The Montopoli site, a reference Local Fauna
in the Pliocene and Pleistocene European Large Mammals Biochronology,
first discovered by Giovanni Capellini (1833-1922)

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ABSTRACT - The Italian paleontologist Giovanni Capellini (1833-1922), internationally renowned for his studies on cetaceans, was the first to discover one of the most important sites for European land mammals biochronology of the Pliocene and Pleistocene, Montopoli (Pisa province; Tuscany). Excavated during the second half of the nineteenth century by the Swiss paleontologist Charles Immanuel Forsyth Major (1843-1923), the fauna from Montopoli differs greatly from the older sites of Italy and Europe. The presence of taxa adapted to more open country environments, typical of arid and progressively cooler habits, contrasts with the faunas of the Early Villafranchian (generally characterized by wooded, tropical/subtropical taxa). This difference led several scholars to regard the fauna of Montopoli as the base of the Middle s. The present study aims to investigate the relationships, in terms of similarity/differences, between the faunal association of Montopoli as compared to other Pliocene and Pleistocene ones from the Old World. Toward achieving this objective we used generic-based resemblance indices and permutative clustering methods attested in literature for their discrimination power. The results of our analysis strengthen the interpretation of the pivotal importance of the faunal association of Montopoli, not only at a regional level but also within a pan-Eurasian Pliocene and Pleistocene framework.

INTRODUCTION

Giovanni Capellini (1833-1922) was a student of the eminent geologist and paleontologist Giuseppe Meneghini (1811-1889) at the University of Pisa. Capellini is renowned for his important works on marine mammals (among others Capellini, 1872, 1873, 1876, 1905) and for his international exposure and commendations (member of the Senate of the Italian Kingdom, Rector of the University of Bologna, President of the Italian Geological Society, promotor of the early stages of the Geological Map of Italy; see Corsi, 2003). Nevertheless, in his early career stages, he had a main role in the discovery of Montopoli, a renowned site in the Lower Valdarno basin of critical importance for European Land Mammal Biochronology (Fig. 1). Capellini was at Montopoli visiting the locality where Count Guicciardini had discovered, in 1854, remains of a large, enigmatic cetacean, which Capellini himself described some years later under the name *Idiocetus guicciardinii* Capellini, 1876 (Fig. 2). At Montopoli, Capellini also discovered the occurrence of terrestrial mammal remains (including a mastodon), and news about this discovery reached the Swiss physician and paleontologist Charles Immanuel Forsyth Major (1843-1923) in the 1870s (Forsyth Major, 1877).

Forsyth Major was an eminent figure among mammal paleontologists, active all across Europe, from the 1870s to the beginning of the 1920s. Of Scottish birth, Forsyth Major graduated in Medicine in Basel in 1868 and started his professional practice in Florence (Italy), where he stayed for about a decade. Like many 19th century physicians, however, he was fascinated by natural history and devoted much of his spare time to the study of fossil mammals (Rook & Alba, 2012). Thanks to the information gathered from the Capellini surveys, in 1880 Forsyth Major conducted paleontological excavations, on behalf of the Geology Laboratory of Florence, in what would become one of the most famous Tuscan conservatories for mammalian paleontology. The results of these early excavations comprise the Montopoli collection still housed in the Museo di Storia Naturale, Geologia e Paleontologia di Firenze.

In this contribution, we critically analyze the large mammal association of Montopoli from a zoogeographic point of view, using several analytic methods in comparison to Pliocene-Early Pleistocene sites from Eurasia and Africa.

STRATIGRAPHIC AND BIOCHRONOLOGICAL SETTING

Montopoli Val d'Arno is a town located in Tuscany, about 27 km east-southeast of Pisa and 40 km west-southwest of Florence. The continental mammal-bearing sands excavated by Forsyth Major outcropped in at least two localities: "L'Uccellatoio" Hill and "Poggio di Montevecchio", both located a few kilometers southeast

Fig. 1- Map of Italy, showing the position of Montopoli.

of the town of Montopoli (De Giuli & Heintz, 1974a, b) (Fig. 1). These sandy sediments, characterized by a yellowish-brownish aspect, alternate with marine littoral deposits in the local stratigraphic setting and overlie, at a regional scale, Upper Pliocene strata (i.e., "middle Pliocene" in papers previous to the IUGS 2009 decision), which are in turn marked by a regression-transgression facies of frequent fluctuation typical of deltaic deposition, and clayish-silty facies of proximal (coastal plain or lagune) or near shore environments (Benvenuti et al., 1995, 2014). The sediments of Montopoli are correlative with the Gauss-Matuyama transition (Lindsay et al., 1980; Benvenuti et al., 1995) and thus with the Plio/Pleistocene boundary (Gelasian Stage, GSSP at Monte San Nicola Section, Sicily; Gibbard et al., 2010).

The fossil mammals from Montopoli have been analyzed by several authors since their discovery (Forsyth Major, 1885; Del Campana, 1915; Merla, 1949; De Giuli & Heintz, 1974a, b; Azzaroli, 1977; Ficcarelli, 1984; Abbazzi & Croitor, 2003; Cherin et al., 2013; Bartolini-Lucenti, 2017; Pandolfi et al., 2017; Rook et al., 2017; Bernor et al., 2018). According to published data, the fauna is composed of sixteen taxa (Tab. 1). The carnivorans taxa here recorded include: *Acinonyx pardinensis* (Croizet & Jobert, 1828) described by Del Campana (1915) as a new species *Felis* (*Cynailurus*) *etruscus*; the enigmatic *Puma pardoides* (Owen, 1846); the large *Pliocrocuta perrieri* (Croizet & Jobert, 1828); and the hypocarnivorous *Nyctereutes megamastoides* (Pomel, 1842). The proboscideans are represented by the bunodont *Anancus arvernensis* (Croizet & Jobert, 1828) and the primitive *Mammuthus rumanus* (Ştefănescu, 1924). The perissodactyls include two rhinocerotids, *Stephanorhinus jeanvireti* (Guérin, 1972)

Fig. 2 - Tridimensional scans of part of the holotype skeleton of *Idiocetus guicciardinii* Capellini, 1876, two tympanic bullae housed at the Museo di Storia Naturale, Geologia e Paleontologia di Firenze. The maximum length of the bullae is 12 cm.

Order	Family	Genus	Species
Carnivora	Canidae	*Nyctereutes*	*megamastoides*
Carnivora	Felidae	*Acinonyx*	*pardinensis*
Carnivora	Felidae	*Puma*	*pardoides**
Carnivora	Hyaenidae	*Pliocrocuta*	*perrieri*
Proboscidea	Anancidae	*Anancus*	*arvernensis*
Proboscidea	Elephantidae	*Mammuthus*	*rumanus**
Perissodactyla	Equidae	*Cremohipparion*	sp.
Perissodactyla	Equidae	*Equus*	cf. *livenzovensis**
Perissodactyla	Rhinocerotidae	*Stephanorhinus*	*jeanvireti*
Perissodactyla	Rhinocerotidae	*Stephanorhinus*	*etruscus**
Artiodactyla	Bovidae	*Gazella*	*borbonica*
Artiodactyla	Bovidae	*Leptobos*	*stenometopon*
Artiodactyla	Cervidae	*Croitzoceros*	*ramosus*
Artiodactyla	Cervidae	*Eucladoceros*	*ctenoides**
Artiodactyla	Cervidae	*Procapreolus*	*cusanus*
Artiodactyla	Cervidae	*Preelaphus*	*lyra*

Tab. 1 - List of taxa occurring in Montopoli. Asterisk indicates the first Italian occurrence for the taxon.

