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Paleobiogeography of early human dispersal in western Eurasia: Preliminary results

Paléogéographie de la dispersion initiale de l'Homme dans l'Ouest de l'Eurasie : résultats préliminaires

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ABSTRACT

A multivariate cluster analysis of western Eurasian regional herbivorous mammalian faunas is applied in order to reveal the paleobiogeographic context of early human dispersal in the area under study. During the early Pleistocene, the North Mediterranean area and Caucasian Land acted as refugia for warm-loving Pliocene faunal holdovers. The Italian Peninsula was biogeographically partially isolated during most of the early Pleistocene due to the forested Dinaric Alps zoogeographic filter, which possibly caused the late arrival of hominines on the Italian Peninsula. A multivariate analysis confirms a firm paleobiogeographic border between the Iberian Peninsula and northwestern Africa. The Pannonian–western European path is proposed here as the most plausible dispersal route for early hominines. The article gives a brief discussion of paleobiogeographic significance of the Alpine-Himalayan Mountain Belt and the Movius Line in western Eurasia.

RÉSUMÉ

L'analyse multivariée des faunes régionales de mammifères herbivores d'Eurasie occidentale est appliquée pour révéler le contexte paléobiogéographique de la dispersion initiale de l'Homme dans la zone étudiée. Au début du Pléistocène, la zone nord-méditerranéenne et le Caucase agissaient comme des refuges pour les animaux du Pliocène de climat chaud. La péninsule Italienne a été biogéographiquement partiellement isolée pendant la majeure partie du Pléistocène inférieur, à cause du filtre zoogéographique créé par les Alpes dinariques forestières, ce qui a peut-être été la cause de l'arrivée tardive d'hominidés dans celle-ci. L'analyse multivariée a confirmé une frontière paléobiogéographique ferme entre la péninsule Ibérique et le Nord-Ouest africain. L'itinéraire Pannonien – Europe de l'Ouest est ici proposé comme la voie de dispersion la plus plausible pour les premiers hominidés. L'article propose une brève discussion sur la signification paléobiogéographique de la ceinture alpine et de la ligne de Movius en Eurasie occidentale.

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1. Introduction

The paleobiogeographic and ecological contexts of the "Out of Africa" early human dispersals into western Eurasia have been intensively discussed; nevertheless, the driving and limiting factors of hominin dispersal are still poorly understood (Moncel, 2010). The initial human dispersal from Africa is often regarded in the context of archaic *Homo* ecologically belonging to the carnivore guild (as a scavenger) and of the assumed commensalism relationship of *Homo* with early Pleistocene large predators, such as the sabertoothed large cats *Megantereon* and *Homotherium* (Arribas and Palmquist, 1999; Blumenschine, 1987; Martinez-Navarro and Palmqvist, 1995). This hypothesis seems to be in accordance with the general zoogeographic context: with a few exceptions, the majority of mammals that dispersed from Africa to Eurasia during the last 2.6 million years were carnivores (Van der Made, 2013). However, the geographic origin of some Villafranchian carnivores is not clear, since their earliest remains are recorded almost simultaneously in the paleontological record of different continents (Bonifay, 1996; Turner, 1990), suggesting rather high ecological polyvalence and ubiquitous distribution including entire continents. Unlike true carnivores, the geographic distribution of hominines during the early Pleistocene was rather limited, suggesting the ecological sensitivity of archaic *Homo* and the existence of certain environmental factors that limited the hominine dispersal. Therefore, the assumed ecological relationship between hominines and large carnivores remains biogeographically elusive. Bar-Yosef and Belmaker (2011) did not find a clear correlation between early hominine and large mammal dispersals from Africa into Eurasia. Similar conclusions are made at a regional paleobiogeographic scale. According to Mussi and Palombo (2001), there is no relationship between hominid dispersal and the dynamics of the carnivore guild in the Italian peninsula.

The paleontological record of western Eurasia is a very promising source of information on environmental and paleobiogeographic limiting factors that controlled the early dispersals of hominines. The dispersal of *Homo* into Europe took place significantly later than in southern and southeastern Asia: the earliest recorded fossil remains of humans in Europe are unearthed from Sima Del Elefante (Spain) dated back to 1.1-1.2 Ma (Carbonell et al., 2008). Archaeological evidence suggests a somewhat earlier dispersal of *Homo* into Europe at ca. 1.4 Ma (de Lumley et al., 2009), while the well-documented paleontological and archaeological evidence reveals a still earlier presence of *Homo* in the Transcaucasian region, dated back to ca. 1.8 Ma (de Lumley et al., 2002). Regional paleobiogeographic evolution may provide some answers on the limiting factors and biogeographic context of early hominine dispersals. Obviously, ubiquitous carnivores are poor biogeographic indicators, unlike herbivorous mammals (Bonifay, 1996), which are proposed as a paleobiogeographic proxy in the present study.

The present paper proposes a multivariate analysis of early Pleistocene faunas from various geographically well-defined areas of western Eurasia compared with coeval faunas from northwestern Africa and eastern Africa in order to reveal the paleobiogeographic context of early human dispersals. The obtained results have a rather preliminary character, since some areas of western Eurasia (such as Near East and newly discovered Anatolian hominin sites) are not considered in the present study. Besides that, taxonomy, synonymy and phylogenetic relationships of some herbivore species still need precision and need to be clarified.

2. Research methods

The research method is based on the multivariate cluster analysis of the West Eurasian regional faunal lists. The applied method is in accordance with the approach used by Palombo et al. (2006) in order to obtain compatible results: the hierarchical clustering paired group algorithm UPGMA was computed using Jaccard Similarity Index for presence-absence data (PAST-3 application: Hammer et al., 2001). The cophenetic correlation coefficient is computed in order to estimate how faithfully a dendrogram preserves the pairwise distances among the original, unmodeled data points (Farris, 1969).

The chosen chronological frame of the paleobiogeographic analysis corresponds to the important middle–late Villafranchian faunal turnovers (Azzaroli, 1983). The database is mostly based on well-dated, species-rich faunal assemblages; however, in some cases sites with poor geochronological control are included (for instance, Salcia, Moldova) in order to estimate the paleobiogeographic affinity of disputable faunas. The analysis is restricted to hoofed mammals and primates, as these are considered ecologically and biogeographically more sensitive than the ecologically polyvalent and biogeographically ubiquitous carnivores. Moreover, carnivore remains are relatively rare in the paleontological record, increasing the risk of data bias.

