4 THE LATE VILLAFRANCHIAN EQUIDS FROM THE LOCALITY TSIOTRA VRYSSI (MYGDONIA BASIN, MACEDONIA, GREECE)

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4.1 INTRODUCTION

The genus *Equus* arrived from North America to Eurasia at the beginning of Pleistocene (2.58 Ma) (Lindsay et al., 1980; Azzaroli, 1983; Bernor et al., 2019; Rook and Martínez-Navarro, 2010; Rook et al., 2019) with its first occurrence marking a faunal turnover and significant environmental changes from humid-warm ecosystems to colder-drier conditions. During the Early Pleistocene, *Equus* had been already significantly radiated in Eurasia, providing several lineages, some of them surviving till recent times.

In Greece, the *Equus* datum is possibly traced in Damatria (Rhodes Island; van der Meulen and van Kolfschoten, 1986). Equids are the most common element in the Pleistocene Greek faunal assemblages, often exceeding 50% of the local finds in number of specimens. Most of the Greek *Equus* remains come from the middle–late Villafranchian and Epivillafranchian. Mygdonia Basin (Central Macedonia, Greece), being at the crossroads of three continents, becomes an important path for faunal dispersals and a gateway for faunas coming from Asia Minor to South-Western Europe and vice versa. Several mammal fossiliferous sites have been discovered in this basin by the Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki (LGPUT) and many fossils have been unearthed, providing important palaeontological and biochronological data for Greece and beyond (Koufos and Kostopoulos, 2016 and references therein). Tsiotra Vryssi (TSR), a fossiliferous locality in Mygdonia Basin, dated between 1.78–1.5 Ma (Konidaris et al., 2021), provided a rich sample of fossil equids. Konidaris et al. (2015) preliminarily reported two species of *Equus* based on their size.

4.2 MATERIALS AND METHODS

More than 440 equid remains have been unearthed from Tsiotra Vryssi and they are stored at the LGPUT. The sample is represented mainly by man-

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Figure 1: Equid remains from Tsiotra Vryssi (TSR): (a) Articulated left hind limb (at the TSR site) preserving all elements from the distal part of tibia to the third phalanx; (b) Left third metacarpal in articulation with the phalanges, TSR-F18-53 (medium-sized); (c) Fragmentary right mandibular body with p2–m2, TSR-F20-15 (medium-sized); (d) Left third metatarsal, TSR-179 (large-sized); (e, f) Third metatarsals, TSR-F17-31d (left), and TSR-F17-12 (right) respectively (medium-sized).

dibular fragments, dental remains and postcranial elements, many of which are articulated (Fig. 1). There is also an extremely fragmentary cranium (TSR-162) belonging to a juvenile individual less than 1 year old based on Levine's (1982) tooth aging tables (with DP1-DP4 and M1 erupting).

The systematics of TSR equids is mainly based on third metacarpals and third metatarsals. We compare them with Eurasian Pleistocene *Equus* species. In particular, the studied material was compared with equids from several Greek and European localities dating from the middle Villafranchian to Epivillafranchian (data from literature are indicated in the parentheses only in the cases where we did not use our personal datasets): *E. stenonis* from Dafnero (Western Macedonia, Greece), Sésklo (Magnesia, Greece), Volax (Drama Basin, Greece), Saint-Vallier (France), Chilhac (France), La Puebla de Valverde (Spain; Eisenmann, 1979), Matassino (Italy), Terranova (Italy), Upper Valdarno (Italy); *E. altidens* (=*E. stenonis mygdoniensis* Koufos, 1992) from Gerakarou and Libakos; *E. altidens* from Krimni-3 (Mygdonia Basin, Greece); *E. altidens* from Dmanisi (Georgia; Bernor et al., 2021), Pirro Nord (Italy), Selvella-Gioiella (Italy; Alberdi and Palombo, 2013); *E. altidens granatensis* from Venta Micena (Eisenmann, 2011); *E. apolloniensis* from Apollonia (Mygdonia Basin, Greece). We used principal component analysis (PCA) in PAST 4.05. Missing values were treated by applying iter-

ative imputation. The nomenclature and measurements follow the recommendations of Eisenmann et al. (1988).

4.3 ANALYSIS AND RESULTS

As originally stated by Konidaris et al. (2015) and recently by Gkeme (2023), two species of *Equus* have been recognized in TSR material based on their size and metapodial slenderness: a medium-sized and a relatively large-sized *Equus*. The medium-sized equid has typically stenonoid cheek teeth (Fig. 1c) with a V-shaped linguaflexid, shallow ectoflexid on premolars and always deep on molars, and relatively long and slender metapodials (Fig. 1b, e, f). The large-sized equid has larger teeth (V-shaped linguaflexid, deep ectoflexid on molars and occasionally on premolars, rounded and often elongated metaconids, lingually pointed metastylids), and the metapodials are longer and more robust (Fig. 1d).