and *Stephanorhinus etruscus* (Falconer, 1868), and two equids, the tridactyl *Cremohipparion* sp. and the earliest European monodactyl horse *Equus* cf. *livenzovensis* Bajgusheva, 1978. Cervids are fairly diverse with four distinct species: the large *Eucladoceros ctenoides* (Nesti, 1841), in some works referred to its junior synonym *Eucladoceros falconeri* (Dawkins, 1868); small- to medium-sized cervids are represented by the primitive roe deer-like *Procapreolus cusanus* (Croizet & Jobert, 1828); the slender-antlered *Preelaphus lyra* (Azzaroli, 1992) and *Croizetoceros ramosus* (Croizet & Jobert, 1828). Lastly, Bovidae are documented by the earliest Italian record of *Gazella borbonica* Depéret, 1816 and the occurrence of the leptobovine *Leptobos stenometopon* Rütimeyer, 1865. Unlike many other fossil localities or faunal units of the Italian Peninsula, no micromammals were recovered from Montopoli, being in general very rare in this timeframe (Masini & Sala, 2007), which is referred to the high portion of the *Mimomys polonicus* zone (Masini & Sala, 2007). Within the Quaternary continental stratigraphic and vertebrate palaeontology community the name of "Montopoli" is well known as a reference for large mammal occurrences typical of the Plio/Pleistocene boundary and was used as type locality of a distinct Faunal Unit (FU) in the Italian biochronological scheme of the Villafranchian by Azzaroli (1977). At a continental scale, Montopoli FU corresponds to MN16b in the European MN mammal unit (Guérin, 1990; Mein, 1999). Originally included in the Early Villafranchian (Azzaroli, 1977; Azzaroli et al., 1988), Montopoli FU is characterized by a major faunal turnover from the earlier Triversa FU, leading authors (e.g., Gliozzi et al., 1997; Rook & Martínez-Navarro, 2010) to reinterpret it as the basal FU of the Middle Villafranchian. Among these turnovers, signals of important environmental changes

include the first arrival in western Europe of particular mammal species such as the monodactyl horse *Equus* cf. *livenzovensis* (see Bernor et al., 2018), of a primitive species of the genus *Mammuthus* (Palombo & Ferretti, 2005), of the large deer *Eucladoceros ctenoides* (De Giuli & Heintz, 1974a), and of *Gazella borbonica* (De Giuli & Heintz, 1974b). In addition, the fauna of Montopoli highlights the disappearance of some of the taxa with subtropical affinities still characterizing the previous Early Villafranchian assemblages (such as *Tapirus arvernensis* Croizet & Jobert, 1828; Pradella & Rook, 2007; Cirilli et al., 2020a), and one of the latest occurring *Cremohipparion* sp. in the European fossil record (Rook et al., 2017; Cirilli et al., 2021a).

MATERIAL AND METHODS

To undertake zoogeographic comparisons between the Montopoli large-mammal assemblage and other Pliocene and Early Pleistocene localities from Africa, Europe and Asia, we performed a pairwise comparison using the genus-rank faunal resemblance indexes (GFRI). We followed the methodology of Bartolini-Lucenti et al. (2022a) calculating both Dice's and Simpson's GFRI (as described by Bernor & Pavlakis, 1987; Fortelius et al., 1996a, b; Bernor et al., 2001, 2009; Lordkipanidze et al., 2007; Bernor & Rook, 2008) and the "closeness index" proposed by Geraads (2010). We selected 58 Old World Pliocene-Early Pleistocene (Gelasian-mid Calabrian) localities (ca 5.3-1.4 Ma) in order to compare them to Montopoli (Tab. 2). The compiled matrix of genus occurrences (Tab. 2) is based on published data (Teilhard de Chardin, 1940; De Giuli, 1986; De Giuli et al., 1986; Willemsen, 1992; Alberdi et al., 1997, 1998; Arribas & Palmqvist, 1998; Sen, 1998; Alberdi & Alcalà, 1999; Kostopoulos & Sen, 1999; Sotnikova et al., 2002; Croitor & Kostopoulos, 2004; Gaudzinski, 2004; Martínez-Navarro, 2004; Mazza et al., 2004; Palombo & Valli, 2004; Qiu et al., 2004; Delson et al., 2006; Montoya et al., 2006; Lordkipanidze et al., 2007; Jin & Liu, 2009; Martínez-Navarro et al., 2009, 2012; Geraads et al., 2010; Rook & Martínez-Navarro, 2010; Werdelin & Sanders, 2010; Kahlke et al., 2011; Petronio & Pandolfi, 2011; Rook, 2013; Rook et al., 2013, 2017, 2019; Wang et al., 2013; Bellucci et al., 2014; Madurell-Malapeira et al., 2014; Bartolini-Lucenti & Rook, 2016, 2018; Gkeme et al., 2017; Piñero et al., 2017; Athanassiou, 2018; Bukhsianidze & Koiava, 2018; Fourvel et al., 2018; Koufos, 2018; Sahnouni et al., 2018; Sen & Sarraç, 2018; Sun et al., 2018, 2021; Bartolini-Lucenti & Madurell-Malapeira, 2020, 2021; Breda et al., 2020; Cirilli et al., 2020a, b, 2021a, b; Bartolini-Lucenti et al., 2021, 2022a; Cherin et al., 2021; Iannucci et al., 2021; Jin et al., 2021; Konidaris et al., 2021; Pandolfi et al., 2021; Paquette et al., 2021). The matrix is available in the online repository Zenodo at the following link: https://dx.doi.org/10.5281/ zenodo.6856564. The fossil specimens of Montopoli are housed in the collection of the Museo di Storia Naturale, Geologia e Paleontologia di Firenze (Italy).

The genus-level faunal resemblance indices were calculated following the formulas provided by Sokal & Sneath (1963) for the Dice's GFRI, Simpson (1943)

Number	Locality	Acronym	Nation	Chronology
1	Montopoli	MON	Italy	Early Pleistocene (early Gelasian)
2	Lothagam Apak Member	LTH-Apa	Kenya	Early Pliocene
3	Lothagam Kaiyumung Member	LTH-Kai	Kenya	Late Pliocene
4	Ahl al Oughlam	AaO	Morocco	Early Pleistocene (early Gelasian)
5	Members C–F, Shungura Formation	OMO C-F	Ethiopia	Late Pliocene-Early Pleistocene
6	Upper Burgi Member, Koobi Fora Formation	U Burgi	Kenya	Early Pleistocene (Gelasian)
7	KBS Member, Koobi Fora Formation	KBS	Kenya	Early Pleistocene (Calabrian)
8	Olduvai Bed 1	Old 1	Tanzania	Early Pleistocene (Calabrian)
9	Sterkfontein Member 4	STK Mb4	South Africa	Early Pleistocene (Gelasian)
10	Kromdraai Member 2	KROM2	South Africa	Early Pleistocene (late Gelasian)
11	Drimolen Main Quarry	DMQ	South Africa	Early Pleistocene (late Gelasian)
12	Maramena	Maram	Greece	Early Pliocene
13	Verduno	Verduno	Italy	Early Pliocene
14	Sable pliocène de Montpellier	MtPel	France	Early Pliocene
15	Perpignan	Perp	France	Early Pliocene
16	Çalta-1	Cal-1	Turkey	Early Pliocene
17	Layna	Lay	Spain	Early Pliocene
18	La Calera	LaCal	Spain	Early Pliocene
19	Wölfersheim	Wölf	Germany	Early-Late Pliocene
20	Milia 5	Milia5	Greece	Late Pliocene
21	Triversa	Triv	Italy	Late Pliocene
22	Collepardo	CPar	Italy	Late Pliocene
23	Kvabebi	KVB	Georgia	Late Pliocene
24	Perrier Les Etouaires	PerEt	France	Late Pliocene
25	El-Rincón	ERic	Spain	Late Pliocene
26	Roca-Neyra	RN	France	Late Pliocene
27	Khapry Faunal Complex	KhFC	Russian Federation	Early Pleistocene (Gelasian)
28	Pardines	Pard	France	Early Pleistocene (Gelasian)
29	Saint Vallier	St.Val	France	Early Pleistocene (Gelasian)
30	Chilhac	Chilh	France	Early Pleistocene (Gelasian)
31	Senèze	Sen	France	Early Pleistocene (Gelasian)
32	Villarroya	VLR	Spain	Early Pleistocene (Gelasian)
33	La Puebla de Valverde	LPVv	Spain	Early Pleistocene (Gelasian)
34	Coste San Giacomo	CSG	Italy	Early Pleistocene (Gelasian)
35	Sesklon Upper Level	SeskU	Greece	Early Pleistocene (Gelasian)
36	Dafnero	DFN	Greece	Early Pleistocene (Gelasian)
37	Vatera	VAT	Greece	Early Pleistocene (Gelasian)
38	Volax	VOL	Greece	Early Pleistocene (Gelasian)
39	Olivola	OLIV	Italy	Early Pleistocene (Gelasian)
40	Fonelas P1	FonP1	Spain	Early Pleistocene (Gelasian)
41	Le Coupet	LeCoup	France	Early Pleistocene (late Gelasian)
42	Tsiotra Vryssi	TsVry	Greece	Early Pleistocene (late Gelasian)
43	Pantalla	Pant	Italy	Early Pleistocene (late Gelasian)

Tab. 2 - Complete list of the localities used in the present work with the time correlation.

