

One step beyond: a revision of Middle Miocene North American *Pliohippus mirabilis* provides new clues about equid evolutionary history

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ABSTRACT - The evolution of North American equids has always been used as a paradigmatic case of macroevolutionary patterns through time and space. Nevertheless, despite many phylogenetic, palaeoecological and macroevolutionary studies, their taxonomy at the genus and species level remains obscure, especially for the tribe Equini. Herein, we describe the cranial and postcranial elements of Middle Miocene *Pliohippus mirabilis*, at different ontogenetic stages, and we compare these with a suite of North American Miocene and Pliocene Equini. Our results clarify the morphology of this species, as well as provide new insights on its position in the evolutionary history of the Equinae that ultimately led to the evolution of the genus *Equus*. Our results support the hypothesis that *Pliohippus mirabilis* represents the basal species of *Pliohippus*, as well as the ancestral form for the radiation of the Equini during the Neogene of North America. Moreover, we provide a comparison of the postcranial morphology of its metapodials, discussing previous hypotheses on the origin of monodactyly. Finally, we present the most up-to-date biochronological framework of the Middle Miocene to Pliocene Equini.

INTRODUCTION

The evolution of the North American equids: A synthesis

The evolutionary history of the North American equids has always been used as a reference to investigate macroevolution (Stirton, 1940; Hulbert & MacFadden, 1991; Hulbert, 1993; MacFadden, 2005; Mhlbachler et al., 2011). From small and forest-habitat dwellers that inhabited the North America region in the Eocene, they flourished during the Miocene and gave rise to multiple lineages and forms adapted to different palaeoenvironments through the Pleistocene (MacFadden & Hulbert, 1988; Hulbert & MacFadden, 1991; Hulbert, 1993; Mhlbachler et al., 2011; Semprebon et al., 2016). However, the classic evolutionary history of equid evolution was previously misrepresented as an example of orthogenesis or progressive evolution. The evolution of horses documented changes in morphology that reflected sequential adaptations to living in a variety of environments including tropical forests, temperate woodlands, woodland/savannas, and eventually to seasonal, arid grasslands (Janis et al., 2002; Janis, 2007).

As reported in Mhlbachler et al. (2011), the Equidae include three main subfamilies identified as: the Eocene “Hyracotherinae”, the late Eocene to Late Miocene “Anchitherinae” and the Early Miocene to recent Equinae (MacFadden, 1992, 2005; Semprebon et al., 2016). Subfamily “Hyracotherinae” includes the basal equid genera *Sifrhippus*, *Minippus*, *Arenahippus*, *Xenichohippus*, *Eohippus*, *Pliolophus*, *Protorohippus*, *Epihippus* and *Orohippus*. These genera were restricted to the Eocene (Froelich, 2002) and their systematics is complex (for a complete summary see Froelich, 2002). Nevertheless, the latest cladistic analyses on these genera do not support

Hyracotherium as member of Equidae but place it as sister taxon of the family Palaeotheriidae (Froelich, 2002). The members of “Hyracotherinae” were relatively small and had a primitive skull morphology (i.e., short face, short diastema) with brachydont and bunolophodont molars and non-molariform premolars (premolars were small and somewhat triangular) (MacFadden, 1986; Semprebon et al., 2016).

Subfamily “Anchitheriinae” includes taxa spanning from the late Eocene to the Late Miocene. Genera included in this subfamily are *Mesohippus*, *Miohippus*, *Kalobatippus*, *Parahippus*, *Desmatippus*, *Hypohippus*, *Megahippus* and *Archeohippus*, with *Parahippus* being the sister taxon to the subfamily Equinae (see Mhlbachler et al., 2011). Compared to “Hyracotheriinae”, the most primitive genera of this subfamily *Mesohippus* and *Miohippus* had slightly larger body size and a functionally three-digit manus and pes (tridactyl condition; Semprebon et al., 2016). They also developed cursorial adaptations such as more elongated metapodials and tight locking of articular surfaces as well as a more advanced molariform dentition (Prothero & Schoch, 1989). Their teeth had more developed transverse lophs which suggests a heavier reliance on shearing vegetation rather than crushing as well as a more fibrous diet. There was also molarisation of the second through fourth premolars (MacFadden, 1992; Semprebon et al., 2016).

Subfamily Equinae includes taxa ranging from Late Miocene to the recent, divided in three tribes: Equini, mainly as being tridactyl or monodactyl and having the protocone connected to the protoloph, including the genera “*Merychippus*”, *Acritohippus*, *Parapliohippus*, *Pliohippus*, *Heteropliohippus*, *Astrohippus*, *Dinohippus*, *Onohippidion*, *Hippidion* and *Equus*. Protohippini,

tridactyl with the protocone initially isolated but then connected to the protocone at later stages-of-wear (Hulbert, 1988a; Pagnac, 2006), including the genera *Protohippus*, *Calippus* and *Scaphohippus*; Hipparionini, tridactyl with the protocone isolated, including the genera “*Merychippus*”, *Merychippus*, *Cormohipparion*, *Neohipparion*, *Pseudohipparion*, “*Hipparion*” and *Nannippus*. These taxa represent the great radiation of the Equidae which began around 20 Ma in North America (MacFadden & Hulbert, 1988; Hulbert & MacFadden, 1991; Hulbert, 1993). Within this temporal interval, derived anchiteriine and basal Equini species evolved larger body size (Cantalapiedra et al., 2017), complete unguligrady, and other cursorial adaptations, although they were still tridactyl. Another important milestone within these taxa was that the cheek teeth evolved a more modern appearance, with increased crown height, presence of well-developed cementum between the lophs, and with cusps positioned in the same basic patterns as seen in modern horses (Semperebon et al., 2016). The reorganisation of the equid cranium also occurred at this time, showing an expanded preorbital region including the preorbital bar associated with enlargement of the cheek teeth. There was a concomitant adaptive shift toward a more abrasive diet, although many diet habits ranging from browser to grazer were experimented with during this time (Janis, 1976; Radinsky, 1983, 1984; Wang et al., 1994; Muhlbachler et al., 2011; Semperebon et al., 2016). The craniodental shifts that began with *Parahippus* and “*Merychippus*” (e.g., several paraphyletic taxa originally included in *Merychippus* but included in the tribe Equini, see later) led to the genus *Equus*, which includes all extant horses that evolved from Pliocene North American *Dinohippus* (MacFadden, 1984, 2005; Azzaroli, 1988; Hulbert, 1993; Maguire & Stigall, 2008; Cirilli et al., 2021a).

Augusto Azzaroli's work on North American equids

Augusto Azzaroli was appointed Assistant Professor of Geology at the University of Florence in 1950 and held that position for 10 years. He worked actively at the Geological Survey on the Geological Map of Italy sheets of the northern Apennines and maintained a longitudinal study of Italian stratigraphy and mammalian fauna of the Villafranchian interval with a particular interest in the taxonomy, systematics and evolution of the genus *Equus* (Rook, 2015). His study of the genus *Equus* and its relationships to the extensive evolutionary radiation of the genus across five continents met with international collaborations and acclaim (Bernor et al., 2019, 2020; Cirilli et al., 2021a, b, 2022).

Initial work on the genus *Equus* was reported by Azzaroli (1965) wherein he found considerable confusion surrounding the genus. In 1867, Cocchi introduced the nomen *Equus stenonis* Cocchi, 1867 without identifying a type specimen. However, Cocchi made specific reference to a complete skull which subsequently Azzaroli (1965) identified as being IGF 560 in the Museum of the University of Florence, Italy. Azzaroli (1965) continued by identifying the correct terminology of *Equus* maxillary and mandibular cheek tooth terminology. He further introduced a lasting morphological definition of the type specimen of *E. stenonis*, as well as other specimens that he referred to this taxon. He also discussed the relationship

of *E. stenonis* smaller contemporary species, *E. stehlini* Azzaroli, 1965. This initial manuscript set the tone for subsequent studies of the origin and evolution of *Equus*.

In 1988, Azzaroli undertook a study of the North American genera *Dinohippus* Quinn, 1955 and *Pliohippus* Marsh, 1874 wherein he clearly differentiated these two lineages. A particular emphasis in this contribution was the contrast between *Pliohippus bakeri* Azzaroli, 1988 (Type UCMP30200) from Coffee Ranch, Texas (late Hemphillian, ca. 5.9 Ma; Tedford et al., 2004) and *Dinohippus leidyanus* Osborn, 1918 (Type AMNH17224; late Hemphillian Snake Creek, Sioux County, Nebraska). Collections from Edson Quarry (Kansas, Guymon area, Texas), Redington Quarry and Old Cabin Quarry, Arizona and the Mt. Eden Fauna, Southern California were also reviewed. Of particular interest was *Dinohippus mexicanus* Lance, 1950 (latest Hemphillian of Yepomera, Chihuahua, Mexico) which Azzaroli identified as being an advanced species of *Dinohippus* which he saw as being ancestral to *Equus* (sensu strictu).

Azzaroli (1992) identified monodactyly as having evolved independently in no less than six distinct lineages: *Pliohippus*, *Hippidion*, *Onohippidium*, *Dinohippus*, *Astrohippus*, and *Equus*. Six lineages differentiated within *Equus* between the Late Pliocene and Early Pleistocene of the Americas. Eurasian Pleistocene *E. stenonis* had several descendants that differentiated in the Early Pleistocene and include six to eight species which became extinct in the Middle Pleistocene with a possible survival into the late Pleistocene in the Indian Subcontinent. *Equus stenonis* was the likely ancestor of several Eurasian species as well as African *Equus koobiforensis* Eisenmann, 1983 and possibly the Grevy's zebra which it closely resembles (Azzaroli, 1992; Bernor et al., 2019; Cirilli et al., 2021a, b). The abundant assemblage of *Equus simplicidens* Cope, 1892 from the Hagerman Horse Quarry, Idaho was characterised by Azzaroli (1992) and Azzaroli & Voorhies (1993) and identified as being a member of the subgenus *Dolichohippus* which also includes the Grevys zebra. Azzaroli (1992) mentioned, but did not embrace the concept of *Allohippus* (Kretzoi, 1938; Gromova, 1949; Samson, 1975; Eisenmann & Baylac, 2000; Eisenmann 2022). A major evolutionary radiation of Eurasian and African horses began soon after the entry of *Equus* ca. 2.6 Ma near the base of the Pleistocene. *Equus simplicidens* Cope, 1892 was acknowledged as being the basal species of the *Equus* radiation across South and North America, Eurasia, India and Africa.

In 1993, Azzaroli & Voorhies discussed the origin of the genus *Equus* in North America during the Blancan, describing the cranial and postcranial morphology of *E. simplicidens*, *Equus stenonis anguinus* Azzaroli & Voorhies, 1993, *Equus idahoensis* Merriam, 1918 and *Equus cummingsii* Cope, 1893. Furthermore, Azzaroli & Voorhies (1993) discussed the evolutionary relationships and palaeobiogeography of *E. simplicidens* with the Eurasian Early Pleistocene taxa *Equus livenzovenis* Bajgusheva, 1978, *E. stenonis* and *E. sanmeniensis* Teilhard de Chardin & Piveteau, 1930, and with the African *E. koobiforensis*.

Azzaroli (1998) reported on his studies of Late Pleistocene Irvingtonian and Rancholabrean age *Equus ferus* Boddaert, 1875, *Equus niobrarenensis* Hay, 1913,

Equus lambei Hay, 1917, *Equus semiplicatus* Cope, 1893, *Equus francisci* Hay, 1915, *Equus freternus* Leidy, 1860, *Equus conversidens* Owen, 1869, *Equus mexicanus* Hibbard, 1955, *Equus excelsus* Leidy, 1858a and *Equus occidentalis* Leidy, 1865, all endemic to North America. He documented their geographic and stratigraphic ranges and distinguished these species by morphological characters of the skulls, dentitions, limb bones and size. These taxa have largely been retained in the comprehensive synthesis of all recognised palaeo-species of *Equus* by Cirilli et al. (2022). In 2003, Azzaroli presented his last view on the phylogeny of *Equus* across North and South America, Eurasia, India and Africa.