Western Eurasia was divided into paleobiogeographic areas corresponding to the geographically delimited zones that yielded characteristic and taxonomically rich herbivores faunas (Fig. 1). Coeval faunas of Tajikistan ("Central Asia") and of Northwest and Northeast Africa are included in the study in order to estimate the importance of Asian or African biogeographic components in the paleobiogeographic areas of European Subcontinent. The analysed faunal lists are built using conservative taxonomic criteria: only species and groups of closely related species are considered (subspecies and local mammal forms are not taken into account). A group of species or morphological forms are regarded as a single faunal element if they are proved to have a direct phylogenetic relationship or if they are distinguished only by body size or minor morphological variants of exosomatic structures (horn-cores, antlers, ossicones).

3. Description

3.1. *"Saint-Vallier Age" (ca. 2.5 Ma)*

This stage of paleobiogeographic evolution is named after the important and well-dated middle Villafranchian reference site of Saint-Vallier, France (Guérin et al., 2004).

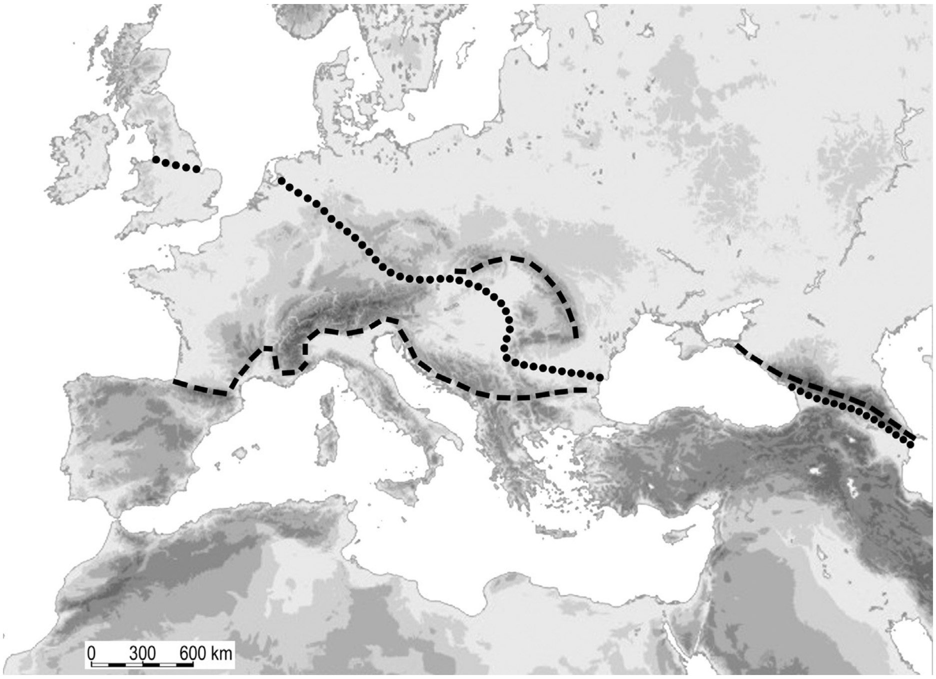

Fig. 1. The map of western Eurasia and North Africa discussed in the article; dashed line: western part of Alpine-Himalayan mountain belt limiting the Mediterranean, Pannonian, and Transcaucasian areas from the north; dotted line: Movius Line.

Fig. 1. La carte d'Eurasie occidentale et d'Afrique du Nord discutée dans l'article ; lignes en tireté : partie ouest de la chaîne montagneuse alpine-himalayenne limitant les zones méditerranéennes, pannoniennes et transcaucasiennes du Nord ; lignes en pointillé : ligne de Movius.

(adapted from Lycett & Bae, 2010).

Some species or groups of species are found in all Eurasian regions included in the study: *Gazella borbonica/Gazella sp.*, *Mammuthus meridionalis/gromovi*, *Stephanorhinus etruscus*, and the stenonid horse *Equus stenonis (vireti, livenzovensis, bressanus, major*).

Western Europe. The middle Villafranchian fauna contains up to six species of bovids: *Gazella borbonica, Gazellospira torticornis, Gallogoral meneghinii, Pliotragus ardei, "Leptobos" stenometopon, "Leptobos" elatus*. Cervids are represented only by three species, two of which (*Croizetocerus ramosus* and *Metacervocerus rhenanus*) are early Villafranchian survivors. *Eucladoceros ctenoides* is a new large cervid of the Saint-Vallier fauna. This species is represented in western Europe by a range of middle and late Villafranchian forms that share the same comb-like antler construction and are distinguished by minor details of antler morphology. Many of these *Eucladoceros* forms are described as separate species (*E. ctenoides, E. tetraceros, E. senezensis, E. tegulensis, E. falconeri*) that generally reflect the morphological variability recorded in subspecies of modern cervids (Croitor, 2014). Therefore, all *Eucladoceros* forms with simple comb-like antlers are regarded here as one species. The only primate from Saint-Vallier, *Macaca sylvanus*, is considered an ecologically flexible species that could tolerate cool climate and treeless landscapes (Delson, 2004).

The Iberian Peninsula. The coeval middle Villafranchian faunas are described from Huelago and Puebla de Valverde fossiliferous sites (Aguirre, 2004). The composition of the herbivore guild is generally very similar to that from the North of the Pyrenees. The "endemic" Iberian bovid *Hesperidoceras merlae* is very close to or may be even synonymous with *Pliotragus ardeus* (Duvernois and Guérin, 1989; Gentry, 2001). Therefore, these two species names are regarded here as a single biogeographic element. Although less diversified than the faunas from Western Europe, the Iberian "Saint-Vallier Age" herbivore guild contains a giraffid *Mitilanotherium inexpectatum* characterized by a disjunct Mediterranean distribution (Van der Made and Morales, 2011). Fragmentary remains of giraffids are less common and are known from the Ponto-Mediterranean area under different names that seem to be synonymous: *Macidonitherium martini* in Greece, *Mitilanotherium inexpectatum* from Southern Romania, *Paleotragus priazovicus* from Azov Sea Area, and *Sogdianotherium kuruksaense* from Tajikistan (Kostopoulos and Athanassiou, 2005). The taxonomic variety of Villafranchian giraffids from western Eurasia is based mostly on minor details of shape of ossicones and metapodial robustness and is regarded as a single ruminant ecological type of Asian origin characteristic of the Ponto-Mediterranean area (Titov, 2008; Van der Made and Morales, 2011). The baboon-like *Paradolichopithecus* from Puebla de Valverde is another region specific species with Mediterranean dispersal limited by the Alpine Mountain Belt from the North (Aguirre and Soto, 1978).

