FOSSIL IMPRINT • vol. 73 • 2017 • no. 1–2 • pp. 115–140
(formerly ACTA MUSEI NATIONALIS PRAGAE, Series B – Historia Naturalis)

NATIONAL MUSEUM

LIGHT AND SHADOWS IN THE EVOLUTION OF SOUTH EUROPEAN STENONOID HORSES

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Palombo, M. R., Alberdi, M. T. (2017): Light and shadows in the evolution of South European stenonoid horses. – Fossil Imprint, 73(1-2): 115–140, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: The appearance of monodactyl equids in Eurasia and their dispersal towards South Europe is a significant event that marks the beginning of the Quaternary period. During the Pleistocene, horses were a common element in most European large mammal faunal assemblages, providing important palaeoecological clues, but their taxonomy, nomenclature and phylogeny, as well as their actual biochronological significance have been widely debated by scholars. The evolutionary history of horses here regarded as "stenonoid" (*Equus livenzovensis*, *Equus stenonis*, *Equus* ex gr. *E. senezensis*, *Equus altidens*, *Equus hydruntinus*, the large-sized horses *Equus major* and *Equus suessenbornensis*, sometimes referred to as the so-called "*Equus bressanus-Equus suessenbornensis* group"), is one of the most intriguing. This study, mainly focusing on the South European representatives of this group, aims to highlight and discuss the major debated issues, re-examining the taxonomy of some Early and early Middle Pleistocene horses. Alternative phylogenetic hypotheses will also be discussed with the aim of providing new clues on the chronology and palaeoecology of some key species/samples.

Key words: Equidae, Early – Middle Pleistocene, South Europe, taxonomy, biochronology

Received: February 25, 2017 | Accepted: May 9, 2017 | Issued: August 15, 2017

Introduction

The evolutionary history of equids is one the most fascinating and intriguing among those of Cenozoic large mammals, but some details still divide scholars and remain unaddressed. There is however a general agreement when considering the appearance of equids in Eurasia that they appeared as the result of various dispersal events from the North American continent, where the main evolutionary history of the Equidae took place (see among others Forsten 1989, 1992a, Eisenmann 1992, Azzaroli and Voorhies 1993). Whether the origin was diphyletic or monophyletic (see e.g. Bennett 1980, Dalquest 1988, Azzaroli 1988, 1992), the first representative of the genus *Equus* appeared in North America about 3.5 Ma, according to the age of the Blancan fauna from Hagerman Quarry (Idaho) (Lundelius et al. 1987, Repenning 1987). The first appearance, however, may be older as suggested by the presence of ?*Equus* sp. reported by Lindsay and Jacobs (1985) in the Concha Fauna (Chihuahua, Mexico) found in strata 25 m higher than those containing the late Hemphillian Yepómera Fauna (Bell et al. 2004). The specimens retrieved from the Late Pliocene deposits of Hagerman Quarry, were originally named *Plesippus shoshonensis* by Giddley (1930). Subsequently most scholars referred the rich equid sample to *Equus simplicidens*, a primitive horse species erected by Cope (1892) for some specimens found in the Early Pleistocene deposits of the Blanco beds (Southern High Plains, Texas) (dated to about 1.6 Ma or older; see Holliday 1988, for a discussion). The species, known from entire skulls and mandibles and numerous well preserved teeth and limb bones (e.g. specimens from the rich early Blancan faunas of Hagerman, Idaho and Broadwater, Nebraska), was quite a large sized horse, 1.5 m high at the shoulder and weighting about 330 kg (Eisenmann 2000) which apparently shows some affinity with the modern zebra, *Equus grevyi*. The apparent affinity prompted some authors to place the American species in the subgenus *Dolichohippus* (see e.g. Skinner and Hibbard 1972), although skull proportions suggest it belongs to a different lineage. In particular, Forsten and Eisenmann (1995) believed that the primitive proportions of vomer and teeth shown by *E. simplicidens*

DE GRUYTER OPEN DOI 10.2478/if-2017-0006

may set it apart from any zebra, and suggested to tentatively include the species in the *Plesippus* subgenus.

During the Pleistocene, representatives of the genus *Equus* widely dispersed across and between continents, inhabiting a variety of environments and giving rise to different lineages, which record radiative and anagenetic evolutionary processes.

The first dispersal event towards Eurasia had probably taken place by the end of the Pliocene, as suggested by the presence of a monodactyl equid, *Equus qingyangensis* closely related to *E. simplicidens* (Deng and Xue 1999a, Eisenmann and Deng 2005) in the deposits of Bajiazui (Qingyang County, Gansu Province, China), which are possibly close in age to the Plio-Pleistocene boundary. Following Eisenmann and Deng (2005), the size, the similar limb bone proportions, and similar morphology of the skull shared by *E. qingyangensis* and "*E. shoshonensis*" (= *E. simplicidens*) would set both species apart from the species *Equus stenonis* to which a number of Eurasian horse have been referred (see below). Therefore, Eisenmann and Deng (2005: 121) hypothesised that the American horse *E. simplicidens*, and its direct Asian descendant *E. qingyangensis*, "both are part of a lineage distinct from *Equus stenonis*". According to these authors, biometrical data would support the existence of two distinct lineages of primitive *Equus* in the Old and New World. In addition Eisenmann and Deng (2005: 121) claimed: "not all Plio-Pleistocene *Equus* of the Old World should be referred to *E. stenonis*. Some taxa seem to resemble more the North-American *E. shoshonensis* (or *E. simplicidens*) but they are not documented enough" and "very scarce fossils represent probably-not-stenonine *Equus* at Huélago and Tegelen". The authors concluded claiming, "the material referred to *E. qingyangensis* is the first evidence complete enough to support the presence of a primitive lineage different from *E. stenonis* in the Old World".

Conversely, Forsten (1986a) believed that the skulls of the most primitive *Equus* representatives from China share various morphological and dimensional traits with *E. stenonis*, an opinion shared by several authors (see e.g. Azzaroli 1987, 1992, Deng 1997, 1999, Alberdi et al. 1998, Deng and Xue 1999b).

As a result a question arises as to how many lineages of monodactyl equids dispersed from America to Asia, and how many were present in Eurasia at the beginning of the Quaternary periods, and, successively, present in Europe during the Early Pleistocene. The genus *Equu*s likely dispersed towards Europe at the time of the Pliocene to Pleistocene transition (termed the *Equus*-Elephant event by Lindsay et al. 1980). Lacombat et al. (2008) hypothesised the presence of *Equus* in the early Villafranchian (Late Pliocene) local faunal assemblage (LFA) of Vialette (Haute-Loire, France), based on a second, quite large phalanx kept in the collection of the Crozatier Museum (Le Puy-en-Velay, France) (Lacombat 2005a). The alleged occurrence of a monodactyl horse in Europe in the Late Pliocene deposits however needs more firm supports. If the second phalanx from Vialette is, on one hand, actually larger than those of any *Hipparion*, its morphology is not taxonomically informative because *Hipparion* and *Equus* do not show any significant difference in morphology of the second phalange of the third finger. Taking into account that the Vialette colletion in the Crozatier Museum also includes a few Miocene specimens (Lacombat 2005b), as well as the presence in the Velay volcanic area of younger Villafranchian LFAs, the hypothesis that the collection may include some spurious remains, and that the equid phalanx might have come from some Early Pleistocene levels cannot be discounted.

The oldest horse representative in Europe correctly assignable to monodactyl equids is recorded in the Early Pleistocene gravel deposits of Livenzovka (= Liventsovka). The specimens found at the site belong to a large equid, first described by Gromova (1949a) as "*Equus stenonis* var. *major*". Later, Baygusheva (1978) erected a new species for these remains, *Equus livenzovensis*, recorded roughly at the same time in Westen Europe (i.e. at Montopoli, Italy, and Huélago, El Rincón, and possibly Barranco de Cañuelas, both Spain). *E. livenzovensis* has been regarded by most authors as closely related to *E. simplicidens*, although larger than the American species, and the ancestor from which minimally all the stenonoid European species would have stemmed (Bonadonna and Alberdi 1987, Azzaroli 1990, 1992, Alberdi et al. 1998, among others). Forsten (1998), however, after having analysed new material from Russian localities, agreed that *E. livenzovensis* should be considered a stenonoid horse, but concluded that Livenzovka monodactyl equid specimens could belong to three taxa, differing in size and bone proportions (i.e. *E. livenzovensis*, *Equus major*, and *Equus* cf. *E. altidens*) (see below for a discussion). Moreover, the Finnish author claimed that "the fossil horses of the genus *Equus* from Livenzovka may indicate a faunal age heterogeneity. The possible presence of *Hipparion* and absence of caballoid *Equus* would point to an early age, in agreement with the assignment of the fauna to the middle Villafranchian. The specific status of the horses could indicate a slightly later age, at least by western European biostratigraphic standards. Thus *E. livenzovensis* does not occur at Montopoli or Huélago, although referred to from these localities, and the occurrence at El Rincón is uncertain. This species does not represent the primordial *Equus* in Eurasia" (Forsten 1998: 654).

During the Early and early Middle Pleistocene various species and ecomorphotypes/subspecies of the genus *Equus* are recorded in several European local faunal assemblages (LFAs). In spite of the rich fossil record and the considerable number of studies, their taxonomy, phylogenetical relationships and chronological distribution are, however, still a matter of debate (for different opinions on systematic and taxonomy see among others Azzaroli 1965, 1979, 1990, 1999, Boeuf 1986, Alberdi et al. 1988, 1998, 2001, Musil 1992, 2001, Eisenmann 1992, 2004, 2010, Caloi 1997, Guerrero-Alba and Palmqvist 1997, Forsten 1999, Alberdi and Palombo 2013a, b, Palombo et al. 2017, and references in those papers). The horses most commonly recorded in the middle and early late Villafranchian European Land Mammal Age, ELMA (= Gelasian, and pre-Jaramillo Calabrian epochs), have been referred by most authors to "*Equus stenonis* group" or "*Equus stenonis* sensu lato". *E. stenonis* has been considered by the majority of researchers as the most "common horse species" in the Early Pleistocene of the Old World, with a geographical range extending from China to North Africa (see e.g. Forsten 1986a, 1999, Azzaroli 1992, Guerrero-Alba and Palmqvist 1997, and references therein). A few other scholars (e.g. Eisenmann 1999) rejected the hypothesis that these Plio-Pleistocene *Equus* specimens from the Old World should be referred to *E. stenonis*.

There is also disagreement among authors regarding the possibility of referring some of the Early – early Middle Pleistocene non-caballine horses to the genus/subgenus *Allohippus* (e.g. Gromova 1949a, Samson 1975, Prat 1980, Eisenmann and Baylac 2000, Eisenmann 2003, 2004, 2006, among others) to which some "primitive" horses have been referred, including those from some South European Early Pleistocene key localities (e.g. Montopoli, Olivola and Valdarno (Italy), Saint-Vallier and Senèze (France), Huélago, El Rincón, and La Puebla de Valverde (Spain), Gerakarou and Vatera (Greece), Sarikol Tepe (Turkey), as well as the specimens from Livenzovka (Russia)). The validity of the genus *Allohippus*, created by Kretzoi (1938) who syntethically described it as a primitive stenonoid form, designating *E. stenonis* as its "genoholotypus", has been questioned by Azzaroli (1992). Some years later, Gromova (1949a), gave a new definition of *Allohippus* based on "*Equus stenonis* var. *major*" (= *E. livenzovensis*). Subsequently the name was regarded as valid, considered by some as subgenus of *Equus* (e.g. among others Samson 1975, Prat 1980), by others elevated to the genus rank (e.g. Eisenmann and Baylac 2000), and Gromova was generally quoted as the author.

Whether the rules of nomenclature were ignored or not, and *Allohippus* is or is not an available name, the question arises if the differences among primitive and modern horses are enough for separating them at a genus level. Given the basic structural homogeneity but the large intra- and interspecific variation shown by fossil monodactyl horses, to employ different genus/subgenus names (e.g. *Plesippus*, *Dolicohippus*, *Allohippus*), sometimes used interchangeably for different designated groups, requires a great deal of caution.