Aims of this work

This work focusses on the Tribe Equini (Equidae, Equinae), and in particular on one of its basal species, *Pliohippus mirabilis* Leidy, 1858a. Although many Middle Miocene species were formerly referred to the genera *Merychippus*, *Pliohippus* and *Protohippus* (Gidley, 1907, Osborn, 1918), a revised taxonomic framework of this tribe has been provided by Quinn (1955), Lance (1950), Hulbert (1988a, b, 1993), Hulbert & MacFadden (1991) and Kelly (1995, 1998). Quinn (1955) erected the genus *Dinohippus*, to distinguish and include some species previously assigned to *Pliohippus*. Hulbert & MacFadden (1991) made a comparison of Early and Middle Miocene North American equids previously included in the genus *Merychippus*, and concluded that only the type species of *Merychippus*, *M. insignis* Leidy, 1856, could be assigned to the genus. Their work provided the basis for a new interpretation of the Tribe Equini given by Kelly (1995, 1998), wherein previously assigned taxa “*Merychippus*” *tertius*, “*Merychippus*” *isonesus* Cope, 1889, “*Merychippus*” *stylodontus* Merriam, 1919 were included in a new genus *Acritohippus* (with the new species *A. quinni* Kelly, 1995), and “*Merychippus*” *carrizoensis* Dougherty, 1940 was referred to a new genus, *Parapliohippus*. Herein we provide a revision of *Pl. mirabilis* from several Middle Miocene localities (late Barstovian of the North American Land Mammal Ages) including those from the Crookston Member and Devil’s Gulch Horse Quarry (Valentine Formation, Nebraska) and from Chama el Rito (New Mexico) (Fig. 1a). Although mentioned in previous works (Osborn, 1918; Hulbert & MacFadden, 1991) these collections have never been described in detail, or quantitatively compared to other North American fossil equids. The biochronology of the North American Equini discussed in the present paper is shown in Fig. 1b.

MATERIAL AND METHODS

Collections and specimens studied

The fossil collections of *Pl. mirabilis* studied herein are housed at the American Museum of Natural History, New York, and at the Smithsonian National Museum of Natural History, Washington D.C., USA. The descriptions of the measurements are reported in Supplementary Online Material (SOM) 1, whereas the measurements of the specimens are given in SOM 2. *Pliohippus mirabilis* has been compared to a suite of Late

Hemingfordian, Barstovian, Hemphillian and Blancan North American equids of the genera *Acritohippus*, *Parapliohippus*, *Pliohippus*, *Dinohippus* and *Equus*. The living zebra *Equus grevyi* Oustalet, 1882 has been chosen as comparison for the extant species. The complete list of the comparative sample is given in Tab. 1. The ages of the formations, member, quarries and sites refer to Woodburne (1996, 2007), Tedford et al. (1987, 2004) and Bell et al. (2004). The Pliocene monodactyl equid fossil species (*E. simplicidens*) is included in the genus *Equus* following the latest cladistic results of Cirilli et al. (2021a), not recognising *Plesippus* or *Allohippus* as either distinct genera or subgenera. Descriptions and comparisons in Systematic Palaeontology are based on *Equus simplicidens* from the Hagerman Horse Quarry (figured later in Figs 7 and 8). Moreover, the maximum, mean and minimum values of each variable described and analysed in the present paper are reported in SOM 3.

Morphometric and statistical analyses

Morphometric analyses have been undertaken on crania, third metacarpals and third metatarsals, including Principal Component Analyses (PCA) and bivariate plots. PCAs have been calculated on crania, third metacarpals and third metatarsal. For crania, two datasets of measurements have been constructed to evaluate the shape and size of the species studied. The first one includes M1 (muzzle length), M2 (palatal length), M3 (vomerine length), M4 (post vomerine length), M5 (post palatal length), M6 (basilar length), M7 (premolar length), M8 (molar length), M9 (upper cheek teeth length), M23 (anterior ocular line), M30 (length of the naso-incisival notch), M31 (cheek length), M32 (distance between the orbit of the preorbital fossa), M33 (length of the preorbital fossa [POF]), M34 (distance between the back of the POF and the infra-orbital foramen), M35 (height of the POF: perpendicular to its maximal length [M33]), M36 (distance between the POF and the facial crest), M37 (height of the back of the infraorbital foramen above the alveolar border) and M38 (height of the back of the POF above the alveolar border). The second one includes the same set of measurements without M3-M6, to increase the sample size with incomplete specimens and to evaluate the morphology of the lateral face of the crania.

PCAs for the third metacarpals and third metatarsals include M1 (maximal length), M3 (minimal breadth), M4 (depth of the diaphysis at level of M3), M5 (proximal articular breadth), M6 (proximal articular depth), M10 (distal maximal supra-articular breadth), M11 (distal maximal width), M12 (distal maximal depth of the keel), M14 (distal maximal depth of the medial condyle). Alongside the PCAs, bivariate plots comparing M1 vs M3 and M1 vs M11 have been calculated for third metapodials.

PCAs and bivariate plots have been calculated in the R Environment v. 1.4.1103 (R Core Team, 2023) using the function *prcomp()* v. 3.6.2 (Venables & Ripley, 2008) and the package “*ggplot2*” v. 3.3.3 (Wickham, 2016). PCAs were calculated using the parameter *scale = T* to have a unit variance before starting the analyses in R. Third metapodials were chosen because they represent the most discriminant postcranial elements to evaluate similarities or differences in morphology among *Equus* species (Bernor et al., 2021; Cirilli et al., 2021a, 2023,

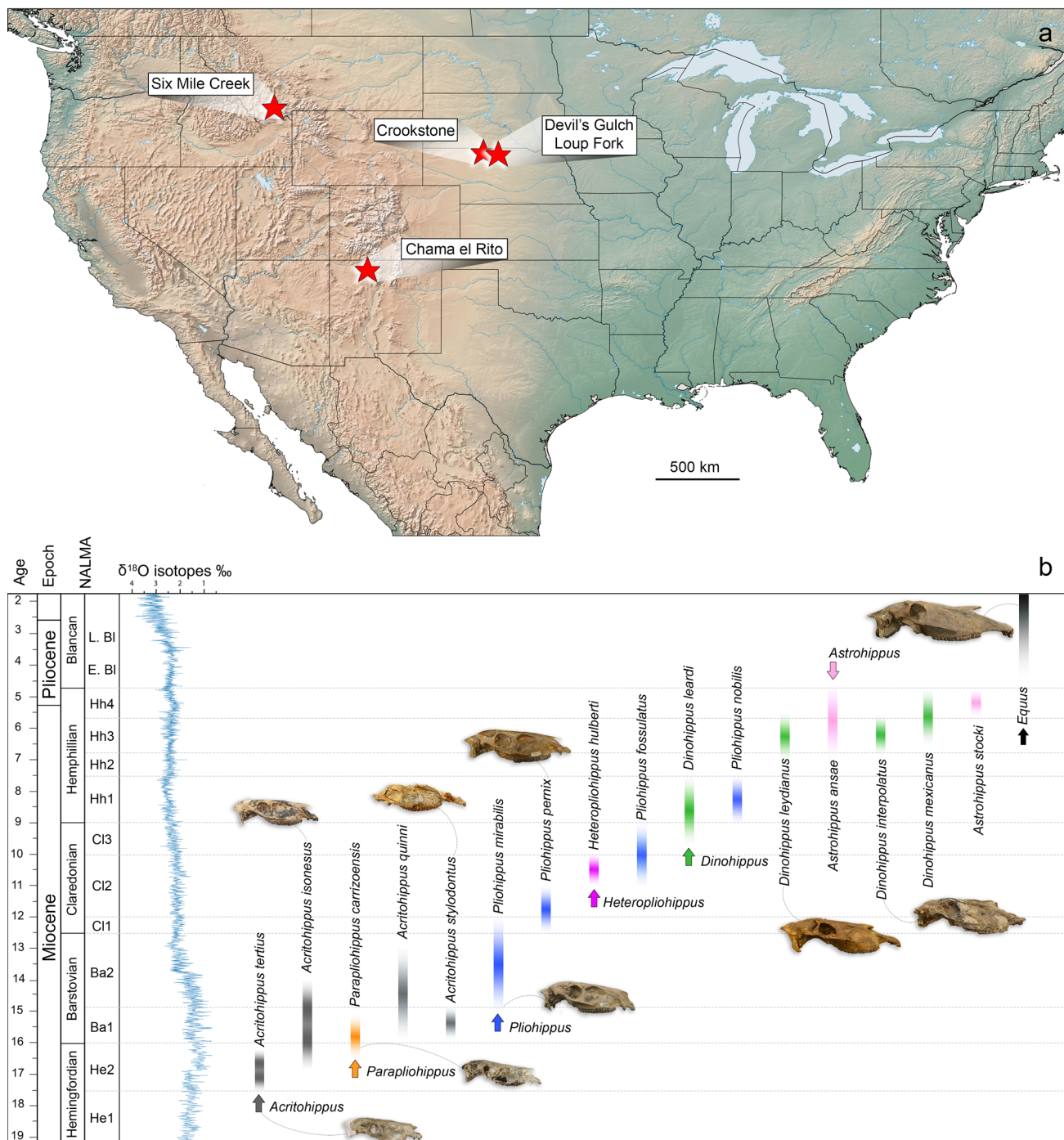


Fig. 1 - (color online) a) Locator map of the late Barstovian *Pliohippus mirabilis* localities discussed in the present paper. b) Biochronology of the North American fossil equid discussed in the paper. Arrows indicate the first occurrence of a genus, here represented by a cranium when available. All crania are scaled as in Fig. 7. Biochronologic ranges are based on direct observations in collections and on the available data reported in Osborn (1918), MacFadden (1986), Azzaroli (1988, 1993), Tedford et al. (1987, 2004), Hulbert & MacFadden (1991), Kelly (1995, 1998), Bell et al. (2004), Muhlbachler et al. (2011) and Sempere et al. (2016). Zonation of North American localities refers to Tedford et al. (2004). $\delta^{18}O$ isotope shift from Raffi et al. (2020).

2024a; Cirilli, 2022; Saarinen et al., 2021), as well as to evaluate the evolution of monodactyly (see later).

The measurements and anatomical nomenclature for cranial and postcranial elements are referred to the international standards for studying fossil equids of Eisenmann et al. (1988) and Bernor et al. (1997) and are shown in SOM 1.