The Italian Peninsula. The Italian middle Villafranchian herbivore guild (Montopoli, Ponte a Elsa, Cava Toppetti) is remarkable in its varied group of cervids (five species), which includes the early Villafranchian holdovers that

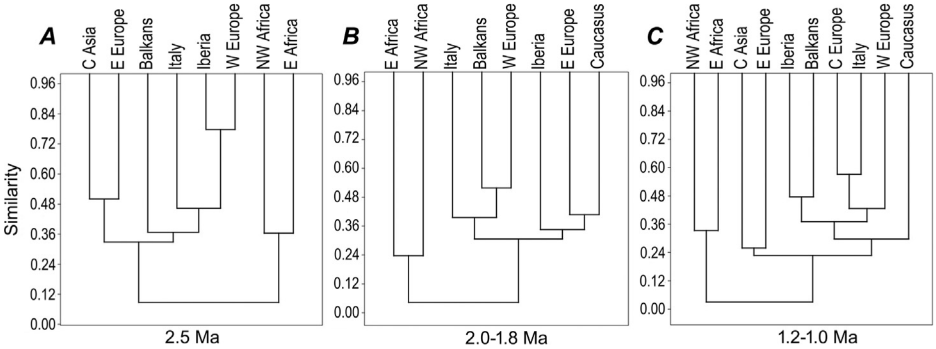

Fig. 2. The dendrogram of the regional composition of faunas: A) “Saint-Vallier age” (ca. 2.5 Ma), Cophenetic Correlation Coefficient = 0.96; B) “Dmanisi age” (2.0-1.8 Ma), Cophenetic Correlation Coefficient = 0.97; C) “Untermassfeld Age” (1.2-1.0 Ma), Cophenetic Correlation Coefficient = 0.93.

Fig. 2. Arborescence de la composition des faunes régionales : A) « âge de Saint-Vallier » (environ 2,5 Ma), coefficient de corrélation cophénétique = 0,96; B) « âge de Dmanisi » (2,0–1,8 Ma), coefficient de corrélation cophénétique = 0,97 ; C) « âge d’Untermassfeld » (1,2–1,0 Ma), coefficient de corrélation cophénétique = 0,93.

disappeared in the rest of Europe: *Procapreolus cusanus, Praeelaphus lyra* (very close or even synonymous with *Praeelaphus perrieri*: Croitor, 2014), and a muntjac-like small cervid “*Eostyloceros*” cf. *pidoplitschkoi* (Abbazzi and Croitor, 2003). The two other cervids are *Croizetoceros ramosus* and the new faunal element represented by the large-sized *Eucladoceros ctenoides*, both are found only in western and Mediterranean Europe (Azzaroli, 2001; Gliozzi et al., 1997).

The Balkan Peninsula. A rich herbivore fauna from the Balkan Area is represented by the middle Villafranchian sites of Varshets and Slivnitsa (Spassov, 2005). The Bulgarian middle Villafranchian herbivore assemblage is characterized by its higher diversity of bovids (seven forms) and contains only three poorly known cervid species, similar to *Metacervocerus, Eucladoceros*, and another cervid of intermediate size (Spassov, 2005). The earliest European occurrence of bovid genera such as *Procamptoceras, Ovis*, and *Hemitragus* represents the biogeographic peculiarity of this region. Scant remains of the giraffid *Mitilanotherium martinii* are reported from the Greek sites of Volakas, Sesklo, and Dafnero (Kostopoulos and Athanassiou, 2005).

Eastern Europe. A rich mammal fauna from eastern Europe coeval with that of Saint-Vallier is produced by Liventsovka sand beds from the northern Azov Sea Area. *Equus livenzovensis* is distinguished from *E. stenonis* from western Europe only by some morphological details of exosomatic body parts: a slight difference is recorded in the relative breadth of incisors, the limb bone robustness and the degree of development of the preorbital pit (Titov, 2008). All large stenonid horses of Europe are regarded in this study as one zoogeographic element, taking into consideration the specific eco-evolutionary strategy and poor evolutionary radiation of horses (Janis, 1976). Similarly, all small hemione-like horses with thin limbs, which are described as *E. stehlini* and *E. altidens* (Forsten, 1999; Gliozzi et al., 1997) are also regarded here as one zoogeographic element. The community of herbivores from Liventsovka is peculiar due to the presence of species and forms that never entered western Europe (*Elasmotherium chaprovicum, Paracamelus alutensis, Paracamelus sp.*) or dispersed westward somewhat later (*Eucladoceros dicranios, Alces gallicus*). *Metacervocerus rhenanus* (= *Cervus (Rusa) philisi* in Titov, 2008) is the only cervid species shared by faunas from Liventsovka and western Europe. Apparently, the rather large *Arvernoceros sp.*, with a body size comparable to that of *Eucladoceros*, belongs to the Asian giant *Rucervus* lineage from the Siwalik fauna (Croitor, 2017).

Central Asia. The fauna from Kuruksai (Tadjikistan) contains open-landscape (*Paracamelus praebactriaus*), savanna (*Sivatherium, Damalops, Gazellospira, Alces cf. gallicus*), and forest (*Paradolichopithecus suschkini, Axis flerovi, Sinomegaceros tadzhikistanis*) species reflecting the vertical montane environmental zonality (Vislobokova et al., 1995). Generally, the warm-loving fauna from Kuruksai shares with the European coeval faunas only the most ubiquitous herbivore species (*Mammuthus meridionalis gromovi, Equus stenonis bactrianus, Dicerorhinus sp.*) and Pliocene holdovers (*Paradolichopithecus, Sivatherium*).

The multivariate analysis includes the coeval faunas from Ahl al Oughlam, Morocco (Geraads, 2002; Geraads et al., 2010) and Bouri Formation from eastern Africa (De Heinzelin et al., 1999). The Q-mode dendrogram reveals a deep divergence between Eurasian and African herbivore faunas. The herbivore community from eastern Europe is clustered together with Central Asia, while western Europe and the Balkan Peninsula form a cluster with increasing similarity from east to west (Fig. 2A).