Eisenmann and Deng (2005), following Eisenmann and Baylac (2000), for instance, did not believe "that any extant species of *Equus* has either *E. stenonis* or *E. shoshonensis* for a direct ancestor", and stated that "all extant *Equus* probably share an apomorphy in their basicranial proportions and may be considered as monophyletic. Although some of the extant *Equus* species are rather *E. stenonis*-like in their body proportions (Plains zebras) while others (Hemiones) are rather *E. shoshonensis*-like, these resemblances very probably result from homoplasies". The authors concluded that "because of frequent homoplasies, the present 'phylogenies' of primitive *Equus* sensu lato can only be very tentative". More recently, Orlando et al. (2013), recalibrating *Equus* evolution by using the genome sequence of an early Middle Pleistocene horse, suggested that the *Equus* lineage, giving rise to all contemporary horses, zebras and donkeys, originated 4.0–4.5 Ma, thus earlier than the conventionally accepted time for the most recent common ancestor of the genus *Equus*, but maybe in accordance with the possible age of the Concha Fauna (Chihuahua, Mexico) (see above).

This argument is beyond the scope of the present study which aims to briefly discuss some of the debated questions which still need a firm answer (e.g. number of phyletic lineages, actual taxonomical rank of some alleged subspecies, phyletic relationships, and biochronological and palaeoecological clues provided by the Early to early Middle Pleistocene stenonoid horses), mainly focusing on horses recorded in the Early and early Middle Pleistocene LFAs from South Europe.

The origin of European horses and their appearance in SW Europe

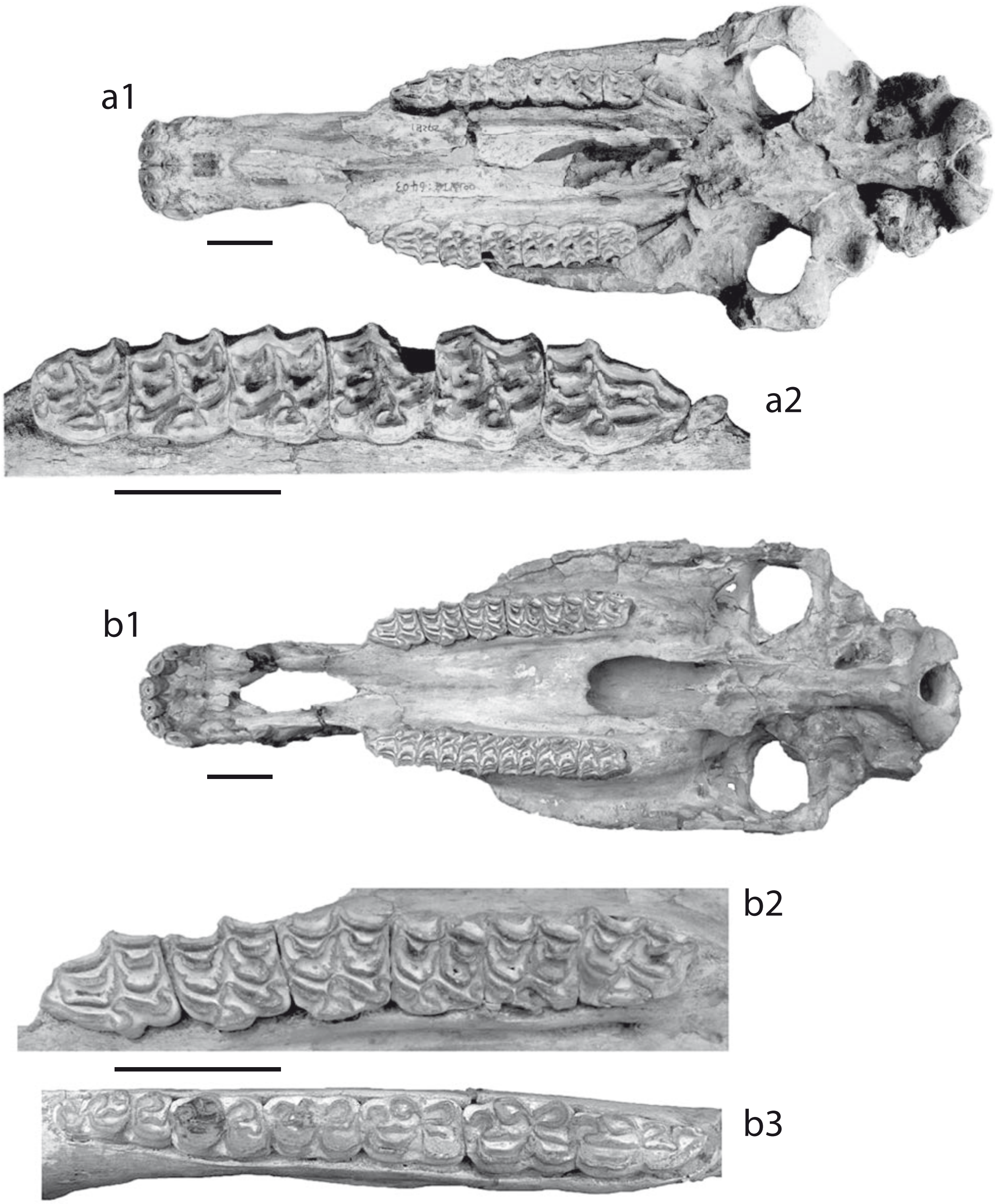
The European Early Pleistocene horses most likely originate from some equid populations from China, where a number of *Equus* species have been reported from localities believed to be close in age to the beginning of the Quaternary (e.g. *Equus yunnanensis*, dated to about 2.48 Ma according to palaeomagnetic evidence, *E. qingyangnensis* possibly around 2.5 Ma, and *Equus sanmeniensis*, and *Equus huanghoensis*) (see e.g. Deng 1997, 1999, Eisenmann and Deng 2005). It is however challenging to hypothesise about any firm phyletic relationship among the oldest representative of the genus *Equus* known in Europe (i.e. *Equus livenzovensis*) and one or other of the Chinese species because of the uncertainty regarding the actual age of some Chinese samples.

On the one hand, for instance, the large horse, *E. huanghoensis* (a species also recorded by cranial remains found at about 1.6 Ma at Yangshuizhan (Nihewan, Hebei province) (Li et al. 2016) and in the Tuozidong fauna believed to be close in age to 2.0 Ma (Dong and Fang 2005)), may be considered as somewhat similar to *E. livenzovensis* in size and a few dental features (Text-fig. 1), but the actual age of the first appearance of the Chinese species is doubtful. An age of about 2.5 Ma has been hypothesised for the few cheek teeth from the Yellow River bank, Sanmen Gorge (Pinglu County, Shanxi Province), the holotype of the species erected by Chow and Liu (1959). Their actual age, however, may be more recent taking into account the geological setting of the area (see e.g. Su et al. 2008).

On the other hand, following Forsten's opinion (Forsten 1986a), the skull and limb bones of *E. sanmeniensis* from the type locality of Nihewan, (Yangyuan, Hebei province), in particular the long and rather slender metapodials and proximal phalanges, share some similarities with the Livenzovka specimens. The age of the Nihewan specimens is, however, younger (~1.66–1.1 Ma) than that of the Russian horse (Deng et al. 2008).

Whichever animal was the direct ancestor of the European species, available data suggest a reasonably rapid dispersal due to the nearly contemporaneous presence of large monodactyl horses near the Southeast European border (Livenzovka and Khapry, near Rostov-Don, Russia), and in South-western Europe (Montopoli, Italy, Huélago and El Rincón, Spain) at the time of the Pliocene-Pleistocene transition.

All the oldest (early middle Villafranchian, Early Gelasian) European horse remains have usually been identified as *E. livenzovensis.* The species is characterised by its large size and quite primitive skull and dental features. In the fragmentary skull, the holotype of the species, the basilar length is about 642 mm (Baygusheva 1978), the maxillary bones and the medium nasal groove are well developed, the



Text-fig. 1. ***Equus huanghoensis*: a) skull (JNTZ28389) from Tuozidong (China) in ventral view (a1) and upper tooth row in occlusal view (a2) (modified from Dong and Fang 2005, Fang and Dong 2007); b) skull (NWUV1403.1) from Nihewan (China) in ventral view (b1), upper cheek tooth row (b2) in occlusal view, and cheek tooth row of the left hemimandible (NWUV1403.2) in occlusial view (b3). Modified from Li et al. (2016). Scale bar = 5 cm.**

braincase is strongly deflected with respect to the face, and the narinal notch reaches the mid point of P2. The upper teeth show a stenonoid morphology with a short protocone (8–9 mm in P3–P4 and 8.5 mm in M1–M2), highly wrinkled enamel and mesostyles without grooves. The lower teeth have a deep ectoflexid and a small isthmus. Although *E. livenzovensis* is larger and heavier than *E. stenonis*, the limb bones are proportionally more elongate (average maximum length of MCIII = 257.9 mm; average maximum length of MTIII = 294.33 mm).

Forsten (1998) questioned the presence of only one horse species at Livenzovka. The Finnish author claimed that, although most remains can be confidently identified as *E. livenzovensis*, the significantly larger or smaller dimensions of a few others could indicate the presence of three different species in the sample, scaling in size, i.e. *Equus major*, *E. livenzovensis* and *Equus* cf. *E. altidens*. Therefore, following Forsten (1998: 654) the alleged presence of "three different species, the fossil horses of the genus *Equus*" would indicate "faunal age heterogeneity…….. Thus *E. livenzovensis* does not occur at Montopoli or Huélago, although referred to from these localities, and the occurrence at El Rincón is uncertain". These hypotheses prompted the author to claim that *E. livenzovensis* "does not represent the primordial *Equus* in Eurasia, as similar forms, mainly of Asiatic origin, are early Pleistocene". It is worth noting, however, that neither geological nor palaeontological evidence support this assertion. Moreover, the key average dimensions of the metapodials of El Rincón horses (range of maximum length = 251–269 mm in MCIII and = 289–296 mm in MTIII; range of the minimal breadth of the diaphysis = 36.2–40.4 mm in MCIII and = 38.9–39.9 mm in MTIII) fall within the 95% equiprobability estimated by Forsten (1998: fig. 2) for the specimens of Livenzovka identified by the Finnish author as *E. livenzovensis* and the 95% equiprobability of Spanish specimens nearly completely overlap that obtained by Forsten (1998: fig. 2) for the Livenzovka horse.

Based on the available date, the hypothesis that at the dawn of Quaternary the changing environmental conditions prompted the dispersal from Asia to and across Europe of large stenonoid horse populations, which led to the appearance and the diffusion of the European species *E. livenzovensis*, seems to be the most rational and parsimonious.

The Gelasian (middle – early late Villafranchian) European horses

During the Gelasian (2.588–1.806 Ma; middle and early late Villafranchian ELMA) large to middle-sized stenonoid equids are recorded in most of European LFAs. The most common horses are those of the so-called "*Equus stenonis* group", which includes quite large stout equids reported in several Eurasian localities, and even in North America (see e.g. Winans 1989, Azzaroli 1992, Guerrero-Alba and Palmqvist 1997, Deng 1997, Alberdi et al. 1998, Deng and Xue 1999b, Forsten 1999).

Excluding horses of very large size (mainly reported in literature as *Equus major*/*Equus bressanus*, see below) the European species show a relatively large variation in morphology and dimensions, which is more evident among horses belonging to "*Equus stenonis* group".

The horses of E. stenonis *group*

Specimens ascribed to the *Equus stenonis* group, although sharing the basic characteristics and bauplane, slightly differ in size and proportions. For the middle and early late Villafranchian European stenonoid horses some authors were prompted to create a number of alleged subspecies (e.g. among others *E. stenonis livenzovensis*, *E. s. stenonis*, *E. s. vireti*, *E. s. pueblensis*, *E. s. guthi*, *E. s. olivolanus*, *E. s. senezensis*, *E. s. mygdoniensis*) whose validity, taxonomic rank and chronological distribution are still a matter of debate (for different opinions on systematic and taxonomy see among others Azzaroli 1965, 1979, 1990, 1999, Boeuf 1986, Bonadonna and Alberdi 1987, Alberdi et al. 1988, 1998, 2001, Musil 1992, Caloi 1997, Forsten 1999, Athanassiou 2001, Eisenmann 2004, 2010, Alberdi and Palombo 2013a, b, Palombo et al. 2017). Although it is challenging to establish whether the differences among samples from different localities may depend on genetic/taxonomic or/and on environmental and/or chronological factors, the hypothesis that differences characterising local populations/ecomorphotypes of horses of the "*Equus stenonis* group" across space and maybe over time are related to environmental characteristics seems to be the most parsimonious. Excluding *E. livenzovensis* (see above), and *E. senezensis* (see below), most of the peculiar features shown by horse populations included in the *E. stenonis* group and recorded in several European LFAs ranging in age from about 2.4 to 1.6 Ma (in particular *E. s. stenonis* recorded in Italy from various Upper Valdarno localities and from Olivola (= *Equus stenonis olivolanus* n. ssp. in Caloi 1997, a poorly characterised taxon whose morphology and dimensions mainly fall within the range of the nominal subspecies), *E. s. vireti* from Saint Vallier and *E. s. guthi* from Chilhac (both France) and horses from La Puebla de Valverde – a sample ascribed by Caloi (1997) to *Equus stenonis pueblensis* n. ssp., but dimensionally and morphologically overlapping the range of *E. s. guthi* (Alberdi et al. 1998), and the large and fairly stout horse from Sésklo (Greece)) may be regarded as intraspecific variations depending on eco-geographic and maybe chronological factors, but without any actual taxonomical significance.