Anatomical abbreviations

POB: preorbital bar; POF: preorbital fossa; IOF: infraorbital foramen; UTR: upper cheek tooth row; LTR: lower cheek tooth row; P2: maxillary second premolar; P3: maxillary third premolar; P4: maxillary fourth premolar; M1: maxillary first molar; M2: maxillary second molar;

Taxon	Locality	NALMA		State	Geographical area	Reference Age
<i>Acritohippus tertius</i>	Thomas Quarry	Hemingfordian	He2	Nebraska	Great Plains	Tedford et al., 2004
<i>Acritohippus tertius</i>	Greenside Quarry	Hemingfordian	He2	Nebraska	Great Plains	Tedford et al., 2004
<i>Acritohippus isonesus</i>	Echo Quarry	Barstovian	Ba1	Nebraska	Great Plains	Tedford et al., 2004
<i>Acritohippus isonesus</i>	Mill Quarry	Barstovian	Ba1	Nebraska	Great Plains	Tedford et al., 2004
<i>Acritohippus isonesus</i>	East Sand Quarries	Barstovian	Ba1	Nebraska	Great Plains	Tedford et al., 2004
<i>Parapliohippus carrizoensis</i>	Yermo Local Fauna	Barstovian	Ba1	Mojave Desert	Northern Great Basin	Tedford et al., 2004
<i>Acritohippus stylodontus</i>	Third Division Fauna	Barstovian	Ba1	Mojave Desert	Northern Great Basin	Tedford et al., 2004
<i>Acritohippus stylodontus</i>	Second Division Fauna	Barstovian	Ba1	Mojave Desert	Northern Great Basin	Tedford et al., 2004
<i>Pliohippus mirabilis</i>	Six Mile Creek Formation	Barstovian	Ba2	Montana	Northern Rocky Mountains	Tedford et al., 2004
<i>Pliohippus mirabilis</i>	Crookston Bridge Member	Barstovian	Ba2	Nebraska	Great Plains	Tedford et al., 2004
<i>Pliohippus mirabilis</i>	Devil's Gulch	Barstovian	Ba2	Nebraska	Great Plains	Tedford et al., 2004
<i>Pliohippus mirabilis</i>	Loup fork as Devil's Gulch	Barstovian	Ba2	Nebraska	Great Plains	Tedford et al., 2004
<i>Pliohippus mirabilis</i>	Chama el Rito, Rio Arriba	late Barstovian - early Claredonian	Ba2 - Cl1	New Mexico	Southern Great Basin	Tedford et al., 2004
<i>Pliohippus pernix</i>	Midway Quarry	Claredonian	Cl1	Nebraska	Great Plains	Tedford et al., 2004
<i>Pliohippus pernix</i>	June Quarry	Claredonian	Cl1	Nebraska	Great Plains	Tedford et al., 2004
<i>Pliohippus pernix</i>	Burge Quarry	Claredonian	Cl2 - Cl3	Nebraska	Great Plains	Tedford et al., 2004
<i>Dinohippus leidymanus</i>	Snake Creek Beds (ZX Bar)	Hemphillian	Hh2 - Hh3	Nebraska	Great Plains	Tedford et al., 2004
<i>Dinohippus leidymanus</i>	Equivalent ZX Bar	Hemphillian	Hh2 - Hh3	Nebraska	Great Plains	Tedford et al., 2004
<i>Dinohippus leidymanus</i>	Edson Quarry	Hemphillian	Hh2 - Hh3	Kansas	Great Plains	Tedford et al., 2004
<i>Dinohippus interpolatus</i>	Coffee Ranch / Miami Quarry	Hemphillian	Hh3	Texas Panhandle	Great Plains	Tedford et al., 2004
<i>Dinohippus interpolatus</i>	Optima / Guyman	Hemphillian	Hh3	Oklahoma	Great Plains	Tedford et al., 2004
<i>Equus simplicidens</i>	Hagerman Horse Quarry	Blancan	Blancan III	Idaho	Northern Rocky Mountains	Bell et al., 2004
<i>Equus simplicidens</i>	Mount Blanco	Blancan	Blancan IV	Texas	Western Gulf Coast	Bell et al., 2004

Tab. 1 - List of the North American fossil equids used for comparative analyses in the present work listed by age, from older to younger, according to the zonation of North American Land Mammal Ages of Tedford et al. (2004) and Bell et al. (2004).

M3: maxillary third molar; p2: mandibular second premolar; p3: mandibular third premolar; p4: mandibular fourth premolar; m1: mandibular first molar; m2: mandibular second molar; m3: mandibular third molar; mc3: third metacarpal; mt3: third metatarsal.

Institutional abbreviations

AMNH:FAM: American Museum of Natural History (Frick Collection, Division of Palaeontology), New York, USA; USNM: Smithsonian National Museum of Natural History, Washington D.C., USA.

SYSTEMATIC PALAEOLOGY

Class MAMMALIA Linnaeus, 1758
 Order PERISSODACTYLA Owen, 1848
 Family EQUIDAE Gray, 1821
 Subfamily EQUINAE Gray, 1821
 Tribe EQUINI Quinn, 1955

Genus *Pliohippus* Marsh, 1874

Pliohippus mirabilis Leidy, 1858a
 (Figs 2-4; SOM 1, Figs S1-S4)

- 1869 *Merychippus mirabilis* LEIDY, p. 299-302, Pl. 17, figs 10-13.
 1892 *Protohippus mirabilis* (Leidy) - COPE p. 32, Pl. 9, fig. 1; Pl. 10, fig. 4.
 1907 *Merychippus campestris* GIDLEY, p. 928-930.
 1918 *Merychippus campestris* Gidley - OSBORN, p. 114, Figs 88-89; Pl. 15, figs 4-5; Pl. 19, figs 3-4; Pl. 26, fig. 1; Pl. 44, fig. 1; Pl. 49, fig. 1; Pl. 50, figs 3, 7.
 1940 *Merychippus (Protohippus) campestris* Gidley - STIRTON, p. 182.

Holotype - USNM V.596, partial right upper cheek tooth row with dP4 and M1, figured in Leidy (1869: pl. 17, figs 10-13) and housed at the Smithsonian National Museum of Natural History, are illustrated here in Fig. 2a.

Paratype - USNM 580, partial right upper cheek tooth row with P4-M3, figured in Leidy (1869: pl. 17, figs 8-9) and housed at the Smithsonian National Museum of Natural History, illustrated here in Fig. 2b.

Type locality - Loup Fork, Niobrara River, Nebraska, USA.

Age range - ca. 15-12.5 Ma, late Barstovian of the North American Land Mammal Ages (Tedford et al., 2004).

Geographic and chronologic distribution - Six Mile Creek Formation, Montana, USA, late Barstovian (Ba 1-2), ca. 15-14 Ma (Tedford et al., 2004); Crookston Bridge Member of the Valentine Formation, Nebraska, USA, late Barstovian (Ba 2), ca. 14-13 Ma (Hulbert & MacFadden, 1991; Tedford et al., 2004); Devil's Gulch Horse Quarry, Devil's Gulch Member of the Valentine Formation, Nebraska, USA, late Barstovian (Ba 2), ca. 13-12.7 Ma (Hulbert & MacFadden, 1991; Tedford et al., 2004); Loup Fork, Devil's Gulch Member of the Valentine Formation, Nebraska, USA, late Barstovian (Ba 2), ca. 13-12.7 Ma (Hulbert & MacFadden, 1991; Tedford et al., 2004); Chama el Rito, Tesuque Formation, New Mexico, USA, late Barstovian (Ba 2), ca. 13-12.5 Ma (Tedford et al., 2004).

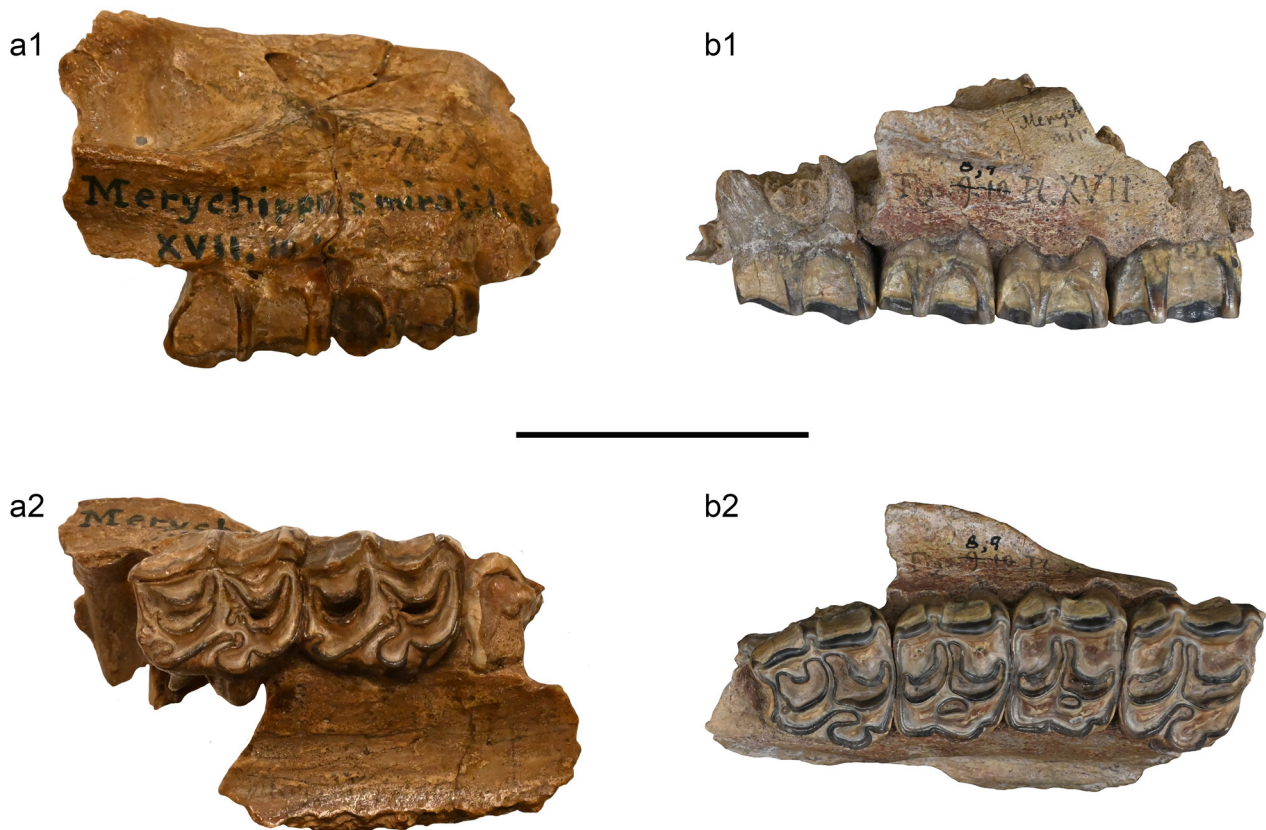


Fig. 2 - (color online) *Pliohippus mirabilis* from Loup Fork, late Barstovian (Ba2), Nebraska. a) Holotype USNM V.596 in labial (a1) and occlusal (a2) views. b) Paratype USNM 580 in labial (b1) and occlusal (b2) views. Scale bar: 5 cm.

Referred material - The *P. mirabilis* collections studied here is reported in SOM 2.

Diagnosis - Cranium having a short nasal notch, with the posterior border anterior to P2; buccinator fossa developed; POF elongated and medially deep, with a horizontal lower rim and a convex upper rim; well-developed malar fossa and a reduced POB; IOF placed at the level of the P4-M1 and at the middle level of the lower rim of the POF; malar crest developed up to the M1 level; large orbit with the anterior margin reaching the M3 mesostyle level; short palatine process; anterior margin of the choanae at the M2. Upper cheek teeth in middle stage-of-wear with a short, sub-triangular and pointed anterostyle in P2; pointed mesostyle; short protocone with a convex lingual margin, longer in molars than in premolars and connected with the protoloph; pli caballin present in P3-P4, very reduced in M2 and absent in P2 and M3; simple pre- and postfossette ornamentation, with one or two plications per margin; large hypocone and distally sub-rounded, separated from the distal wall of the teeth by a tiny hypoconal groove in P2-P4, connected to the distal wall in M1, and separated in M2-M3. Lower cheek teeth in middle stage-of-wear with a small, sub-triangular and round paraconid in p2; reduced preflexid with no plications; more elongated postflexid with few plications; small and round metaconid and metastylid, with a closed and pointed linguaflexid (V-shaped but very rudimentary); pointed ectoflexid, deep in p3-p4 up to the

metaconid-metastylid; small, short and round entoconid; pli caballinid absent. Tridactyl (but not functional during locomotion), small and slender third metapodials, with a small diaphysis.

Description - The *Pl. mirabilis* holotype and paratype are figured in Fig. 2a and Fig. 2b, respectively. The holotype, USNM V.596 (Fig. 2a), is a fragmented juvenile right upper maxilla, with dP4 and M1. The IOF is apparent on the lateral side, and it is placed above the dP4-M1 limit, whereas the maxillary crest extends anteriorly to the M1 mesostyle. The paratype, USNM 580 (Fig. 2b), is an incomplete right upper maxillary fragment with P4-M3 preserved. The teeth are in a late stage-of-wear and the crown height is very reduced. The maxillary crest extends anteriorly to the level of the M1 mesostyle (Fig. 2b1). The morphology of the occlusal surface of the upper teeth is almost obliterated from the late stage-of-wear, without salient morphological features being observable. The protocone is found to be connected to the hypocone in the M1 and M2, with a rounded lingual margin. No pre- and postfossette plications are present, and the mesostyle is very reduced.

