than the Liventsovka ones (Garrido and Arribas, 2008; Godina and Baygusheva, 1985; Samson and Radulesco, 1966; Titov, 2008; Van der Made and Morales, 2011). Although giraffids are represented during the Pleistocene in Europe possibly by a single taxon, *Palaeotragus inexpectatus* (Athanassiou, 2014), we prefer to refer the TSR giraffid to as *Palaeotragus* sp. awaiting more material.

3.2. *Platanochori-1*

The best-preserved specimen in the PLN fauna is a juvenile maxilla fragment of a rhinocerotid bearing the DP2–DP4 (Fig. 3l). The DP2 is characterized by a rather complicated crochet, double crista, weak anterocrochet and closed mediofossette; the DP3 is characterized by a single crochet and protocone constriction and the DP4 by an open mediofossette and absence of crista. The dental morphology among the European Pleistocene *Stephanorhinus* species, *S. etruscus*, *S. hundsheimensis*, *S. hemitochus* and *S. kirchbergensis*, is quite similar but the combination of the above features points to *S. hundsheimensis* (Lacombat, 2006a).

As in the TSR fauna, the equids are the most abundant faunal element in the PLN collection. The equid from PLN is known by postcranial material that belongs to a single large-sized species (Fig. 3m). The dimensions of the specimens are clearly larger than the medium-sized equid from GER, KRI, KRM and TSR and are within the size variation

of *E. apolloniensis* from APL, allowing an attribution to this species (Koufos et al., 1997).

A large bovid from PLN is known from some isolated upper teeth, which are hypsodont and bear cement, have strong entostyles reaching the half of the crown and rectangular-shaped central cavities. In these features, they are similar to the APL and TSR *Bison* material. Additionally, a distal metatarsal end presents the pronounced tubercles above the trochleas typical for *Bison* (Fig. 3n). Among the PLN collection, there is also a torsioned horn-core fragment with triangular to elliptical-rounded cross-section. These features are similar to the homonymously spiral horned antelope *Pontoceros ambiguus* from APL and Libakos (Greece) (Kostopoulos, 1997; Steensma, 1988) and permit the attribution to this species. A large-sized upper molar with slightly rugose enamel, strong protoconal fold, hypoconal spur and low entostyle marks the presence of a large cervid in the PLN fauna, which is also supported by a distal metacarpal end. Additionally, a large-sized ulna diaphysis indicates the presence of a proboscidean.

4. Biochronology – Conclusions

The presence of *P. brevirostris* in the TSR fauna clearly indicates a late Villafranchian age. The invasion of this large-sized hyaenid in Europe and its great impact in the Early Pleistocene faunal assemblages, is referred to as the “*Pachycrocuta brevirostris* event”, dated around 2.0 Ma (Martínez-Navarro, 2010). During this event, the wolf-sized dog *C. etruscus* becomes also widespread (Sotnikov and Rook, 2010), additionally supporting a late Villafranchian age for TSR. In the TSR fauna, there are two *Equus* species: the medium-sized one, which is similar to *E. stenonis mygdoniensis* from GER, and the large-sized one similar to *E. apolloniensis* from APL. This indicates that TSR is intermediate between GER and APL faunas. According to Eisenmann (2002), during the beginning of the Early Pleistocene (~ 2.5 – 1.7 Ma), usually one equid species was present, whereas in younger localities the co-existence of two species became more frequent. This co-existence is reported from several localities such as Dmanisi (Georgia), Selvella, Pirro Nord (Italy), Fuente Nueva-3, Barranco León-5 (Spain) and Untermassfeld, dated after the terminal Tasso Faunal Unit (FU) of the Italian Early Pleistocene, and coincides with the earliest hominin dispersals into Europe (Alberdi and Palombo, 2013; Lordkipanidze et al., 2007; Rook and Martínez-Navarro, 2010). However, to date, the strongest biochronological indicator recovered from TSR is *Bison* sp. In the Olivola, Tasso and Farneta FUs large bovines are represented by *Leptobos*, a genus, which is thought to have been replaced by *Bison* in Europe during the Pirro FU (Masini et al., 2013). Although bisons originated before 2.0 Ma in Asia and are recognized in Dmanisi around 1.77 Ma (Akbar Khan et al., 2010; Lordkipanidze et al., 2007), they dispersed into Europe slightly later. The oldest occurrences of *Bison* in south-western Europe are traced between 1.6–1.3 Ma (Pirro FU) (Arzarello et al., 2012; Masini et al., 2013; Pavia et al., 2012). Primitive bisons in Europe are reported from Pirro Nord, Venta Micena, Atapuerca TE9 (Sima del Elefante), Fuente Nueva-3, Barranco León-5 and Untermassfeld, many of which preserve evidence for early