Cocchi (1867) created the species *Equus stenonis* for the equid remains found in the Early Pleistocene deposits of Olmo (Arezzo, Italy) (Text-fig. 2). This horse is characterised by large size and heavy proportions. The braincase is deflected and small in comparison with the face length. The skull shows a transversely concave-convex forehead, a narinal notch deep at the level of the third premolar, an elongated snout, and a very long diastema (ranging from 122 to 150 mm in the upper tooth row, and from 112 to 124 mm in the lower tooth row). The upper cheek teeth have short protocones, similar in shape to the protocones of *E. livenzovensis*, but smaller. The morphology of the lower cheek teeth is typically stenonoid, showing the characteristic rounded double-knot form (metaconid-metastylid) the latter sometimes sharp-pointed, a V-shaped linguaflexid, a sometimes deep ectoflexid. The dimensions of limb bones show a wide range of variation. The average maximal length of MCIII and MTIII are respectively 241.23 and 273.92 mm in *E. s. stenonis*, 229.1 and 264.4 mm in *E. s. vireti*, and 224.81 and 262.3 mm in *E. s. guthi*. The horses from Saint Vallier (*E. s. vireti*) mainly differ from *E. s. stenonis* in having wider styles on the upper premolars, and more robust metapodials with an articular facet on the second carpal and more developed distal articular keel. In specimens ascribed to *E. s. guthi*, the skull in dorsal view appears slightly narrower than that of *E. s. vireti* with a more oval orbital shape, the dental arch is straighter than in the other *E. stenonis* subspecies, and limb bones, although large and heavy, are smaller and more slender than those of *E. s. vireti*.

Text-fig. 2. Skull of *Equus stenonis* (Type IGF-560) from Upper Valdarno, stored in the Natural History Museum, Geology and Palaeontology section (University of Florence, Italy) in dorso-lateral left view (a), dorso-lateral right view (b), and ventral view (c).

Some subspecies of *E. stenonis* have also been proposed for a number of Asian stenonoid horses which share similarities with the European species, such as "*Equus* (*Hippotigris*) *pamirensis*", a taxon created by Sharapov (1986) for an Early Pleistocene stocky horse from Kuruksay (Tajikistan), with rather short and massive limbs (Azzaroli 1990, 1992, Forsten and Sharapov 2000).

E. stenonis was believed to be present even in North America, where "*Equus stenonis anguinus*" was created by Azzaroli and Voorhies (1993) for a complete skull and jaw found in the late Blancan Grand View fauna retrieved from the highest level of the Glenns Ferry Formation (Idaho), older than the Olduvai palaeomagnetic event (Neville et al. 1979, Repenning et al. 1995).

Although the range limit of *E. stenonis* most likely did not extend so far, the presence of *E. stenonis*-like equids in China (cf. Forsten 1999) and North America accounts for parallel evolutionary trends, with the development of similar traits, maybe connected to global climate and environmental changes, which developed in related, but distinct lineages of monodactyl equids, possibly descending from the same ancestral stock.

The intriguing question of horses included in E. senezensis *group*

During the middle and early late Villafranchian slender horses which were slightly smaller than the typical *E. stenonis* have been reported from some European localities. Their phylogeny and taxonomic rank divides authors. Eisenmann (2004), for instance, suggested the presence of two horse species at Huélago (Spain), one referred by the French author to "*Allohippus stenonis*", the other included in a group comprising slender horses, with metapodials "avec des diamètres antéro-postérieurs très développés qui évoquent parfois des hémiones actuels" Eisenmann (2004: S302). It is worth noting, however, that dimensions and proportions of these metapodials are not convincing due to the poor state of preservation (Alberdi and Ruiz Bustos 1989, Alberdi et al. 1998, and MTA personal observation). Moreover, the body mass estimations, based on dimensions of these metapodials, are higher than those obtained for the metapodials from the same locality, included by Eisenmann in the *E. stenonis* group (Eisenmann 2004: S299, tab. 18).

A medium-small sized stenonoid horse, "*Equus stenonis mygdoniensis*", is recorded in the middle Villafranchian LFA of Gerakarou and in a few others Greek localities (Koufos and Melentis 1983, Koufos 1992). The validity of the subspecies has been questioned by some authors (e.g. Forsten (1999: 1393) who claimed that this species "falls inside the samples from Valdarno, but also resembles *E. altidens* from Süssenborn…..."), while others erected it at a species rank (i.e. *Allohippus mygdoniensis* in Eisenmann 2004). Forsten (1999: 1393) believed that the small, slender Greek horses previously attributed to *E. stenonis mygdoniensis* excepted for "the horse from Riza…. evidently do not represent *E. stenonis*; they rather resemble *E. stehlini* or belong, with the gracile horses from Libakos and Petralona," to the horse group "pooled under the name *E.* cf. *altidens*" by the Finnish author.

The hypothesis that during the Gelasian in South Europe a stenonoid lineage was represented by horses slightly smaller and more gracile than the typical *E. stenonis*, finds support in the morphology, dimensions and proportions of specimens found at Senèze (France), on average more slender and slightly smaller in size than *E. stenonis*, and which had been originally ascribed to a subspecies of *E. stenonis*, i.e. *E. stenonis senezensis* (Prat 1964). The Senèze LFA, dated between 2.09 Ma and 2.2 Ma (Delson et al. 2006, Nomade et al. 2014, Pastre et al. 2015), was generally considered as belonging to the late Villafranchian ELMA, although the overall faunal composition (i.e. the presence of *Pliocrocuta perrieri*, the absence of *Pachycrocuta brevirostris*) suggests the fauna belongs to an older faunal complex (cf. Palombo 2014 and references therein). *E. senezensis* may actually be regarded as a bona fide species, as suggested by the results of morphometric multivariate analyses and the application of a "neighbour-joining-method" (Saitou and Nei 1987) performed by Alberdi et al. (1998). These authors included in *E. senezensis* two geographical subspecies, i.e. the nominotypical subspecies, recorded at Senèze and also reported in a few other younger LFAs, such as Blassac-la-Girondie, France (Beden and Guth 1970, Prat 1980), and Libakos, Greece (Steensma 1988), and the subspecies *Equus senezensis stehlini*, slightly smaller in size and characterised by proportionally shorter metapodials, mainly recorded in Italy in some LFAs slightly younger than the type locality of *E. senezensis* (late Villafranchian ELMA, post-Olduvai/pre-Jaramillo Calabrian) (e.g. *Equus stehlini* from Casa Frata, Upper Valdarno, and Farneta, Val di Chiana; Azzaroli 1965, 1984, Caloi and Palombo 1982). Forsten (1999), conversely, elevated *E. stehlini* to species rank, and referred to it also the slender and medium-small sized specimens from Pirro (Italy), Pyrgos (Greece), Dmanisi (Georgia), which had been identified as *E. stenonis* by most other authors (e.g. Vekua and Lordkipanidze 1998, Hemmer et al. 2011), and Poilu (Azerbaijan), the latter regarded as similar to *E. senezensis* by Kuzmina and Sablin (1992). Accordingly, the range limits of this horse would extend from South Europe to the Caspian Sea.

Horses believed to be smaller and more gracile than *E. senezensis* and identified as *E. stehlini*, have also been reported from Senèze (De Giuli 1972, Delson et al. 2006). The alleged presence of two horses differing in size, if truly sympatric, would imply a specific distinctness, thus questioning the conspecificity of *E. senezenzis* and *E. stehlini.* Although we believe that the differences may not be enough to support this hypothesis, pending a detailed study and a full description of the new material found at Senèze (Delson et al. 2006), we provisionally include the middle

Text-fig. 3. Skull of *E. senezensis* (number 210993, stored in the University Claude Bernard, Lyon, France) from Senèze (France) in lateral right view (a), dorsal view (b), and ventral view (c).

Text-fig. 4. Skull of *Equus senezensis stehlini* (Type IGF-563) from Upper Valdarno, stored in the Natural History Museum, Geology and Palaeontology section (University of Florence, Italy), in ventral view.

to early late Villafranchian medium – small sized, slender horse from South Europe in the *Equus senezensis* group.

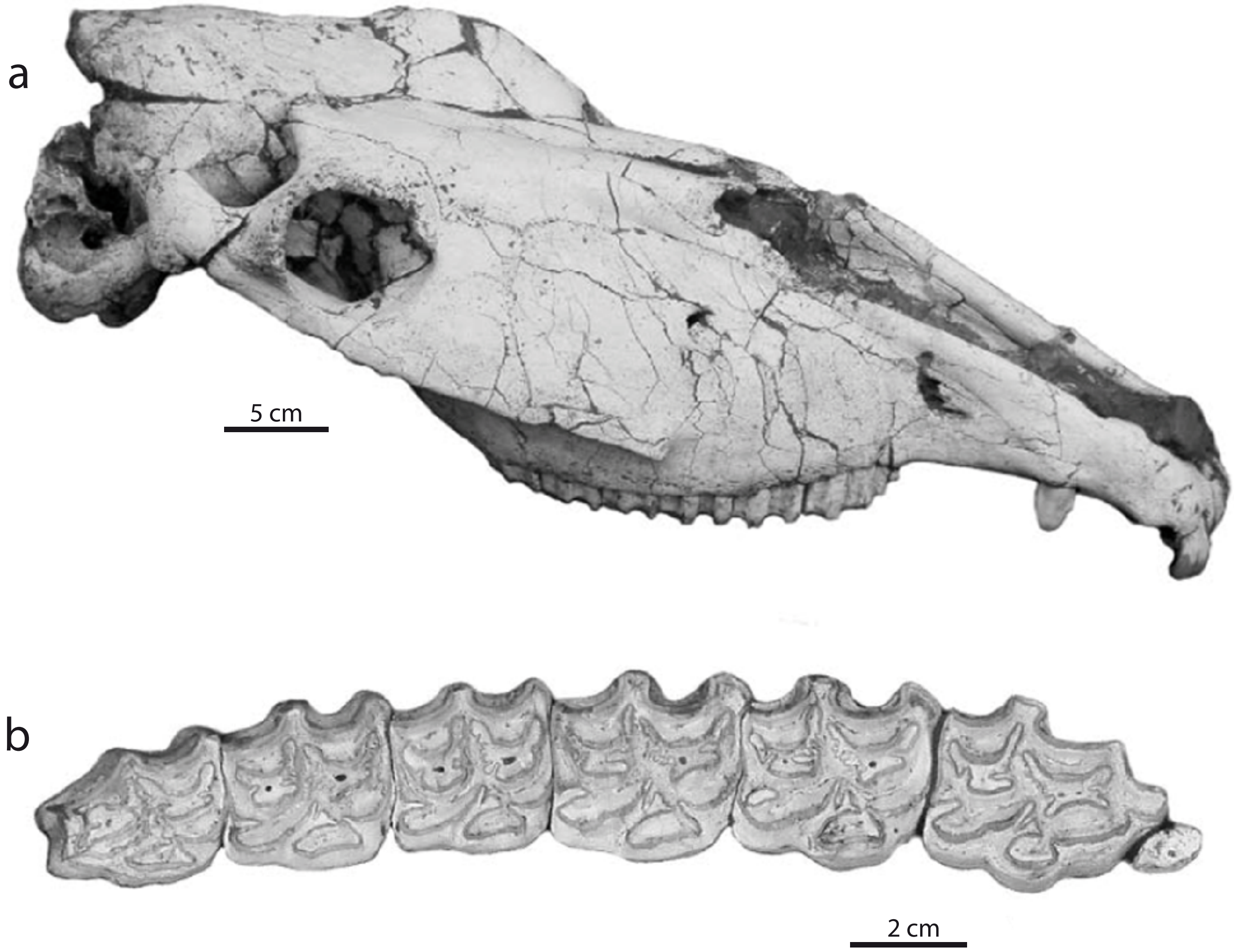
The species *E. senezensis* is characterised by a long and relatively narrow skull, with a basal length of about 480–497 mm, a cephalic index equal to 37.7, and a short muzzle (Text-fig. 3). This stenonoid horse shows tooth morphology closer to *E. s. stenonis* than to *E. s. vireti* (e.g. short protocone with an average length of 8.8 mm in P3 – P4 and 9.7 mm in M1 – M2). Conversely, the limb bones are less elongate that those of *E. s. stenonis*. In particular, the metapodials are shorter but more slender than in *E. s. stenonis*.