CRANIA - The best-preserved *Pl. mirabilis* crania from Crookston Member of the Valentine Formation, Devil's Gulch Horse Quarry and Chama el Rito are illustrated in Figs 3-4. The crania are ordered by age, from juvenile to more senile individuals, based on the wear stages of the upper cheek tooth rows. Sex determination, males and

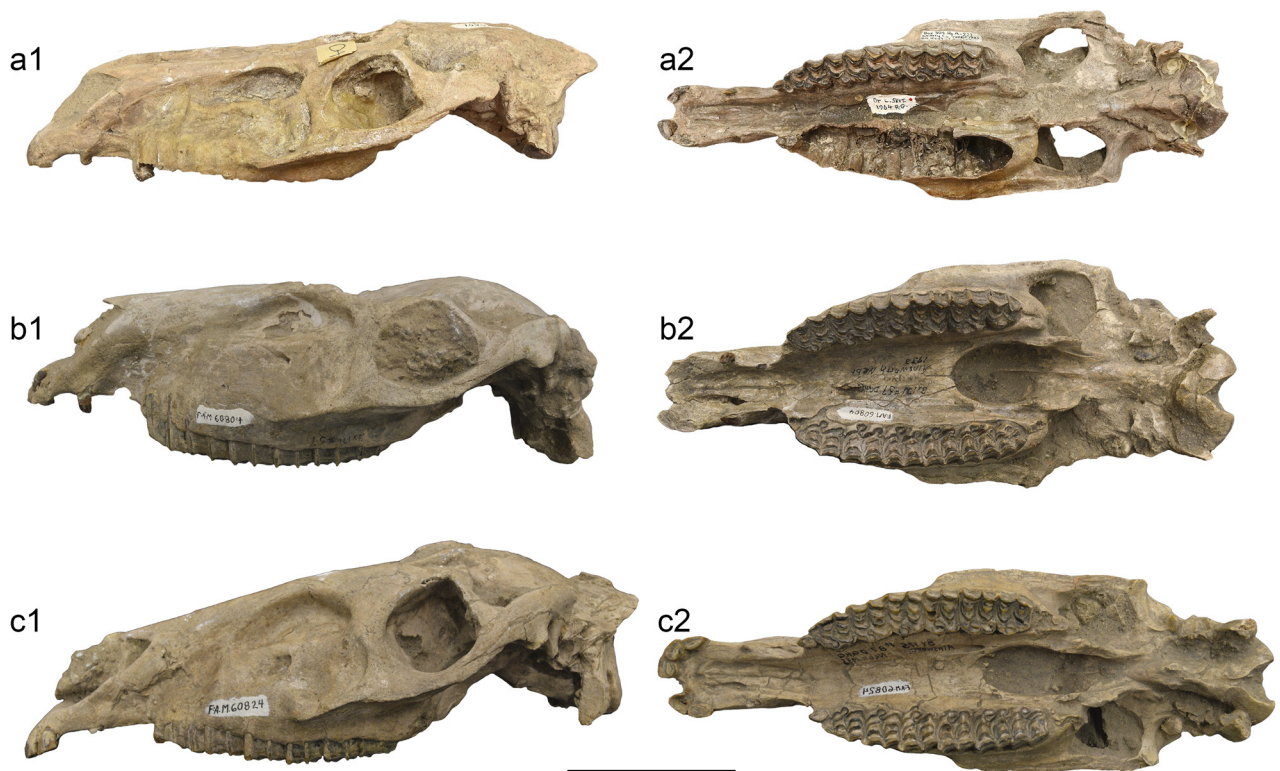


Fig. 3 - (color online) *Pliohippus mirabilis* crania in lateral (1) and ventral (2) views. a) AMNH:FAM60801, Crookston Member of the Valentine Formation. b) AMNH:FAM60804, Devil's Gulch Horse Quarry of the Valentine Formation. c) AMNH:FAM60824, Devil's Gulch Horse Quarry of the Valentine Formation. Scale bar: 10 cm.

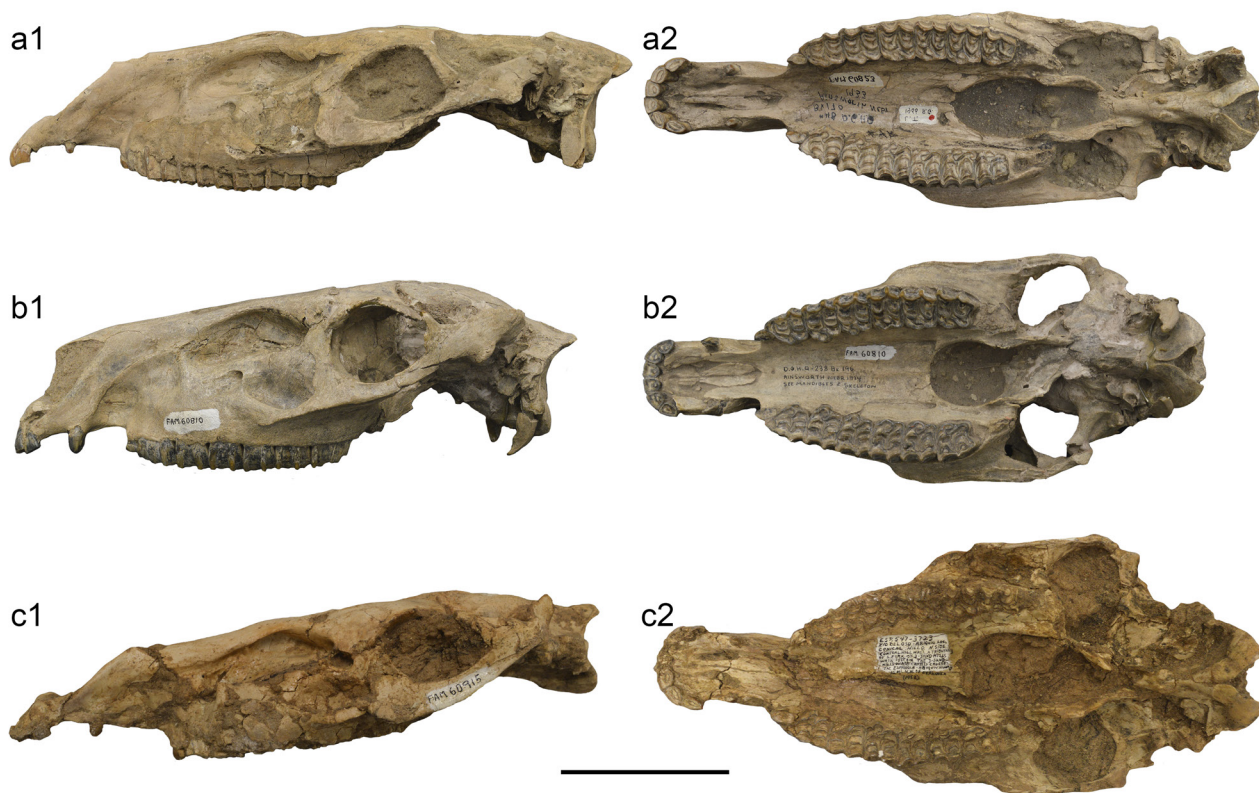


Fig. 4 - (color online) *Pliohippus mirabilis* crania in lateral (1) and ventral (2) views. a) AMNH:FAM6083, Devil's Gulch Horse Quarry of the Valentine Formation. b) AMNH:FAM60810, Devil's Gulch Horse Quarry of the Valentine Formation. c) AMNH:FAM60915, Chama el Rito, Tesuque Formation. Scale bar: 10 cm.

females, is based on the presence of the canine. Large and present canines represent male individuals, whereas absent or vestigial canines represent females.

Figure 3a is AMNH:FAM60801 from Crookston Member of the Valentine Formation in lateral and ventral view. The cranium is of a male juvenile individual, with P2-P4 in an early stage-of-wear, and M3 not erupted. It is also deformed, dorsoventrally and bilaterally compressed. On the lateral side, the cranium has a short nasal notch with the posterior border anterior to the P2, a moderately developed buccinator fossa, an elongated and deep POF, with a flattened lower margin, and a convex upper rim, a large and well-developed malar fossa, and a reduced POB. The IOF is positioned at the level of the P4-M1, placed at the middle level of the lower rim of the POF. The maxillary crest extends to the P4-M1 limit, and the orbit is large, with the anterior margin extended up to the M3 level. In ventral view, the cranium is bilaterally compressed. The palatine process is slender, whereas the anterior margin of the choanae extend to the M1-M2 limit. The anterior margin of the vomer is slightly in advance compared to the occipital bones.

Figure 3b is AMNH:FAM60804 from Devil's Gulch Horse Quarry of the Valentine Formation in lateral and ventral view. The cranium represents a young adult male individual, with M3 erupted but unworn. The cranium is almost complete, although damaged at the level of the frontal bones, and deformed in the vomer and in the basisphenoid. The right side is damaged and the zygomatic

arch is missing. On the lateral side, the cranium has a short nasal notch with the posterior border in front of the P2, the buccinator fossa is developed and deep, an elongated and deep POF, with a flattened lower margin and a convex upper rim, a well-developed malar fossa, and a reduced POB. The IOF is placed at the level of the P4-M1 and at the middle level of the lower rim of the POF. The maxillary crest is at the level of the P4-M1, whereas the orbit is large, with the anterior margin reaching the M2-M3 limit. In ventral view, the palatine process is short and thick, and the anterior margin of the choanae reach the M1-M2 boundary. The anterior margin of the vomer is slightly in advance compared to the occipital bones.

Figure 3c is AMNH:FAM60824 from Devil's Gulch Horse Quarry of the Valentine Formation in lateral and ventral view. The cranium represents a female adult individual, with a reduced canine and with all the upper cheek teeth in a middle stage-of-wear (P2-M3 erupted and worn, with all the dental structures visible). The cranium is complete, and it shows a bilateral compression, with the vomer and basisphenoid slightly deformed. On the lateral side, the cranium shows a more elongated nasal notch than AMNH:FAM60804, with the posterior border in front of the P2. The buccinator fossa is less developed than AMNH:FAM60804, whereas the POF is elongated and deep, with a flattened lower margin and a convex upper rim. The cranium has a well-developed malar fossa and a very short POB. The IOF is placed at the level of the P4-M1 and at the inferior middle level of the POF

ventral rim. The maxillary crest extends to the level of the P4-M1, below the IOF and the orbit is large, with the anterior margin reaching the M3 mesostyle level. In ventral view, the palatine process is more elongated than AMNH:FAM60804, and the anterior margin of the choanae reach the M1-M2 boundary. The anterior margin of the vomer is slightly in advance compared to the occipital bones.

Figure 4a is AMNH:FAM60823 from Devil's Gulch Horse Quarry of the Valentine Formation in lateral and ventral view. The cranium is of an adult female individual, with a reduced canine and all the upper cheek teeth in a middle stage-of-wear. The cranium is complete, and it shows a dorso-ventral and a bilateral deformation. On the lateral side, the cranium shows an elongated nasal notch as AMNH:FAM60824, with the posterior border in front of the P2. The buccinator fossa is well developed, whereas the POF is elongated and deep, with a flattened lower margin and a convex upper rim. Although damaged, the cranium has a well-developed malar fossa and a short POB. The IOF is placed at the level of the P4-M1 and at the middle level of the lower rim of the POF. The maxillary crest is damaged but extends to the level of the P4-M1 below the IOF. The orbit is large, with the anterior margin reaching the M3 mesostyle level. In ventral view, the palatine process is elongated as in AMNH:FAM60824, and the anterior margin of the choanae reach the M1-M2 boundary. The anterior margin of the vomer is slightly in advance compared to the occipital bones.