Figure 2 (a, b) exhibits the PCA results for (a) third metacarpals (MCIII) and (b) third metatarsals (MTIII). The PC1 and PC2, for the third metacarpals, account for most of the variance with 87.4 % (PC1=60.63%; PC2=26.8%), and for the third metatarsals, with 93.6% (PC1=74.7%; PC2=18.9%). The PC1 indicates a progressively slenderer morphology from positive to negative values, whereas PC2 separates species by the maximum length (M1) with more to less elongated metapodials (from positive to negative values) (Fig. 2a, b). The third metacarpals of the medium-sized species from TSR, overlap with the equids from Libakos and Krimni-3, and as it seems, they are slightly longer than those from Gerakarou (Fig. 2a, 2c1). Furthermore, the MCIII from TSR overlaps with *E. altidens* from Pirro Nord and mostly from Venta Micena. Generally, the equids from the Greek localities Tsiotra Vryssi, Krimni-3, Gerakarou and Libakos overlap with the European *E. altidens* samples, and they all differentiated from the various *E. stenonis* Greek (Dafnero, Sésklo, Volax) and the rest of the European (Saint-Vallier, Olivola, Upper Valdarno, Chilhac) samples because of their slenderness (Fig. 1a).

The third metatarsals of the TSR medium-sized species overlap with Gerakarou and Libakos, while Krimni-3 shows slightly longer metatarsals as it is shown in the PCA analysis (Fig. 2b). Here too, the equids from these localities overlap with the samples of *E. altidens*, and they are distinguished from *E. stenonis* based on their slenderness. There are two specimens, TSR-179 (Fig. 2b) and TSR-D16-41 (large-sized species) that plot outside the convex hull of *E. altidens* and within the variation of *E. stenonis* and *E. apolloniensis*. These third metatarsals are relatively long, but more robust than those of the medium-sized species. The slenderness index, minimal breadth at the middle of the diaphysis (M3) / maximal length (M1) % (Alberdi et al., 1998; Eisenmann, 2002) is 11.8 and 13 for TSR-179 and TSR-D16-41, respectively, versus 11.4 (n=11; min=10.9, max=11.9) for the medium-sized species.

4.4 DISCUSSION

The taxonomy of the slender late Villafranchian European equids is still a matter of debate (Koufos 1992; Alberdi et al. 1998; Forstén 1999; Eisenmann 2010; Gkeme et al. 2017; Bernor et al. 2021; Cirilli et al. 2021; Gkeme 2023 among others). The TSR equids provide some new insights into the late Villafranchian equid faunal assemblages of Greece and southwestern Europe. The presence of a medium-sized equid in the TSR fauna similar in size and slenderness to *E. altidens* (=*E. stenonis mygdoniensis* Koufos, 1992) from Gerakarou and Krimni-1, 3 (see Koufos et. al. 2022; Gkeme 2023) and the other European samples of *E. altidens* (including *E. a. granatensis* from Venta Micena) may