"*E. stehlini*" (Text-fig. 4), a species created by Azzaroli (1965: 9–11) for late Villafranchian specimens from Upper Valdarno (Italy) is smaller than *E. stenonis*, and shows some asinine-like features, such as "a skull much smaller in size and shorter and more slender muzzle than *E. stenonis* ….. a narrow symphysis, a small size of the cheek teeth, … nasal opening as far back as P2". Later, Azzaroli (1990) noted that *E. stehlini* shares many cranial specializations (deep narinal notch, shallow preorbital pits, deep groove along the sagittal suture of the nasal) with *E. senezensis* from Senèze, although these similarities also apply when compared to *E. stenonis*. Alberdi et al. (1998), in their revision of the stenonoid horses from Europe, considered this horse a subspecies of *E. senezensis*, as suggested by the skull morphology and results obtained by multivariate statistical analysis. The Italian horse differs from the French ones in having shorter metapodials and deeper ectoflexids on the lower premolars.

Recently, a horse smaller than the typical *E. stenonis* has been reported from Coste San Giacomo (Italy), in a LFA similar in age to Senèze (Bellucci et al. 2012, 2014, Palombo et al. 2017), and tentatively identified as *E. senezensis* aff. *E. sen. stehlini*. The presence in Coste San Giacomo of horse remains similar to those typically found in the Valdarno deposits, puts back their appearance to the middle Villafranchian, and poses some questions about the actual origin of "*E. stehlini*" that Azzaroli (1990) believed to have originated by cladogenesis/sympatric speciation from *E. stenonis*. Palombo et al. (2017), implicitly assuming that only one middle-sized horse species was present in Senèze, proposed different hypotheses to explain the origin of pre-Olduvai middle-sized horses and their relationship with the early post-Olduvai ones. The first hypothesis would assume that in the early middle Villafranchian two stenonoid lineages stemmed from the European *E. livenzovensis* group. One included the large and ecologically flexible horses, belonging to the *E. stenonis* group, and the other the relatively smaller, more slender and specialized horses of the *E. senezensis* group. From these horses, present in the pre-Olduvai middle Villafranchian in a few South European LFAs (e.g. Senèze, France, Vatera, Greece and Coste San Giacomo, Italy), could have originated in the early late Villafranchian, a slightly more robust ecomorphotype/subspecies (i.e. *E. sen. stehlini).* A second hypothesis would presume that early on smaller, more slender and specialized different species (i.e. *E. senezensis*, *E. stehlini* and perhaps *Equus* sp. from Vatera) originated independently through cladogenic processes from local populations of *E. stenonis.* According to a third hypothesis *E. altidens* could have derived from *E. stenonis*, shortly before the Jaramillo submagnetochron, replacing the horses of medium size already present since the middle Villafranchian.

Available data, however, fail to provide compelling support for any of the alternative hypotheses. As a result, any questions about the taxonomical rank and actual phylogenetic relationships of the middle sized, slender middle Villafrachian horses cannot be convincingly answered.

We should also mention a further alternative hypothesis proposed by Eisenmann (2010) who believed that *E. altidens*, regarded as phylogenetically unrelated to stenonoid horses, could be part of an Eurasian group stemmed from a North American lineage about 2 Ma ago (see below). In our opinion, the stenonoid characters of *E. altidens* and related species



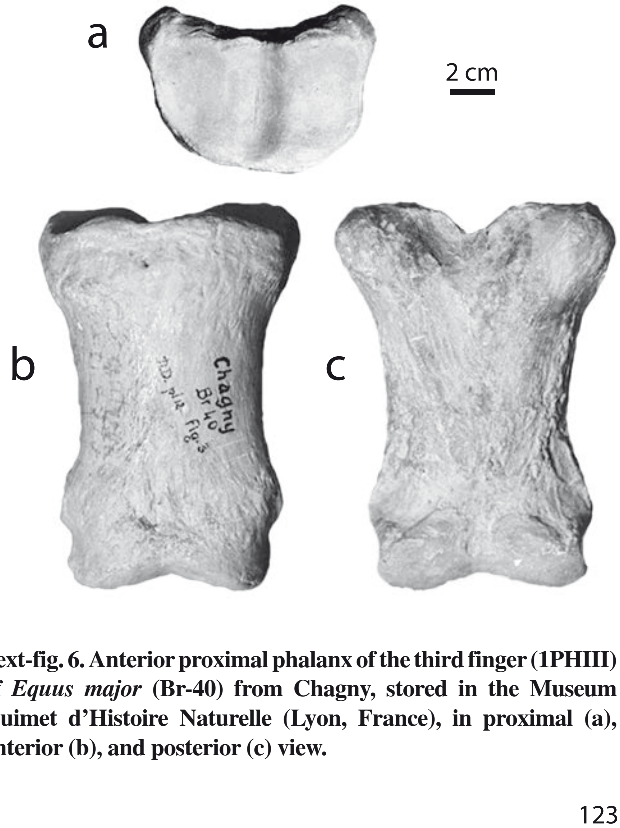
Text-fig. 5. *Equus* cf. *E. major* from Fonelas 1 (Guadix Baza basin, Spain). a) skull in right rostro-lateral view; b) right tooth upper row in occlusal view (modified from Garrido 2008).

(i.e. *E. senezensis*/“*E. stehlini*”), as well as the continuous, although sporadic, presences of the middle sized, slender horses in the middle and early late Villafranchian (e.g. among other Senèze, Coste San Giacomo, Matassino (De Giuli 1972 and unpublished data), and Valdarno LFAs) seem to deny the hypothesis.

The large sized Equus major

During the first part of the Early Pleistocene (Gelasian Epoch), horses larger than those belonging to “*E. stenonis* group”, usually reported as “*Equus bressanus*” or *Equus major* (a senior synonym and the valid name according to the ICZN nomenclature rules), were not frequent. The nomenclature of these very large equids and their relationships with taxa of “*E. stenonis* group” have been widely discussed by several authors (see e.g. Azzaroli 1992, Alberdi et al. 1998, Forsten 1999, Eisenmann 2006).

E. major is recorded in various localities by the few remains, sometimes found together with either *E. stenonis* (e.g. Upper Valdarno) or *E. senezensis* (e.g. Senèze) specimens. At Fonelas, however, the quite rich equid sample includes only a stenonoid horse provisionally identified as *E.* cf. *major* (Garrido 2008) (Text-fig. 5). *E. major* shows dental



Text-fig. 6. Anterior proximal phalanx of the third finger (1PHIII) of *Equus major* (Br-40) from Chagny, stored in the Museum Guimet d’Histoire Naturelle (Lyon, France), in proximal (a), anterior (b), and posterior (c) view.

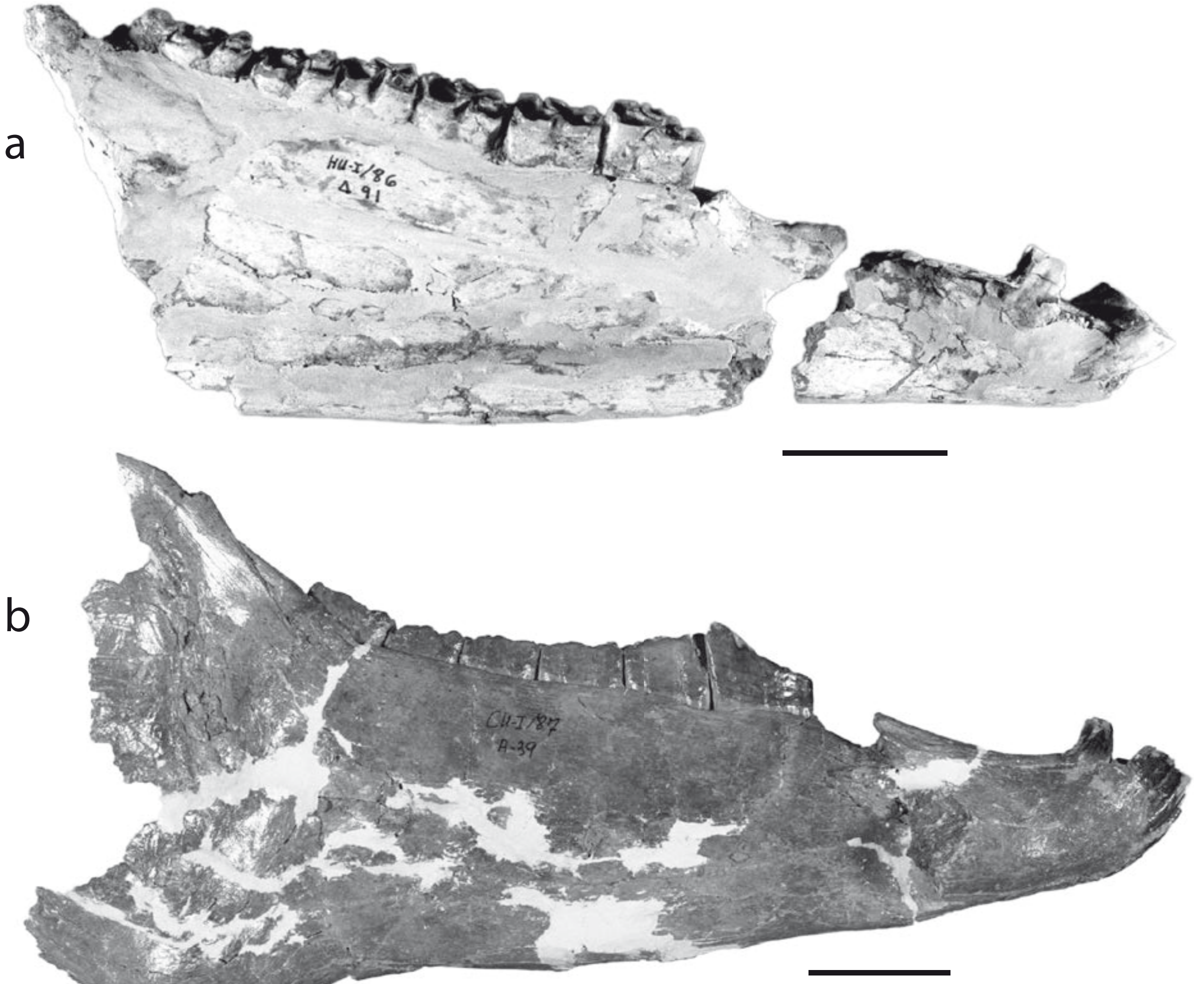
stenonoid features (e.g. short protocones and developed pli caballin), but limb bone morphology, although sharing many features with stenonoid horses, also has some apparent caballoid traits. It was the biggest stenonoid horse, even larger and heavier than *E. livenzovensis*, showing more marked dimensional differences in the first phalanx (Text-fig. 6) rather than in the metapodials (average lengths of MCIII and MTIII = 271 and 329 mm respectively). According to Alberdi et al. (1998), *E. major*-*E. suessenbornensis* monophyletic group may have stemmed from *E. livenzovensis*.

The horse turnover during the post Olduvai late Villafranchian

Evidence from terrestrial fossil plants and vertebrates indicates that during the post-Olduvai Early Pleistocene, open and somewhat dry environments progressively expanded in South Europe. A gradual renovation of large mammal communities occurred in a period recording the first evidence of the incoming marked climatic upsetting known as the Mid-Pleistocene Revolution/Transition (see e.g. Magri and Palombo 2013, Sadori et al. 2013, Palombo 2014, 2017, and references therein). A few anagenetic processes within already present phyletic lineages, and discrete dispersal bioevents of taxa originally coming from both Asia and Africa led to the appearance of new taxa and triggered new faunal dynamics.

Two horses are reported for the first time, since about 1.5 Ma, in South Europe during the post-Olduvai Early Pleistocene, a slender, middle-sized horse here identified as *Equus altidens*, and a larger more robust equid here identified as *Equus suessenbornensis*. These equids were first recorded in Italy (Selvella and Pirro Nord LFAs), then in Spain (Barranco Léon 5 and Fuente Nueva 3 LFAs), and even later in France (?Solilhac LFA) (Prat 1980, Alberdi 2010, Alberdi and Palombo 2013a, b, Palombo 2016, 2017 and references therein).