Figure 4b is AMNH:FAM60810 from the Devil's Gulch Horse Quarry of the Valentine Formation in lateral and ventral view, respectively. The cranium represents a male adult individual, with a prominent canine and all the upper cheek teeth in an advanced stage-of-wear (P2-M3 erupted with most of the dental morphology obliterated). The cranium is complete, and it shows an antero-posterior deformation. On the lateral side, the cranium shows a short nasal notch, probably as a result of the deformation, with the posterior border in front of the P2. The buccinator fossa is well developed, whereas the POF is elongated and deep, with a flattened lower margin and a convex upper rim. The cranium shows a well-developed malar fossa and a reduced POB. The IOF is placed at the level of the P4-M1 and at the middle level of the lower rim of the POF. The maxillary crest is strong and extends to the level of the M1 mesostyle. The orbit is large, with the anterior margin reaching the M3 mesostyle level. In ventral view, the palatine process is short, and the palatine bones are fragmented, as a result of the antero-posterior deformation. The anterior margin of the choanae reaches the M2, whereas the vomer and the basisphenoid are crushed.

Figure 4c is AMNH:FAM60915 from Chama el Rito (Tesuque Formation) in lateral and ventral view. The cranium represents a male adult individual, with a prominent canine and all the upper cheek teeth in an advanced stage-of-wear. The cranium is complete but heavily damaged, with a dorso-ventral deformation and a poor preservation of its ventral morphology. On the lateral side, the cranium shows an elongated nasal notch as in AMNH:FAM60823 and AMNH:FAM60824, with the posterior border in front of the P2. The buccinator fossa is not well preserved, whereas the POF is elongated and

deep, with a flattened lower margin and a convex upper rim. The malar fossa is present but crushed, with a reduced POB. The IOF is not preserved as well as the malar crest. The orbit is large, with the anterior margin reaching the M3 level. In ventral view, the palatine process is short and deformed, as a result of the deformation affecting the cranium. The anterior margin of the choanae reaches the M2, whereas the vomer and the basisphenoid are crushed.

MAXILLARY CHEEK TOOTH ROWS - Figure S1 depicts the occlusal view of the *Pl. mirabilis* UTRs of the best-preserved crania from Crookston Member of the Valentine Formation and Devil's Gulch Horse Quarry. The UTR of AMNH:FAM60915 from Chama el Rito has not been included because of its poor preservation.

Figure S1a is AMNH:FAM60801 from Crookston Member of the Valentine Formation. The UTR shows a well-developed dP1, a worn M1, whereas P2-P4 and M2 are in an early stage-of-wear. The P2 has a short, sub-triangular and pointed anterostyle. All cheek teeth have a labially pointed mesostyle in occlusal view. The protocone is short with a convex lingual margin. It is connected to the protoloph in P2, P3 and M1, and it is not connected in the P4 and M2, where it shows a well-developed spur towards the protoloph. This is effect of the early stage-of-wear of the UTR. No pli caballin is observed at this stage, and the pre- and postfossettes ornamentation is simple or absent. The hypocone is small and distally pointed, separated from the distal wall of the teeth with a well-developed hypoconal groove.

Figure S1b is AMNH:FAM60804 from the Devil's Gulch Horse Quarry of the Valentine Formation. The dP1 is not present, and the UTR shows an early to middle stage-of-wear with the M3 not worn. The P2 has a short, sub-triangular and pointed anterostyle. All cheek teeth have a labially pointed mesostyle in occlusal view. The protocone is short with a convex lingual margin, being serially longer in molars than in premolars. At this stage, protocone is always connected with the protoloph. The pli caballin is present in P2-P4, very reduced in M1 and absent in M2-M3. The pre- and post-fossettes ornamentation is simple, with one or two plications per margin. The hypocone is large and distally sub-rounded, separated from the distal wall of the teeth by a small hypoconal groove.

Figure S1c is AMNH:FAM60824 from the Devil's Gulch Horse Quarry of the Valentine Formation. The dP1 is preserved, triangular and pointed at the mesial margin. The UTR is in a middle stage-of-wear, with all cheek teeth worn. The P2 has a short, sub-triangular and pointed anterostyle. All cheek teeth have a labially pointed mesostyle in occlusal view. The protocone is short with a convex lingual margin, being serially longer in molars than in premolars. At this stage, it is always connected with the protoloph and it is remarkably close to the hypocone in M1-M2. The pli caballin is present in P3-P4, very reduced in M2 and absent in P2 and M3. The pre- and post-fossette ornamentation is simple, with one or two plications per margin, or obliterated. The hypocone is large and distally sub-rounded, separated from the distal wall of the teeth by a tiny hypoconal groove in P2-P4, connected to the distal wall in M1, and separated in M2-M3.

Figure S1d is AMNH:FAM60823 from the Devil's Gulch Horse Quarry of the Valentine Formation. The dP1 is preserved, oval-shaped and pointed at its mesial margin.

The UTR is in a middle to late stage-of-wear, with all the teeth in advanced wear. The P2 has a short, sub-triangular and pointed anterostyle. All cheek teeth have a pointed mesostyle in occlusal view. The protocone is short with a convex lingual margin, being serially longer in molars than in premolars. At this stage, protocone is always connected to the protoloph and it is remarkably close to the hypocone in M1-M2. The pli caballin is very short in P3-P4 and absent in P2, M1-M3. Pre- and postfossette ornamentation is virtually obliterated. The hypocone is connected to the distal wall of the teeth, separated only in M2-M3 by a small hypoconal groove.

Figure S1e is AMNH:FAM60810 from the Devil's Gulch Horse Quarry of the Valentine Formation. The UTR is in a late stage-of-wear. The dP1 has an elongate-oval

contour. The P2 has a short, sub-triangular shape and pointed anterostyle. All cheek teeth have a sub-squared mesostyle in occlusal view. The protocone is short, sub-rounded with a convex lingual margin. At this stage, the protocone is always connected with the protoloph by a large isthmus and is confluent with the hypocone in M1-M2. Pli caballin is absent in P2-M3. The pre- and postfossette ornamentation is obliterated in P2-M3. The hypocone is always confluent with the distal wall of the teeth, separated only in M3 by a small hypoconal islet.

MANDIBULAR CHEEK TOOTH ROWS - Figure S2 depicts the occlusal view of the *Pl. mirabilis* LTRs of the best-preserved mandibles from Crookston Member of the Valentine Formation and Devil's Gulch Horse Quarry. The LTRs are shown by age, from young to more senile individuals.

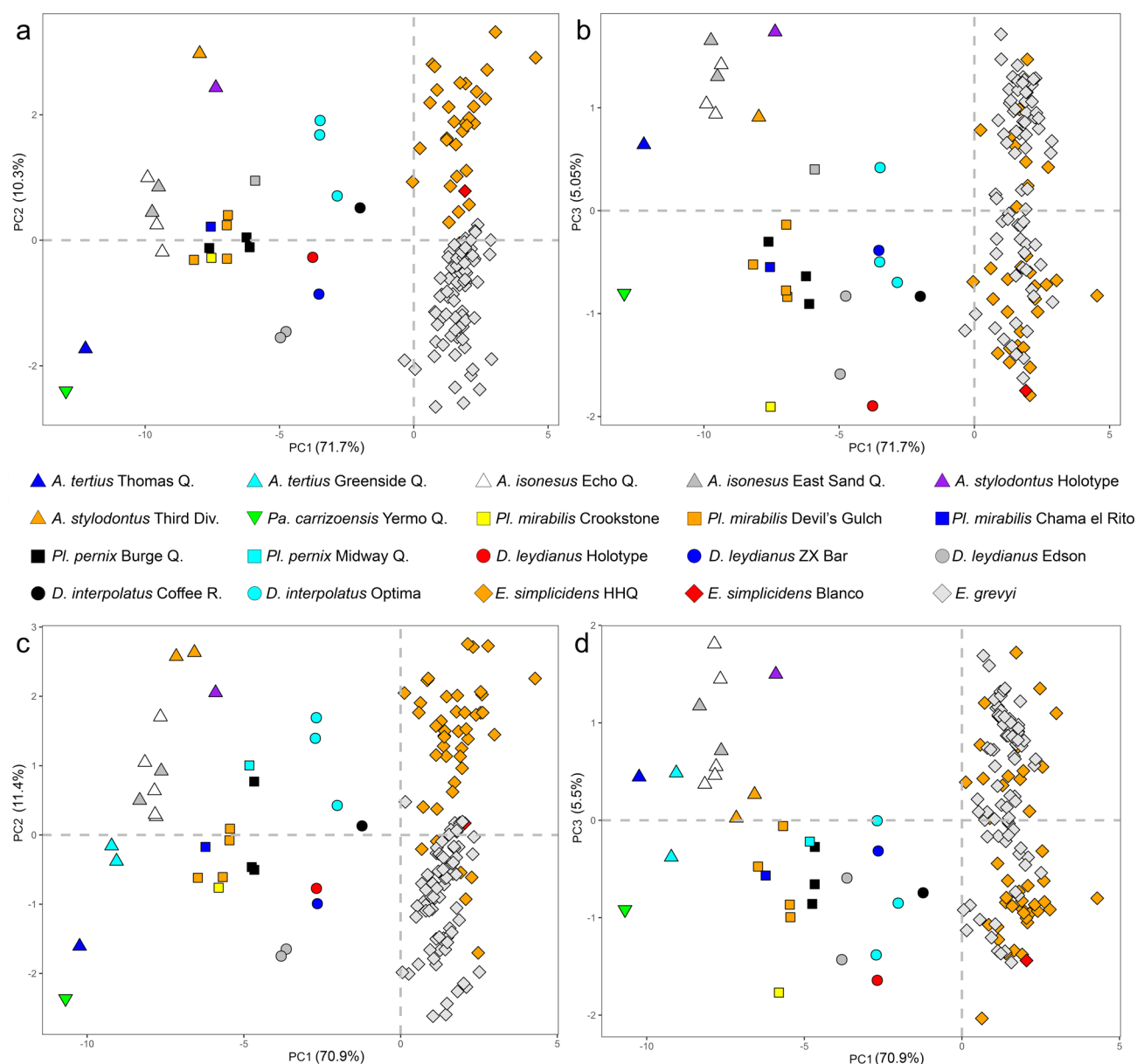


Fig. 5 - (color online) Principal component analysis comparing *Pliohippus mirabilis* with a suite of fossil Miocene, Pliocene and extant crania. Species are ordinated by age (Ma) from oldest to youngest, following the info reported in Tab. 1. Moreover, the same symbol identifies the same genus, to have a better understanding of the image. The PC components and the loadings distribution are reported in SOM Tab. S3. Abbreviations: *A.*: *Acritiohippus*; *Pa.*: *Parapliohippus*; *Pl.*: *Pliohippus*; *D.*: *Dinohippus*; *E.*: *Equus*.

Figure S2a is AMNH:FAM60801 from the Crookston Member of the Valentine Formation. The LTR is in an early stage-of-wear, with m1 and m2 worn, p2-p4 in an early stage-of-wear and m3 unworn. The p2 has a small, sub-triangular and pointed paraconid. The preflexid is large and deeply extended in the p2-p4, reduced in m1-m2. The metaconid and metastylid are small and round, with a close and pointed linguaflexid (V-shaped but very rudimentary). The postflexid is large and extended in p2-p4, reduced in m1-m2, with few plications. The ectoflexid is pointed lingually and large, and it separates the metaconid and metastylid. The entoconid is small, short and round. Pli caballinid absent.

Figure S2b is AMNH:FAM126880 from the Devil's Gulch Horse Quarry of the Valentine Formation. The LTR is in a middle stage-of-wear, with all the teeth worn. The p2 has a small, sub-triangular and round paraconid. The preflexid is small with no plications, whereas the postflexid is more elongated than the preflexid with few plications. The metaconids and metastylids are small and round and not meso-distally aligned, with a close and pointed linguaflexid (V-shaped but very short). In p2, the metaconid is very reduced, and the metastylid is more developed and oval shaped. The ectoflexid is pointed at the top, deep in p3-p4 up to the metaconid-metastylid and large, and it separates well the protoconid from the hypoconid. In p2, the ectoflexid reaches the middle plane of the teeth. The entoconid is small, short and round. Pli caballinid is absent.