3.2. “Dmanisi Age” (2.0-1.8 Ma)

Athough geographically restricted to the Caucasus, this paleobiogeographic stage of faunal evolution from western Eurasia is remarkable for the earliest arrival of *Homo* in western Eurasia, recorded at the paleoanthropological site of Dmanisi (Gabunia et al., 2000; de Lumley et al., 2002). Within this stage, only two herbivore species or groups of species are recorded in all considered biogeographic areas: the stenonid horse *Equus stenonis* (*cf. stenonis, cf. namadicus, mygdoniensis, olivolanus, senezensis, major, athanasiui*) and *Stephanorhinus etruscus*.

Western Europe. This stage of paleobiogeographic evolution is presented by the fauna of Tegelen and partially by the Sénèze fauna. The paleontological record from

Tegelen represents a humid biotope and is characterized by presence of cervids *Eucladoceros ctenoides* (= *E. tegulensis*) and *Metacervocerus rhenanus*, a large bovid *Leptobos sp.*, a primate *Macaca sylvanus florentina* (Vervoort-Kerkhoff and van Kolfschoten, 1987). The fauna of Sénèze represents a mammal community from a drier environment characterized by presence of a diversified community of bovids (*"Leprobos" etruscus, Gallogoral meneginii, Pliotragus ardeus, Megalovis latifrons, Procamptoceras brivatense*), a new cervid of Asian origin *Alces gallicus*, and local forms of *Eucladoceros ctenoides* (= *E. senezensis*), *Metacervocerus rhenanus*, and *Croizetoceros ramosus* (Pastre et al., 2015).

The Iberian Peninsula. The fauna from Fonelas-1 (Spain) yielded a rich herbivore association very similar to that of Sénèze (Arribas et al., 2009). Unlike the coeval faunas from northwestern Europe, the fauna of Fonelas-1 lacks *Alces gallicus* and contains such endemic and/or new forms as *Mitilanotherium sp.*, *Capra baetica*, and *Anancus* cf. *arvernensis* (Arribas et al., 2009).

The Italian Peninsula. For long time, the fauna from Olivola was known as an important record of dispersal of *Canis etruscus* and *Pachycrocuta brevirostris* in western Europe (Azzaroli, 2001). The fauna of herbivores is represented by "*Leptobos" etruscus*, *Gallogoral meneghinii, Eucladoceros ctenoides* (= *E. dicranios olivolanus*) and two smaller cervids *Praeelaphus* cf. *lyra* and *Cervus nestii* (=*Dama nestii*) (Croitor, 2014). *Praeelaphus* cf. *lyra* is a remarkable Pliocene holdover from the fauna of Olivola, while *C. nestii* is a new faunal element closely related to modern red deer. The absence of *Alces gallicus* is noteworthy.

The Balkan Peninsula. The synchronous Olivola faunas from the Balkan Peninsula are poor. However, they provide the main paleozoogeographic characteristics of this region. The site of Leu (Southern Romania) yielded remains of *Alces gallicus*, *Eucladoceros* cf. *dicranios*, "*Leptobos*" *etruscus*, *Pliotragus ardeus* (Croitor and Popescu, 2011). The site of Gerakarou (Greece, MNQ18) yielded the easternmost remains of *Croizetoceros ramosus* (Koufos and Kostopoulos, 1997).

Eastern Europe. Possibly, the closest to the above discussed faunas from eastern Europe is the site of Salcia Quarry from Moldova. The fauna of Salcia is considered mixed (Abbazzi et al., 1999). However, the more general biogeographic context may suggest a peculiar regional character of the fauna. The herbivore community from Salcia contains the large cervids *Praemegaceros obscurus* (= *Megaceroides obscurus*), *P. pliotarandoides* (= *Psecupsoceros orientalis*), *Arvernoceros verestchagini* (possibly closely related to "*Cervus*" *colberti* from the Sivalik Hills), *Alces gallicus*, a fallow deer *Dama sp.* (similar to *D. eurygonos*), *Bison (Eobison) sp., Paracamelus gigas, Elasmotherium sp., Stephanorhinus* cf. *etruscus*, and a stenonid horse.

The Caucasus. The fauna of Dmanisi provides the first well-dated record in western Eurasia of *Bison (Eobison), Pontoceros, Soergelia*, and the giant cervid *Praemegaceros obscurus* (Vekua et al., 2010). *Gallogoral* and *Paleotragus* are faunal holdovers characteristic of the fauna of Dmanisi (Bukhsianidze, 2016). The medium-sized cervid "*Cervus* (ex. gr. *Arvernoceros ardei*)" (Vekua, 1996) is a Ruscinian/early Villafranchian holdover closely related to *Praeelaphus perrieri* (Croitor, 2017). The primitive small-sized cervid closely related to modern red deer *Cervus nestii* (= *C. abesalomi*; = *Pseudodama nestii*) is a new faunal element of Central Asian origin. Both *C. nestii* and *Praeelaphus sp.* (cf. *P. lyra*) are shared with fauna from Olivola (Italy). Although *Eucladoceros* was reported in the composition of the Dmanisi fauna (Vekua, 1996), there is no well-preserved fossil evidence confirming this. *Arvernoceros insolitus* Vekua et al., 2010 is an oriental faunal element showing a great similarity to *Sinomegaceros*. The herbivore fauna associated with paleoanthropological finds is very peculiar and has a clear Eurasian and Asian origin (Gabunia et al., 2000).

The coeval faunas from Ain Bucherit in Northwest Africa (Arambourg, 1979; Geraads et al., 2010) and Melka-Kunturé in East Africa (Geraads et al., 2004) are included in the analysis. The Q-mode dendrogram shows a basal dichotomy between African and Eurasian regional faunas, while the regional faunas of European subcontinent show an unexpected split between western Europe, Italy and the Balkans on the one hand and Iberia, eastern Europe and the Caucasus on the other (Fig. 2, B).

3.3. *"Untermassfeld Age" (1.2–1.0 Ma)*

The rich fossiliferous site of Untermassfeld (Germany) dated back to ca. 1 Ma (Kahlke, 2006) is chosen as a reference site for the next stage of paleobiogeographic evolution. The species or species groups recorded in all considered Eurasian paleobiogeographic areas are *Equus altidens/wuesti/granatensis* (see Lister et al., 2010), *Mammuthus meridionalis/tamanensis*, and *Stephanorhinus etruscus/brachycephalus*.