Number	Locality	Acronym	Nation	Chronology
44	Gerakarou-1	GER	Greece	Early Pleistocene (early Calabrian)
45	Dmanisi	DMA	Georgia	Early Pleistocene (early Calabrian)
46	Poggio Rosso	PR	Italy	Early Pleistocene (late Gelasian)
47	Libakos	LIB	Greece	Early Pleistocene (early Calabrian)
48	Casa Frata	CF	Italy	Early Pleistocene (Calabrian)
49	Farneta Unit	Farn	Italy	Early Pleistocene (Calabrian)
50	Venta Micena	VM	Spain	Early Pleistocene (Calabrian)
51	Pirro Nord	Pirro	Italy	Early Pleistocene (Calabrian)
52	'Ubeidiya	UBEI	Israel	Early Pleistocene (Calabrian)
53	Shihuiba	SHB	China	Early Pliocene
54	Longdan locality	Longdan	China	Early Pleistocene (Gelasian)
55	Zhoukoudian Locality 18	ZKD18	China	Early Pleistocene (Gelasian)
56	Renzidong Cave	RZD	China	Early Pleistocene (late Gelasian)
57	Xiashagou, Classic Nihewan	Nihew	China	Early Pleistocene (early Calabrian)
58	Jinyuan Cave Lower fauna	JYCLow	China	Early Pleistocene (late Gelasian)

Tab. 2 - Continuation.

for Simpson's, Geraads (2010) for the closeness index. They are calculated as follows: the Dice's GFRI is 2A/(2A+B+C) in which A is the number of genera shared by both faunas; B is the number of genera exclusive of the first fauna; C is the number of genera exclusive of the second fauna; the Simpson's index is calculated by A/(A+E) in which E is the smallest number of taxa between B and C. Lastly, the closeness index is calculated as A (A+B+ C)/(A+B) (A+C) (where A, B and C are the same as for Dice's and Simpson's indexes). The use of different indices allows us to detect differing degrees of similarity as maintained by many scholars (Archer & Maples, 1987; Maples & Archer, 1988; Fortelius et al., 1996a, b; Geraads, 2010; Bartolini-Lucenti et al., 2022a). Dice's GFRI is affected by the record of the taxa in each site, as it strictly takes into account the recorded taxa in both of the compared sites (Archer & Maples, 1987; Maples & Archer, 1988). Simpson's GFRI is valuable as it is demanding of the record (indeed the number of different taxa between the sites considered by the index is limited to the smallest of the two). In this way, the effect of the missing record is mitigated, although not removed (Fortelius et al., 1996a, b). On the other hand, the closeness index is less affected by unequal sample representation in the analyzed sites, as explained by Geraads (2010).

Following Bartolini-Lucenti et al. (2022a), we selected three of the oldest and most similar localities to Montopoli to cross-test pairwise affinities to the other Old-World sites. In order to measure the proximity of Montopoli to other fossil localities considered in this study, we performed a bootstrapping cluster analysis (BCA) on the occurrences of all the considered fossil sites. This partitioning methodology has been found to be useful for testing the robustness of the clustering results as shown in various papers (Raia et al., 2009; Carotenuto et al., 2016; Bartolini-Lucenti et al., 2022a, b). The procedure and steps of the BCA have been detailed in Bartolini-Lucenti et al., (2022a, b). We calculated BCA by using the package "pvclust" v. 2.2-0 (Suzuki et al., 2019) for R v. 3.6.0 (R Core Team, 2020) in RStudio v. 2021.09.1 (build 372).

MONTOPOLI AND THE PLIOCENE MAMMAL RECORD OF EUROPE

GFRI and closeness index for Montopoli

The results of the pairwise comparisons between Montopoli and the Pliocene-Early Pleistocene Old World vertebrate localities considered here using Dice's, Simpson' GFRI and closeness indices are shown in Fig. 3. It is evident that the Montopoli fauna is closer to Western Eurasian sites, rather than the Asian and, especially, to African ones. Particularly, the highest values of the three indexes are found in the Early and Middle Villafranchian localities of Western Europe and of the circum-Mediterranean area, including: Collepardo (Italy), El-Rincón and La Puebla de Valverde (Spain) and St. Vallier, Pardines, and Chilhac (France). Table 3 summarizes the ranks of the various localities for each index. Nevertheless, fairly high values are also shown by earlier faunas of Layna (Spain), or the younger Villarroya and Fonelas P1 (Spain), Coste San Giacomo (Italy), Le Coupet (France), Sèsklo Upper Level and Vatera (Greece). Nevertheless, the Montopoli fauna appears to be rather different compared to Asian localities (i.e., coeval, or much younger than Montopoli). The only locality with higher values is represented by Jinyuan Cave Lower Fauna (China) showing the following values Dice's GFRI = 0.261, Simpson's GFRI = 0.400 and closeness index = 0.516 (Tab. 3). The age of the African localities does not increase the low affinities with Montopoli. The highest GFRI and closeness indices of the African localities are those of Ahl al Oughlam (Morocco): Dice's GFRI = 0.189, Simpson's GFRI = 0.333 and closeness index = 0.421,
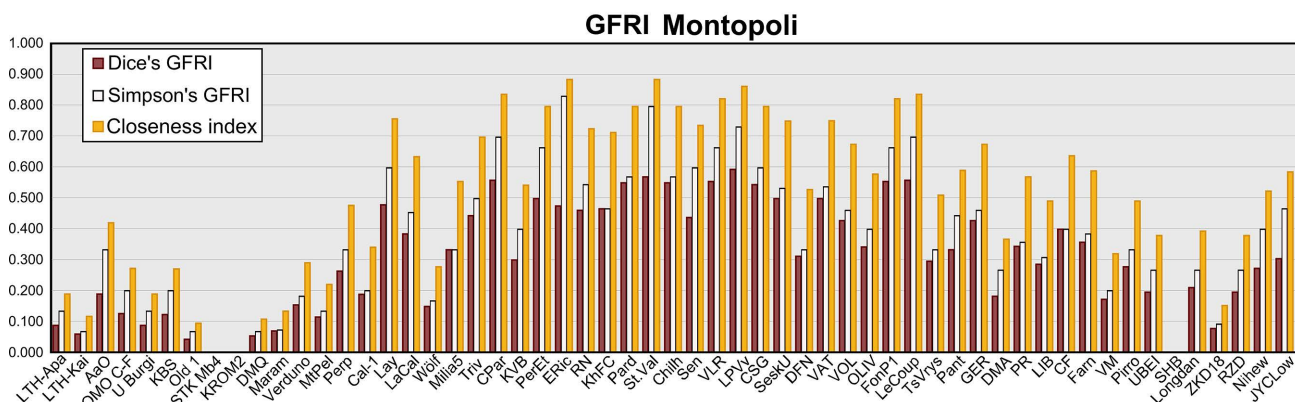
Fig. 3 - Histogram showing the degree of similarities resulting from the pairwise comparison between Montopoli and other selected localities of the Old World, using both Dice's (brown), Simpson's genus faunal resemblance index (white) and the closeness index (yellow). Montopoli shows clear resemblance with Eurasian faunas, especially of the Early and Middle Villafranchian. Abbreviations: LTH-Apa: Lothagam Apak Member (Kenya); LTH-Kai: Lothagam Kaiyumung Member (Kenya); AaO: Ahl al Oughlam (Morocco); OMO C-F: Members C-F, Shungura Formation (Ethiopia); U Burgi: Upper Burgi Member, Koobi Fora Formation (Kenya); KBS: KBS Member, Koobi Fora Formation (Kenya); Old 1: Olduvai Bed 1 (Tanzania); STK Mb4: Sterkfontein Member 4 (South Africa); KROM2: Kromdraai Member 2 (South Africa); DMQ: Drimolen Main Quarry (South Africa); Maram: Maramena (Greece); Verduno: Verduno (Italy); MtPel: Sable pliocène de Montpellier (France); Perp: Perpignan (France); Cal-1: Çalta-1 (Turkey); Lay: Layna (Spain); LaCal: La Calera (Spain); Wölf: Wölfersheim (Germany); Milia5: Milia 5 (Greece); Triv: Triversa (Italy); CPar: Collepardo (Italy); KVB: Kvabebi (Georgia); PerEt: Perrier Les Etouaires (France); ERic: El-Rincón (Spain); RN: Roca-Neyra (France); KhFC: Khapry Faunal Complex (Russian Federation); Pard: Pardines (France); St.Val: Saint Vallier (France); Chilh: Chilhac (France); Sen: Senèze (France); VLR: Villarroya (Spain); LPVv: La Puebla de Valverde; CSG: Coste San Giacomo (Italy); SeskU: Sesklon Upper Level (Greece); DFN: Dafnero (Greece); VAT: Vatera (Greece); VOL: Volax (Greece); OLIV: Olivola (Italy); FonP1: Fonelas P1 (Spain); LeCoup: Le Coupet (France); TsVrys: Tsiotra Vryssi (Greece); Pant: Pantalla (Italy); GER: Gerakarou-1 (Greece); DMA: Dmanisi (Georgia); PR: Poggio Rosso (Italy); LIB: Libakos (Greece); CF: Casa Frata (Italy); Farn: Farneta Unit (Italy); VM: Venta Micena (Spain); Pirro: Pirro Nord (Italy); UBEI: 'Ubeidiya (Israel); SHB: Shihuiba (China); Longdan: Longdan locality (China); ZKD18: Zhoukoudian Locality 18 (China); RZD: Renzidong Cave (China); Nihew: Xiashagou, Classic Nihewan (China); JYCLow: Jinyuan Cave Lower fauna (China).

all rather low (Tab. 3). Indeed, Ahl al Oughlam ranks as the 39th, 30th and 36th (out of 57) most similar locality to Montopoli (Tab. 3), respective to the Dice's, Simpson's and closeness indices.