Figure S2c is AMNH:FAM60824 from the Devil's Gulch Horse Quarry of the Valentine Formation. The LTR is in a middle to late stage-of-wear, and the enamel morphology is less preserved than the previous individuals. The p2 has a small, sub-triangular and round paraconid. The preflexid and postflexid are both obliterated by wear. Only the metastylid is present and is round. The p3 and p4 are also heavily worn with only p3 metastylid preserved. Likewise m1-m3 are heavily worn. The ectoflexid is pointed lingually, not extending as far as metaconid-metastylid contact. The entoconid is large, open and sub-rounded. Pli caballinid absent.

Figure S2d is AMNH:FAM60810 from the Devil's Gulch Horse Quarry of the Valentine Formation. The LTR is in a late stage-of-wear, and the enamel morphology is obliterated. The P2 has a small, sub-triangular and round paraconid. The metaconid and metastylid are barely shown. The ectoflexid is short not extending in between metaconid and metastylid in any of the teeth. The protoconid and the hypoconid are very large, occupying most of the teeth. The entoconid is large, open and sub-rounded. Pli caballinid absent.

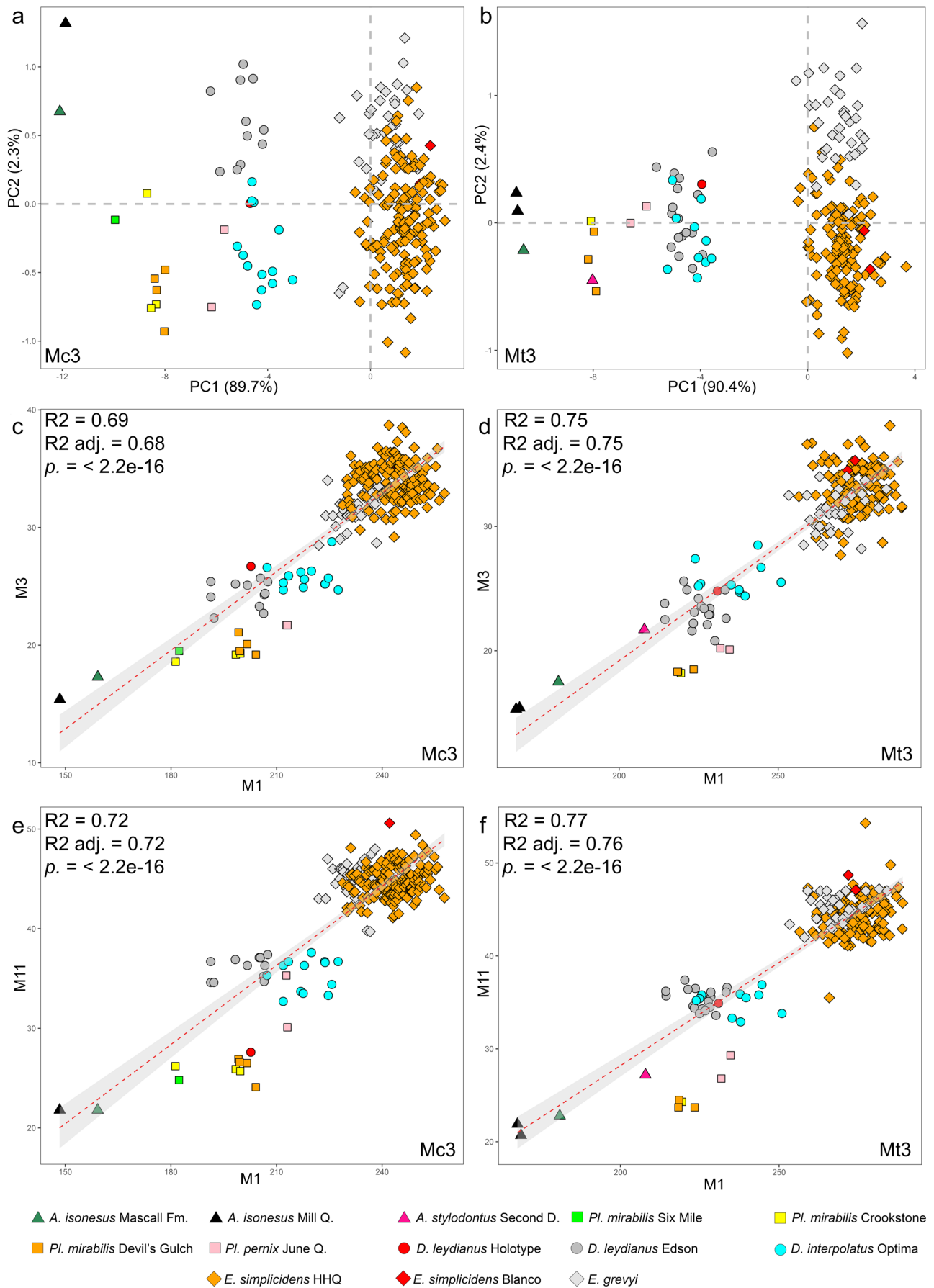
THIRD METACARPALS - Figure S3 illustrates the cranial, caudal and lateral morphology of the *Pl. mirabilis* third metacarpals from Six Mile Creek (Montana; Fig. S3a), Crookston Member (Fig. S3b-d) and Devil's Gulch Horse Quarry of the Valentine Formation (Nebraska; Fig. S3e-f). The third metacarpals are small and gracile with a small diaphysis. The proximal end has tiny articular facets for the second and fourth metacarpal, and a flat articular surface that articulates with the magnum; the distal epiphysis has reduced medial and lateral supra-articular processes, with a small medial and lateral trochlea. The crista sagittalis in between is reduced and not pronounced.

The lateral second and third metapodials extend up to the supra-articular processes, with small first, second and third phalanges of the second and fourth digits (Fig. S3a, c, f). Although these metacarpals exhibit a tridactyl morphology, the extremely reduced second and fourth phalanges were vestigial and did not have an effective locomotor function.

THIRD METATARSALS - Figure S4 exhibits cranial, caudal and lateral morphology of the *P. mirabilis* third metatarsals from Crookston Member (Fig. S4a) and Devil's Gulch Horse Quarry of the Valentine Formation (Nebraska; Fig. S4b-c). As in the mc3s, the third metatarsals are small and slender, with a small diaphysis. The proximal end has tiny articular facets for the second and fourth metatarsals, and a flat and circular articular surface for the cuneiforme; the distal epiphysis has reduced medial and lateral supra-articular processes, with a small medial and lateral trochlea. The crista sagittalis in between is small and unpronounced. As with the mc3s, the lateral second and fourth metatarsals extended up to the supra-articular processes. No lateral phalanges are preserved in the mt3s, but the existing morphology suggests that, although tridactyl, the lateral metapodials (second and fourth) did not function in locomotion.

RESULTS

The results of the morphometric and statistical analyses on cranial and postcranial elements are given in Figs 5 and 6. A complete summary of the PC components and of the loadings distribution is reported in SOM 4. Figure 5a-b depict the results of the PCA undertaken on the first dataset on complete crania. Figure 5a compares PC1 and PC2, accounting for the 82.0% of the total variance (PC1 = 71.7%; PC2 = 10.3%). PC1 clusters species by size of the crania (all measurements except M33 and M35), smaller to larger from negative to positive values, whereas PC2 separates species by the dimensions of the POF (M33 and M35), smaller in negative values and larger in positive values. *Pliohippus mirabilis* from Devil's Gulch Horse Quarry plots close to *Pl. pernix* Marsh, 1874 from Burge and Midway Quarry, and its range of variability includes the crania from Crookstone Member of the Valentine Formation and from Chama el Rito. The *Pliohippus* species (*Pl. mirabilis* and *Pl. pernix*) are separated from the species of the genus *Acritohippus* (including *A. tertius* Osborn, 1918 from Thomas Quarry, *A. isonesus* from Echo and East Sand Quarry, and *A. stylodontus* from the Third Division) characterised by a very short POB and a dorsoventrally high POF. *Acritohippus tertius* and *Parapliohippus carrizoensis* from Yermo Quarry are plotted closely, even if the latter shows similar proportions to *Pliohippus* but smaller (see PC1 vs PC3). *Pliohippus mirabilis* is also well separated from the younger species of *Dinohippus*, where two ranges of variability might be identified. The first one proper of *D. leydianus* (including the holotype, the cranium from the ZX Bar, and the sample from Edson Quarry), and another of *D. interpolatus* Cope, 1893 from Optima. Here, the cranium described by Azzaroli (1988) as *Pl. bakeri* (here *D. interpolatus*) plots close to the variability of the Optima population. *Equus simplicidens* from the Hagerman Horse Quarry



(HHQ) and extant *E. grevyi* are the assemblages with the largest species in this analysis, and they are mostly separated by their POF dimensions which are larger in the HHQ population than in living Grevy's zebras. The *E. simplicidens* cranium from Blanco is included in the lower part of the HHQ *E. simplicidens* range.

Figure 5b compares PC1 vs PC3 of the same dataset, accounting for the 76.8% of the total variance (PC1 = 71.7%; PC3 = 5.05%). PC1 clusters species by size (as above), smaller to larger from negative to positive values, whereas PC3 separates species by the dimensions of the POF (M33 and M35) and by M34 (distance of the IOF from the posterior margin of the POF), smaller in negative values and larger in positive values. The results are similar to those shown in Fig. 9a, but with some slight differences. *Pliohippus mirabilis* from Devil's Gulch plots close to *Pl. pernix* from Burge and Midway Quarry, and its range of variability includes the cranium from Chama el Rito, whereas the cranium from Crookston Member of the Valentine Formation is slightly separated from the range of variability shown by the Devil's Gulch Horse Quarry for its dorso-ventral deformation. The *Pliohippus* species (*Pl. mirabilis* and *Pl. pernix*) are separated from species of the genus *Acritohippus* (including *A. tertius* from Thomas Quarry, *A. isonesus* from Echo and East Sand Quarry, and *A. stylodontus* from the Third Division) characterised by a very small POB and a dorsoventrally extensive POF, and herein *A. tertius* and *Pa. carrizoensis* are separated, the latter showing more similar proportions to *Pliohippus* albeit with a much smaller size. This evidence supports the original interpretation of Hulbert & MacFadden (1991) and Kelly (1995, 1998) about the close evolutionary relationship between *Parapliohippus* and *Pliohippus*. *Pliohippus mirabilis* is still well separated from *D. leydianus* and *D. interpolatus* from Optima. Again, the cranium described by Azzaroli (1988) as *Pl. bakeri* (here *D. interpolatus*) still plots close to the variability of the Optima population. *Equus simplicidens* from Hagerman Horse Quarry (HHQ) and extant *E. grevyi* overlap extensively, and the *E. simplicidens* cranium from Blanco is included within the lower part of their variability in the PC3.

Figure 5c-d illustrates the results of the second dataset on crania (without M3-M6), including an increase in the number of specimens which has increased the comparative sample. Overall, the results are similar to the previous ones. In Fig. 5c, PC1 and PC2 account for the 82.4% of the total variance (PC1 = 70.9%; PC2 = 11.4%). PC1 clusters species by size, smaller to larger from negative to positive values, whereas PC2 separates species by the dimensions of the POF (M33 and M35), smaller in negative values and larger in positive values. *Pliohippus mirabilis* from Devil's Gulch Horse Quarry includes the crania from Crookstone Member of the Valentine Formation and from Chama el Rito, whereas *Pl. pernix* from Burge and Midway Quarry are slightly separated

and do not overlap as in Fig. 5a. The *Pliohippus* species (*Pl. mirabilis* and *Pl. pernix*) are separated from species of the genus *Acritohippus* (including *A. tertius* from Thomas Quarry and Greenside Quarry, *A. isonesus* from Echo and East Sand Quarry, and *A. stylodontus* from the Third Division) characterised by having a very short POB and a wide dorsoventrally high POF. *Acritohippus tertius* from Thomas Quarry and *Pa. carrizoensis* from Yermo Quarry are still plotted closely, although *A. tertius* from Greenside Quarry is more closely placed to *A. isonesus* (Echo and East Sand Quarry). *Pliohippus mirabilis* is also well separated from the younger species of *Dinohippus*, wherein two clusters can be identified. The first one proper of *D. leydianus* (including the holotype, the cranium from the ZX Bar, and the sample from Edson Quarry), and another of *D. interpolatus* from Optima. The *Pl. bakeri* cranium (here *D. interpolatus*) plots close to the variability of the Optima population. *Equus simplicidens* from HHQ and *E. grevyi* exhibit a large range of variability, and the *E. simplicidens* cranium from Blanco is still included in the lower part of the HHQ population range, although they are slightly separated by higher values of PC2 on average for *E. simplicidens*.