Scholars disagree on the systematics and taxonomy of *E. altidens* and *E. suessenbornensis* that have been regarded either as phylogenetically related species or as belonging to different phyletic lineages. Eisenmann (2004, 2010) considered both species, as well as "*Equus*



Text-fig. 7. Mandibles of *E. altidens* from the Guadix-Baza Basin (Spain), stored in the Museo Nacional de Ciencias Naturales, CSIC (Madrid, Spain). a) mandible from Huéscar-1 in buccal view; b) mandible from Cúllar de Baza in lingual view. Scale bar = 5 cm.

granatensis" (here considered a younger synonym of *E. altidens*) as bona fide species not phylogenetically linked to stenonoid horses (see e.g. Eisenmann 1999, 2006, 2010 for a discussion), and assigned them to the new subgenus *Sussemionus* (type species *E. coliemensis*, from the late Early Pleistocene deposit of Kolima, Siberia). The subgenus would include "species" showing a mixture of osteological characters (e.g. following Eisenmann's classification, the Asian horses *E.* (*Sussemionus*) *verae* and *Equus* (*Sussemionus*) *hipparionoides*, and the European *E.* (*Sussemionus*) *suessenbornensis*, *E.* (*Sussemionus*) *altidens*, *E.* (*Sussemionus*) *granatensis*, and *E.* (*Sussemionus*) *marxi*), some of which characterised the fossil equids from Süssenborn (Germany), and some others observed in extant hemiones. In spite of this apparent similarity, sussemiones formed a separate monophyletic group with no extant relatives, as supported by mtDNA analyses of specimens from Khakassia (SW Siberia) (Orlando et al. 2009). According to Eisenmann (2010), the subgenus *Sussemionus* could have stemmed from equid stock present in North American around 2 Ma, where very small horse species were reported in the late Blancan of Arizona (Azzaroli and Voorhies 1993). *Sussemionus* would have had a wide geographical (from Arizona to Ethiopia) and chronological range (from about 2 Ma to 45–50 ka). The last representative of the subgenus, *Equus ovodovi*, is indeed recorded in Proskuriakova Cave (Khakassia, Southwestern Siberia) in deposits carbon dated to 40 ka (Eisenmann and Sergej 2011). As discussed above, in our opinion, available data on the one hand fail to fully support this hypothesis, on the other confirm the basic stenonian morphology of *E. altidens* teeth and limb bones.

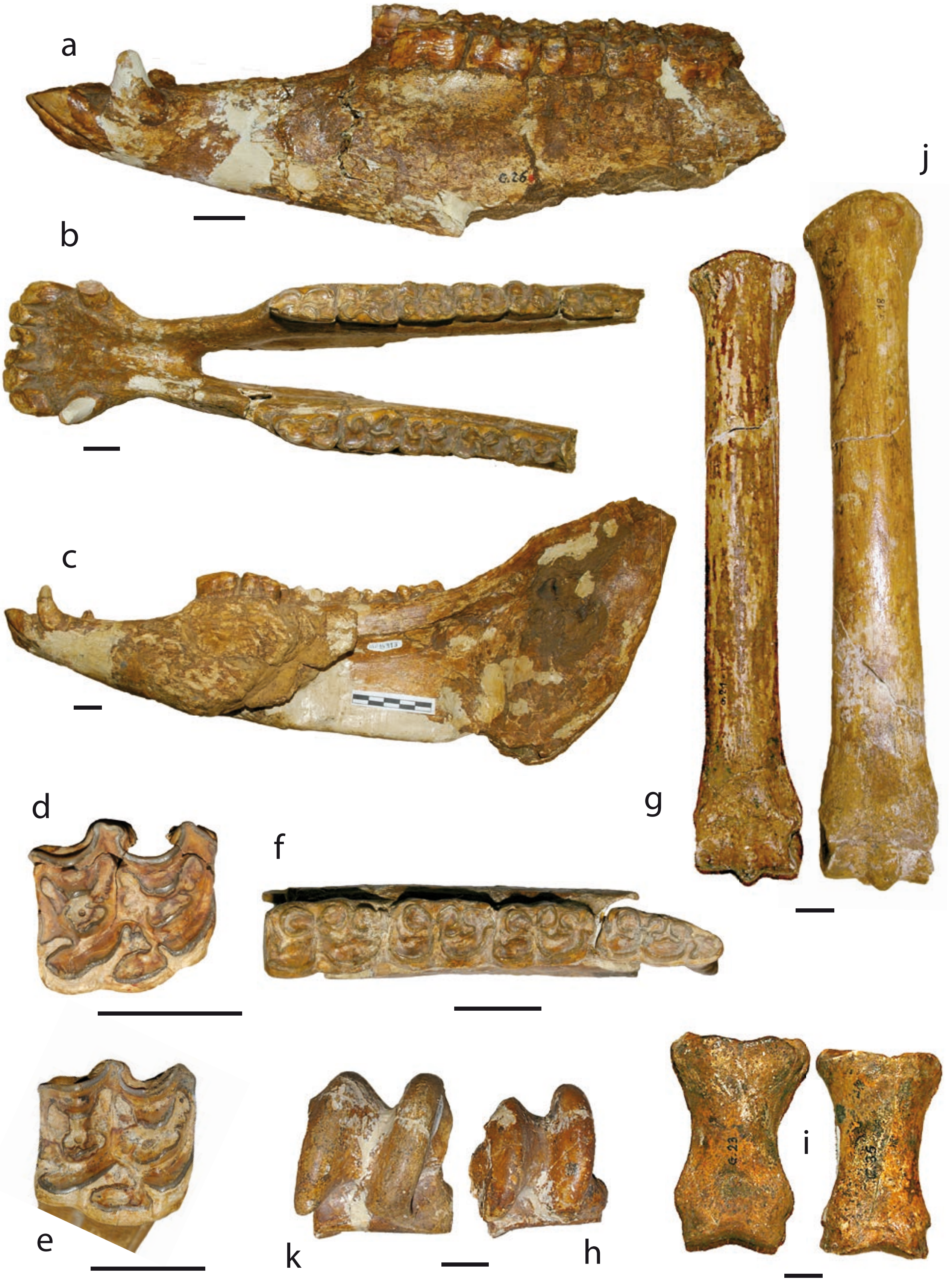
The slender horse Equus altidens

Von Reichenau (1915) created the species *E. altidens* for the small size horse remains found in the early Middle Pleistocene locality of Süssenborn (Germany). This species shows dental morphology (i.e. shape of protocones and double-knot) quite similar to that of *E. stenonis*, but is smaller than the latter, more slender than *E. senezensis*, the distal part of the protocone is more elongated than in *E. stenonis*. Moreover, metapodials and phalanges are more slender than in any other stenonoid horse. *E. altidens* is reported in South, Central and possibly Eastern Europe during the post-Olduvai Early and the early Middle Pleistocene (Cúllar de Baza, Huéscar, Quibas in Spain, Pirro Nord, Venosa and Ponte Galeria in Italy, Solilhac in France, and several localities in Germany including the type locality of Süssenborn) (Text-figs 7, 8, 9). The species is associated with *E. suessenbornensis* in most of the deposits, but the relative percentage of these equids varies from one site to another.

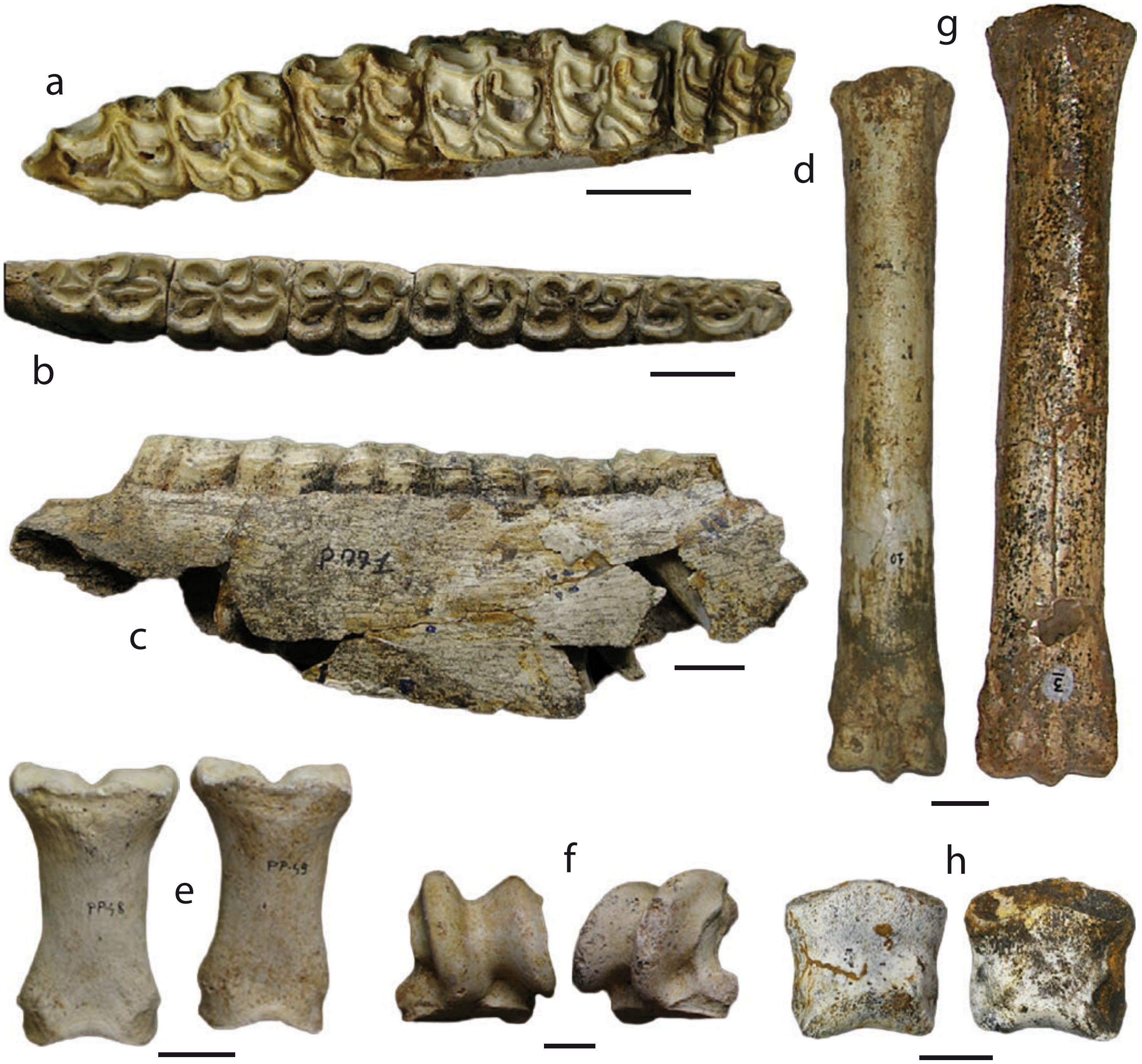
E. altidens has been regarded either as a species originated from a pre-existing European lineage (sees e.g. Forsten 1986b, 1999, Azzaroli 1990, 1992, Alberdi et al. 1998, Alberdi and Palombo 2013a, b, van der Made 2013 for a discussion) or a new Early Pleistocene incomer, which originated from an African species (*Equus tabeti*, *Equus numidicus*) (e.g. Eisenmann 1992, Guerrero-Alba and Palmqvist 1997, Fleagle et al. 2010), or from the Chinese lineage of *E. qinyangensis* (see above, Eisenmann and Deng 2005).