Comparative similarity indices for three Old-World sites similar to Montopoli

The resemblance and closeness indices of the three European, Asian and African sites most similar to Montopoli, respectively are St. Vallier (France), Jinyuan Cave Lower Fauna (China) and Ahl al Oughlam (Morocco). These values are shown in Fig. 4 while Tabs S1-S3 of the Supplementary Online Material (SOM) illustrate the ordered values for the three sites. In the case of St. Vallier, the most similar faunal associations are El-Rincón, Pardines, Chilhac, La Puebla de Valverde, Perrier Les Etouaires and Senèze, although a high level of resemblance is shared with other 2.5-2.0 Myr-old European sites from Greece, Italy and Spain. It is evident that St. Vallier GFRI and closeness index values are very low (i.e., fauna fairly different) from African localities, with the only exception of Ahl al Oughlam (Fig. 4). On the contrary, Asian sites have higher values (for instance Nihewan and Jinyuan Cave Lower Fauna) as opposed to African ones even not so high, roughly comparable to those of Calabrian European sites (Casa Frata, Venta Micena, Pirro Nord) (Fig. 4). As expected, the pattern of GFRI and closeness index for Jinyuan Cave Lower Fauna shows high values for the chronologically correlating Chinese localities like Xiashagou or Longdan, but also for some Western European localities (e.g., Poggio Rosso, Tsiotra Vryssi, and Olivola). A lower degree of similarity

with Jinyuan Cave Lower Fauna is seen with the Late Pliocene and Gelasian localities from Western Europe (Fig. 4). Comparison histograms with Ahl al Oughlam (Fig. 4) show a generalized pattern of low values for all the localities considered (highest Dice's index = 0.435; highest Simpson's = 0.700 and highest closeness index = 0.755). The localities to which Ahl al Oughlam has higher affinities are the Early Pleistocene East African localities (e.g., Upper Burgi and KBS members of Koobi Fora). Nevertheless, it should be pointed out that there is a certain degree of similarity between the Moroccan site and other Pliocene-Early Pleistocene Western European sites like Layna (with which Ahl al Oughlam has the highest Simpson's GFRI and closeness index; Tab. S3), Roca-Neyra or St. Vallier (as noted above). At the same time other Eurasian localities show high values like 'Ubeidiya and Longdan.

Classification of Montopoli according to its faunal composition

Figure 5 shows the dendrogram resulting from the bootstrapping cluster analysis (BCA) carried out on the absence-presence matrix of the Old-World localities of Tab. 2. Values reported for the branching nodes indicate the identification number (grey), and the percentage *p*-values supporting each node: in blue those *p*-values below 95% of support, and in bold red those above 95%. As visible in Fig. 5 analysis retrieved numerous clusters. The first branching separates old MN14 localities of Europe and China (Maramena, Greece; Verduno, Italy; Shihuiba, China) from the rest of the analyzed sites. Within this larger cluster two subgroups branch out at node 55: one

Dice's GFRI			Simpsons's GFRI			Closeness Index		
1	LPVv	0.595	1	ERic	0.833	1	ERic	0.889
2	St.Val	0.571	2	St.Val	0.800	2	St.Val	0.889
3	CPar	0.560	3	LPVv	0.733	3	LPVv	0.867
4	LeCoup	0.560	4	CPar	0.700	4	CPar	0.840
5	VLR	0.556	5	LeCoup	0.700	5	LeCoup	0.840
6	FonP1	0.556	6	PerEt	0.667	6	VLR	0.825
7	Pard	0.552	7	VLR	0.667	7	FonP1	0.825
8	Chilh	0.552	8	FonP1	0.667	8	PerEt	0.800
9	CSG	0.545	9	Lay	0.600	9	Pard	0.800
10	PerEt	0.500	10	Sen	0.600	10	Chilh	0.800
11	SeskU	0.500	11	CSG	0.600	11	CSG	0.800
12	VAT	0.500	12	Pard	0.571	12	Lay	0.760
13	Lay	0.480	13	Chilh	0.571	13	VAT	0.754
14	ERic	0.476	14	RN	0.545	14	SeskU	0.753
15	KhFC	0.467	15	VAT	0.538	15	Sen	0.738
16	RN	0.462	16	SeskU	0.533	16	RN	0.727
17	Triv	0.444	17	Triv	0.500	17	KhFC	0.716
18	Sen	0.439	18	KhFC	0.467	18	Triv	0.700
19	VOL	0.429	19	JYCLow	0.467	19	VOL	0.677
20	GER	0.429	20	VOL	0.462	20	GER	0.677
21	CF	0.400	21	GER	0.462	21	CF	0.640
22	LaCal	0.385	22	LaCal	0.455	22	LaCal	0.636
23	Farn	0.357	23	Pant	0.444	23	Pant	0.593
24	PR	0.345	24	KVB	0.400	24	Farn	0.590
25	OLIV	0.343	25	OLIV	0.400	25	JYCLow	0.587
26	Milia5	0.333	26	CF	0.400	26	OLIV	0.580
27	Pant	0.333	27	Nihew	0.400	27	PR	0.571
28	DFN	0.313	28	Farn	0.385	28	Milia5	0.556
29	JYCLow	0.304	29	PR	0.357	29	KVB	0.544
30	KVB	0.300	30	AaO	0.333	30	DFN	0.529
31	TsVrys	0.296	31	Perp	0.333	31	Nihew	0.524
32	LIB	0.286	32	Milia5	0.333	32	TsVrys	0.511
33	Pirro	0.278	33	DFN	0.333	33	LIB	0.492
34	Nihew	0.273	34	TsVrys	0.333	34	Pirro	0.492
35	Perp	0.263	35	Pirro	0.333	35	Perp	0.478
36	Longdan	0.211	36	LIB	0.308	36	AaO	0.421
37	UBEI	0.195	37	DMA	0.267	37	Longdan	0.394

Tab. 3 - Resuming GFRI values for Montopoli obtained applying different indices (Dice's, Simpson's, and closeness index). Abbreviations: AaO: Ahl al Oughlam (Morocco); Cal-1: Çalta-1 (Turkey); CF: Casa Frata (Italy); Chilh: Chilhac (France); CPar: Collepardo (Italy); CSG: Coste San Giacomo (Italy); DFN: Dafnero (Greece); DMA: Dmanisi (Georgia); DMQ: Drimolen Main Quarry (South Africa); ERic: El-Rincón (Spain); Farn: Farneta Unit (Italy); FonP1: Fonelas P1 (Spain); GER: Gerakarou-1 (Greece); JYCLow: Jinyuan Cave Lower fauna (China); KBS: KBS Member, Koobi Fora Formation (Kenya); KhFC: Khapry Faunal Complex (Russian Federation); KROM2 = Kromdraai Member 2 (South Africa); KVB: Kvabebi (Georgia); LaCal: La Calera (Spain); LeCoup: Le Coupet (France); LIB: Libakos (Greece); Longdan: Longdan locality (China); LPVv: La Puebla de Valverde; LTH-Apa: Lothagam Apak Member (Kenya); LTH-Kai: Lothagam Kaiyumung Member (Kenya); Maram: Maramena (Greece); MON: Montopoli (Italy); MtPel: Sable pliocène de Montpellier (France); Nihew: Xiashagou, Classic Nihewan (China); Old 1: Olduvai Bed 1 (Tanzania); OLIV: Olivola (Italy); OMO C-F: Members C-F, Shungura Formation (Ethiopia); Pant: Pantalla (Italy); Pard: Pardines (France); PerEt: Perrier Les Etouaires (France); Perp: Perpignan (France); Lay: Layna (Spain); Pirro: Pirro Nord (Italy); PR: Poggio Rosso (Italy); RN: Roca-Neyra (France); RZD: Renzidong Cave (China); Sen: Senèze (France); SeskU: Sesklon Upper Level (Greece); SHB: Shihuiba (China); STK Mb4: Sterkfontein Member 4 (South Africa); St.Val: Saint Vallier (France); Triv: Triversa (Italy); TsVrys: Tsiotra Vryssi (Greece); U Burgi: Upper Burgi Member, Koobi Fora Formation (Kenya); UBEI: 'Ubeidiya (Israel); VAT: Vatera (Greece); Verduno: Verduno (Italy); VLR: Villarroya (Spain); VM: Venta Micena (Spain); VOL: Volax (Greece); Wölf: Wölfersheim (Germany); Milia5: Milia 5 (Greece); ZKD18: Zhoukoudian Locality 18 (China).