Figure 5d compares PC1 versus PC3 of the second dataset on crania, with the total variance accounting for 76.4% (PC1 = 70.9%; PC3 = 5.5%). PC1 cluster species by size, smaller to larger from negative to positive values, whereas PC3 separates species by the dimensions of the POF (M33 and M35) and by M34 (distance of the IOF from the posterior margin of the POF), smaller in negative values and larger in positive values. The results are similar to those shown in Fig. 5b, but with some differences. *Pliohippus mirabilis* from Devil's Gulch plots close to *Pl. pernix* from Burge and Midway Quarry, and its range of variability includes the cranium from Chama el Rito, whereas the cranium from Crookston Member of the Valentine Formation is slightly separated from the range of variability shown by the Devil's Gulch Horse Quarry for its dorso-ventral deformation. The *Pliohippus* species (*Pl. mirabilis* and *Pl. pernix*) are separated from the species of the genus *Acritohippus* (including *A. tertius* from Thomas Quarry and Greenside Quarry, *A. isonesus* from Echo and East Sand Quarry, and *A. stylodontus* from the Third Division) characterised by a very short POB and a dorsoventrally large POF. Here, *A. tertius* from Thomas Quarry plots close to the sample of Greenside Quarry, separated from *Pa. carrizoensis*. *Pliohippus mirabilis* is still well separated from *Dinohippus*, and in this plot *D. leydianus* and *D. interpolatus* overlap their range of variability. *Equus simplicidens* from Hagerman Horse Quarry (HHQ) and *E. grevyi* overlap extensively, and the *E. simplicidens* cranium from Blanco is included in the lower part of their variability.

Figure 6 plots the results for the PCAs and bivariate plots for mc3s and mt3s. Figure 6a provides the outcomes

Fig. 6 - (color online) Principal component analysis and bivariate plots on third metacarpals and third metatarsals, *Pliohippus mirabilis* with a suite of fossil Miocene, Pliocene and extant species. a) PCA on third metacarpals. b) PCA on third metatarsals. c) Bivariate plot on third metacarpals (M1 vs M3). d) Bivariate plot on third metatarsals (M1 vs M3). e) Bivariate plot on third metacarpals (M1 vs M11). f) Bivariate plot on third metatarsals (M1 vs M11). Species are ordinated by age (Ma) from oldest to youngest, following the info reported in Tab. 1. Moreover, the same symbol identifies the same genus, to have a better understanding of the image. The PC components and the loadings distribution are reported in SOM Tab. S3. M1, M3 and M11 refer to the measurements of Eisenmann et al. (1988) and Bernor et al. (1997). Abbreviations: *A.*: *Acritohippus*; *Pl.*: *Pliohippus*; *D.*: *Dinohippus*; *E.*: *Equus*.

of the PCA on mc3s in *Acritohippus*, *Pliohippus*, *Dinohippus* and *Equus*. PC1 and PC2 account for 92.0% of the total variance (PC1 = 89.7%; PC2 = 2.3%). PC1 separates species by size (M3-M14 in Material and Methods), smaller to larger from negative to positive values, whereas PC2 segregates species by the total length of the metapodial (M1), shorter to longer from positive to negative values. *Pliohippus mirabilis* from Crookston Member of the Valentine Formation and from the Devil's Gulch Horse Quarry are plotted together, showing a small and slender morphology of their mc3s. The single mc3 from Six Mile Creek Formation plots close to them, and it is well separated from *A. isonesus* from Mascall Formation and Mill Quarry. On the other hand, *Pl. pernix* is separated from *Pl. mirabilis* (not clustering with the latter), and it is placed close to *Dinohippus*. Here, two *Dinohippus* clusters can be identified, *D. leydianus* from Edson Quarry and *D. interpolatus* from Optima. The holotype of *D. leydianus* plots close to the smallest individuals of *D. interpolatus*, a reflection of its young age; the holotype skeleton is based on a young individual (see Osborn, 1918; Azzaroli, 1988). *Equus simplicidens* from HHQ and *E. grevyi* overlap extensively, and the *E. simplicidens* from Blanco is included within the HHQ variability.

Similar results can be observed in Fig. 6b, the PCA based on mt3s. Here, PC1 and PC2 account for the 92.8% of the total variance (PC1 = 90.4%; PC2 = 2.4%). The distribution of the data in the morphospace is mostly influenced by PC1, clustering species by size from negative to positive values (smaller to larger), whereas PC2 segregates species by robustness, more robust in negative values and less robust in positive values. *Pliohippus mirabilis* from Crookstone Member of the Valentine Formation and Devil's Gulch Horse Quarry still plot together, although their variability also includes *A. stylodontus* from the Second Division. *Acritohippus isonesus* from the Mascall Formation and Mill Quarry are still well separated from *Pl. mirabilis*, and *Pl. pernix* from June Quarry plots between *Pl. mirabilis* and *Dinohippus*. In this plot, *D. leydianus* and *D. interpolatus* overlap extensively their range of variability, not showing two different clusters as in Fig. 6a. Nevertheless, as for the mc3s, *E. simplicidens* from HHQ and *E. grevyi* overlap extensively, and the *E. simplicidens* from Blanco is included in the HHQ variability.

Figure 6c-f provides bivariate plots comparing the maximum length (M1) versus midshaft width (M3) in mc3s (Fig. 6c) and in mt3s (Fig. 6d), and the maximum length (M1) versus M11 distal articular maximum width (M11) in mc3s (Fig. 6e) and in mt3s (Fig. 6f). The results differ little from those shown in Fig. 6a-b. There is a general increase in size from older to younger taxa in *Acritohippus*, *Pliohippus*, *Dinohippus* and *Equus*. This size increase is not only found between genera, but also in younger species of the same genus (see *A. stylodontus* compared to *A. isonesus* and *Pl. pernix* compared to *Pl. mirabilis*). *Dinohippus interpolatus* is slightly larger than *D. leydianus* but shows an overlap in their ranges of variability. *Equus simplicidens* and *E. grevyi* remain the largest species included in the analyses, with *E. simplicidens* being slightly larger than *E. grevyi*.

DISCUSSION

Our revision of late Barstovian *Pl. mirabilis* has included our evaluation of its morphology at different ontological stages compared with other North American fossil equids. This has further led to our interpretation of its evolutionary relationships, especially within the Tribe Equini. In its cranial size and metapodial size, *Pl. mirabilis* occupies a place between the small-sized *Acritohippus* and *Parapliohippus* and the medium-sized *Dinohippus*.

Evolution of cranial anatomy in Pliohippus mirabilis and related North American fossil equids

Figure 7 provides a morphological comparison of the cranial lateral morphology for *Parahippus cognatus* Leidy, 1958 (Fig. 7a; USNM 531638, cast), *Acritohippus tertius* (Fig. 7b; AMNH:FAM109955, Thomas Quarry, He2), *Acritohippus isonesus* (Fig. 7c; AMNH:FAM71154, East Sand Quarry, Ba1), *Acritohippus stylodontus* (Fig. 7d; AMNH:FAM144661, Third Division, Ba1), *Parapliohippus carrizonesis* (Fig. 7e, AMNH:FAM110128, Yermo Quarry, Ba1), *Pliohippus pernix* (Fig. 7g, AMNH:FAM60800, Midway Quarry, Cl1), *Dinohippus leydianus* (Fig. 7h; AMNH:FAM172224, Snake Creek, He2-3), *Dinohippus interpolatus* (Fig. 7i; AMNH:FAM128158, Optima, He3) and *Equus simplicidens* (Fig. 7j; AMNH:FAM32551, Hagerman Horse Quarry, late Blancan) scaled for their relative size.

Pliohippus mirabilis (Fig. 7f, AMNH:FAM60810) cranium from the Devil's Gulch Horse Quarry, exhibits the typical apomorphies of the genus having a medium sized cranium, a short nasal notch, a well-developed buccinator fossa, a large POF with a flattened lower and convex upper rim, a large and well developed malar fossa, a short POB and a relatively large orbit, with its anterior margin placed above M3. The same general features can be identified in *Pliohippus pernix* (Fig. 7g), although the cranium is distinguished from *Pl. mirabilis* by a larger size, a reduced malar fossa and less defined POF. Hulbert (1993) suggested that evolution proceeded anagenetically within the genus *Pliohippus* and our results are in agreement with his hypothesis.

Pliohippus mirabilis is distinguished from *Acritohippus* by its larger size and in particular by the morphology of the facial region. *Acritohippus* had a very short POB and a dorsoventrally and antero-posteriorly extensive POF, occupying most of the maxillary and malar surfaces. The malar fossa is barely present in *A. tertius*, and slightly more developed in *A. isonesus* and *A. stylodontus*, although as not as in *Pl. mirabilis*. These observations are reflected in the cranial PCAs (Fig. 5), where the species included in the genus *Acritohippus* are separated from *Pliohippus* by general size, length of POB and size of POF. These features might be considered plesiomorphies retained from the genus *Parahippus*, from which *Acritohippus* is believed to have evolved (see Kelly, 1995, 1998; Maguire & Stigall, 2008).

The genus *Parapliohippus* is represented by a single species, *Pa. carrizoensis* (Fig. 7e; Kelly, 1995), and although the PCAs place it close to *A. tertius* (Fig. 5) by its small size, its lateral cranial morphology exhibits a longer POB and a smaller POF when compared to *Acritohippus*,

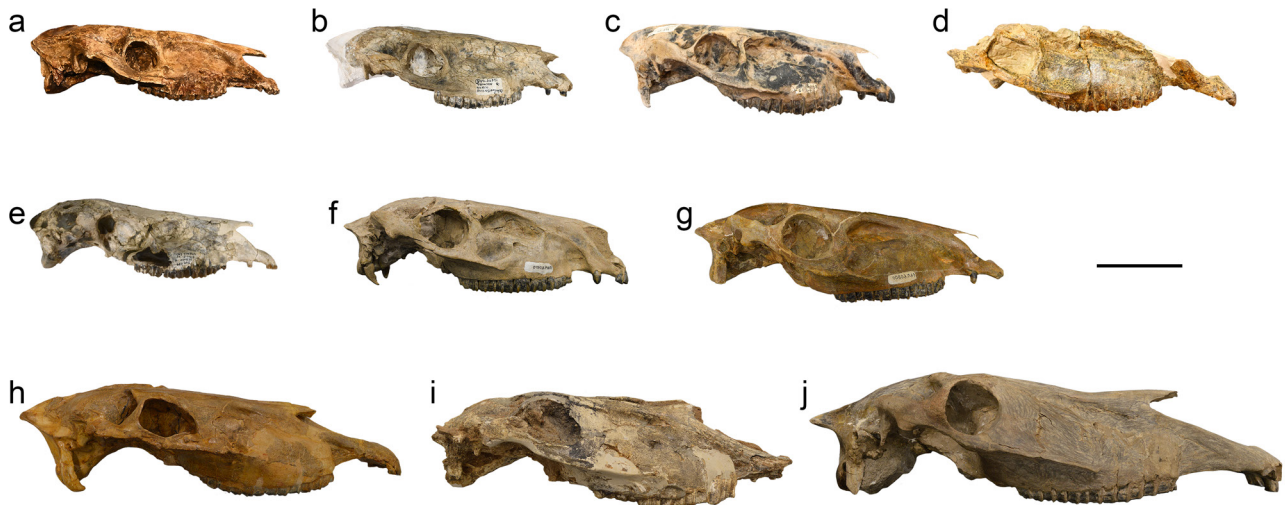


Fig. 7 - (color online) North American fossil crania of *Parahippus*, *Acritohippus*, *Parapliohippus*, *Pliohippus*, *Dinohippus* and *Equus* in lateral view. a) Cast of *Parahippus cognatus*, USNM 531638. b) *Acritohippus tertius*, AMNH:FAM109955, Thomas Quarry, He2. c) *Acritohippus isonesus*, AMNH:FAM71154, East Sand Quarry, Ba1. d) *Acritohippus stylodontus*, AMNH:FAM144661, Third Division, Ba1. e) *Parapliohippus carrizonesis*, AMNH:FAM110128, Yermo Quarry, Ba1. f) *Pliohippus mirabilis*, AMNH:FAM60810, Devil's Gulch Horse Quarry, Ba2. g) *Pliohippus pernix*, AMNH:FAM60800, Midway Quarry, Cl1. h) *Dinohippus leydianus*, AMNH:FAM172224, Snake Creek, He2-3. i) *Dinohippus interpolatus*, AMNH:FAM128158, Optima, He3. j) *Equus simplicidens*, AMNH:FAM32551, Hagerman Horse Quarry, late Blancan. Zonation of North American localities refers to Tedford et al. 2004. Scale bar: 10 cm.

with a more developed malar fossa. Moreover, according to Hulbert & MacFadden (1991), it shows also rapidly connected protocones and relatively simple fossette margins in the upper teeth, features not always present in the genus *Acritohippus* (Kelly, 1995), but attributed to *Pliohippus* and younger Equini. As reported by Hulbert & MacFadden (1991) and shown in the phylogenetic analyses of Hulbert (1993), Kelly (1995, 1998) and Maguire & Stigall (2008), *Parapliohippus* is closely related to *Pliohippus*, although being a mesodont equid (Mihlbachler et al., 2011).