The sample of the middle-sized horse from the late Villafranchian Italian site of Selvella (De Giuli 1987) (inferred age of about 1.5; Napoleone et al. 2003) may provide some clues regarding the origin of this slender species. In the Selvella LFA, a large, robust and a middle sized, slender horse is present. Authors disagree about the taxonomical identification of the latter, which was recorded in the literature, for instance, as *E.* cfr. *E. stenonis* (De Giuli 1987), *E. stenonis* ssp. (Caloi and Palombo 1987), a possible distinct subspecies of *E. stenonis* (Azzaroli 1990), a species very close to *E. tabeti* (Eisenmann 1992), *E. altidens* (Caloi 1995), *E. altidens altidens* (Alberdi and Palombo 2013a, b), and an *E. stenonis* representative with slender phalanges and metapodials and quite peculiar proportions (Forsten 1999). The relatively rich sample of middle-sized horses from Selvella includes isolated teeth, mandibles and limb bones, but not skulls (De Giuli 1987, Alberdi and Palombo 2013a, b). The teeth and postcranial bones, although sharing a few plesiomorphic traits with *E. stenonis* (e.g. a quite short protocone and the double-knot shape) show morphological traits similar to those characterising the basic morphology of *E. altidens* (e.g. some limb bones proportions) (Text-fig. 8). In the upper premolars and molars, for instance, the mesial part of the protocone is short while the distal is moderately elongate, and a concave lingual rim prevails, the pli caballin is generally present, the hypocone is mainly open and oval-triangular in shape with marked distal, and slightly marked mesial grooves, the hypocone is isolated inside the loph of some M3. The lower premolars show a double knot with short, rounded metaconids and metastylids, sometimes clearly pointed metastylids, "V-shaped" linguaflexid. The ectoflexid is shallow and does not enter the isthmus in the premolars, but in the molars it is deep and penetrates the isthmus making contact with the linguaflexid. The dimensions of limb bones are consistent with those of *E. altidens*, and the gracility indices of the middle-sized metapodials (ranging from 12.90 to 14.72 in metacarpals, and from 11.69 to 11.87 in metatarsals) indicate that the Selvella equid was a slender horse, similar in proportions to some early Middle Pleistocene *E. altidens.*

The European horse samples referred to *E. altidens* show a nearly uniform tooth morphology, while the size and metapodial and phalange gracility vary from one sample to another as highlighted by the results of the multivariate analysis performed by Alberdi et al. (1998), according to which two groups differing in the proportions of metapodium and acropodium bones may be detected. This prompted Alberdi et al. (1998) to split *E. altidens* in two subspecies, *E. a. altidens*, and, the latter larger with less slender but shorter limb bones. *E. a. granatensis* "subspecies" is mainly recorded in Early Pleistocene Spanish LFAs (e.g. Venta Micena, Lachar, Fuensanta, Fuente Nueva 3, Barranco León 5 in Spain, possibly Sainzelles in France). *E. altidens* is probably present at Sima del Elefante and Pinal. The nominotypical subspecies is mainly recorded in early Middle Pleistocene LFAs, but is also present in a few Early Pleistocene sites, such as Pirro Nord (Italy) LFA (Text-fig. 9) close in age to the Spanish Venta Micena LFA (see among others Prat 1980, Alberdi et al. 1998, Alberdi 2010, Alberdi and Palombo 2013a, b, van der Made 2013, Piñero and Alberdi 2015 and references in those papers).



Text-fig. 8. ***Equus altidens*** **and** ***Equus suessenbornensis*** **from Selvella (Italy).** ***E. altidens*****: a–b) Mandible (IGF-14312) in lateral view (a) and occlusal (b) view; c) Mandibles (IGF-14312) in lateral view; d) right P3 – P4 (IGF-14338) in occlusal view; e) right M1 – M2 (IGF-14340) in occlusal view; f) left p4 – m3 (IGF-14314) in occlusal view; g) third left metatarsal (IGF-14184) in anterior view; h) right astragalus (IGF-14191) in anterior view; i) left posterior (IGF-14324) and right anterior (IGF-14323) proximal palanx in anterior view.** ***E. suessenbornensis*****: j) third left metatarsal (IGF-14185); k) right astragalus (IGF-14190) in anterior view. Scale bar = 2 cm. Modified from Alberdi and Palombo (2013a). (IGF = Geological and Paleontological Museum, University of Florence).**



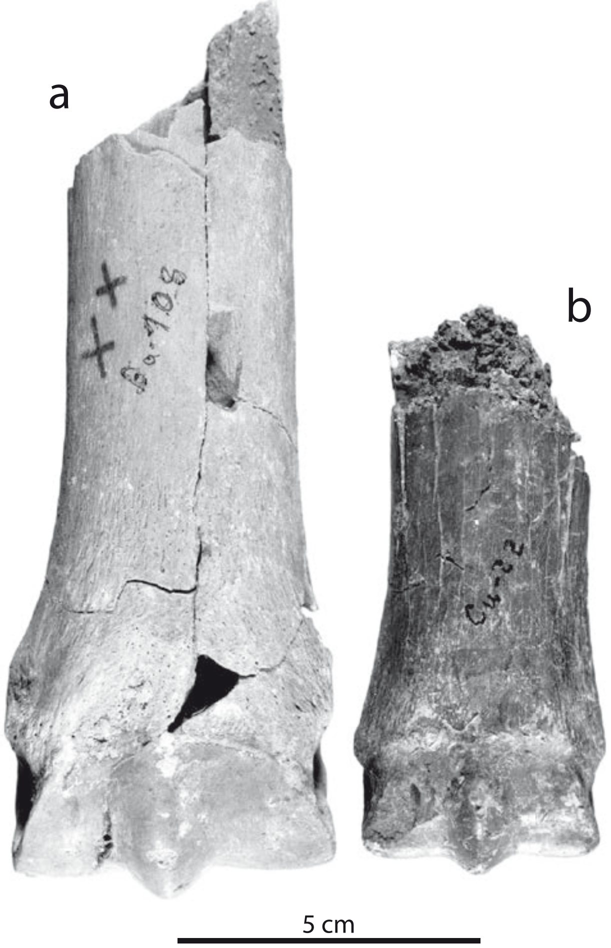
Text-fig. 9. ***Equus altidens*** **and** ***Equus suessenbornensis*** **from Pirro Nord (Italy).** ***E. altidens*****: a) left P2 – M3 (without number) in occlusal view; b–c) left p2 – m3 (P771) in occlusal (b) and lateral (c) view; d) left MTIII (10 PA) in anterior view; e) proximal phalanges (PP-48 and PP-49) in anterior view, f) right (DE 12.1) (on the right) and left (PP-43) (on the left) astragalus in anterior-lateral view;** ***E. suessenborrnensis*****: g) third right metatarsal (n. 32) in anterior view; h) second phalanx (PU-106721) in posterior and anterior view. Stored in the Geological and Palaeontological Museum of Florence (Italy). Scale bar = 2 cm. Modified from Alberdi and Palombo (2013a).**

The nearly contemporaneous occurrence of local populations slightly differing in morphological traits, size and limb bone proportions, makes it difficult to depict the evolutionary scenario of *E. altidens* and the actual significance of alleged geographic subspecies, especially because of the lack of well-preserved skull remains. Whether "*E. a. granatensis*" was a primitive representative of the *E. altidens* lineage or merely an ecomorphotype mainly present in Spain, and maybe in France (Sainzelles), is unclear. Horses ascribed to "*E. a. granatensis*" and "*E. a. altidens*", share a number of features, although some plesiomorphic features shown by the teeth of *E. a. granatensis* may suggest that it is less advanced than "*E. a. altidens*". The presence in the Selvella LFA, of a horse whose traits seem to be intermediate between the alleged subspecies stresses the difficulty in discriminating between evolutionary and ecomorphological traits. Although the hypothesis that differences in size and limb bone proportions may be related to dissimilar environmental conditions cannot be discounted.

All thing considered, the main morphological traits, especially those of teeth, and some tendency to evolve towards ecomorphotypes with more slender metapodials shown by the representatives of *E. stenonis* group, support the hypothesis that *E. altidens* originated in Europe by an anagenetic evolutionary process within the stenonian lineage as a response to the changing climatic and environmental conditions. The appearance of *E. altidens* in SW Europe, whatever related to in loco origination or to a dispersal event, confirms, indeed a spread of open landscapes that time by time modified the vegetation physiognomy across the region and had a significant influence on the ecological structure of large mammal palaeocommunities.

The large and robust horse Equus suessenbornensis

The species *E. suessenbornensis*, created by Wüst (1900) for some large sized remains from the early Middle Pleistocene site of Süssenborn (Germany), is characterised by a mixture of stenonoid and caballoid features, in particular by upper cheek teeth with a complicated enamel pattern. This large horse, smaller than *E. major*, with very robust metapodials (average maximum length: MCIII = 271 mm, MTIII = 293.07 mm), appeared in Europe at about 1.5–1.4 Ma, when it is reported, for instance, in Italy (Pirro Nord) (Alberdi and Palombo 2013a, b), and in Spain (Barranco León 5 and Fuente Nueva 3) (Alberdi 2010, Oms et al. 2010a, b, Duval et al. 2012, Álvarez et al. 2015) (Text-figs 9, 10). The fossil record, rather scarce during most of the Early Pleistocene, increased since about 0.9 Ma throughout the early Middle Pleistocene.



Text-fig. 10. Third metacarpal (distal part) of *E. suessenbornensis* (a) and *Equus altidens altidens* (b) from Cúllar de Baza (Guadix-Baza Basin) in anterior view. Stored in the Museo Nacional de Ciencias Naturales, CSIC (Madrid, Spain).

The unique mix of stenonoid and caballoid characters shown by *E. suessenbornensis* led some authors to suggest it could be an evolutionary intermediate between stenonoids and caballoids, or to consider it a stenonoid horse showing some features converging towards those of caballine horses. In particular some authors consider *E. suessenbornensis* a descendant of *E. major* (Grossouvre and Stehlin 1912, Forsten 1999, Alberdi et al. 2001), which is last recorded in Europe about 1.7 Ma (Musil 1992), others considered it to be close to, or a direct descendant of *E. stenonis* (Nobis 1971, Samson 1975, Azzaroli 1984), while others reject any affinity between *E. suessenbornensis* and *E. stenonis* (Musil 1969, 1992), considering it an archaic caballoid or a true caballine (Gromova 1949a, b). Some features of *E. suessenbornensis* (complicated enamel pattern, upper cheek teeth with rather long protocones with concave lingual borders, lower cheek teeth with marked protostylids) actually look like those of caballoid equids (Gromova and Dubrovo 1975), but some other dental characteristics (e.g. the stenonian shape of the double-knot, although more derived than in *E. stenonis*) clearly indicate an advanced taxon within the basic stenonoid type.

All in all, morphological and biometrical data support the existence of a long lasting *E. major-E. suessenbornensis* lineage, and the hypothesis that it may have originated from the *E. livenzovensis* clade, seems to be the most parsimonious.

How many horse species were in Europe during the late Early Pleistocene?

From shortly before the Jaramillo palaeomagnetic event to the early Middle Pleistocene, the increasing climatic instability connected to the onset of a new global climatic regime/system (the so-called Mid-Pleistocene Revolution/Transition, MPR/T, broadly speaking from about 1.2 to 0.6 Ma; Maslin and Ridgwell 2005) characterised by increased severity and duration of cold stages, had a profound effect and prompted important changes in the structure of terrestrial ecosystems especially in the northern hemisphere (Head and Gibbard 2005). The climate forcing, in particular precessions that have an important control on seasonality, induced deep, more or less gradual alterations and latitudinal displacements in European terrestrial biomes, and was a critical factor in driving faunal turnovers by removing keystone species, and exerting great influence on dispersal and dispersion of mammalian taxa across and between continents. This in turn triggered new competition-coevolution dynamics that contributed to either the extirpation of some taxa or to the appearances of others by anagenetic evolution in some phyletic lineages. In SW Europe, in spite of a continuing change in the structure of large mammal palaeocommunities, *E. altidens* and *E. suessenbornensis* stenonoid horses were recorded throughout the MPR. The SW European *E. altidens* populations slightly differentiated from each other, possibly as a response to the wide array of environments present during the late Early to Middle Pleistocene in the Mediterranean area, while *E. suessenbornensis* did not undergo any important local differentiation (e.g. Alberdi and Palombo 2013a, b and references therein).

In this scenario it is complicated to understand the details and explain the appearance in Europe of the gracile *Equus* *wuesti* by the time of the Jaramillo submagnetochron (only recorded with certainty in Germany in the Untermassfeld LFA) (Musil 2001), and the more robust *Equus apolloniensis*, reported from some Greek LFAs (Koufos et al. 1997, Koufos 2001, Athanassiou 2002, Konidaris et al. 2015) and possibly present also in Turkey roughly during the same period (Boulbes et al. 2014, Lebatard et al. 2014, Mayda et al. 2015).