Dice's GFRI			Simpsons's GFRI			Closeness Index		
38	RZD	0.195	38	UBEI	0.267	38	UBEI	0.379
39	AaO	0.189	39	Longdan	0.267	39	RZD	0.379
40	Cal-1	0.188	40	RZD	0.267	40	DMA	0.368
41	DMA	0.182	41	OMO C-F	0.200	41	Cal-1	0.341
42	VM	0.171	42	KBS	0.200	42	VM	0.320
43	Verduno	0.154	43	Cal-1	0.200	43	Verduno	0.291
44	Wölf	0.148	44	VM	0.200	44	Wölf	0.278
45	OMO C-F	0.125	45	Verduno	0.182	45	OMO C-F	0.273
46	KBS	0.122	46	Wölf	0.167	46	KBS	0.271
47	MtPel	0.114	47	LTH-Apa	0.133	47	MtPel	0.220
48	LTH-Apa	0.087	48	U Burgi	0.133	48	LTH-Apa	0.189
49	U Burgi	0.087	49	MtPel	0.133	49	U Burgi	0.189
50	ZKD18	0.077	50	ZKD18	0.091	50	ZKD18	0.152
51	Maram	0.069	51	Maram	0.071	51	Maram	0.133
52	LTH-Kai	0.059	52	LTH-Kai	0.067	52	LTH-Kai	0.116
53	DMQ	0.053	53	Old 1	0.067	53	DMQ	0.107
54	Old 1	0.041	54	DMQ	0.067	54	Old 1	0.094
55	STK Mb4	0.000	55	STK Mb4	0.000	55	STK Mb4	0.000
56	KROM2	0.000	56	KROM2	0.000	56	KROM2	0.000
57	SHB	0.000	57	SHB	0.000	57	SHB	0.000

Tab. 3 - Continuation.

includes all the African localities (node 51) and the second one the Pliocene and Pleistocene Eurasian sites (node 53). The support of these groupings is high (respectively 88% and 91%). The large Eurasian group includes four major subclusters (Fig. 5): node 53 and 52 separate the European MN15 localities with Kvabebi; node 48 is composed by two clusters made of the 3.2 - 1.9 Ma European localities and another large group, defined respectively by nodes 46 and 44. Node 44 includes Early Pleistocene Chinese localities (of these, node 23 - the group of Longdan, Xiashagou and Jinyuan Cave Lower Fauna - is characterized by one of the highest percentual p-value of the analysis = 99%), whereas node 40 comprises the European Late Villafranchian sites and 'Ubeidiya (Levant). Node 31 clusters the ca. 2.0 - 1.4 Ma localities from Georgia (Dmanisi), Greece (Libakos, Tsiotra Vrissy), Italy (Casa Frata, Farneta, Olivola, Pantalla, Pirro Nord, Poggio Rosso), and Spain (Venta Micena). Lastly, node 46 includes the Western European and Mediterranean sites dated between ca. 3.2 and 1.9 Ma, together with the Khapry Faunal Complex. The latter is the most different locality of the cluster, branching out at node 46 (Fig. 5). The Late Pliocene-earliest Pleistocene cluster further subdivides into three well-supported groups (node 39 percentual p-value = 88%, 93% for the node 35 and 94% for node 20). Roca-Neyra and El-Rincón are the first to separate from the other localities and are clustered together (node 22). Montopoli is rooted in one of these three subclusters (node 32), coupled with Collepardo (node 26) and close to Triversa (node 28), Perrier Les Etouaires and Villarroya (node 6) (Fig. 5). The other localities from France, Greece, Italy, and Spain form another fairly well supported subcluster at node 34 (Fig. 5). Gerakarou-1 probably branched off from this large group defined at node 34 because of the relatively low generic diversity.

DISCUSSION

The Montopoli fauna represents an important documentation of the mammal faunal turnover in Western Eurasia at the Pliocene/Pleistocene transition. Several taxa recorded at Montopoli are common in the Late Pliocene of Eurasia, such as *Cremohipparion* sp., *Nyctereutes megamastoides*, *Pliocrocuta perrieri*, *Preelaphus lyra*, *Procapreolus cusanus*, but several others underline the turnover that was undergoing across Europe by the end of the Pliocene. The species included within this turnover are *Equus* cf. *livenzovensis*, *Eucladoceros ctenoides*, *Mammuthus rumanus*, which all verify the increase of wider semi-open or open environments in Europe, although these taxa probably still maintained a mixed-feeding, if not browsing, diet (Rivals et al., 2015; Rook et al., 2017; Strani et al., 2018; Saarinen et al., 2021). The increase of open environments is clearly evident when analyzing paleobotanical records. In the Pliocene succession of San Miniato-Montopoli, the levels underlying the mammal fauna evidenced the passage from warm-temperate forests to cooler ones, characterized by the prevalence of conifers (Benvenuti et al., 2007). Mediterranean data such as those collected from Garraf 1 (Spain) highlight the progressive opening of the vegetation during the cold phases from MIS 108 to MIS 98 (~2.7-2.5 Ma; Suc & Popescu, 2005), and from the Italian Peninsula steppe and open vegetation are already recorded at Rena Bianca succession of the Upper
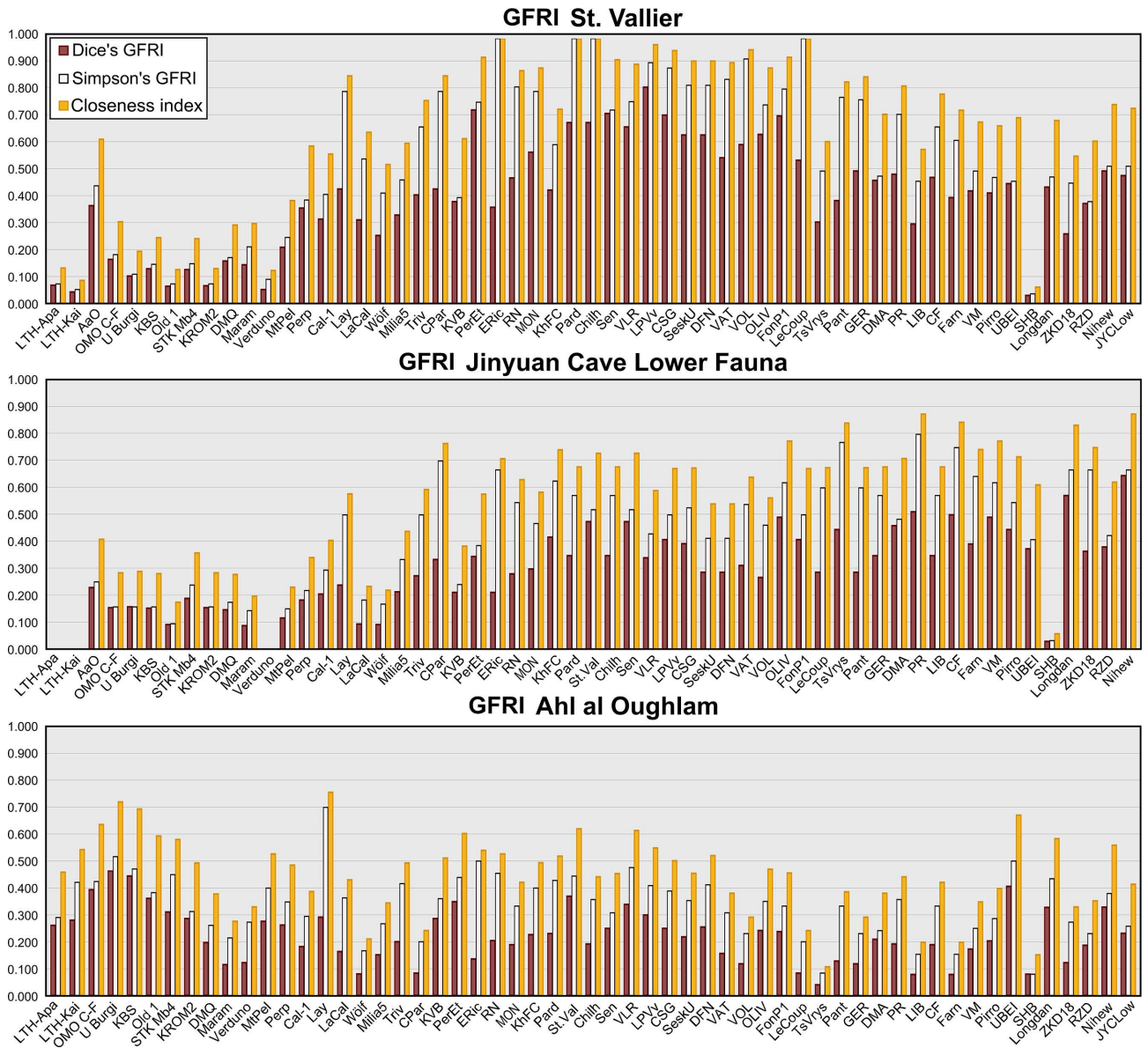
Fig. 4 - Histograms showing the pairwise comparison between the three sites from Europe (St. Vallier), Asia (Jinyuan Lower Fauna) and Africa (Ahl al Oughlam) (the most similar sites to Montopoli) compared to the other selected localities of the Old World, using both Dice's (brown), Simpson's genus faunal resemblance index (white) and the closeness index (yellow). Abbreviations: LTH-Apa: Lothagam Apak Member (Kenya); LTH-Kai: Lothagam Kaiyumung Member (Kenya); AaO: Ahl al Oughlam (Morocco); OMO C-F: Members C-F, Shungura Formation (Ethiopia); U Burgi: Upper Burgi Member, Koobi Fora Formation (Kenya); KBS: KBS Member, Koobi Fora Formation (Kenya); Old 1: Olduvai Bed 1 (Tanzania); STK Mb4: Sterkfontein Member 4 (South Africa); KROM2: Kromdraai Member 2 (South Africa); DMQ: Drimolen Main Quarry (South Africa); Maram: Maramena (Greece); Verduno: Verduno (Italy); MtPel: Sable pliocène de Montpellier (France); Perp: Perpignan (France); Cal-1: Çalta-1 (Turkey); Lay: Layna (Spain); LaCal: La Calera (Spain); Wölf: Wölfersheim (Germany); Milia5: Milia 5 (Greece); Triv: Triversa (Italy); CPar: Collepardo (Italy); KVB: Kvabebi (Georgia); PerEt: Perrier Les Etouaires (France); ERic: El-Rincón (Spain); RN: Roca-Neyra (France); MON: Montopoli (Italy); KhFC: Khapry Faunal Complex (Russian Federation); Pard: Pardines (France); St.Val: Saint Vallier (France); Chilh: Chilhac (France); Sen: Senèze (France); VLR: Villarroya (Spain); LPVv: La Puebla de Valverde; CSG: Coste San Giacomo (Italy); SeskU: Sesklon Upper Level (Greece); DFN: Dafnero (Greece); VAT: Vatera (Greece); VOL: Volax (Greece); OLIV: Olivola (Italy); FonP1: Fonelas P1 (Spain); LeCoup: Le Coupet (France); TsVrys: Tsiotra Vryssi (Greece); Pant: Pantalla (Italy); GER: Gerakarou-1 (Greece); DMA: Dmanisi (Georgia); PR: Poggio Rosso (Italy); LIB: Libakos (Greece); CF: Casa Frata (Italy); Farn: Farneta Unit (Italy); VM: Venta Micena (Spain); Pirro: Pirro Nord (Italy); UBEI: 'Ubeidiya (Israel); SHB: Shihuiba (China); Longdan: Longdan locality (China); ZKD18: Zhoukoudian Locality 18 (China); RZD: Renzidong Cave (China); Nihew: Xiashagou, Classic Nihewan (China); JYCLow: Jinyuan Cave Lower fauna (China).