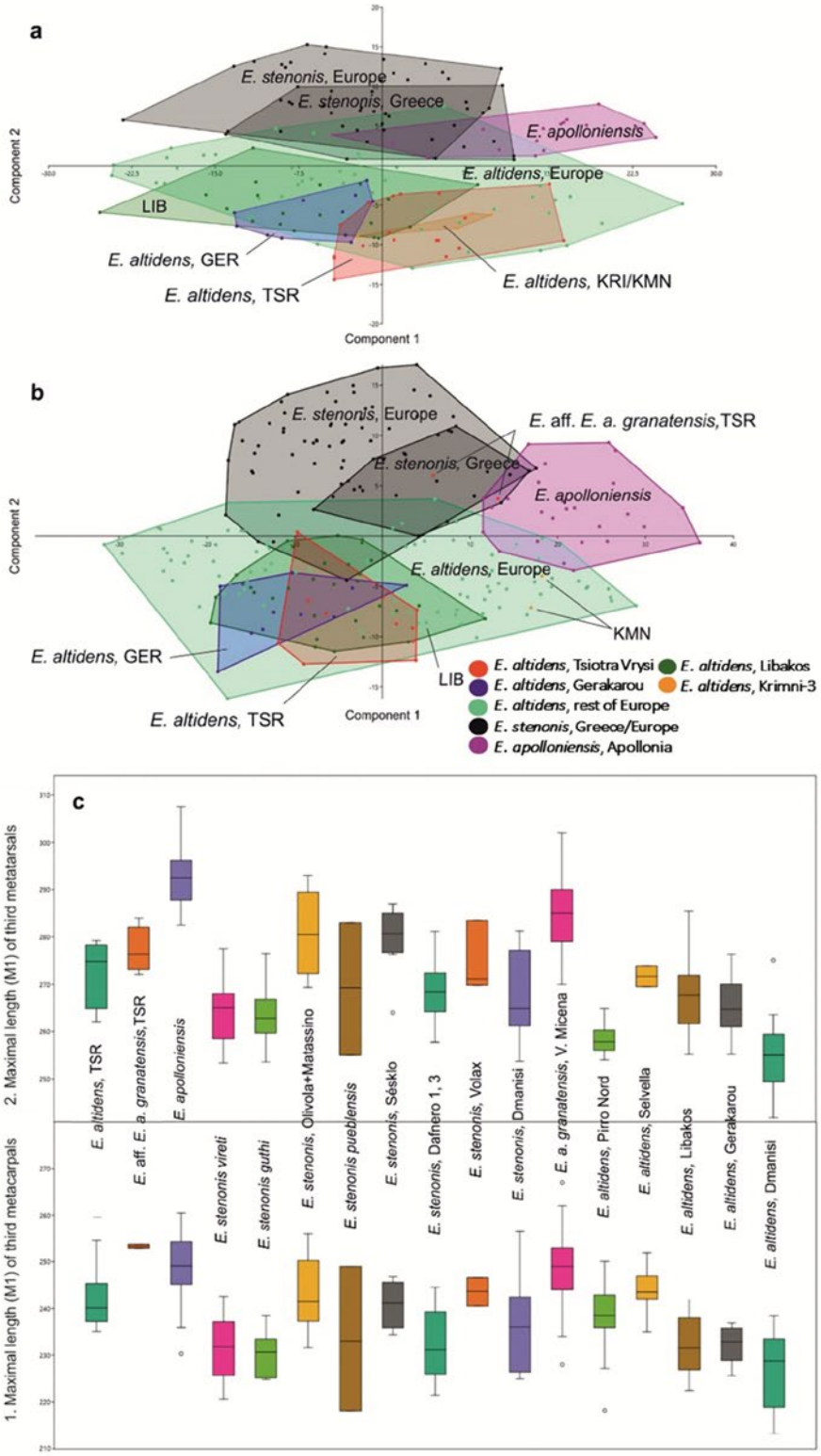

Figure 2: (a, b) PCA of the third metacarpals and third metatarsals, respectively, from Tsiotra Vryssi (TSR) in comparison with those from various Greek and other European localities; (c) Boxplots comparing the maximum length of the third metapodials from TSR with other Greek and European samples. Boxplots include minimum, median and maximum values with first and third quartile of each sample and outliers.

give some new information about the systematic position of this taxon. The equid from Gerakarou (including the equid from Krimni 1) was originally described by Koufos (1992) as a distinct subspecies of *E. stenonis* (*E. stenonis mygdoniensis*) despite its much slenderer built and smaller overall size. Forstén (1999) and Gkeme et al. (2017) referred the equid from Libakos to *E. altidens*, an equid identical to the one from Gerakarou, suggesting that they both belong to *E. altidens*. However, Eisenmann (2017) considered '*E. s. mygdoniensis*' as a valid taxon and raised it at the species level (*Allohippus mygdoniensis*), while she suggested the cautious use of the name *E. altidens*, because the erection of this species was mainly based on teeth. Recently, Cirilli et al. (2021), Bernor et. al. (2021) and Gkeme (2023) considered '*E. s. mygdoniensis*' as a junior synonym of *E. altidens*, thus favoring the preliminary work of Gkeme et al. (2017) and the recent review of the Early Pleistocene slender equids from Greece by Koufos et al. (2022). The presence of *E. altidens* at TSR possibly validates this theory, since the variability reported by the European *E. stenonis* populations seems to be similar in Gerakarou, Libakos, Tsiotra Vryssi, Krimni and the European *E. altidens* samples.

The large-sized *Equus* from TSR is less abundant, at least in number of identified specimens (less than 20). Some of the dental remains (belonging to the larger species) exhibit peculiar features like those described by Eisenmann (2010) as common features of the *Sussemionus* subgenus and in particular those from Venta Micena (see Gkeme, 2023). Furthermore, according to Gkeme (2023: fig.5.40a), the third metacarpals from TSR exhibit the same morphology and morphometry as those of *E. altidens granatensis* from Venta Micena. However, the metatarsals resemble both *E. stenonis* and *E. apolloniensis* based on their slenderness and size. For this reason, the large-sized *Equus* is pulled under the name *Equus* aff. *E. a. granatensis* following Gkeme's (2023) commendation. The presence of two species of *Equus* in the TSR fauna validates its young age (slightly younger than Gerakarou and older than Apollonia) marking an important faunal turnover at the late Early Pleistocene: slender equids (eg. *E. altidens*) replaced the more robust and archaic ones (*E. stenonis*).

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