Equus wuesti: *an intriguing slender stenonoid horse*

The species *Equus wuesti* was created by Musil (2001) for the rich sample of a slender horse but which was significantly larger than *E. altidens.* The sample was from the well-known German LFA of Untermassfeld, regarded as the epitome of the so-called Epivillafranchian ELMA (Kahlke 2006, 2007). The fossil record of *E. wuesti* includes a number of long bones as well as mandibles and isolated teeth which show a mix of primitive and derivative characters. This evidence prompted Musil (2001) to consider the Untermassfeld equid as more advanced than the nearly contemporaneous European stenonoid horses. A comparison with the quite rich sample of *E. altidens* from Pirro Nord (Alberdi and Palombo 2013b) may suggest some similarities in the size of teeth and long bone of the samples from both localities. The maximum length of the Untermassfeld metapodials, for instance, fall within the range of variation for the specimens of *E. altidens* from Pirro Nord and other localities included in the comparison material used by Alberdi and Palombo (2013b). It is difficult, however, to appreciate the actual difference in proportions possibly exhibited by *E. wuesti* based on literature data. This is because measurements taken by Musil (2001) differ from those suggested and standardized during the *Hipparion* Conference (New York, November 1981; see Eisenmann et al. 1988).

All in all, the morphological traits shown by these teeth warrant consideration of the similarities with *E. altidens*, while the metapodials and phalanges of the German horse, although similar in size to those of *E.altidens*, seem to be more robust.

E. wuesti has been, indeed considered a stenonoid horse by most authors, showing some similarities with *E. altidens.* Forsten (1999), for instance, had already considered the horse from Untermassfeld to be similar to *E. altidens*, suggesting some relationships with either the slender equid identified by the Finnish author at Livenzovka (see above) or with Asian horses, such as those found at Nalaikha (Mongolia) (i.e. *Equus nalaikhaensis*) (but see Eisenmann and Kuznetsova 2004) and Nihowan (China). Some other authors considered the Untermassfeld horse the putative ancestor of *E. altidens*, in spite of the presence of the latter species in LFAs older than the German site (Musil 2001, Lister et al. 2010). It is, however, challenging to fully understand its origin and clarify the actual phylogenetic relationship of the Untermassfeld species with the *E. altidens* populations recorded in Europe by the end of the Early Pleistocene and those typically present in German LFAs during the early Middle Pleistocene, such as *E. altidens* from Süssenborn (Musil 1969, Forsten 1986b, 1988).

Whether *E. wuesti* could have originated from an unknown Asian species that enlarged the limits of its range towards central Europe at the time of MPR when open landscapes extended to the west triggering the discrete dispersals of ungulates inhabiting grasslands, or could have originated from the local evolution of the stenonoid population, or alternatively may represent a local morphotype within the *E. altidens* group, still remain unanswered questions.

The east Mediterranean horse Equus apolloniensis

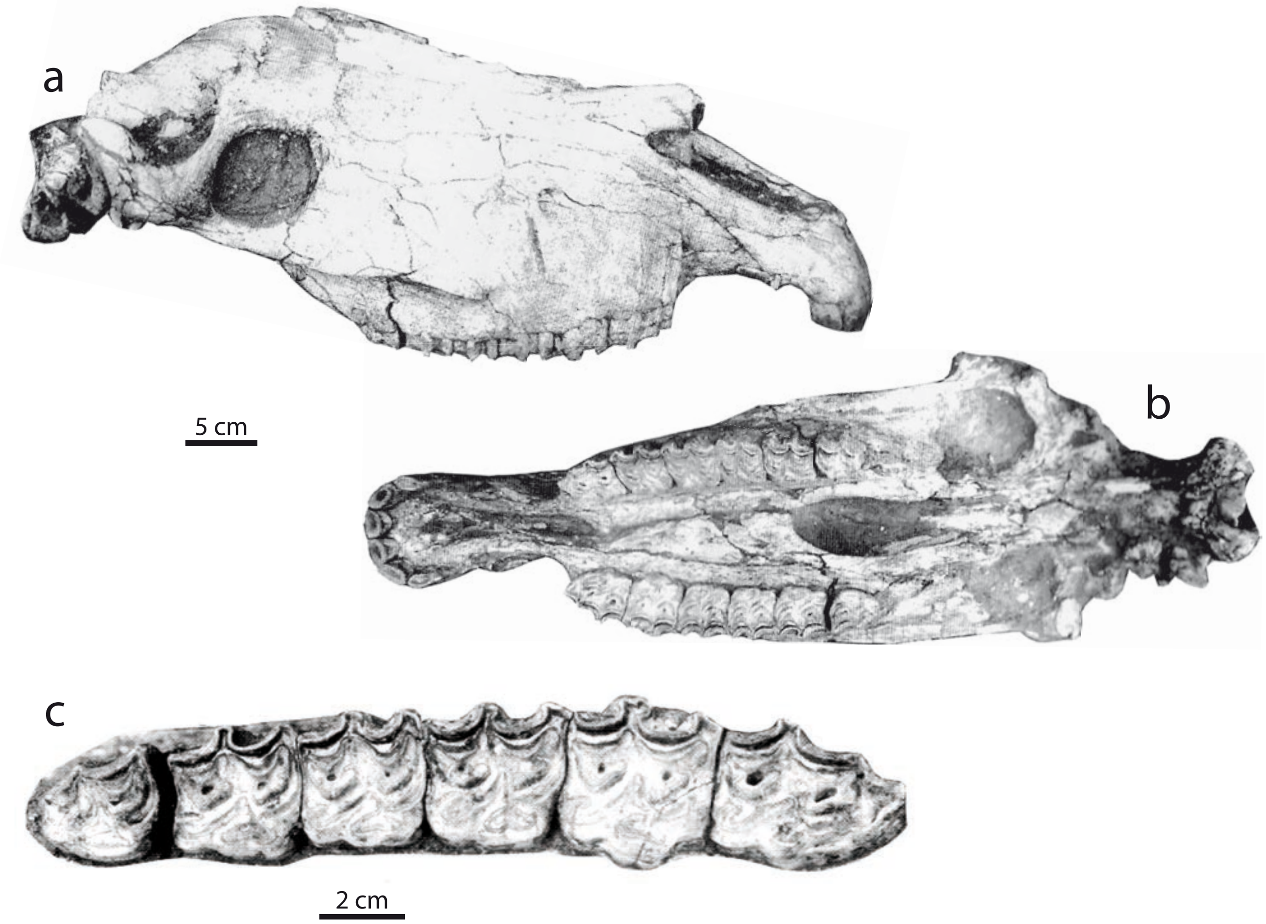
The species *Equus apolloniensis* (Text-fig. 11) was created by Koufos et al. (1997) for the rich equid sample found in the late Early Pleistocene LFA of Apollonia 1, dated to about 1.2–0.9 Ma (Koufos and Kostopoulos 2016). The Apollonia horse was regarded by the authors of the species as a stenonoid horse, which could "represent a transitional form from the typical *E. stenonis* to the Middle Pleistocene horses (*Equus* ex gr. *E. suessenbornensis*)". The species, known by a number of well preserved remains, including cranial and limb bones, is characterized by "large size, short and deep muzzle, short palate, elongated choanae, shallow narinal notch, far posteriorly situated orbit, elongated supra occipital crest, relatively long protocones, elongated and slender metapodials" (see Koufos et al. 1997: 50).

A comparison with tooth remains of *E. altidens* and *E. suessenbornensis* from some Early Pleistocene South European sites (Pirro Nord, Venta Micena, Fuente Nueva 3, Huéscar-1) shows that the Apollonia horse had large teeth, on average larger than the largest teeth of *E. altidens*, but the average size of metapodials (in particular the maximum length) fall roughly within the range of *E. altidens*. If compared with *E. wuesti*, *E. apolloniensis* shows definitely larger teeth, while the metapodials are similar in length, but more robust, confirming the peculiar proportion and characteristics of the skeleton of the Apollonia horse.

Koufos et al. (1997) noted that "the similarity in proportion of the Apollonia metapodials with the older local subspecies *E. s. mygdoniensis*" would suggest that "a gradual adaptation in situ from this form is possible, while the slenderness, the short muzzle, the less cursorial proportion of Apollonia horse indicate also cool conditions" (Koufos et al. 1997: 49, 55). The presence in the late Villafranchia LFA of Tsiotra Vryssi (Mygdonia Basin, Macedonia) of scanty remains of two horses, *Equus* sp. medium-sized and *Equus* sp. large-sized respectively similar in size to *E. s. mygdoniensis* and *E. apolloniensis* (Konidaris et al. 2015), would contradict the idea of *E. apolloniensis* originating from the slender Villafranchian stenonoid horse reported in Greece.

The origin and phyletic relashionships of *E. apolloniensis* are a matter of debate: Eisenmann and Kuznetsova (2004: 524) noted that although the exact taxonomic position of *E. apolloniensis* is unknown, the basicranial proportions indicate that the species does not belong to *Allohippus*, but to *Equus*, while upper cheek teeth "resemble hemiones and some asses by their deep postprotoconal grooves and lack of plis caballins", and lower teeth "are absolutely ass-like: rounded double knots, shallow ectoflexids on molars".

All in all, based on the available data, the correct taxonomical position of *E. wuesti* and *E. apolloniensis*, and their relationships with stenonoid horses recorded in Europe during the Early Pleistocene remain controversial, although



Text-fig. 11. Skull of *Equus apolloniensis* from Apollonia (Macedonia, Greece) (APL-148) in lateral (a), and ventral (b) view. c) the right upper tooth row in occlusal view (modified from Koufos et al. 1997).

the hypothesis that the German and the Greek horses may represent local representatives respectively of *E. altidens* and *E. suessenbornensis* lineages would merit further investigation.

The decline of *E. altidens* and *E. suessenbornensis* and the appearance of new equids during the Middle Pleistocene

During the early Middle Pleistocene, *E. altidens* and *E. suessenbornensis* are reported from a number of European localities. The type locality of Süssenborn (Germany), about 0.6 Ma old, records a rich sample of both species, which occur in approximately equal proportions (Musil 1969, Forsten 1986b). The relative abundance of these horse species across Europe varies according to the climatic region, geographical position, environmental conditions, in particular the vegetation cover and productivity, characterising the localities in which they were found. In SW Europe, for example *E. altidens*, was definitely more abundant than *E. suessenbornensis* in the late Early than in the early Middle Pleistocene LFAs, when the frequency of both species, as regards the number of sites and number of specimens decreased. Conversely, *E. suessenbornensis* was generally only sporadically recorded in South Europe in both periods. The two equids probably differentiated in their ecology and the notable differences in size likely prevented any interspecific competition. To avoid competition for resources, indeed, sympatric horse species with wide ecological requirements have to have different ecological niches, as it may be inferred sometimes more from their different size than from their actual morphology. Accordingly, it is rational to suppose that the appearance in the European early Middle Pleistocene of a large caballine horse (i.e. *Equus mosbachensis*) had some influence on the disappearance of the large stenonoid *E. suessenbornensis*.

The replacement of large stenonoid horses by caballine horses

Von Reichenau (1903) created the species *E. mosbachensis* for a rich horse sample found in the youngest fossiliferous layer (Graues Mosbach/Mosbach 2) of the well-known stratigraphic succession of Mosbach quarries (Rhineland, Germany). The level, which yielded the majority of mammal remains, may be tentatively correlated with MIS 13 or MIS 15 (Maul et al. 2000, Hemmer et al. 2008). The species, showing clear caballine features, although primitive (see e.g. Eisenmann 1979, 1980, Azzaroli 1990), likely originated from an Asian population and dispersed towards

Europe at the beginning of the Middle Pleistocene. The hypothesis may be supported by the presence of caballine horses in the Tiraspolian Kolkotova Balka LFA (Moldova), correlated to MIS 17, or even to the final part of the Matuyama and the beginning of the Brunhes epochs, based on paleontological, bioclimatic and paleomagnetic data (Markova 2007, Markova and Vislobokova 2016).

The species has been reported in some European early Middle Pleistocene localities ranging in age from about 0.6 to 0.5 Ma, or even slightly older. In Germany, for instance, caballine remains have been found at Mauer (MIS 15, 0.609 Ma ± 40 ka; Wagner et al. 2010, 2011), in Spain at Galería GII (between 0.6 and 0.5 Ma; Berger et al. 2008), in France at Pont-du-Château (0.6–0.5 Ma; Raynal et al. 1996), in Italy at Notarchirico (about 0.6 Ma; Pereira et al. 2015), and Cesi (early Brunhes, about 0.7 Ma; Ficcarelli et al. 1997, Napoleone et al. 2003), and at La Caune de L'Arago, where the oldest *E. mosbachensis* remains are present in the lowermost levels of the stratigraphic succession, correlated with MIS 14 (Moigne et al. 2006 and references therein). The age of about 0.55 Ma previously proposed by de Lumley et al. (2000) was recently confirmed by new ESR/U-Series dates obtained by Falguères et al. (2015) on herbivorous teeth coming from the lowest excavated layers (Q–P levels). According to the available data, *E. mosbachensis* appeared in Europe when *E. suessenbornensis* was still present in the region, and the two large horse species coexisted for a while. Their sympatry would also be supported by the alleged occurrence of both species in the same stratigraphic level at West Runton (Britain) (large stenonoid horse, cf. *Equus suessenbornensis* and *E.* cf. *ferus mosbachensis* in Lister et al. 2010) together with *E. altidens*. As noted by Lister et al. (2010), however, the identification of the caballoid horse has to be considered provisional, due to the small sample and the mix of stenonoid and caballoid features detectable in *E. suessenbornensis* upper teeth. A caballoid horse has been hypothesized to occur together with *E. suessenbornensis* and *E. altidens*, also at Süssenborn (Musil 1969, Forsten 1986b), although its actual presence in this level needs confirmation (cf. Forsten 1999).