Western Europe. The site of Ceyssaguet (France) yielded the richest well-dated fauna (1.2 Ma) of western Europe with an interesting herbivore community, containing typical Villafranchian ruminants like *Eucladoceros ctenoides*, *Metacervocerus rhenanus*, *Dama sp., Praemegaceros obscurus*, *"Leptobos" sp*. (closely related to "*L.*" *etruscus*), *S. etruscus*, a stenonid horse (Croitor and Bonifay, 2001). The fauna from Ceyssaguet represents a paleobiogeographic interest as a remnant of typical archaic Villafranchian fauna.

Central Europe. The Epivillafranchian fauna of Untermassfeld (Germany) is just slightly younger than the fauna from Ceyssaguet, but it contains a significantly renewed community of herbivores: a large long-limbed *Bison menneri*, *Arvernoceros giulii* (= *Eucladoceros giulii*), *Capreolus cuzanoides*, *Dama vallonnetensis*, *Alces carnutorum*, *Hippopotamus amphibius*, and *Macaca sylvanus* (Kahlke, 2006). Only the smaller horse *Equus wuesti* is present in the Untermassfeld fauna, which, according to Lister et al. (2010), is closely related to hemionus-like *Equus altidens*. Poor antler fragments that were interpreted as *Eucladoceros* of *ctenoides* type most probably belong to *Praemegaceros* similar to *P. pliotarandoides* (Croitor and Kostopoulos, 2004). A similar fauna has been reported from Rosières near Saint-Florent-sur-Cher situated in the northern plain of France (de Grossouvre and Stehlin, 1912). The fauna of Rosières contains a large cervid described by Stehlin as *Cervus* (*Megaceros*) *dupuisi* that is a forgotten senior synonym of *Arvernoceros giulii*. Although the faunas from Untermassfeld and Ceyssaguet are not strictly coeval, most probably they coexisted during a certain geological period, since the late early and early middle Pleistocene faunas of western Europe contain comparatively specialized forms of *Eucladoceros ctenoides tetraceros* and *Praemegaceros dawkinsi*, a dwarfed descent of *P. obscurus* that survived in the climate refugia of northwestern Europe (Croitor and Brugal, 2007).

The Iberian Peninsula. The transitional early–middle Pleistocene fauna from Iberian Peninsula is reported from Cueva Victoria (Clols et al., 1999). The site yielded the only fossil evidence of the African cercopithecid *Theropitecus* in Europe (Gibert et al., 2016). The community of herbivores also includes an archaic *Dama*, the European endemic cervid genus *Praedama*, an Asian tahr *Hemitragus*, *Bison*, and *Hippopotamus*. The occurrence of the oldest European Acheulean tools from the contemporaneous nearby site of Cueva Negra attests to a hominine presence in the Iberian Peninsula (Gibert et al., 2016). The slightly older Iberian site of Quibas yielded a similar faunal assemblage that additionally attests to the presence of *Macaca sylvanus* (Alba et al., 2011). *Praemegaceros* cf. *obscurus* from Barranco Leon-5 (Martínez-Navarro et al., 2004b: Fig. 9) lacks the characteristic of *P. obscurus* basal tine resting on the burr and is rather close to *P. orientalis*, but the distal portion of the antler under discussion is simplified, which may represent a taxonomically meaningful character. Even if the antler of *Praemegaceros* from Barranco Leon-5 belongs to an endemic Iberian species, it is regarded here as a part of the *P. pliotarandoides* dispersal event. The open landscape dwellers *Alces carnutorum* and *Bison menneri* are not present in the Iberian Peninsula.

The Italian Peninsula. The fossiliferous site of Madonna della Strada (L'Aquilla, Italy) yielded remains of *Arvernoceros giulii* that possibly coexisted with the first *Praemegaceros* on the Italian Peninsula (Petronio and Pandolfi, 2011). Remains of *Bison (Eobison) sp*. and *Dama eurygonos* (= *D. nestii eurygonos*, = *Pseudodama nestii*, = *Axis nestii*) are known from Capena (Croitor, 2016; Gliozzi et al., 1997; Petronio, 1979). Poor remains of *Alces* cf. *carnutorum* were discovered in the fauna from Leffe (Pre-Alps, northern Italy); this cervid was present only in the northern part of the Italian Peninsula together with *Hippopotamus* and *Praemegaceros* (Breda and Marchetti, 2007). Obviously, the dispersal of *Alces* was restricted to the northern part of the Italian Peninsula. The cervical vertebrae from Pirro Nord ascribed to *Theropithecus* were reassigned to the porcupine *Hystrix refossa* (Gibert et al., 2016). Therefore, this primate is excluded from the Italian paleontological record in the present work.

The Balkan Peninsula. The latest Villafranchian site of Apollonia-1 (Greece) yielded a specific herbivore fauna with *Praemegaceros pliotarandoides*, giant *Arvernoceros* cf. *verestchagini*, *Bison (Eobison)* sp., *Soergelia brigittae*, *Praeovibos* sp., *Pontoceros ambiguus*, and Caprinae (Croitor and Kostopoulos, 2004; Kostopoulos, 1997; Koufos, 2001). The coeval fauna of Voulgarakis yielded remains of *Hippopotamus amphibius* (Koufos, 2001). The similar fauna from Kalamoto (Greece) contains also remains of fallow deer *Dama sp*. and another unidentified medium-sized deer (Tsoukala and Chatzopoulou, 2005).

Eastern Europe. The Tzimbal fauna, described by Vereshchagin (1957) from the Tamanian Peninsula, is an important reference fauna for the South of the European part of Russia. The specific faunal elements of Tamanian fauna are *Elasmotherium caucasicus, Sus tamanensis, Paracamelus cf. kujalnikensis, Tragelaphus sp., Gazella sp., Bison (Eobison) tamanensis, Bison menneri* (= *B.* cf. *schoetensacki fide* Vereshchagin, 1957: Figs. 26, 28-1), *Praemegaceros obscurus* (= *Megaceros sp. fide* Vereshchagin, 1957: Fig. 19), *Praemegaceros pliotarandoides* (= ex gr. *Cervus elaphus fide* Verestchagin, 1957: Figs. 21, 22), *Praemegaceros solilhacus* (= *Tamanalces caucasicus*; = Cervidae gen et sp. *fide* Vereshchagin, 1957: Pl. VIII, Figs. 7, 8), and a medium-sized deer described as *Eucladoceros sp*. 1 (Croitor, 2014, 2016; Vereshchagin, 1957). Vereshchagin's "*Eucladoceros sp*. 1" differs from *Arvernoceros giulii* from Untermassfeld in its significantly shorter metapodials and possibly is similar to the medium-sized deer from Kalamoto.