Valdarno (Gauss/Matuyama boundary; Bertini, 2010), characterized by the abundance of *Artemisia*.

Besides Montopoli, the large *E. livenzovensis* (or *Equus* cf. *livenzovensis*) is found in the ca. 2.6 Ma European localities of El-Rincón (Spain), Roca-Neyra (France) and

Liventsovka (Khapry Faunal Complex, Russia) (Alberdi et al., 1998; Azzaroli, 2000; Bernor et al., 2018, 2019; Cirilli et al., 2021a, b, c). In Asia, one of the earliest species of monodactyl equid is *Equus eisenmannae* Qiu et al., 2004 from Longdan (slightly younger than Montopoli, 2.55 Ma;

Rook et al., 2019). This equid resembles *E. livenzovensis*, especially in size and postcranial elements, even if its cranial morphology shows more primitive features similar to the North American *E. simplicidens*, whereas *E. livenzovensis* appears to be closely related to *E. stenonis* (Cirilli et al., 2021a, b). Regarding carnivorans, the most peculiar taxon recovered in Montopoli is the Eurasian puma, *Puma pardoides* (previously *Panthera schaubi* or *Viretailurus schaubi*). It was a somewhat elusive carnivoran, documented in Western Eurasia during the Early-Middle Villafranchian, in localities such as Kvabebi, St. Vallier, La Puebla de Valverde and doubtfully in Perrier-Les Etouaires. Although not so informative about the environmental conditions of Montopoli, its record in Italy documents the westward dispersal of an Asian taxon (Madurell-Malapeira et al., 2010; Cherin et al., 2013), being previously recorded in Shamar (Mongolia, MN15), and Beregovaya (Transbaikalia, MN15) (Sotnikova, 1978). The combination of the earlier and younger taxa accounts for the peculiar pattern of affinity of Montopoli for both the European localities of the Late Pliocene and those of the Early Pleistocene (Fig. 3). The lesser resemblance between African localities and Montopoli (and by extension European sites) might suggest that the biotic connections between Africa and Eurasia were limited in the Late Pliocene and possibly restricted to some taxa and to certain areas (e.g., the North Africa). Indeed, the absence of numerous wild pig genera and bovids, including the tribes Alcelaphini, Hippotragini, Reduncini, and Tragelaphini, marks the difference between African sites and Eurasian sites (as also observed by Bartolini-Lucenti et al., 2022a). The most similar African locality to Montopoli is Ahl al Oughlam, but even with this site the values of both GFRI and closeness index are fairly low (Tab. 2). Applying the same indices to the three most similar localities, St. Vallier (France), Jinyuan Cave Lower Fauna (China) and Ahl al Oughlam (Morocco), allows the evaluation of their affinity towards other Old-World faunas.

Like in the case of Montopoli, the closest associations to St. Vallier are those of the Early-Middle Villafranchian sites such as La Puebla de Valverde, El-Rincón, Perrier Les Etouaires and Senèze (Alberdi et al., 1997a, b; Palombo and Valli, 2004; Delson et al., 2006), and of the beginning of the Late Villafranchian such as Le Coupet (Palombo & Valli, 2004). Younger European sites, i.e., Late Villafranchian ones, and Asian ones show comparable degree of similarity (as shown in Fig. 4 and Tab. S1). Among these localities, there is Gerakarou-1 (Gkeme et al., 2017), Jinyuan Cave Lower Fauna and Nihewan (Wang et al., 2013; Jin et al., 2021). The African localities have very low GFRI and closeness index, generally lower than 0.300 (Fig. 4 and Tab. S1). An exception is the abundant fauna of Ahl al Oughlam, characterized by numerous Eurasian taxa recorded, namely *Nyctereutes*, *Pliocrocuta*, *Lynx* and *Ursus* (Geraads et al., 2010).

Jinyuan Cave is one of the richest sites of northeastern China, composed of two faunal accumulations of the late Gelasian-early Calabrian and of the latest Calabrian (Jin et al., 2021). The older association (Lower Fauna) has affinity to other chronological coeval Chinese localities such as Xiashagou or Longdan (Qiu et al., 2004; Wang et al., 2013), but also shows relatively high values of GFRI

and closeness index with Western European localities of Casa Frata, Dmanisi, Farneta, Olivola, Poggio Rosso, Tsiotra Vryssi (De Giuli, 1986; De Giuli & Masini, 1986; Rook et al., 2013; Konidaris et al., 2021; Bartolini-Lucenti et al., 2022a). To a lesser extent, the Jinyuan Cave Lower Fauna resembles also older sites like St. Vallier, Senèze, El-Rincón (Viret, 1954; Alberdi et al., 1997; Delson et al., 2006) and younger ones such as Venta Micena (Madurell-Malapeira et al., 2014). At a larger geographic scale, St. Vallier and Jinyuan Cave Lower Fauna share numerous genera, as exhibited by their GFRI scores (Fig. 4 and Tab. S2). This is due to the common occurrence of numerous carnivorans but also *Equus*, *Leptobos*, *Macaca*, *Mammuthus*, *Stephanorhinus* and *Sus*. Compared to the African localities, geographic distance can be accounted as the major responsible for the differences between these sites and the Jinyuan Cave Lower Fauna. Indeed, the GFRI and closeness index with them are quite low. Even in the case of Ahl al Oughlam (Geraads et al., 2010) those values are fairly low, despite the fact this site has the highest values among the African ones.