The contemporaneous presence of two large horses in the same area may imply different ecological requirements and a low level of competition, de facto making it more difficult to decipher causal factors behind the replacement of large stenonoid horses by caballine horses in Europe. There are also uncertainties with regard to the disappearance of the middle sized *E. altidens* and the origin of the small late Middle Pleistocene – Holocene species *Equus hydruntinus.*

Was Equus hydruntinus *the last stenonoid horse?*

Equus hydruntinus was a small, gracile horse, with very hypsodont cheek teeth, slender limbs and body proportions suggesting a marked cursorial habit and an adaptation to semi-arid conditions. The species is reported from a number of European and western Asian (e.g. Iran and Israel) sites ranging in age from the late Middle Pleistocene to the Holocene, possibly until the historical time (Wilms 1989, Mashkour 2002, Antunes 2006). The small, slender equid was largely present in Middle and Late Palaeolithic archaeological contexts and was frequently represented in the parietal and portable art (Text-fig. 12). The morphology of the upper cheek teeth, characterised by a short protocone, on one hand shares some features with the zebras, on the other hand shows some similarities with asses. The morphology of the lower teeth (double-knot, deep vestibular groove in molars) is similar to that of stenonoid horses, while the limb bones resemble those of hemiones (see below). These peculiar features make the systematic affiliation of the species controversial. Moreover, in spite of the wide geographical distribution and the rich fossil record, the morphology of the skull of the small equid was for a long time poorly known. This fact and the presence of a mix of morphological characteristics in the teeth and bones contribute to the disparity of opinions among scholars regarding its systematic position relative to other equid lineages. *E. hydruntinus* was considered by some authors to be a zebra (Davis 1980), by other an ass (Stehlin and Graziosi 1935, Gromova 1949a, b), or a stenonoid horse which may have been derived from *E. altidens* (e.g. Forsten 1986b, 1999, Forsten and Ziegler 1995, Alberdi and Palombo 2013a, b), while Azzaroli (1979: 37) noted that the species "... recall hemiones in the slenderness of the limbs, asses in the microdonty, zebras in the enamel pattern of the cheek teeth ...". Eisenmann and Mashkour (1999: 120, 121), while discussing the possible range of morphological and dimensional variation of their newly created hemione subspecies (*Equus hemionus binagadensis* from Binagady, Azerbaijan) did not exclude the hypothesis that it may "include teeth and bones presenting characters of *E. hydruntinus*", and consequently "that *E. hydruntinus* was basically a variation of Hemione, not a Zebra nor an *E. stenonis*, or that the morphologies considered as specific for *E. hydruntinus*, developed several times in different places, and inside different phylogenetic lines". Van der Made et

Text-fig. 12. Engraving of *Equus hydruntinus*, Grotta del Genovese on the Island of Levanzo (Egadi, Sicily, Italy), dated at about 12 cal ka BP (Tusa 1999) (modified from Antonioli et al. 2016).

Text-fig. 13. Skull of *E. hydruntinus* from Kabazi II (Crimea), lateral view (modified from Burke et al. 2003).

al. (2016) stated that it was probably closely related (or ancestral) to the living *Equus hemionus*.

The morphology and proportions of two quite well preserved skulls, one nearly complete (Text-fig. 13), found at the end of the last century (excavated in 1995) in the Late Pleistocene deposits of Kabazi II (Western Crimea, Ukraine) suggest that the species is more closely related to the hemiones than to any other equid (Burke et al. 2003), as supported by results obtained from DNA analysis (Orlando et al. 2006).

Assuming that *E. hydruntinus* did not originate from *E. altidens*, the question arises on the time and the causal factors behind the disappearance of the slender stenonoid horses and the appearance of a new equid, smaller in size, retaining some plesiomorphic traits in dentition, but showing a higher degree of hypsodonty.

In SW Europe an equid smaller and more slender than *E. altidens* is recorded in France at Lunel-Viel, a site that has been dated to about 0.38 Ma by Bonifay (1973), and correlated to MIS 11–9 by Lacombat (2009), and to MIS 11–10 by Brugal and Boudadi-Maligne (2011). The Lunel-Viel horse is smaller than *E. hydruntinus* specimens found in the Late Pleistocene deposits, as highlighted by its designation as *E. hydruntinus minor* proposed by Bonifay (1991). Although Azzaroli (1990) questioned the identification of the Lunel-Viel horse as *E. hydruntinus*, most authors regarded the French horse as the oldest European representative of the species. Eisenmann (1992: 166) had already emphasised that "the skull shape of the small equid from Lunel-Viel is closer to hemiones than to any other equid species", although "metapodials are often more robust than in hemiones … but other proportions are close to those of hemiones". The French author noted that "quite similar metapodials were also found at Dawson, Gold Run and Lost Chicken Creeks (Yukon and Alaska) and at Fossil Lake (Oregon)" and in China, while typical hemiones are recorded in North America in Irvingtonian LFAs. Accordingly Eisenmann (1992) suggested a "possible migration of *E. hydruntinus*… from the New World". Assuming that *E. hydruntinus* is phylogenetically linked to hemiones, not to stenonoid horses, the hypothesis that it originated from some Asian species and dispersed to Europe by the end of the early middle Pleistocene seems to be the most parsimonious. The occurrence, reported by Baryshnikov (2002), of *E. hydruntinus* in layer 6, Azykh (= Azokh) Cave (Trancaucasia), in a fauna correlated by the author to MIS 15–13, if confirmed, may support this hypothesis.

Remarks

Although during the last couple of decades developing research, including those genetic based (e.g. George and Ryder 1986, Forsten 1992b, Oakenfull et al. 2000, Orlando et al. 2006, 2008, 2009, 2011, 2013) has led to a continuously increasing amount of data, the evolutionary dynamics of monodactyl equids in Europe during the Early Pleistocene is still imperfectly understood and a number of issues remain unaddressed. Evidence provided by the equid fossil record suggests that by the end of the Pliocene, at the transition to the Pleistocene, stenonoid horses similar in size and morphology to *E. livenzovensis* from the type locality of Livenzovka, dispersed from Asia to Europe. The nearly contemporaneous occurrence of large stenonoid horses in the Rostov-on-Don (SW Russia) region and SW Europe, on the one hand may indicate a rapid diffusion and shift of the geographic limits of the rank of a single species, but on the other raises a doubt as to whether Russian and European populations, although descendant from the same ancestor, may actually belong or not belong to the same species. The scantiness of the European samples, in particular the lack of cranial remains, hampers any attempt to scrutinize the validity of this hypothesis. Taxonomical and systematic issues concerning the large horses from Montopoli, Huéscar and Huélago, commonly referred to *E. livenzovensis*, are further complicated by the presence of two stenonoid equids, i.e. *E. stenonis* and *E. major*, in the French LFAs of Pardines and Le Coupet, dated to about 2.6 Ma and 2.5 respectively (Nomade et al. 2014). More data is needed to answer the question as to whether the Spanish and Italian remains may be confidently ascribed to the Russian species, and considered the common ancestor of the three, differently sized, stenonoid lineages that are recorded in SW Europe during the Gelasian. During the course of the Gelasian, slender horses, here tentatively included in the *E. senezensis* group, were indeed recorded sporadically in Europe, in addition to the most widespread lineage of quite large stout horses of the *E. stenonis* group, and *Equus major*, larger but less abundant. Evidence from the fossil record is not sufficient to endorse or deny the assumption that the increase in taxonomic diversity and morphological disparity resulted from an evolutionary radiation, due to adaptive change or the opening of ecospace. On the one hand, samples from the few populations of slightly smaller horses with more slender metapodials than the average in the contemporaneous *E. stenonis* that appeared in SW Europe (e.g. in France at Senèze, in Italy at Coste San Giacomo, and in Greece at Gerakarou) about 2.2 Ma, differ from each other in amount, typology and preservational status of specimens, making it sometimes challenging to correctly understand the actual differences, if any, in morphology, bone proportions and size. Conversely, the number of "subspecies" into which authors split *E. stenonis*, accounts for the variation in size and proportions also within this lineage, while the scantiness of *E. major* remains (with the possible exception of the sample from the Spanish latest Gelasian LFA of Fonelas 1; see Garrido 2008) hampers the recognition of its actual, apparently low range of intra-specific variation. Based on available data on environmental characteristic, vegetation cover, and fauna structure and functional diversity of the middle to early late Villafranchian South European sites recording stenonoid horse (see Palombo et al. 2017 and references therein), the hypothesis that local specific ecological conditions may have triggered the appearance/differentiation of ecomorphotypes (sometimes regarded as geographical subspecies) seems quite reasonable. Moreover, primary productivity and faunal structure, in particular resources partitioning and competition among primary consumers, may be more favourable for large, heavy and stout horses, and may have affected the diffusion of equids of the *E. senezensis* group across Europe. It is worth noting, however, that the representatives of the three middle and early late Villafranchian horses most likely had different ecological requirements, and did not compete directly with each other for the same resource, due to their contemporaneous, although infrequent, presence in the same LFA.

Climate and ecosystem changes in the post-Olduvai Early Pleistocene (from about 1.5 Ma onwards) are probably among the most influential factors driving the evolution and dynamics of European horse populations. The wide array of environments present throughout the post-Olduvai Early Pleistocene in Europe, particularly in the Mediterranean area, consistently led to the differentiation of horses due to their ecological flexibility and the changing local environmental conditions.

Together with the environmental changes, the increase in aridity and some spread of savanna-like environments and grasslands (e.g. Pons et al. 1995, Tzedakis et al. 2006, Joannin et al. 2007, Magri and Palombo 2013, Sadori et al. 2013), a shift towards smaller size, with some oscillations, and slender limb proportions is traceable in the *E. major*-*E. suessenbornensis* lineage. Climate and environmental changes most likely also led to the disappearance of *E. stenonis* and horses of the *E. senezensis* group. Assuming it to be true that *E. altidens* is anagenetically derived from European *E. stenonis* populations, it may be hypothesised that the shift towards smaller size and slender limb proportions underwent by *E. stenonis* led to an at least partial overlap between the niche of the relatively diversified new species, i.e. *E. altidens*, and the last representatives of the *E. senezensis* group, causing the disappearance of the latter species. More data, however, are required to support the hypothesis.

Since its appearance, *E. altidens* showed morphological and biometrical intra-specific variation. Whether these differences may have any taxonomical significance or are merely traits separating the local ecomorphotypes, is still a matter of debate. More data is needed to decipher, for instance, the actual meaning and the causal factors behind the different sizes characterising "*E. a. granatensis*" (average body mass 359 kg) and "*E. a. altidens*" (average body mass 297 kg). The almost contemporaneous occurrence of local populations with peculiar morphotypes makes it difficult to depict the evolutionary scenario of middle-sized stenonoid horses during the Early Pleistocene. The origin of *E. wuesti* and its relationships with the Middle Pleistocene *E. altidens* from Süssenborn, the actual phylogenetical position of *E. apolloniensis* and related issues are among the most intriguing, still unanswered questions, pending a complete comparative revision of the medium-sized equids of the late Early Pleistocene European localities.

The long evolutionary history of European stenonoid horses reached its end during the early Middle Pleistocene, when the large taxa were replaced by the first true horse (*E. mosbachensis*), and the niche of the now extinct *E. altidens* became available for a newcomer, the small slender horse, *E. hyduntinus.*

Acknowledgments

We are grateful to the guest editors for giving us the opportunity to honour two great scientists, Professor Rudolf Musil and Professor Oldřich Fejfar, whose researches provided an outstanding contribution towards elucidating the evolution of Neogene and Quaternary mammals. We thank also the reviewers, J. Arroyo-Cabrales and A. Athanassiou, for critically reading the manuscript.

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