The Caucasus. The site of Akhalkalaki (Georgia) yielded a rich fauna that is slightly younger than 1 Ma (Tappen et al., 2002). The fauna contains *Praemegaceros, Dama, Bison, Capra, Pontoceros, Hippopotamus antiquus* (= *H. georgicus*), *Equus suessenbornensis* and endemic *Equus hipparionoides* (Bukhsianidze and Hertler, 2013; Tappen et al., 2002; Vekua, 1986). The small horse *Equus hipparionoides* is regarded here as a biogeographic analogue of the European *Equus altidens*.

Central Asia. The roughly coeval faunas of Lakhuti-1 and Obigharm (Tajikistan) contain *Paracamelus* cf. *gigas, Gazella sp., Cervus (Rusa) sp., Dicerorhinus* cf. *etruscus, Dicerorhinus mercki, Equus mosbachensis*, and a stenonid horse similar to *E. stehlini* (Forsten and Sharapov, 2000). The slightly younger fauna of Lachuti-1 is characterized by the presence of *Palaeoloxodon*, *Praemegaceros, Sinomegaceros, Gazellospira*, and *Bison* (Vangengeim et al., 1988).

The Northwest African faunas included in the analysis come from the Thomas Quarry 1 (L) (Morocco) and Aïn Hanech (Algeria) (Arambourg, 1979; Geraads et al., 2010; Sahnouni and de Heinzelin, 1998; Sahnouni et al., 2002). The coeval faunas from Buia (Eritrea) and Daka Member of Bouri Formanion (Ethiopia) represent in the study the East African biogeographic region (Gilbert and Asfaw, 2008; Martínez-Navarro et al., 2004a). The Q-mode dendrogram shows a deep dissimilarity between African and Eurasian herbivore communities (Fig. 2C). Among the Eurasian regional faunas, a clear dichotomy is observed between the eastern Europe–Central Asia and the western Europe–Caucasus clusters. The Iberian regional herbivore fauna is clustered together with the Balkan biogeographic region.

4. Discussion

The "Saint-Vallier stage" of paleobiogeographic evolution presents a record of the important faunal turnover and the deep change of ecological structure of the herbivore community that defined the character of early Pleistocene faunas in Europe (Brugal and Croitor, 2007). Climate change was caused by the establishment of the 41 kyr glacial cycles and was marked in Europe by increased seasonality and significantly decreased precipitation (De Menocal, 2004; Mosbrugger et al., 2005). The increased paleobiogeographic regionalism in western Eurasia is one of the important consequences of this climate change (Bonifay, 1996).

The herbivore community of the Iberian Peninsula is quite similar to that of western Europe north of the Pyrenean Mountains, but somewhat impoverished: *Gazellospira, Gallogoral*, and *Metacervocerus* are not recorded in the middle Villafranchian of the Iberian Peninsula. However, the giraffid *Mitilanotherium* and *Paradolichopithecus* are specific warm-loving Iberian faunal elements missing in western Europe north of the Pyrenean Mountains. The Pyrenean Mountains seem to have an insignificant role as a geographic barrier; however, the specific climatic and ecological conditions (dry and warm) may have determined Iberian mammalian distributions (O'Regan, 2008).

The middle Villafranchian fauna of the Italian Peninsula is remarkable due to the presence of such Pliocene cervid holdovers as *Praeelaphus lyra*, *Procapreolus cusanus*, and "*Eostyloceros*" *pidoplitschkoi* that disappeared on the European subcontinent north of the Alps. Apparently, the Italian Peninsula acted as a forest refugium for archaic cervid species and was in greater zoogeographic isolation than Iberia during the middle Villafranchian.

The coeval faunas of the Balkan Peninsula are characterized by the more diversified group of bovids and attest to the first appearance of *Megalovis, Hemistagus*, and *Ovis* on the European subcontinent (Spassov, 2005). Despite their different biogeography, the three large southern peninsulas of the European Subcontinent all acted as climate refugia for early Villafranchian warm-loving mammals: forest-dwelling Pliocene cervids continue to be present in the biogeographic isolation of the Italian Peninsula, while the faunas of Iberia and the Balkans contained such savanna dwellers as *Paradolichopithecus* and paleotragine giraffids.

The Khaprovian fauna from eastern Europe shows some affinities with the Kuruksai fauna from the Tajik Depression of Central Asia: both faunas contain paleotragine giraffids, *Gazellospira torticornis/gromovi*, *Alces gallicus*, and a large bovid similar to *Leptobos*. Perhaps the large *Arvernoceros sp*. from Khapry is a specific South Asian faunal element that belongs to a *Rucervus sivalensis* – *"Cervus" colberti* phylogenetic stock from the Sivalik Hills (see the overview of cervids from the Sivalik Hills in Croitor, 2017).

The "Dmanisi Age" was marked by further climate cooling and higher amplitude 41 kyr cycles that caused increased seasonality and, for the first time in Europe, the drop of the mean temperature of the coldest months below the freezing point, as was shown for Central Europe (Mosbrugger et al., 2005). The faunal evolution in the European subcontinent is marked by the first dispersal of the giant scavenger *Pachycrocuta brevirostris* and an increased importance of smaller cursorial collective hunters like *Canis etruscus* (the "Wolf event" according to Azzaroli, 1983). The dispersal of several new large ruminants in western Eurasia is the most remarkable change in the community of herbivorous mammals (Brugal and Croitor, 2007). The faunal change suggests a predominating deforestation of the European subcontinent (Bar-Yosef and Belmaker, 2011).