human presence (e.g., Arzarello et al., 2012; Carbonell et al., 2008; Martínez-Navarro, 2010; Toro-Moyano et al., 2013). In the Mygdonia Basin, *Leptobos* is known from GER and VSL, correlated to the Olivola FU, while *Bison* is present in APL, KAL and KLT (Kostopoulos, 1997; Tsoukala and Chatzopoulou, 2005). Therefore, TSR should be younger than GER and VSL. *M. rhenanus* is known from the middle and late Villafranchian (Croitor, 2006); in Mygdonia Basin it occurs in GER. *Palaeotragus* is well recorded during the middle Villafranchian (Athanasidou, 2014), as well as in the late Villafranchian localities Fonelas P-1, Dmanisi, Libakos and Denizli-Kocabaş (Turkey) (Boulbes et al., 2014; Garrido and Arribas, 2008; Lordkipanidze et al., 2007; Steensma, 1988), but it is so far not recorded in Pirro Nord, the Orce sites and APL. In conclusion, the current data suggest that TSR is placed chronologically between GER-VSL (middle/late Villafranchian boundary, ~1.8 Ma) and APL [latest Villafranchian, ~1.2 Ma; following the recent biochronological concepts of Rook and Martínez-Navarro (2010); Toro-Moyano et al. (2013); Belluci et al. (in press)], showing more geological and palaeontological similarities to the localities Krimni-1 (KRI) and Kalamoto-2 (KLT).

Concerning the PLN fauna, *S. hundsheimensis* has a biochronological range in Europe lasting from the late Villafranchian to the beginning of the Middle Pleistocene (Lacombat, 2006b). In the Mygdonia Basin, the species is possibly known from APL. The similarity of the PLN *Bison* with the primitive bisons from Venta Micena, Pirro Nord and APL indicates a similar latest Villafranchian age. Additionally, the presence of *E. apolloniensis* in the PLN fauna makes it comparable with its type locality APL. The most important biochronological marker for the PLN fauna is the presence of *P. ambiguus*. Although rare, this species is known in Greece from Libakos and APL. In conclusion, all the taxa found so far in PLN, are also present in APL (latest Villafranchian), indicating close affinities with this locality and a similar age.

Although several fossiliferous localities in the Mygdonia Basin have been discovered during the last decades and the study of their faunal assemblages has enriched significantly our knowledge on the Pleistocene of Greece and the wider region, several biostratigraphical issues still exist concerning the correlation among them. This is mainly due to two factors. First, the Mygdonia Basin covers a large area, which has been severely affected by neotectonics, leading to a very dense network of faults. Consequently, the correlation even between adjacent sections is difficult and becomes more puzzling in the case of red beds. Lateral transitions of sediments due to different depositional environments further complicate correlation efforts. Another reason is that apart from the fossil-rich localities of GER and APL, the material from VSL, KRI, KRM and RIZ is rather limited, while the assemblages from RVL and MAR, with the exception of relatively few macro-mammals from the former locality, consist mainly of micro-mammals, making direct comparisons and correlations difficult.

The discovery of new material from TSR and PLN is deemed essential in order to i) enrich the collection, ii) follow more densely the local mammal faunal succession through time, iii) add further data for a more detailed age, and iv) contribute to enhance our knowledge about the

relationships among the Mygdonia Basin localities in particular, and the Pleistocene sites of Greece and the wider SE European region in general. Importantly for the objectives of PaGE, the new sites will provide additional geographical and ecological information about a crucial interval of time for mammal migrations and turnovers and of the first hominin dispersals from Africa to Europe.

Acknowledgments

This research was supported by the ERC STG no. 283503 (“PaGE”) awarded to K. Harvati. We are grateful to A. Darlas of the Ephoreia of Palaeoanthropology and Speleology (Northern Greece) for his support, as well as to the field team members for their contribution during the fieldwork. We thank B. Martínez-Navarro and two anonymous reviewers for their constructive comments.

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