The analysis of the GFRI and closeness index for Ahl al Oughlam yielded interesting results: as pointed out above, the occurrence in this locality of elements common in coeval or closely dated sites of both Africa and Eurasia yields a generalized pattern of rather low values with most of the localities, especially with old (MN14) or Late Villafranchian European sites. East African sites, especially Koobi Fora members, are relatively similar to Ahl al Oughlam. The high Simpson's GFRI and closeness index between Ahl al Oughlam and Layna (Alberdi & Alcalà, 1999) is the result of the abundance of Eurasian carnivores of Ahl al Oughlam, yet not supported when the whole fauna is considered (e.g., in the case of the Dice's GFRI). Although, the Moroccan site has the highest values of the resemblance indices of the African localities from Montopoli, their affinity is scarce (Fig. 4 and Tab. S3).

The results of the GFRI and closeness index overall suggest an expected pattern of affinity explained by geographic position and chronology of the localities. Eurasian sites possess a degree of higher similarity with one another more than to African ones. The indices for Montopoli fit this general scheme. Nevertheless, an interesting element should be pointed out. All the comparisons (Figs 3 and 4) point out a biotic connection between Circum-Mediterranean Europe and North Africa during the earliest Pleistocene as important, if not more, than that with East and South Africa. It also should be noted that this connection was apparently limited to certain taxa (mainly carnivores), possibly as a result of ecological mechanisms filtering the dispersal from and to Africa of mammals in key contact area (e.g., the Levantine corridor; inter alios Martínez-Navarro, 2004). This second element explains the limited affinity between African (especially East and South ones) and Eurasian localities, which are characterized by important faunal differences especially in the omnivore and herbivore guild. In Africa, the niches of medium- to large-sized cervids, browsing/mixed feeding taxa widespread in Eurasia, are occupied by the varied array of antelope-like bovids, similar to the occurrence of *Sus* in the Pliocene and Pleistocene of Eurasia opposed to the numerous suids of Africa (e.g., *Kolpochoerus*, *Metridiochoerus*, *Hylochoerus*,

Phacochoerus, etc.). Apparently, the peri-Mediterranean connection interrupted shortly after 2.5 Ma, probably for the increasing effect of climatic deterioration at mid-latitudes and their environments.

Observing the results of the BCA, the first branch of the dendrogram (node 56) includes older MN14 Eurasian localities. The association of Shihuiba, Verduno and Maramena can be explained by the persistence of older Miocene taxa which are not found in younger faunas. Among the early taxa exclusive to these localities are *Amphimachairodus*, *Choerolophodon*, *Euprox*, *Indarctos*, *Oioceros* and *Proputorius*. In the BCA, the African localities are separated from the others in a well-supported cluster (percentage *p*-value = 88%), due to the presence of certain genera like *Dinofelis*, *Kobus*, *Panthera*, *Parapapio*, *Theropithecus* and *Tragelaphus* although not shared by all. Within the African cluster, localities are divided partially according to two different criteria: their chronology, as identified by the subcluster of Lothagam, Apak and Kaiyumung Members (node 21; respectively MN14 and MN15-16; Leakey & Harris, 2003), and their position, evident in the grouping of South African Sterkfontein Member 4, Kromdraai Member 2, and Drimolen Main Quarry (Werdelin & Sanders, 2010; Adams et al., 2016; Fouvel et al., 2018) separated from Ahl al Oughlam (Geraads et al., 2010) and the East African localities of Olduvai Bed 1, C-F levels of Shungura Formation and Koobi Fora members (Werdelin & Sanders, 2010). These groups are justified by their composition with some important distinctions between Northern, Eastern and South African localities: for instance, the former share the presence of *Acinonyx*, *Gazella*, *Pelorovis*, *Pseudocivetta*, all missing in the latter. South African localities are characterized by *Caracal*, *Hystrix*, *Megantereon*, and *Suricata* or taxa rare in North and East Africa such as *Chasmaporthetes*, *Damaliscus*, *Papio* and *Vulpes*. The other Eurasian localities are all arranged in a large, well-supported cluster with many subgroups in it. The first two to branch (nodes 53 and 52) include the MN15 localities of Europe with Kvabebi, recently dated at ca. 2.8 Ma (Bukhsianidze & Koiava, 2018; Lazarev et al., 2021). These localities are arranged into two groups of four localities. Their distinction from the rest of Eurasian sites is plausibly rooted in the presence of some taxa typical of the first half the Pliocene, as *Pliorhinus* or *Eucyon*, the sporadic persistence of other earlier forms (e.g., *Propotamochoerus*), or peculiar records like *Agriotherium* in Montpellier and Milia 5, *Parailurus* in Wölfersheim, *Parastrepsiceros* in Kvabebi and *Plioviverrops* in Çalta-1. The first of the two subgroups (node 47; Fig. 5) includes Kvabebi, Çalta-1, Layna, and La Calera, which are associated for the shared records of *Gazella*, the early one of *Lynx* and *Nyctereutes*, and those of *Chasmaporthetes* (except for La Calera) and *Eucyon* (except for Layna) (Sen, 1998; Alberdi & Alcala, 1999). Milia 5 (Kostopoulos et al., 2014), Montpellier, Perpignan, and Wölfersheim are grouped for the presence of *Anancus* (often in association with *Mammut*), *Tapirus*, and the early presence of *Ursus* (Tobien, 1953; Morlo & Kundrát, 2001; Palombo & Valli, 2004). Further relevant forms for the group are also *Dolichopithecus* (absent in Milia 5), *Proboscidipparion* (absent in Wölfersheim). In contrast to the MN15-16 localities, two large groups

of localities branch from node 48. The first (node 44) is further divided into two subgroups, one of Early Pleistocene European sites and the other only of Chinese localities (respectively nodes 40, 37 and 23; Fig. 5). The position of 'Ubeidiya and particularly Dmanisi, Venta Micena and Pirro Nord concurs with the result described by Bartolini-Lucenti et al. (2022a). Opposite to this group, at node 30, the localities of Tsiotra Vryssi (Konidaris et al., 2021), Libakos (Gkeme et al., 2017), Pantalla (Cherin et al., 2021), Casa Frata (De Giuli, 1986), Farneta (De Giuli et al., 1986), Olivola and Poggio Rosso (Mazza et al., 2006) are clustered together in a well-supported group (percentage *p*-value = 93%). The similarity is due to the common record of carnivores (*Canis*, *Homotherium*, *Lynx*, *Pachycrocuta*) and other typical Late Villafranchian elements such as *Equus*, *Mammuthus*, *Pseudodama*, *Stephanorhinus* and *Leptobos*.

In the Chinese group Nihewanian age localities (2.6-1.6 Ma; Wang et al., 2013), Jinyuan Cave Lower Fauna, Longdan, and Xiashagou are grouped together, and their clustering may be related to the co-occurrence of several carnivorans (*Canis*, *Meles*, *Pachycrocuta*, *Ursus*) and some ungulates (like *Equus* and *Cervus*) (Qiu et al., 2004; Wang et al., 2013; Jin et al., 2021).