The geographically limited presence of *Homo* ex gr. *erectus* in the Transcaucasus and its paleobiogeographic context suggest a specific character of the earliest hominine dispersal in western Eurasia. The explanation should be sought in the peculiar paleogeographic conditions of the Caucasian land at that time. Transcaucasia at the epoch of the Dmanisi fauna rather was a large peninsula separated from the West and from the East by Kujalnik (Black) and Akchagyl (Caspian) seas, respectively, and by the Manych Strait from the north (Gabunia et al., 2000). The mountain range of the Greater Caucasus protected the Caucasian land from the North and apparently created specific mild climate conditions as in the case of large European southern peninsulas protected from the north by the Alpine-Himalayan mountain belt (Fig. 1). All ruminant species associated with *Homo* in Dmanisi are of Asian origin and many of them represent a strong South Asian biogeographic component: *Bison* (*Eobison) georgicus* is closely related to *Bison (Eobison) sivalensis*; *Praemegaceros obscurus* is a form of giant deer known only from the Near East and southern and western Europe, while *Cervus nestii* is a central Asian form that represents an early stage of evolution of modern *Cervus elaphus* (Croitor, 2014). Some species dispersed further westward (*Cervus nestii* is found also in Olivola, Italy) or northward (*Eobison* and *Praemegaceros obscurus* are recorded in Salcia, Moldova). The Caucasian Peninsula also was one of two last refugia for the early Pliocene cervid genus *Praeelaphus* (the Italian Peninsula is the second area of isolated survival of this cervid genus) and for the warm-loving palaeotragine giraffids. One may assume that the seasonal drop of temperature below freezing to the north of the Alpine-Himalayan mountain belt was the main limiting factor for the hominine dispersal. It is necessary to point out that, unlike ubiquitous carnivores with a vast area of distribution, the earliest Eurasian hominines biogeographically behaved very differently and their area of distribution was limited by the Alpine-Himalayan mountain belt, suggesting a different, more stenobiont hominine ecological and biological strategy (Croitor, 2011). Actually, the advantages of an ecological link between early hominines and large saber-toothed felid predators assumed by Blumenschine (1987) seem to be very unlikely, since hominines are poorly adapted for the commensalist ecological niche of a saber-toothed predator because of their low olfactory capacity and specific physiology of thermoregulation (sweating), which reveals the hominine presence to a predator (Croitor, 2008). Taking into account the morphofunctional adaptation of saber-toothed felids for ambush hunting in wooded environments (Croitor and Brugal, 2010), the chances of hominines to survive are very low in this case, since the visual survey of a potential danger and interaction within a hominin group become difficult in forests (Croitor, 2008). Carotenuto et al. (2016) reported a negative interrelationship between the presence of *H.* ex *gr. erectus* and the density of large carnivores, suggesting that carnivore avoidance was important for early hominins.

The Italian paleontological record supplies the evidence for a partial biogeographic isolation of the Italian peninsula at that time: the Dinaric Alps acted as a zoogeographic filter that impeded the dispersal of some specialized open-landscape species (such as *Alces gallicus* and possibly *Mitilanotherium* and *Gazellospira torticornis*) and slowed down the dispersal of some Oriental mammals like *Eucladoceros dicranios* (Croitor and Popescu, 2011). It is interesting that during the late Villafranchian, two endemic large bovid forms with similar body size and eco-morphological characteristics repeatedly evolved on the Italian peninsula and remained locked in the southern arid part of the region: the bison-like *"Leptobos" vallisarni*, and the stunted *B. (Eobison) degiulii* that substituted *"L." vallisarni* during the final stage of Villafranchian. Apparently, the Alps and the forested Dinaric Mountains represented a selective biogeographic filter that impeded the distribution of open-landscape hoofed mammals (*Alces gallicus, Eucladoceros dicranios, Bison (Eobison) tamanensis/georgicus*) into the Italian peninsula during most of the early Pleistocene (Croitor and Popescu, 2011). Possibly, this partial biogeographic isolation during most of the early Pleistocene caused the late arrival of *Homo* on the Italian Peninsula. One can assume that the forested Dinaric Alps represented a biogeographic obstacle for *H.* ex gr. *erectus* that avoided dense forests.

The comparatively high degree of similarity between the Balkan and West European faunas (Fig. 2, B) suggests an intensive dispersal connection between those two paleobiogeographic areas. The Balkan–western European paleobiogeographic connection is very interesting, since it may explain the most probable path of colonization of western Europe by hominines, which took place somewhat later, ca. 1.4 Ma (de Lumley et al., 2009). The Balkan Peninsula protected from the North by mountain chains is the most probable springboard for hominine colonization of the European subcontinent, since *H.* ex gr. *erectus* remained preferentially associated with low/middle latitude (i.e., comparatively warm) sites throughout its colonization history (Carotenuto et al., 2016). Fenced from the north and east by the Carpathian Mountains, the Pannonian plain apparently acted as a bridge for hominin dispersal toward western Europe.

The "Untermassfeld stage" of paleobiogeographic evolution coincides with further climate deterioration caused by the onset of the high-amplitude 100 ka cycles ca. 1.0 Ma ago (De Menocal, 2004). This paleobiogeographic age is characterized by the important faunal turnover known as the "end-Villafranchian event" (Azzaroli, 1983), which deeply changed the structure of both herbivore and carnivore mammal guilds followed by the extinction of the major part of Villafranchian taxa (Brugal & Croitor, 2007; Croitor and Brugal, 2010). The end of the partial biogeographic isolation of the Italian Peninsula is marked by the arrival of such Asian forms as *Bison (Eobison) sp., Arvernoceros giulii*, and *Alces carnutorum*.

The paleobiogeographic similarity between Iberian and Balkan biogeographic areas is caused by the presence of common African (*Hippopotamus*) and Mediterranean faunal elements (*Dama* cf. *vallonnetensis, Praemegaceros pliotarandoides, Praeobivos sp., Praedama sp.*), while the new species that dispersed from temperate Asia (*Alces carnutorum, Capreolus cuzanoides, Bison menneri, Arvernoceros giulii*) did not enter the areas under discussion. The giant *Arvernoceros* cf. *verestchagini* from Apollonia seems to be closely related to "*Cervus*" *colberti* from the Sivalik Hills and represents a remarkable South Asian faunal element together with *Bison (Eobison) sp.*