Dinohippus leydianus (Fig. 7h) and *D. interpolatus* (Fig. 7i) are distinguished from *Pl. mirabilis* (and by extension *Pliohippus*) by their larger size, longer snout, a reduced POF, a longer POB and having the orbit posterior to the M3. Quinn (1955) distinguished the genus *Dinohippus* from *Pliohippus* by its lack of a malar fossa. In the crania illustrated herein, the malar fossa is not as prominent as in *Pliohippus*, and it appears as a slight depression in the maxilla and zygomatic bones. These features are also evident in *E. simplicidens* (Fig. 7j), where the cranium is larger, more elongated, and the POF is more reduced than in *Dinohippus* and *Pliohippus*. Overall, these morphological comparisons, aligned with the morphometric characterisations, place *Pl. mirabilis* at the base of Equini clade, and are in agreement with the previous phylogenetic results of Hulbert & MacFadden (1991), Hulbert (1993), Kelly (1995, 1998), Maguire & Stigall (2008), Mihlbachler et al. (2011), Fraser et al. (2015), and Cantalapiedra et al. (2017).

Palaeodietary reconstructions in Pliohippus mirabilis and related North American fossil equids

Figure S5 depicts a comparison of the palaeodietary reconstruction using mesowear values for North American genera and species of Equini discussed in this paper (data

from Mihlbachler et al., 2011). *Pliohippus mirabilis* has a mesowear average (using the “ruler” scale of Mihlbachler et al., 2011) of ca. 2.5, suggesting a mixed-feeding habit of the Devil's Gulch Horse Quarry population. Its mesowear values are comparable to those of *A. tertius* (Greenside Quarry), *A. isonesus* (Echo Quarry, Mill Quarry, East Sand Quarry) and *A. stylodontus* (Greenside Quarry, Yermo Quarry) (Fig. S5). *Acritohippus tertius* from Thomas Quarry has intermediate adaptations between browser and mixed-feeders (average values of 2.08, see supplementary material of Mihlbachler et al., 2011), whereas *Pa. carrizoesis* from Yermo Quarry had a more browsing diet than *Acritohippus* and *Pliohippus* species. The *Pl. pernix* population from Burge Quarry and other Claredonian 1 and 2 sites shows also comparable values with *Pl. mirabilis*. Nevertheless, *D. leydianus* (Edson) and *D. interpolatus* (Coffee Ranch and Optima) have higher mesowear values, showing a greater tendency toward a grazing diet than *Pliohippus* (Fig. S5). *Equus simplicidens* from HHQ has a similar grazing adaptation to living *E. grevyi* (Cirilli et al., 2024b). The main mixed feeding adaptations shown by the Middle and Late Miocene North American horses (including *Pl. mirabilis* from the Devil's Gulch Horse Quarry) reflect the great diversity of palaeoenvironments and habitats promoted by the spread of the C3 grasses (Strömberg, 2004, 2006; Mihlbachler et al., 2011), whereas C4 grasses began to expand in the Great Plains of North America between the very Late Miocene and Pliocene (Mihlbachler et al., 2011; Strömberg & McInerney, 2011).

Postcranial morphology of Pliohippus mirabilis and related North American fossil equids with remarks on the origin of monodactyly

Recently, several researchers have investigated when, how, and why monodactyly appeared in horses through

biomechanical, palaeoecological, macroevolutionary and histological approaches. A consensus concerning these various questions has yet to be completely reached (McHorse et al., 2017, 2019; Parker et al., 2018; Solounias et al., 2018; Janis & Bernor, 2019). McHorse et al. (2017, 2019) and Parker et al. (2018) suggested that the evolution

of a functional monodactyly in horses was not caused by a single evolutionary driver because climate changes, open habitats, changes in substrate, changes in foot posture and changes in body size could have operated together and influenced the selective regime wherein monodactyly eventually emerged (McHorse et al., 2019).



Fig. 8 - (color online) Palmar view of the North American fossil third metacarpals of *Acritohippus*, *Pliohippus*, *Dinohippus* and *Equus* compared to *Equus grevyi* and *Hippotherium primigenium*. a-b) *Acritohippus isonesus*, AMNH:FAM 69512, Mill Quarry, Ba1 (a metacarpal, b metatarsal). c-d) *Pliohippus mirabilis*, AMNH:FAM60810, Devil's Gulch Horse Quarry, Ba2 (c metacarpal, d metatarsal). e-f) *Pliohippus pernix*, AMNH:FAM60803, June Quarry, C11 (e metacarpal, f metatarsal). g-h) *Dinohippus leydianus*, AMNH:FAM172224, Snake Creek, He2-3 (g metacarpal, h metatarsal). i-j) *Equus simplicidens*, AMNH:FAM32552, Hagerman Horse Quarry, late Blancan (i metacarpal, j metatarsal). k-l) *Equus simplicidens*, AMNH:FAM20076, Mount Blanco, late Blancan (k metacarpal, l metatarsal). m) *Equus grevyi*, USNM241009 (metacarpal). n) *Equus grevyi*, USNM49796 (metatarsal). o-p) *Hippotherium primigenium*, SMNK Hö A, Höwenegg, 10.3 Ma (o metacarpal, p metatarsal). Zonation of North American localities refers to Tedford et al. (2004). Scale bar: 10 cm.

Parker et al. (2018) provided evidence contrary to the classic hypothesis that derived equid traits such as large body size, hypsodonty and monodactyly evolved as a suite of adaptations concomitant with the spread of grassland environments in North America. Species of Equini, Protohippini and Hipparionini shared multiple habitats concurrently (Parker et al., 2018). The palaeoecological and evolutionary models provided by Parker et al. (2018) show that the evolution of large body size, hypsodonty, and monodactyly were not correlated and that the lack of habitat partitioning suggests that these equid traits did not evolve within a single strict selective regime in newly-opened grasslands, but they were the result of a complex set of heterogeneous selective pressures of the various habitats where the Miocene and Pliocene equids lived. In addition to these hypotheses, Janis & Bernor (2019) proposed that monodactyly had originated by a difference in diet and foraging behavior in North American equids. According to Janis & Bernor (2019), North American Miocene monodactyl horses adopted a feeding regime that involved a greater extent of roaming behavior, on a daily and/or seasonal basis, which would have led to selection for limb morphology that supported more efficient distance transport through trot gait rather than running-walk as shown in Hipparionini (Renders, 1984; Janis & Bernor, 2019). In this sense, monodactyly could represent a case of exaptation (Gould & Vrba, 1982) for cooler and more arid world of the Plio-Pleistocene and the present day, having its origin in divergent foraging behaviors of Late Miocene North American hipparionin and equin lineages, leading to selection in the latter lineage for a its greater locomotor efficiency.

The identification of how, when and why monodactyly emerged as a distinct trait in Equini is beyond the scope of the present work, but the study of the morphology of *Pl. mirabilis* provided herein might add some new clues about it. Figure 8 shows the caudal view of the metacarpals and metatarsals in *A. isonesus* (Fig. 8a-b; Ba1), *Pl. mirabilis* (Fig 8c-d; Ba2), *Pl. pernix* (Fig. 8e-f; Cl1), *D. leydianus* (Fig. 8g-h; He2-3), *E. simplicidens* (Fig. 8i-l; Late Blancan), *E. grevyi* (Fig. 8m-n) and in *Hippotherium primigenium* von Meyer, 1829 (Fig. 8o-p; MN9 of the European Land Mammal Ages; Bernor et al., 1997, 2022). Compared to the functional tridactyl *H. primigenium* (Bernor et al., 1997; Janis & Bernor, 2019), the third metapodials of *Pl. mirabilis* are more gracile in their build, with a reduced length of the second and fourth metapodials. As shown in Fig. S3 and here in *Pl. pernix* (Fig. 8e), the lateral first, second and third phalanges are much more reduced than in *H. primigenium*, and not functional as reported also by Hulbert & MacFadden (1991) and Janis & Bernor (2019). The lateral metapodials (second and fourth) are more reduced in *D. leydianus* (Fig. 8g-h), extended up to the lateral protuberances of the distal articular epiphysis, with no second or fourth phalanges preserved. Eventually, in *Equus* (*E. simplicidens* and *E. grevyi*, Fig. 8i-n), the lateral metapodials are even more retracted compared to *Dinohippus*, with the fourth metapodial more reduced than the second (more evident in the mc3s than mt3s). This line of evidence shows that *Pliohippus mirabilis* had a foot morphology similar to *Pl. pernix* from Burge (Janis & Bernor, 2019), and, although tridactyl, its locomotion was actually

functionally monodactyl. As previously argued by Hulbert & MacFadden (1991) and Janis & Bernor (2019), incipient monodactyly appeared in the Middle Miocene of North America (late Barstovian of the NALMA, ca. 15-12 Ma), and *Pl. mirabilis* apparently represented the first taxon to exhibit this morphology. More studies of North American equid postcranial anatomy are needed to understand when the lateral phalanges were lost and full monodactyly was achieved. As shown in Fig. 8g-h, the holotype of *D. leydianus* from Snake Creek (Nebraska, ca. 7 Ma; Skinner et al., 1977; Skinner & Johnson, 1984; Tedford et al., 2004), does not preserve any medial or lateral phalanges, suggesting that this transition might have occurred during the late Clarendonian - early Hemphillian interval of the NALMA in the Equini tribe.

CONCLUSIONS

Our study of Middle Miocene *Pl. mirabilis* samples has led to a comprehensive morphologic and morphometric characterisation of the species. *Pliohippus mirabilis* was intermediate in its size and morphology between *Parapliohippus* and *Dinohippus* and at the same time distinct from *Acritohippus*. Its biochronologic age was late Barstovian (NALMA Ba2; Tedford et al., 2004). Our re-evaluation of *Pl. mirabilis* supports the hypotheses of Hulbert & MacFadden (1991), Kelly (1995, 1998) and Maguire & Stigall (2008) that this species represents the base of the *Pliohippus* radiation and subsequent taxa of the North American tribe Equini, eventually leading to the origin of *Equus*. Our contribution represents a step in clarifying the phylogeny of Equinae.

SUPPLEMENTARY ONLINE MATERIAL

Supplementary data generated and analysed in this contribution are available on the BSPI website at: <https://www.paleoitalia.it/bollettino-spi/bspi-vol-641/>

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