Similarly, Zhoukoudian Loc. 18 and Renzidong are clustered together for several shared carnivore genera (e.g., the mustelid *Martes*, *Meles*, *Mustela*) and few herbivores (*Equus*, *Muntiacus*) (Teilhard de Chardin, 1940; Jin & Liu, 2009). The second large group branching from node 48, includes European sites dated between 3.2 and ca 1.9 Ma (node 46, Fig. 5). The peculiar position of Khapry Faunal Complex accounts for the difference between this locality and the others of the group: the presence of peculiar taxa, some of which with clear Asian affinity, like *Elasmotherium*, *Palaeotragus* and *Paracamelus*, or the early records of *Arvernoceros* and *Pannonictis*, explains the position in the dendrogram. Roca-Neyra and El-Rincón are close to the other Late Pliocene and Gelasian localities, yet distinct, probably for their limited record, rather than great generic differences (Alberdi et al., 1997; Cirilli et al., 2021a; Bartolini-Lucenti & Spassov, 2022). After the branching of Roca-Neyra and El-Rincón, the European localities are arranged in two groups (node 32 and node 33): the distinction between them is fairly supported for node 34 (percentage *p*-value = 79%) but reduced for node 32 (percentage *p*-value = 68%). The lower support suggests the occurrence of taxa in their faunal compositions is not clearly distinct, and this confounds the BCA results. Nevertheless, some inferences comparing the generic composition can be drawn. Groups connected by node 32 are characterized by the presence, in most cases, of taxa typical of the Late Pliocene, such as *Preelaphus*, *Tapirus*, the persistence of three-toed equids of the genera *Cremohipparion* or *Plesiohipparion*. Moreover, this group represents a combination of missing relevant and younger genera (e.g., *Equus*, *Eucladoceros*, *Gallogoral*, *Gazellospira*, *Mammuthus*, *Meles*, *Metacervoceros*), which are instead typical of the Gelasian localities of the cluster branching from node 33. Indeed, the latter sites (Fig. 5), despite the difference in age between them, generally share numerous species, in addition to the one just mentioned, like the carnivores *Pliocrocuta* or *Homotherium*, the
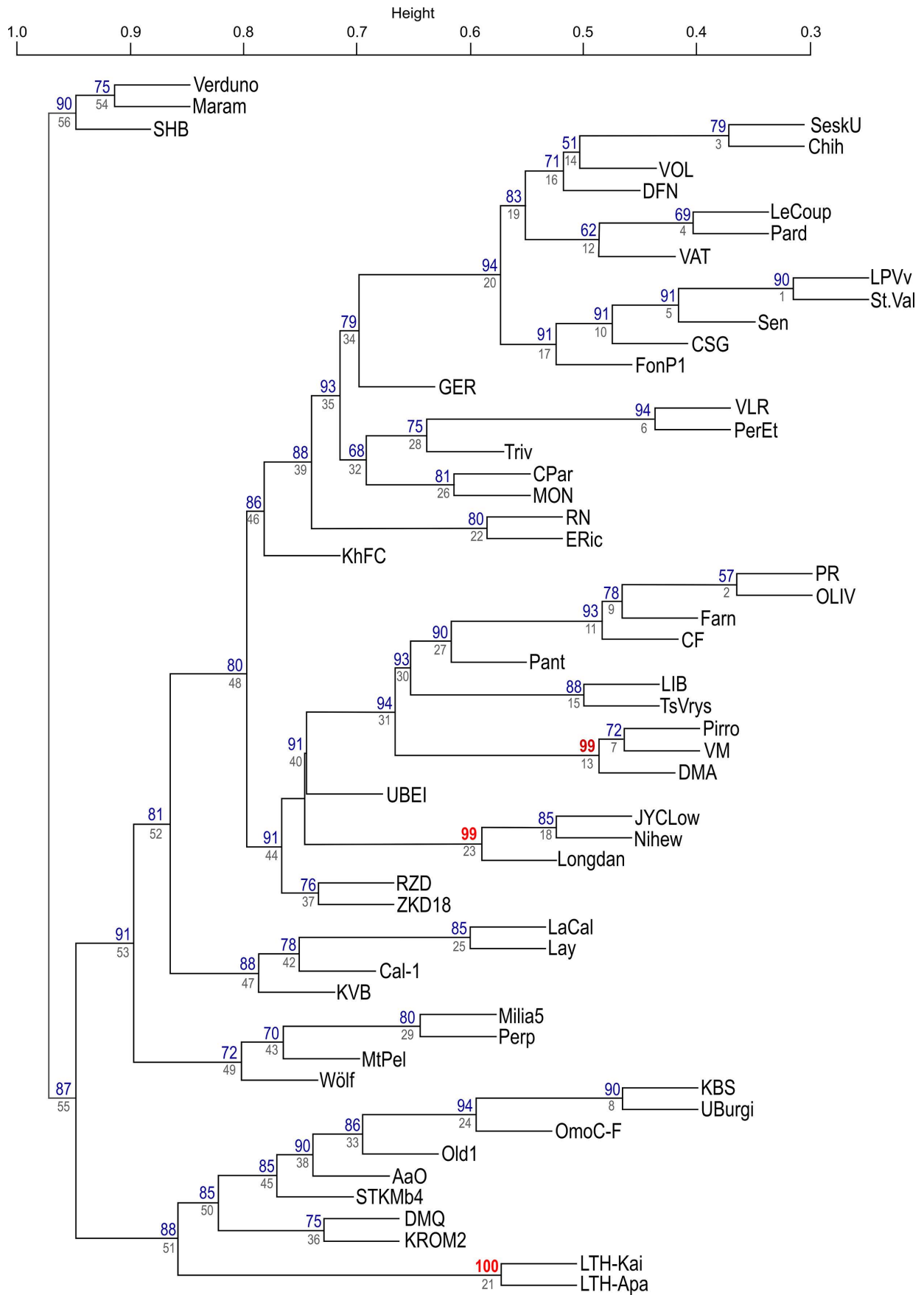
Fig. 5 - Dendrogram resulting from the bootstrapping cluster analysis (BCA) based on the presence/absence genera matrix of 58 localities across the Old World. Numbers in grey represent the number of the node, whereas the one in blue or red are the percentage *p*-values supporting that node: values below 95% are in blue, whereas those above 95% are in bold red.

cervid *Croitzoceros*, the leptobovine *Leptobos* and the rhinocerotid *Stephanorhinus*. Montopoli lies among the sites of the last group of node 32. It is characterized by co-occurring taxa such as *Anancus*, *Preelaphus* and *Procapreolus*, typical of earlier faunas, combined with the new arrival of *Equus, Eucladoceros* and *Mammuthus*. Its peculiar composition explains the position and the pattern of the dendrogram. This intermediate similarity between the Late Pliocene (Early Villafranchian) occurrences and new arrival typical of the Early Pleistocene (Middle Villafranchian) fits with results of the generic resemblance and closeness indices (Fig. 5), as mentioned above.

CONCLUSIONS

The fauna of Montopoli is among the most diverse localities in Europe related to the Pliocene/Pleistocene boundary. Even more than a century after its discovery, the assemblage represents a reference for the European land mammal communities, identifying a time frame of radical changes in the terrestrial ecosystems. The first occurrence of some genera and species that ultimately characterize the entire Quaternary period, such as *Equus* and *Mammuthus*, is associated with the decline of typical late Neogene species, underlying a complex event in the faunal turnover with a short-term replacement of Ruscinian species. From the analyses undertaken here, it is clear that the faunal composition of Montopoli is strongly influenced by its geographic position and, to lesser extent by its chronology (Figs 3-5). The position of Montopoli is clearly with a group of French, Italian and Spanish localities (in turn framed within a larger cluster with other western and Mediterranean European sites), dated to the Late Pliocene and erliest Pleistocene.

The aridification trend that is documented in western Eurasia around 2.6 Ma, had already affected Central Asia around 3.6 Ma (Guo et al., 2004; Alexeeva, 2005; Jiang et al., 2005; Wu et al., 2011). This was probably related to a combination of factors, such as the long general cooling trend of the high latitudes, the stabilization of the permanent Arctic and Antarctic ice caps, as well as regional factors like the uplift of the Tibetan Plateau (Guo et al., 2004) for the Chinese area. Such local climatic changes drove the radiation of taxa related to open, drier environments during the Late Pliocene, as indicated by the records correlated to the central-northern Chinese Mazegouan Land Mammal Age (Qiu et al., 2013) or in the Udunganian-Chikoian Faunal Complexes of Transbaikalia (Erbajeva & Alexeeva, 2013). The importance of this open-habitat fauna was probably favored by the subsistence of similar conditions of increased aridity, and then cooling, affecting other parts of Eurasia, allowing the thriving and the westward dispersal of such elements during the whole Late Pliocene, especially after ~2.8 Ma when, apparently at intercontinental scale, thermophilus-tropical environments of mid-latitudes declined till their almost complete disappearance (Bertini, 2010; Combourieu-Nebout et al., 2015; Momohara, 2016; Vieira et al., 2018). Right at the Pliocene/Pleistocene boundary, around 2.6 Ma, the dry-cool trend apparently reached a maximum across the whole Eurasia, as testified to by many authors using different climatic proxies (see Jiang et al., 2005; Suc & Popescu, 2005; Bertini, 2010; Wu et al., 2011; Li et al., 2019). From this moment on, the climatic deterioration toward cooler/dryer stages remained steady and involved the large mammal associations. Interestingly, these climatic shifts also seemed to disrupt the peri-Mediterranean connections between Europe and North Africa (as evidenced by the high similarity indices of the present analyses), leading then to a higher degree of provinciality of some areas of the Old-World like, e.g., East Africa. The site of Montopoli, with its record, undoubtedly constitutes a pivotal reference of the changes that affected Eurasia by the end of the Pliocene, not only at a regional level.

SUPPLEMENTARY ONLINE MATERIAL

Supplementary data of this work are available on the BSPI website at: https://www.paleoitalia.it/bollettino-spi/early-access/. Supplementary Online Material (SOM) includes the tables resulting from the GFRI and closeness index comparison of three Old-World localities.

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