The Iberian Peninsula is the only region of western Europe that provides evidence of the earliest and sustained presence of a *Homo* population (Carbonell et al., 2008). The isolated occurrence of the African primate *Theropitecus* in combination with *Hippopotamus* and *Equus altidens*, which is assumed to have an African origin, is regarded as an argument for a direct dispersal connection between the Iberian Peninsula and northwestern Africa (Gibert et al., 2016). However, the present multivariate analysis of herbivore associations revealed a significant gap between the coeval faunas of northwestern Africa and Iberia, suggesting rather a strong Asian/Oriental component in the Iberian dispersal events. Clear evidence of faunal exchange between northwestern Africa and the Iberian Peninsula after the Messinian Salinity Crisis is missing (Straus, 2001). Despite some indirect archaeological arguments from Atapuerca in favor of the early "out of Africa" hominin dispersals via the Gibraltar route (Aguirre and Carbonell, 2001), the paleontological and zoogeographic data indicate that the Strait of Gibraltar was an effective natural barrier for humans and mammal faunas throughout the Pleistocene (Currant, 2000; Garcia et al., 2013; O'Regan, 2008). According to Straus (2001), the trans-Gibraltar human contacts were possible only during the terminal Phase of the late Paleolithic.

The "Levant Corridor", or the eastern Mediterranean dispersal route, is the most plausible way of dispersal of early hominines and African large mammals into temperate western Eurasia (Arambourg, 1962). It is important to mention that all African species recorded in the Iberian Peninsula are also found in the eastern Mediterranean area (O'Regan, 2008). Therefore, the Pannonian Plane and western Europe are the most probable biogeographic bridge connecting the Iberian Peninsula and the eastern Mediterranean area. The peculiar biogeographic role of central and western Europe in the colonization of Iberia by African species is not confirmed by paleontological data yet, while the dispersal of *Hippopotamus* via eastern Europe poses fewer questions, since it is confirmed by the geographically continuous paleontological record of the genus from the Near East to western Europe. One can assume that the seasonal temperature drop and the general continentality of the climate in western Europe during the early Pleistocene was mitigated by the influence of the Gulf Stream as suggested for the early middle Pleistocene, when western Europe acted as a "Wet-climate refugium" for some Villafranchian faunal holdovers (Croitor & Brugal, 2007). Interestingly enough, the early Paleolithic of western Europe is detached from the rest of the continent by the so-called Movius Line that represents an imaginary northern and eastern border of distribution of the Acheulian industry and represents a geographic and cultural boundary between the Acheulian (handaxe and cleaver) and the non-Acheulian (chopper/chopping tool) technologies in the East and West of the Old World (Movius, 1948). The eastern part of the Movius Line is drawn along Tien Shan and Himalayas Mountains, Brahmaputra River until the Bay of Bengal and represents an effective biogeographic boundary. The western part of the Movius Line ranges from the Thames River to the Black Sea (Lycett and Bae, 2010) and does not coincide with important geographic obstacles (Fig. 1). Southwest of this line, handaxes are abundant. The lithic technology was interpreted as increasing in complexity west of the Movius Line, while east of this hypothetical line only the record of conservative, unspecialized and "non-progressive" core artifacts was found (Movius, 1948). Although Acheulian-like bifaces were discovered recently in eastern Asia, they are very rare there and the Movius Line *sensu lato* is still regarded as a valid phenomenon (Keates, 2002; Lycett and Bae, 2010). According to Lycett and Norton (2010), the Movius Line is a crossing of a demographic threshold, which delimited the area with a lower density of human population that defined the level of social interconnectedness and, as a result, influenced the effective transmission of technological skills and practices. This hypothesis is very interesting in a paleobiogeographic context, since it presumes specific climate and environmental conditions in the early Paleolithic of western Europe that caused both higher human population density and the survivorship of the last Villafranchian faunal elements.

5. Conclusions

The area of sustainable presence of *Homo* ex gr. *erectus* in the Early Pleistocene of western Eurasia was limited by the Alpine Mountain Belt from the north. The Iberian, Italian and Balkan Peninsulas, protected from the increased seasonality and seasonal drop of temperatures by the Alpine mountain belt, acted as refugia for warm-loving Pliocene faunal holdovers, but the region-specific biome characteristics of each peninsula formed a specific group of holdover species for each paleobiogeographic zone. The dry and warm Iberian and Balkan paleobiogeographic zones acted as refugia for the last European *Mitilanotherium* and *Paradolychopithecus*, while the cervid genera *Praeelaphus, Procapreolus*, and the muntjac-like *"Eostyloceros" pidoplitschkoi* survived in the more humid and forested biomes of the Italian Peninsula. The Italian Peninsula remained partially isolated until the end of the Villafranchian due to the forested Dinaric Alps, which acted as a zoogeographic filter impeding the dispersal of open-landscape dwellers in the peninsula. Apparently, the late arrival of *Homo* on the Italian Peninsula was caused by the Dinaric zoogeographic filter. The herbivore fauna associated with the earliest *Homo* in western Eurasia from Dmanisi (Georgia) contains new South-Asian ruminant species and a few endemic holdovers similar to those of Mediterranean refugia (*Palaeotragus* and *Praeelaphus*). Therefore, the paleobiogeography of early human dispersals in western Eurasia characterizes *H.* ex gr. *erectus* as a temperature sensitive stenobiont, that failed to disperse north of the Alpine Mountain Belt, unlike ubiquitous carnivorans of presumed African origin (*Megantereon, Pachycrocuta*) or South-Asian herbivores (*Eobison, Praemegaceros obscurus, Arvernoceros verestchagini*). The geographically restricted earliest human presence in the Iberian Peninsula should be regarded as evidence of the sustainable presence of human population in this isolated area. The multivariate analysis of regional faunas from western Eurasia supports the paleobiogeographic model of the hominine dispersal to Iberia from the eastern Mediterranean through the Balkans, the Pannonian plain and western Europe, thus confirming the early hominine dispersal model in Europe proposed by Carotenuto et al. (2016). The Pannonian plain situated southwest of the Carpathian Mountains was apparently characterized by a comparatively warm climate similar to that of the Mediterranean area, while the climate of the western European paleobiogeographic area was mitigated by the Gulf Stream influence and could support episodic hominin dispersals toward the Iberian Peninsula. The "wet-climate refugia" for the last Villafranchian herbivores in western Europe (Croitor and Brugal, 2007) and the archaeological artefact based Movius Line separating western Europe from the rest of northern Eurasia confirm the peculiar paleobiogeographic significance of the western European area and its importance for early hominin dispersals to the Iberian Peninsula.

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